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## REVIEW OF THE PALEOZOIC AND MESOZOIC FAMILIES MEGAKHOSARIDAE AND BLATTOGRYLLIDAE (INSECTA: GRYLLOBLATTIDA)

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Relationship of the families Blattogryllidae, Megakhosaridae, Plesioblattogryllidae and Grylloblattidae is discussed. The diagnoses of Blattogryllidae and Megakhosaridae are clarified. New synonymy is proposed: Blattogryllidae Rasnitsyn, 1976 = Plesioblattogryllidae Huang, Nel et Petrulevicius, 2008, **syn. n.** New genus *Blattokhosara* Storozhenko et Aristov, **gen. n.** (type species: *Megakhosarina minuscula* Aristov, 2008 from the Middle Permian Soyana locality in Russia) is described. Genera *Protoblattogryllus* Storozhenko, 1992, *Mesoblattogryllus* Storozhenko, 1992, *Megablattogryllus* Storozhenko, 1992 and *Madygenocephalus* Aristov, 2011 are transferred from Blattogryllidae to Megakhosaridae. New combinations are proposed: *Mesoblattogryllus conjunctus* Storozhenko, 1992 = *Costatoviblatta conjuncta* (Storozhenko, 1992), **comb. n.**, *Mesoblattogryllus longipennis* Storozhenko, 1992 = *Costatoviblatta longipennis* (Storozhenko, 1992), **comb. n.** Genus *Blattogryllulus* Storozhenko, 1988 is excluded from Blattogryllidae and transferred to Grylloblattida incertae sedis.

KEY WORDS: Insecta, Grylloblattida, Blattogryllidae, Megakhosaridae, Plesioblattogryllidae, taxonomy, phylogeny, Permian, Triassic, Jurassic.

**С. Ю. Стороженко, Д.С. Аристов. Обзор палеозойских и мезозойских семейств Megakhosaridae и Blattogryllidae (Insecta: Grylloblattida) // Дальневосточный энтомолог. 2014. N 271. С. 1-28.**

Обсуждаются взаимоотношения семейств Blattogryllidae, Megakhosaridae, Plesioblattogryllidae и Grylloblattidae. Уточнены диагнозы Blattogryllidae и Megakhosaridae. Предложена новая синонимия: Blattogryllidae Rasnitsyn, 1976 = Plesioblattogryllidae Huang, Nel et Petrulevicius, 2008, **syn. n.** Описан новый род *Blattokhosara* Storozhenko et Aristov, **gen. n.** (типовой вид: *Megakhosarina minuscula* Aristov, 2008 из местонахождения Сояна, средняя пермь России). Рода *Protoblattogryllus* Storozhenko, 1992, *Mesoblattogryllus* Storozhenko, 1992, *Megablattogryllus* Storozhenko, 1992 и *Madygenocephalus* Aristov, 2011 перенесены из Blattogryllidae в Megakhosaridae. Предложены две новые комбинации: *Mesoblattogryllus conjunctus* Storozhenko, 1992 = *Costatoviblatta conjuncta* (Storozhenko, 1992), **comb. n.**, *Mesoblattogryllus longipennis* Storozhenko, 1992 = *Costatoviblatta longipennis* (Storozhenko, 1992), **comb. n.** Род *Blattogryllulus* Storozhenko, 1988 исключен из Blattogryllidae и отнесен к гриллоблаттидовым неясного положения (*Grylloblattida incertae sedis*).

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## INTRODUCTION

The Paleozoic and Mesozoic families Blattogryllidae and Megakhosaridae are considered as stem-group of extant family Grylloblattidae, or ice crawlers (Rasnitsyn, 1976; Storozhenko, 1998). Family Megakhosaridae was established by Sharov (1961) for Permian genus *Megakhosara* Martynov, 1937. Rasnitsyn (1976) described family Blattogryllidae for Jurassic genus *Blattogryllus* Rasnitsyn, 1976. Family Plesioblattogryllidae was established for Jurassic genus *Plesioblattogryllus* Huang, Nel et Petrulevicius, 2008 (Huang *et al.*, 2008). Moreover, the formal cladotypic taxon Blattogrylloptera is established for majority of the species currently assigned to Blattogryllidae, Plesioblattogryllidae and Grylloblattidae (Cui, 2012). Still now 32 Permian, Triassic and Jurassic genera are described in Megakhosaridae, Blattogryllidae and Plesioblattogryllidae, or transferred to these families from other families (Martynov, 1937; Handlirsch, 1939; Bode, 1953; Sharov, 1961, 1962; Riek, 1973, 1976; Rasnitsyn, 1976; Storozhenko, 1988, 1990, 1992, 1993, 1994a, 1994b, 1998, 2002; Carpenter, 1992; Novokshonov, 1998; Dijk & Geertsema, 1999; Aristov, 2000, 2004a, 2004b, 2008a, 2008b, 2009a, 2009b, 2010, 2011a, 2011b, 2013a, 2013b; Huang *et al.*, 2008; Aristov & Zessin, 2009; Aristov *et al.*, 2011; Ren & Aristov, 2011).

