ISSN 0031-0301, Paleontological Journal, 2006, Vol. 40, No. 1, pp. 79–89. © Pleiades Publishing, Inc., 2006.
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Taxonomy of the Fossil Grylloblattid Nymphs (Insecta: Grylloblattida)

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Received November 3, 2004

Abstract—Nymphs of fossil grylloblattid insects are revised. Newly described taxa are *Lemmatonympha gracilissima* gen. et sp. nov. and *Kaltanympha vorcutensis* sp. nov. from the Verkhne-Syr'yaginsk locality (Ufimian, Lek-Vorkuta Formation in the Vorkuta Coal Basin), genera *Sylvalitoralis* gen. nov. and *Tshebardanympha* gen. nov. from the Tshekarda locality (Kungurian, Koshelevka Formation, Middle Urals), *Tataronympha kamensis* gen. et sp. nov. from the Tikhie Gory locality (Lower Kazanian, linguloid beds of the Baitugan Formation, Tatarstan), and *Kaltanympha ornata* sp. nov. from the Kerbo locality (Upper Tatarian, lower part of the Degali Formation, Evenki Autonomous Region). *Liomopterites* (?) *gracilis* Sharov, 1961 from Lower Kazanian deposits of the Kuznetsk Formation in the Kuznetsk Basin is transferred to the genus *Kaltanympha* Sharov, 1961; *Permonympha arcuata* Sharov, 1957 from the same locality is synonymized under *Permonympha gracile* Sharov, 1957; the nymph described from the Karatau locality (Upper Jurassic, Karabastau Formation in southern Kazakhstan) as *Blattogryllus karatavicus* Rasnitsyn, 1976 is excluded from grylloblattids. Keys to extinct grylloblattid nymphs are provided.

DOI: 10.1134/S0031030106010096

Key words: Insecta, Grylloblattida, nymphs, fossils, taxonomy, new taxa, new combinations.

INTRODUCTION

The most ancient grylloblattid nymphs are known from the Lower Permian. Carpenter (1935) recognized three groups of nymphs on the basis of extensive fossil material from the Artinskian locality of Elmo in the United States (over 80 specimens, comprising 10% of all grylloblattids in this locality); however, these groups remain undescribed. The richest collection of nymphs comes from the Kungurian locality of Tshekarda, the Middle Urals. Here, over 250 specimens (approximately 15% of grylloblattids) were collected, with the majority belonging to *Kirkorella mira* (family Atactophlebiidae). The nymphs of ten other species, *Gurianovella silphidoides, Sylvonympha tshekardensis, Sylvaclinicus echinatus, Permedax effertus, Lemmatonympha gracilis, Tshekardites comitialis, Sylvalitoralis calcomessor, S. curculianicus, Tshebardanympha lienterica*, and *Tsh. bardensis*, are infrequent. *Thaumatophora pronotalis* Riek, 1976 has been described from Haakdoornfontein in South Africa (Lower Permian, Middle Ecca).

Upper Permian grylloblattid nymphs are less abundant and diverse. The Ufimian locality of Verkhne-Syr'yaginskoe (Vorkuta Coal Basin; the Ufimian age of the Vorkuta deposits was discussed elsewhere (Aristov, 2004)) yields several compression fossils of nymphs belonging to the species *Lemmatonympha gracilissima* gen. et sp. nov. (family Lemmatophoridae) and *Kaltanympha vorkutensis* sp. nov. Two representatives of the genus *Kaltanympha*, *K. thysanuriformis* and *K. gracilis*, have been described from another Ufimian or, according to other data (Shcherbakov, 2000), Lower Kazanian locality of Kaltan (Kuznetsk Basin). In addition to a dozen complete nymphs, numerous isolated wing sheaths have been found in Kaltan. Scarce remains of *Permonympha gracile* also come from this locality. The Lower Kazanian locality of Tikhie Gory in Tatarstan has yielded several compression fossils of *Tataronympha kamensis* gen. et sp. nov. Isolated wing sheaths have been found in the locality of Kityak, the Kazanian of the Kirov Region. *Kaltanympha ornata* sp. nov. is described from the Upper Tatarian locality of Kerbo, Evenki Autonomous Region.

An unidentified wing sheath and a nymph of *Triasseuryptilon acostai* (Marquat, 1991) have been found in the Triassic localities of Babii Kamen' (Lower Triassic, Mal'tseva Formation in the Kemerovo Region) and Cacheuta (Middle Triassic, Potrerillos Formation in Argentina). An exuvia of a nymph (Fig. 3f) was described as a paratype of *Blattogryllus karatavicus* of the family Blattogryllidae from the locality of Karatau, Upper Jurassic of southern Kazakhstan (Rasnitsyn,

†Deceased.

1976). Judging from the color pattern, strongly curved CuP in the forewing pad, and the setation pattern of the fore tibia, this specimen is a cockroach exuvia.

Like adult representatives of this order, grylloblattid nymphs are distinct in their high morphological diversity. There are aquatic rheophilous forms and undoubted land dwellers, including free-living forms and herpetobionts. Giving this, characters separating grylloblattid nymphs from other insects orders should be defined before one starts discussing their systematics. There are not likely to be many such characters.

Grylloblattid nymphs possessed a hypognathous head with filiform antennae, a pronotum, often with paranota, comparable in its size to the head, hind femora not widened basally, tibiae unarmed in their middle part, tarsi with one, two, or five tarsomeres, and paired long cerci. Grylloblattid nymphs are generally similar to stoneflies, but differ in having the tarsi with one, two, or five tarsomeres and in the presence of paranota on the abdominal tergites. The last two features are not necessarily present in all grylloblattid nymphs, but the presence of either is sufficient to affirm that a given specimen is not a stonefly. Some grylloblattid nymphs are similar to cockroach nymphs, from which they differ in a frequently occurring 1–4 segmented tarsus, the fore margin of the pronotum not being rounded and/or the presence of long cerci (to date, no cockroach nymphs with long cerci have been recorded).

To characterize grylloblattid nymphs in more details, it would be more convenient to consider aquatic and terrestrial forms separately. These ecological groups clearly differ in their sets of morphological adaptations to their corresponding lifestyles.