The composition and classification of the families Megakhosaridae, Blattogryllidae and Plesioblattogryllidae are discussed below. Herein the wing-venation of fore wings is considered as the most important taxonomic character for separating these families. Special attempt is made for re-examination of tarsal segments of the extinct and extant representatives of the order Grylloblattida.

## TARSI OF GRYLLOBLATTIDAE, BLATTOGRYLLIDAE AND PLESIUBLATTOGRYLLIDAE AS TAXONOMIC CHARACTER

Still now the tarsal segments of legs are considered as main feature for separating families Grylloblattidae, Plesioblattogryllidae and Blattogryllidae. In extant Grylloblattidae all tarsi are 5-segmented; the dorsal side of 1-4-th segments is provided by a pair of euplantulae on each segment; dorsal side of 5-th segment furnish with an unpaired euplantula and two apical claws; pulvillus between claws absent (Figs. 4, 5). According to original description of *Blattogryllus karatavicus* the apex of 5-th tarsal segments of this species is characterized by presents of large pulvillus and absents of claws (Rasnitsyn, 1976). Such structure of apical segments of legs is unusual for almost all known insects (except some very small-sized Thysanoptera) and has been used for separating Blattogryllidae from Grylloblattidae (Storozhenko, 1998; 2002). By presents of large claws and by absents of pulvillus at the top of the apical tarsal segments of legs (Fig. 3) the family Plesioblattogryllidae was established for *Plesioblattogryllus magnificus* (Huang *et al.*, 2008), while the shape of body and wing-venation of *Blattogryllus* and *Plesioblattogryllus* are very similar (Cui, 2012).

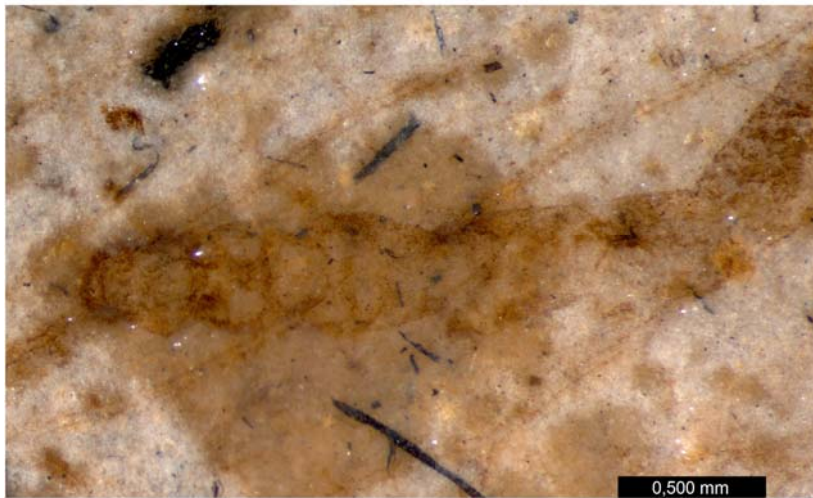
We re-examined the paratypes of *Blattogryllus karatavicus* with well preserved legs at large magnification and find that the tarsal segments of this species are not so strongly differ from Grylloblattidae and Plesioblattogryllidae. In *B. karatavicus* all tarsi are also 5-segmented; each of 1-4-th segments are provided by a pair of dorsal euplantulae; the unpaired euplantula on dorsal side of 5-th segment is very large and slightly surpassing the apex of segment; two very small claws present, but weakly sclerotized; pulvillus between claws absent (Figs 1, 2, 6, 7). In *Blattogryllus* the length of all tarsal segments are almost equal (like in *Plesioblattogryllus*, see Figs. 3, 8), while in extant Grylloblattidae 1-st and 5-th segments are distinctly longer than other segments (Figs. 4, 5). As contrasted to Grylloblattidae the 5-th tarsal segment of *Blattogryllus* and *Plesioblattogryllus* are inflated. The enlarged apical euplantulae in *Blattogryllus* are devices similar in operation with large arolium at the top of the apical tarsal segments of legs in phytophilous insects (for example, grasshoppers). We believe what *Blattogryllus* is the genus specialized for living on leaf of plants, while *Plesioblattogryllus* inhabits the soil. The presence of phytophilous and geophilous forms in the same family is common situation in insects. Thus, there are no any reasons for dividing Blattogryllidae and Plesioblattogryllidae in different families based only on adaptation for habitat on different substrate, and new synonymy is proposed herein: Blattogryllidae Rasnitsyn, 1976 = Plesioblattogryllidae Huang, Nel et Petrulevicius, 2008, **syn. n.**