Terrestrial grylloblattid nymphs are characterized by the presence of pronotal paranota without incisions on their fore margins, by the middle and hind tibiae directed backward (knees are directed outward or forward) and having apical setation, tarsi not shortened, with three to five tarsomeres, and by the abdominal tergites often bearing paranota. *Kirkorella, Permonympha, Kaltanympha, Thaumatophora, Permedax, Sylvaclinicus, Tshekardites, Tshebardanympha* gen. nov., *Tataronympha* gen. nov., *Sylvalitoralis* gen. nov. and *Lemmatonympha* gen. nov. belong to this group.

Aquatic nymphs are characterized by pronotal paranota with incisions on their fore margins, by the middle, and quite often hind tibiae, directed forward (actually, the position of the tibiae can vary, but it is important that the knees are always directed backward or toward the median line, not outward or forward as in terrestrial nymphs), by their generally unarmed tibiae, by shortened tarsi with one to three tarsomeres, by the coxal gills that are present in the majority of members of this group, and by the abdominal tergites possessing paranota. This group is less numerous and is represented by the genera *Gurianovella, Triasseuryptilon*, and *Sylvonympha*.

Due to their strong resemblance, grylloblattid and stonefly nymphs are often difficult to separate. One such example is the stonefly *Spinoperla spinosa* from the locality of Novospasskoe, Lower–Middle Jurassic, Ichetui Formation of Transbaikalia (Sinichenkova, 1985). Having typical stonefly habitus, this nymph has the middle and hind tibiae directed backward. Its good preservation suggests that the tibiae did not change their position after burial.

Fundamental differences in the locomotion of terrestrial and aquatic insects are determined by absolutely different physical tasks. A terrestrial insect's life is profoundly affected by its body weight, whereas dynamic resistance of the environment can be ignored (vice versa in aquatic insects). That is why terrestrial insects have to utilize a supportive mode of locomotion, which provides stability of their bodies under gravity. This task is solved by a well-known method; the six legs of an insect are divided into two groups, each forming a tripod, the most stable support in the world.

The essence of walking in a terrestrial insect is in transferring its body weight from one support (tripod) onto another, the center of gravity of the body should not leave the perimeter of the triangle formed by the fulcra to keep stability. To provide maximum stability, it is necessary that the distance between the fulcra is as great as possible, and the center of gravity is exactly within the tripod projection. This is achieved by turning the fore and hind tibiae in different directions and by shifting the leg bases toward the median plane of the insect.

The life of an aquatic insect is much less affected by the weight of its body; therefore, the center of gravity, the weight of the body etc. can be ignored, and locomotion stops being supportive. Correspondingly, the two tripods disappear due to their complete uselessness, and the legs constituting them are used for pulling the body. At the same time, under high dynamic resistance of the environment, hydrodynamic stability becomes more important. This problem is solved by separation of the center of force application (in the area of attachment to the ground) and the center of hydrodynamic force; the body of an insect becomes a sort of weathercock, which is capable of self-orientation along the direction of movement. To provide the maximum hydrodynamic stability, it is advantageous for an insect to bring its legs forwards and outwards as much as possible (outwards, to create a long lever while keeping the smallest clearance between the ventral side of the body and the ground) and to move the center of hydrodynamic forces backwards as much as possible. That is why the tibiae in all benthic insects are turned forward and moved apart, whereas the leg bases are shifted towards the anterior end of the body.

Benthic insects are characterized by the middle and hind tibiae being directed forwards; this is a universal feature regardless whether insects are stagnophilous or rheophilous. Exceptions are active swimmers. Giving that grylloblattids are not recorded in Novospasskoe

(Jurassic grylloblattids are rather rare generally), one can surmise that we are dealing with an amphibious or terrestrial stonefly nymph. There are modern stoneflies that inhabit wet moss, whereas there are no aquatic stoneflies with the tibiae directed backward. It is impossible to explain the position of the tibiae of *Spinoperla* by an actively swimming mode of life, due to the general body shape and the absence of adaptations for swimming, such as, for example, a swimming fringe on the legs.

MATERIAL

The material examined is housed in the collections of the Paleontological Institute (PIN), Russian Academy of Sciences, and the State Geological Vernadsky Museum (SGM), Russian Academy of Sciences.

Identification key to genera of grylloblattid nymphs

1 (2) Pronotum with paranota wider than mesonotum……*Thaumatophora* Riek, 1976

2 (1) Pronotum with paranota narrower than or equal to mesonotum

3 (10) Pronotum with paranota 2 times as wide as head

4 (7) Pronotal paranota with incisions on their anterior margin, tibiae unarmed, middle tibiae directed forward

5 (6) Abdominal paranota wide, hind tibiae directed backward……*Gurianovella* G. Zalessky, 1939

6 (5) Abdominal paranota narrow, hind tibiae directed forward……*Sylvonympha* Novokshonov et Pan'kov, 1999

7 (4) Pronotal paranota without incisions on their anterior margin, tibiae armed, middle tibiae directed backward

8 (9) Pronotal paranota drawn laterally and narrowly rounded, middle tibiae widened apically……*Sylvaclinicus* Aristov, 2004

9 (8) Lateral sides of pronotal paranota broadly rounded, middle tibiae not widened apically……*Kirkorella* G. Zalessky, 1939

10 (3) Pronotum with paranota less than twice width of head

11 (12) Middle and/or hind tibiae directed forward……*Triasseuryptilon* Storozhenko, 1997

12 (11) Middle and hind tibiae directed backward

13 (18) Abdominal tergites without paranota

14 (15) Body strongly elongated……*Permedax* Aristov, 2004

15 (14) Body not elongated

16 (17) Legs elongated……*Lemmatonympha* gen. nov.

17 (16) Legs not elongated……*Sylvalitoralis* gen. nov.

18 (13) Abdominal tergites with paranota

19 (20) Abdominal tergites with broad paranota……*Permonympha* Sharov, 1957

20 (19) Abdominal tergites with narrow paranota

21 (22) Tarsus 3-segmented……*Tshekardites* Aristov, 2004

22 (21) Tarsus 5-segmented

23 (24) Pronotum longer than wide……*Tataronympha* gen. nov.

24 (23) Pronotum not longer than wide

25 (26) Pronotum quadrate……*Tshebardanympha* gen. nov.

26 (25) Pronotum transverse……*Kaltanympha* Sharov, 1961

Undescribed nymphs from the locality of Elmo (Carpenter, 1935) differing from known grylloblattid nymphs in having short and transverse pronota (Figs. 1e, 1f) are not included in this key.

SYSTEMATIC PALEONTOLOGY

Order Grylloblattida Walker, 1914

Suborder Lemmatophorina Storozhenko, 1997

Family Atactophlebiidae Martynov, 1930

Genus *Kirkorella* G. Zalessky, 1939

Kirkorella: G. Zalessky, 1939, p. 62.
Peremella: G. Zalessky, 1939, p. 63.
Czekardia: Martynov, 1940, p. 27.
Mariella: G. Zalessky, 1955, p. 161.

Type species. *K. mira* G. Zalessky, 1939; locality of Tshekarda; Lower Permian, Kungurian, Iren' Horizon, Koshelevka Formation.

Diagnosis (Fig. 1g). Pronotum with paranota twice as wide as head and as wide as mesonotum. Pronotal paranota without incisions on their anterior margins, their lateral margins broadly rounded. Middle tibiae directed backward, tibiae armed and not broadened apically, tarsus short with two to five tarsomeres. Abdominal tergites with paranota, body colored. Length of nymph body, 4.5–43 mm; length of subimago, 41 mm; and length of imago, 47.1–49.8 mm.

Species composition. Type species.

Remarks. This genus was described from the Koshelevka Formation simultaneously with *G. silphidoides* and *Peremella ambigua* G. Zalessky, 1939. All three species were synonymized along with *Czekardia blattoides* Martynov, 1940 and *Mariella gracilis* G. Zalessky, 1955 under *G. silphidoides* by Sharov (1962). Reexamination of the holotypes revealed that *Gurianovella* in a separate genus, whereas the others are junior synonyms of the genus *Kirkorella* (Aristov, 2004).

To date, *Kirkorella* is the only grylloblattid genus represented by nymphs, subimagoes, and imagoes. Study of extensive material from the PIN collection allowed recognition of nine nymphal stages, two subimaginal stages, and one imaginal stage (Storozhenko, 1998; Aristov, 1999). Additionally, only for this genus, a gradual increase of the number of tarsomeres during development is confidently recorded.

In its body shape (especially the shape of the pronotum), the leg setation and specific color pattern, *K. mira* is the most cockroach-like nymph among grylloblattids.

Family Lemmatophoridae Sellards, 1909

Genus *Lemmatonympha* Aristov, Novokshonov et Pan'kov, gen. nov.

Etymology. From the genus *Lemmatophora* and the Greek *nympha* (nymph).

Type species. *Tshekardites gracilis* Aristov, 2004; Tshekarda, Koshelevka Formation.

Diagnosis. Nymphs with slender body. Head large with long antennae. Pronotum as wide as head, transverse, with narrow paranota. Mesonotum somewhat wider than pronotum, trapezoid; metanotum equal to mesonotum. Legs elongated and lender, middle and

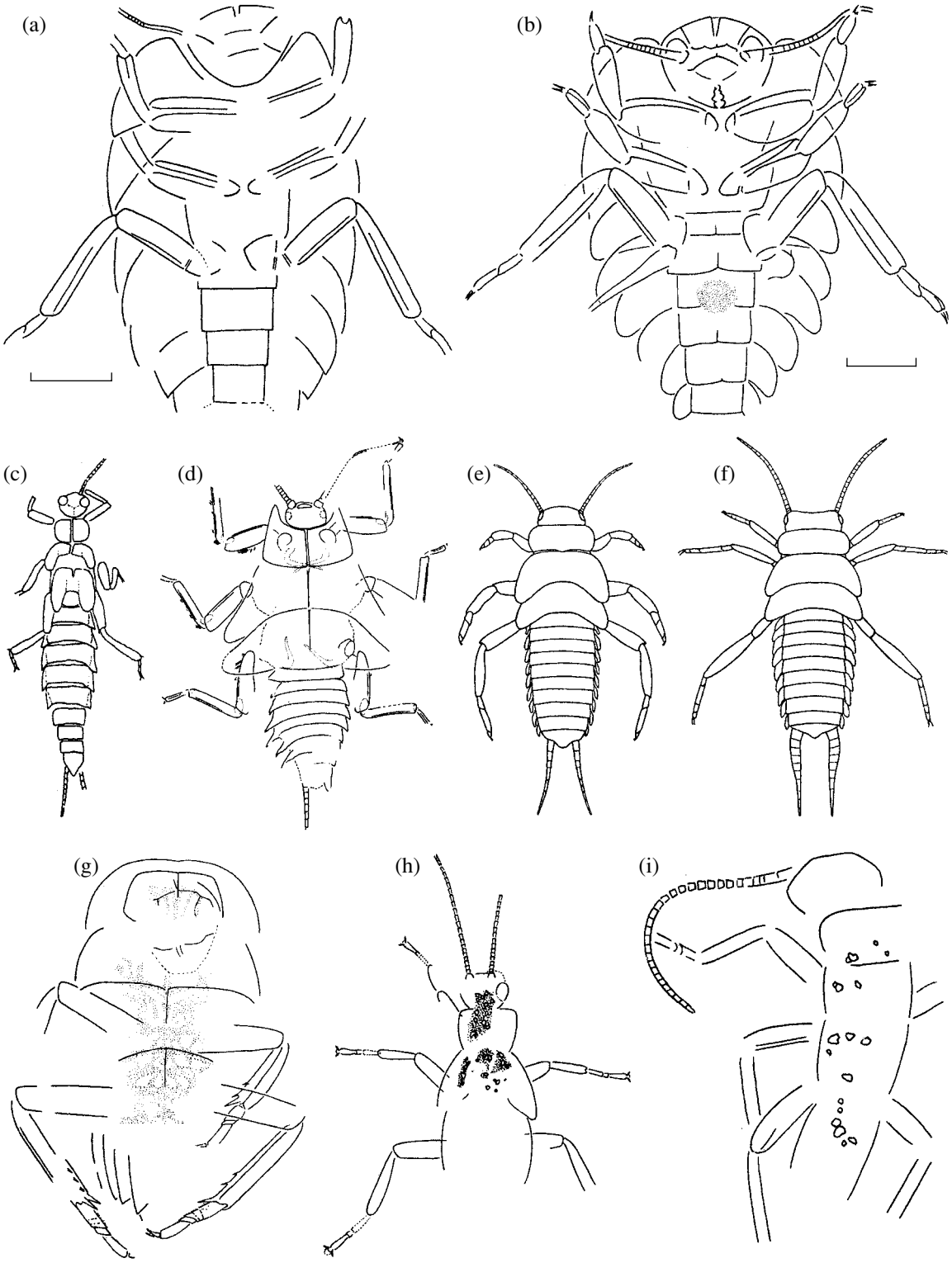

Fig. 1. Grylloblattid nymphs: (a, b) *Gurianovella sylphidoides* G. Zalessky, 1939: (a) holotype (after Aristov, 2004), (b) specimen PIN, no. 1987/51 (orig.); (c) *Triasseuryptilon acostai* (Marquat, 1991) (after Storozhenko, 1997); (d) *Sylvonympha tshekardensis* Novokshonov et Pan'kov, 1999 (after Novokshonov and Pan'kov, 1999); (e, f) undescribed nymphs from the locality of Elmo (after Carpenter, 1935); (g) *Kirkorella mira* G. Zalessky, 1939; (h) *Sylvalitoralis calcomessor* (Aristov, 2004); (i) *S. curculianicus* (Aristov, 2004) (after Aristov, 2004). Scale bar 2 mm in Figs. 1a and 1b, other figures are not to scale.

hind tibiae directed backward, tarsus long, 5-segmented. Abdominal tergites without paranota, cerci very long.

Species composition. *L. gracilis* comb. nov. and *L. gracilissima* sp. nov.

Remarks. There are two characters typical for this genus, i.e., elongated legs with long (especially in *L. gracilissima* sp. nov.) 5-segmented tarsi and long cerci. This combination of characters occurs only in imagoes of the family Lemmatophoridae (e.g., genera *Paraprisca* and *Sylvaprisca*) only. On the basis of this similarity, the genus is being described within lemmatophorids.

Undescribed nymphs from Elmo (Figs. 1e, 1f) may also belong to this family. Carpenter (1935) assigned them to lemmatophorids apparently on the basis of peculiarities of the Elmo oryctocenosis, which is characterized by the abundance of these nymphs along with the domination of adult Lemmatophoridae. However, representatives of eight more grylloblattid families are known from Elmo, and there are no reasons in their morphology to exclude the possibility that these nymphs belong to any of them. The abundance of nymphs cannot serve as reliable evidence that they belong to Lemmatophoridae, the imagoes of which dominate there. It is worth taking into account that in Tshekarda nymphs predominate over infrequent imagoes in the family Atactophlebiidae; by contrast, only two nymphs are found along with three hundred imagoes in the family Tylliardembiidae (Aristov, 2004). Additionally, Lemmatophoridae is also one of the dominant families in Tshekarda (over hundred impressions), although there is only one undoubted nymph. It is interesting that lemmatophorids in Tshekarda are represented chiefly by the same genera as in Elmo, mainly by the genus *Artinska*. Thus, attribution of the nymphs discussed to lemmatophorids is doubtful.

Identification key to species of *Lemmatonympha*

1 (2) Legs moderately elongated, middle tibiae not bent, hind tibiae less than twice as wide as femora (Fig. 2a)……
……*L. gracilis* (Aristov, 2004)

2 (1) Legs strongly elongated, middle tibiae bent, hind tibiae twice as wide as femora, body length, about 16 mm (Fig. 2b)……
……*L. gracilissima* sp. nov.

***Lemmatonympha gracilissima* Aristov, Novokshonov et Pan'kov, sp. nov.**

Etymology. From the Latin *gracilissima* (most slender).

Holotype. PIN, no. 1631/372, part and counterpart of well-preserved nymph fragment; Komi Republic, Vorkuta, borehole KhK-650, depth 187 m; Upper Permian, Lek-Vorkuta or Inta formations, border between Members M and L (Pukhonto, 1998).

Description (Fig. 2b). The nymph has a slender body. The pronotum is as broad as the mesonotum; both the mesonotum and metanotum are transverse; the wing sheaths are small. The middle and hind legs are very long. The femora are twice as broad as the tibiae; the tibiae are longer than the femora and slightly bent; the tarsi are as long as the femora, 5-segmented, the first tarsomere is longest. The abdomen is as long as the rest of the body, the tergites lack paranota. The cerci are thin and very long, their first segments are slightly broader than long.

Measurements, mm. Length of body without cerci, about 16.

Material. Holotype.

Suborder Protoperlina Storozhenko, 1997

Family Tillyardembiidae G. Zalessky, 1938

Genus *Permedax* Aristov, 2004

Type species. *P. effertus* Aristov, 2004; locality of Tshekarda; Lower Permian, Kungurian, Iren' Horizon, Koshelevka Formation.

Diagnosis (Figs. 2c, 2d). Body strongly elongated. Large head, pronotum and mesonotum equally broad. Legs shortened, hind tibiae directed backward. Abdominal tergites without paranota, cerci long. Body length, 14–15 mm.

Species composition. Type species.

Remarks. The genus *Permedax* is characterized by a large head, a strongly elongated body with shortened legs, and by long cerci. This combination of features is typical only for the family Tylliardembiidae, where *P. effertus* is transferred to from Grylloblattida incertae sedis where it was described. The absence of close similarity to any of tylliardembiid genera demands that *Permedax* be considered as a separate genus.

Protoperlina incertae sedis

Genus *Sylvaclinicus* Aristov, 2004

Type species. *S. echinatus* Aristov, 2004; locality of Tshekarda; Lower Permian, Kungurian, Iren' Horizon, Koshelevka Formation.

Diagnosis (Fig. 2e). Body stocky. Pronotum with paranota twice as broad as head and as broad as mesonotum. Pronotal paranota without incisions on their fore margins, drawn laterally and narrowly rounded. Middle tibiae directed backward; tibiae armed, broadened apically; tarsi shortened. Body length, 12–13 mm.

Species composition. Type species.

Remarks. Among grylloblattids, the tibiae being broadened apically in combination with shortened tarsi are known in the family Probnidae only. Another grylloblattid family with 3-segmented tarsi, Tshekardominidae of the suborder Protoperlina, does not have broadened tibial apices. However, the stocky body and small head of *Sylvaclinicus* do not allow its inclusion in Probnidae. The pronotal paranota being strongly

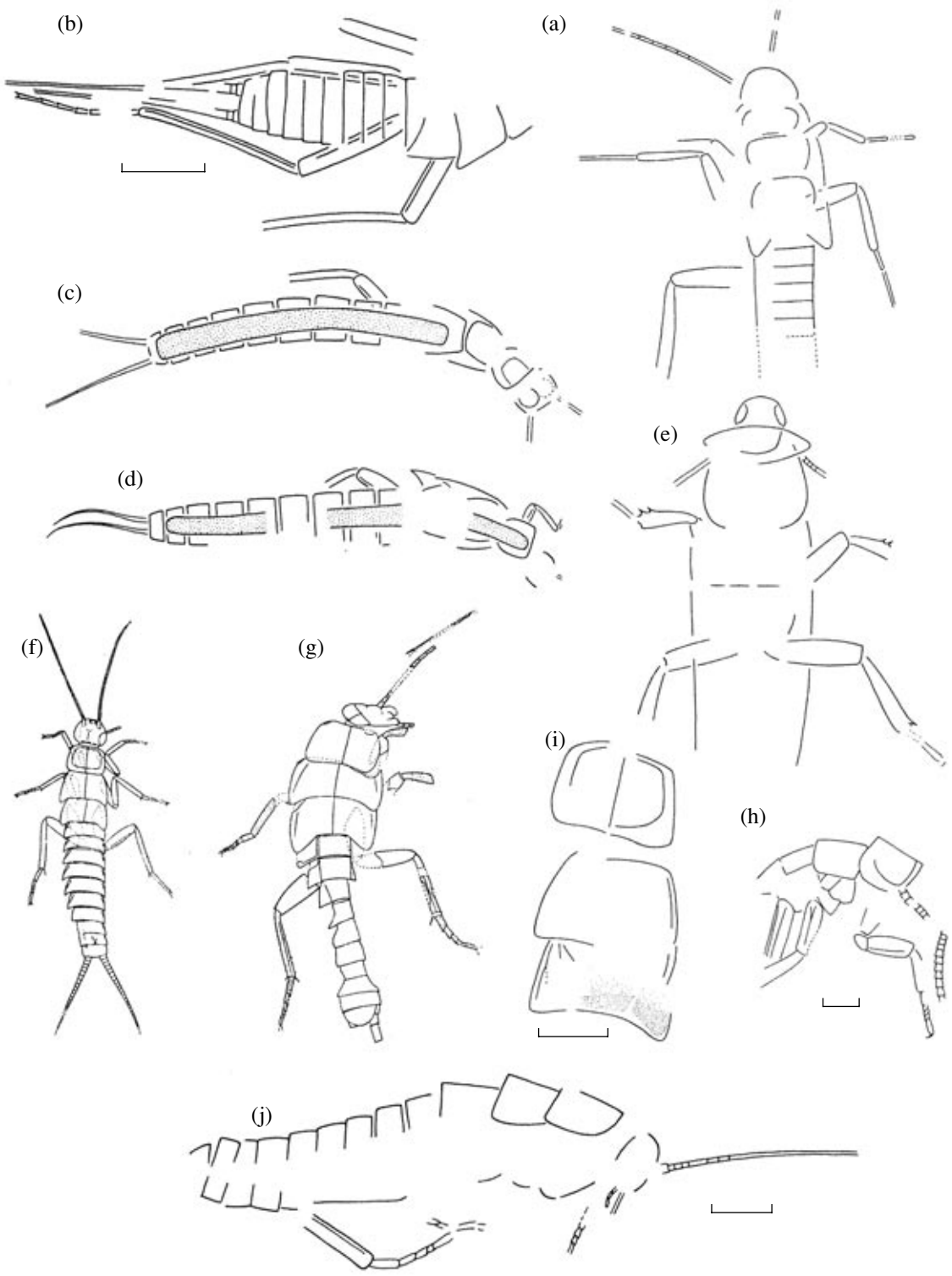

Fig. 2. Grylloblattid nymphs: (a) *Lemmatonympha gracilis* (Aristov, 2004) (after Aristov, 2004); (b) *L. gracilissima* sp. nov., holotype PIN, no. 1631/372 (orig.); (c, d) *Permedax effertus* Aristov, 2004; (e) *Sylvaclinicus echinatus* Aristov, 2004 (after Aristov, 2004); (f) *Kaltanympha gracilis* Sharov, 1961 (after Sharov, 1961); (g, h) *K. thysanuriformis* Sharov, 1961: (g) holotype (after Sharov, 1961), (h) specimen PIN, no. 679/69 (orig.); (i) *K. ornata* sp. nov., holotype PIN, no. 2987/313 (orig.); (j) *K. vorkutensis* sp. nov., holotype PIN, no. 1631/160 (orig.). Scale bar 2 mm in Figs. 2b, 2h, 2j, and 2i, other figures are not to scale.

stretched out in association with apically broadened armed tibiae and shortened tarsi are characters known in neither Lemmatophorina nor Grylloblattina. Therefore, this genus has been transferred, on the basis of similarity to the Probnidae, from Grylloblattida incertae sedis, where it was described, into Protoperlina incertae sedis.

Suboder Grylloblattina Walker, 1914

Family Liomopteridae Sellards, 1909

Genus *Kaltanympha* Sharov, 1961

Type species. *K. thysanuriformis* Sharov, 1961; Kaltan, Kuznetsk Formation.

Diagnosis. Head large, with large eyes. Pronotum with paranota as broad as head and mesonotum. Pronotum transverse, broadening backward, paranota narrow. Fore and middle legs approximately equally long, hind legs noticeably longer. Middle and hind tibiae directed backward, tarsus 5-segmented. Abdominal tergites with narrow paranota.

Species composition. Besides the type species, *K. gracilis* (Sharov, 1961) comb. nov., *K. vorkutensis* sp. nov. and *K. ornata* sp. nov. from the same locality.

Remarks. This genus was described from the locality of Kaltan and assigned to Liomopteridae, probably on the basis of the domination of liomopterid imagoes in this locality. As discussed earlier, the domination of imagoes of any taxon cannot prove assignment of abundant nymphs to the same taxon. However, *Kaltanympha* has been left within Liomopteridae, since its morphology does not contradict this assignment.

With certain hesitation, the species *K. gracilis* was originally referred to the genus *Liomopterites* Sharov, 1961. Due to the lack of essential differences from *Kaltanympha*, this species is transferred to the latter genus.

Identification key to species of *Kaltanympha*

1 (4) Mesonotum as long as metanotum.

2 (3) Hind femora armed, first segment of hind tarsus almost as broad as hind tibia. Body length, 14 mm (Figs. 2g, 2h)……
……*K. thysanuriformis* Sharov, 1961

3 (2) Hind femora unarmed, first segment of hind tarsus 0.5 times as broad as hind tibia. Body length, 16 mm (Fig. 2j)……
……*K. vorkutensis* sp. nov.

4 (1) Mesonotum longer than metanotum.

5 (6) Metanotum not colored. Body length, 9 mm (Fig. 2f)……
……*K. gracilis* (Sharov, 1961)

6 (5) Metanotum colored. Length of notum, about 8.5 mm (Fig. 2i)
……*K. ornata* sp. nov.

***Kaltanympha vorkutensis* Aristov, Novokshonov et Pan'kov, sp. nov.**

Etymology. From Vorkuta.

Holotype. PIN, no. 1631/160, adequately preserved impression of the body of a nymph; Komi republic, locality of Verkhne-Syr'yaginskoe, borehole VSK-186, depth 144 m; Upper Permian, Ufimian, Lek-Vorkuta Formation, Ayach'yaginsk Subformation, Member R (Pukhonto, 1998).

Description (Fig. 2j). The head is oval-shaped in profile; the antennae are long, the first antennomere is enlarged, basal antennomeres are as long as wide, distal segments are elongated. The thoracic sections are equally long; the abdomen is longer than the thorax. The legs are rather short, the forelegs are approximately 0.5 times as long as the hindlegs. The hind femora are unarmed; the tibia and tarsus are approximately equal in their lengths, the first segment of the hind tarsus is half as broad as the hind tibia.

Measurements, mm. Body length, 16.

Remarks. The hind tibiae are directed forward apparently due to postmortem deformation.

Material. Holotype.

***Kaltanympha ornata* Aristov, Novokshonov et Pan'kov, sp. nov.**

Etymology. From the Latin *ornata* (ornamented).

Holotype. PIN, no. 2987/313, deformed part and counterpart of the dorsal side of the thorax; Evenki Autonomous Region, right bank of the Taimura River near the factory (trading station) of Kerbo; Upper Permian, Upper Tatarian, lower part of the Degali Formation.

Description (Fig. 2i). The pronotum is trapezoid, broadening backward, with a longitudinal suture. The paranota are narrow and broadening backward. The mesonotum and metanotum are trapezoid, the mesonotum is longer than the metanotum. The wing sheaths are small; the rear margin of the metanotum is colored.

Measurements, mm. Length of notum, about 8.5.

Material. Holotype.

Grylloblattina incertae sedis

Genus *Tataronympha* Aristov, Novokshonov et Pan'kov, gen. nov.

Etymology. From Tatarstan and the Greek *nympha* (a nymph).

Type species. *T. kamensis* sp. nov.

Diagnosis. Pronotum with paranota as broad as mesonotum and less than twice as broad as head. Pronotum elongate, slightly broadening to base. All three pairs of legs approximately equally long. Middle and hind tibiae directed backward; tarsus shortened, 5-segmented. Abdominal tergites with narrow paranota.

Species composition. Type species.

Remarks. The nymphs under description were originally attributed to *Atactophlebia termitoides* Martynov, 1928 of the family Atactophlebiidae (Storozhenko, 1994). In the locality of Tikhie Gory, Atactophlebiidae is a dominating family, constituting about 85% of all grylloblattids that can be identified to the family level. As previously mentioned, the domination

of imagoes of any taxon cannot prove assignment of abundant nymphs to the same taxon. Additionally, the described nymphs differ from *K. mira*, the only undoubted atactophlebiid nymph, both in morphology and in its presumed mode of life. Judging from their scarcity in the presence of a large amount of adults, *Tataronympha* lived some distance from the water, so should not be considered in the same family as near-water *Kirkorella*. The absence of apparent similarity to other families prompts the description of this nymph as a new genus of Grylloblattina incertae sedis.

***Tataronympha kamensis* Aristov, Novokshonov et Pan'kov, sp. nov.**

Etymology. From the Kama River.

Holotype. PIN, no. 2295/49, nymph impression; Tatarstan, right bank of the Kama River, locality of Tikhie Gory; Upper Permian, Kazanian, Lower Kazanian, linguliod beds of the Baitugan Formation.

Description (Fig. 3d). The head is rounded, middle-sized; the antennae are short. The mesonotum is as long as the metanotum. The fore legs are somewhat shorter than the middle and hind legs; the tibiae bear small spines; the first and fifth tarsomeres are of equal length, other tarsomeres are equal, and shorter than these two. The cerci are moderately long, with short segments.

Measurements, mm. Body length, 15–18.

Material. Besides the holotype, paratypes PIN, nos. 2295/56, 2295/86, 2295/88, and 2295/89 from the same locality.

Genus *Tshebardanympha* Aristov, Novokshonov et Pan'kov, gen. nov.

Etymology. From the localities of Tshekarda and Barda and the Greek *nympha* (a nymph).

Type species. *Tshekardites lientericus* Aristov, 2004; Tshekarda, Koshelevka Formation.

Diagnosis. Head large with small eyes. Pronotum with paranota as broad as mesonotum and less than twice as broad as head. Pronotum quadrate, paranota narrow. Fore and middle legs of approximately equal length, hind legs noticeably longer. Middle and hind tibiae directed backward, tarsus 5-segmented. Abdominal tergites with narrow paranota.

Species composition. *T. lienterica* (Aristov, 2004) comb. nov. and *T. bardensis* (Aristov, 2004) comb. nov. from the coeval locality of Barda.

Identification key to species of *Tshebardanympha*

1 (2) Wing sheaths rounded, middle femora longer than fore femora, fore tarsus comparable to tibia in its length. Body length, 13 mm (Fig. 3b)……*Tsh. lienterica* (Aristov, 2004)

2 (1) Wing sheaths tapered, fore femora as long as middle ones, fore tarsus much shorter than tibia. Body length, 25 mm (Fig. 3a) ……*Tsh. bardensis* (Aristov, 2004)

Genus *Sylvalitoralis* Aristov, Novokshonov et Pan'kov, gen. nov.

Etymology. From the Sylva River and the Latin *litoralis* (coastal).

Type species. *Tshekardites calcomessor* Aristov, 2004; Tshekarda, Koshelevka Formation.

Diagnosis. Head large, with thick antennae. Pronotum with paranota narrowing backward, less than twice as broad as head and as broad as mesonotum. Middle and hind tibiae unarmed, directed backward; middle tarsus as long as tibia; tarsus 3-segmented, first tarsomere as long as third. Abdominal tergites without paranota.

Species composition. *S. calcomessor* (Aristov, 2004) comb. nov. and *S. curculianicus* (Aristov, 2004) comb. nov. from the same locality.

Identification key to species of *Sylvalitoralis*

1 (2) Pronotum as long as wide, hind femora longer than fore femora. Length of body without abdomen 19 mm (Fig. 1h)…… ……*S. calcomessor* (Aristov, 2004)

2 (1) Pronotum wider than long, fore femora approximately as long as hind ones. Body length 11 mm (Fig. 1j)…… ……*S. curculianicus* (Aristov, 2004)

Genus *Tshekardites* Aristov, 2004

Type species. *T. comitialis* Aristov, 2004; locality of Tshekarda; Lower Permian, Kungurian, Iren' Horizon, Koshelevka Formation.

Diagnosis (Fig. 3c). Pronotum with paranota as long as wide, less than twice as broad as head and as broad as mesonotum. Paranota narrow. Hind legs longer than middle legs. Middle and hind tibiae armed and directed backwards; middle tibia longer than 3-segmented tarsus; first tarsomere longer than third. Abdominal tergites narrow, with small paranota. Body length, 20 mm.

Species composition. Type species.

Remarks. Although originally described as a formal genus (Aristov, 2004), this genus is considered to be natural in the present study.

Genus *Permonympha* Sharov, 1957

Type species. *P. gracile* Sharov, 1957; Kemerovo Region, Kuzedeevo District, outcrop 1300, locality of Kuznetsk Basin; Upper Permian, Kazanian, Lower Kazanian, Kuznetsk Formation.

Diagnosis (Figs. 3g, 3h). Pronotum trapezoid, slightly wider than long, without paranota, as broad as head and mesonotum. Wing sheaths long, with poorly visible traces of venation. Middle and hind legs equally long, fore legs slightly shorter. Middle and hind tibiae directed backward. Abdominal tergites with median crest, broad pointed paranota and rather long unsegmented cerci.

Species composition. Type species.

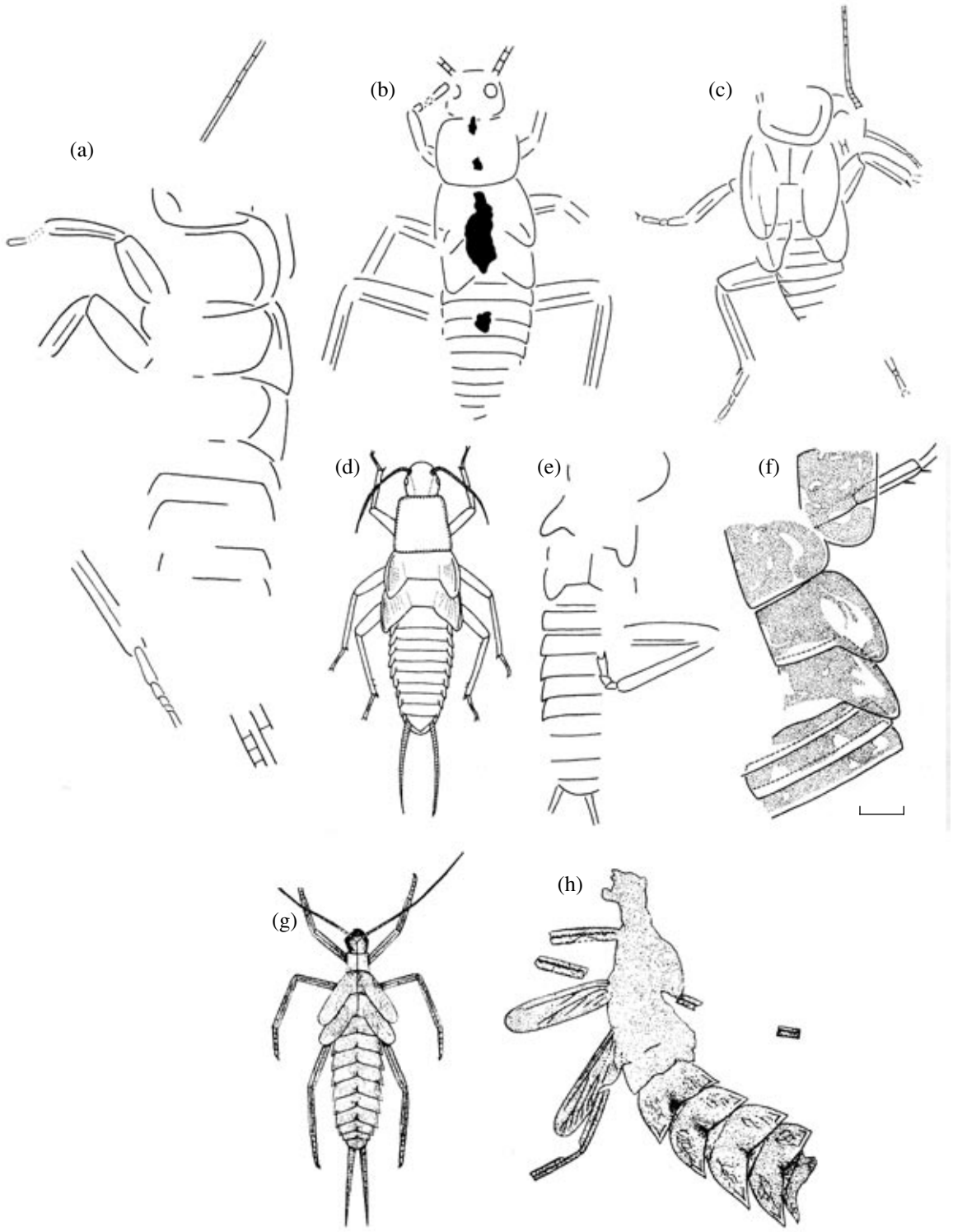

Fig. 3. Grylloblattid and cockroach nymphs: (a) *Tshebardanympha bardensis* (Aristov, 2004); (b) *Tsh. lienterica* (Aristov, 2004); (c) *Tshekardites comitialis* Aristov, 2004 (after Aristov, 2004); (d) *Tataronympha kamensis* sp. nov., reconstruction (after Storozhenko, 1994); (e) *Thaumatophora pronotalis* Riek, 1976 (orig. drawing after photograph from Riek, 1976); (f) cockroach exuvia, specimen PIN, no. 2384/8 (orig.); (g, h) *Permonympha gracile* Sharov, 1957: (g) reconstruction, (h) specimen PIN, no. 600/496 (after Sharov, 1957). Scale bar 2 mm in Fig. 3f, other figures are not to scale.

Remarks. These nymphs had been described within the order Miomoptera as a separate genus, which was subsequently synonymized under the genus *Delopterum* Sellards, 1909 (Sharov, 1957, 1961). Traces of the wing sheath venation was the reason for their assignment to miomopterans. However, the poor preservation of the wing sheaths and the fact that miomopterans were holometabolous insects (Rasnitsyn, 1977) prevent allocation of *Permonympha* to this order. At the same time, nymphs of *Permonympha* have no features that would contradict their inclusion into the order Grylloblattida.

Two species, *P. gracile* and *P. arcuata* Sharov, 1957, differing in their size and in the shape of the lateral margins of their abdominal tergites, were described in this genus. The fact that the first character depends on the instar of a nymph and the second character can vary due to the state of preservation does not allow us to consider these nymphs as representatives of different species. Therefore, *P. arcuata* (Sharov, 1957, p. 1107, text-fig. 2) is here proposed as a junior synonym of *P. gracile*.

Genus *Thaumatophora* Riek, 1976

Type species. *T. pronotalis* Riek, 1976; Republic of South Africa, Hammanskraal, Pretoria; Lower Permian, Middle Ecca (not examined).

Diagnosis (Fig. 3e). Pronotum broadening forward, pronotum with paranota broader than mesonotum. Hind tibiae directed backwards, unarmed. Tarsus shortened, 3-segmented; first two tarsomeres short and equal to each other. Abdominal tergites with paranota. Body length, about 18 mm.

Species composition. Type species.

Genus *Gurianovella* G. Zalessky, 1939

Type species. *G. silphidoides* G. Zalessky, 1939 locality of Tshekarda; Lower Permian, Kungurian, Iren' Horizon, Koshelevka Formation.

Diagnosis (Figs. 1a, 1b). Pronotum with paranota twice as broad as head and as broad as mesonotum. Each pronotal paranotum with incision on its fore margin. Fore femora thickened; tibiae unarmed, fore and middle tibiae directed forward, hind tibiae directed backward. Fore and middle tarsi unsegmented, hind tarsus 2-segmented. Body length, 13–14 mm.

Species composition. Type species.

Remarks. Since the holotype had been redescribed (Aristov, 2004), a better preserved specimen from the same locality was discovered (PIN, no. 1987/51, Fig. 1b). This specimen demonstrates previously unknown for *Gurianovella* chewing mouthparts, unsegmented fore and middle tarsi, coxal gills, and gut contents with sand grains.

Genus *Sylvonympha* Novokshonov et Pan'kov, 1999

Type species. *S. tshekardensis* Novokshonov et Pan'kov, 1999; locality of Tshekarda; Lower Permian, Kungurian, Iren' Horizon, Koshelevka Formation.

Diagnosis (Fig. 1d). Pronotum with paranota twice as broad as head and as broad as mesonotum. Each pronotal paranotum with incision on its fore margin. Tibiae unarmed, all three pairs directed forward; tibiae and femora with hairs; tarsus shortened, most probably 3-segmented. Coxal gills visible near fore and hind coxae. Abdomen somewhat narrowed near its base, abdominal paranota narrow. Body length, 14.5 mm.

Species composition. Type species.

Remarks. This genus was described as Plecopteroidea incertae sedis (Novokshonov and Pan'kov, 1999), was later treated as a grylloblattid nymph (Storozhenko, 2002), and finally transferred to Grylloblattida incertae sedis (Aristov, 2004).

Genus *Triasseuryptilon* Storozhenko, 1997

Type species. *Delopterum acostai* Marquat, 1991; Argentina, Mendosa Prov., Cacheuta; Middle Triassic, Potrerillos Formation (not examined).

Diagnosis (Fig. 1c). Pronotum without incision on its fore margin, pronotum with paranota less than twice as broad as head and as broad as mesonotum. All three pairs of tibiae directed forward; tarsi shortened, with three subequal segments. Abdominal tergites with paranota. Body length, 18.5 mm

Species composition. Type species.

Remarks. This genus was first described as a miomopteran larva (Marquat, 1991) and later transferred as a new genus to the family Atactophlebiidae (Storozhenko, 1997). The comparison with the genus *Kirkorella* revealed that the only similarity between them is in the presence of paranota on the abdominal tergites. Unlike cockroach-like *Kirkorella*, *Triasseuryptilon* is the most stonefly-like grylloblattid nymph (differs from stonefly nymphs only in having abdominal paranota) and cannot be considered as a member of the same family.

ACKNOWLEDGMENTS

The authors are most grateful to A.P. Rasnitsyn (PIN) for valuable consultations. The study was supported by the Russian Foundation for Basic Research, project no. 04-04-48296.

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