## WING-VENATION OF MEGAKHOSARIDAE AND BLATTOGRYLLIDAE AS TAXONOMIC CHARACTER

The examination of the additional material of *Megakhosarina minuscula* Aristov, 2008 allows us to establish new genus (see below under description of *Blattokhosara* gen. n.) and to clarify the differences in wing-venation of Megakhosaridae and



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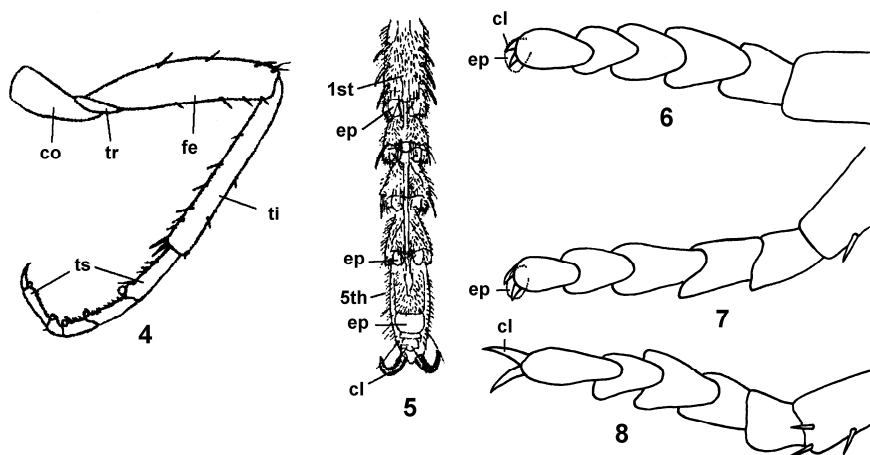


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Figs. 1–3. Tarsi of Blattogryllidae. 1, 2 – *Blattogryllus karatavicus* (spec. PIN No 2384/205): 1 – mid leg; 2 – hind leg; 3 – *Plesioblattogryllus magnificus*, hind leg. (Fig. 3 after Huang *et al.*, 2008). Scale bars = 0,5 mm.



Figs. 4–8. Legs of Grylloblattidae and Blattogryllidae. 4 – *Grylloblattella pravdini*, hind leg, lateral view; 5 – *Grylloblatta campodeiformis*, tarsus of hind leg, ventral view; 6, 7 – *Blattogryllus karatavicus* (spec. PIN No 2384/205): 6 – tarsus of mid leg, 7 – tarsus of hind leg; 8 – *Plesioblattogryllus magnificus*, tarsus of hind leg. Abbreviations: cl – claws; co – coxa; ep – euplantulae; fe – femur; ti – tibia; tr – trochanter; ts – tarsus; 1st – first tarsal segment; 5th – fifth tarsal segment.

Blattogryllidae. Previously these families differ by position of *M* in forewing: in Megakhosaridae the base of *M* is distinctly separated from base of *CuA* and *M* connected with *CuA* by oblique vein ( $M_5$ ), and in Blattogryllidae the base of *M* is partly or completely fused with *CuA* (Storozhenko, 1998; Cui, 2012). But in *Megakhosarina minuscula* this feature is variable within the same species (Figs 9-22) and wherefore don't be used for identification of families Megakhosaridae and Blattogryllidae. Herein we propose that the most important feature for separation of these families is the position of bases of *M*, *MA* and *MP* in forewing. The genera with the base of *M* in forewing distinctly separated from *CuA* (plesiomoprphy) or with *MA* and *MP* arise from *CuA* as single vein (in this case the base of *M* always present) are deposited in Megakhosaridae. The genera with *MA* and *MP* in forewing arise from *CuA* separately (synapomorphy) are placed herein in Blattogryllidae. Such conception support the hypothesis (Storozhenko, 1998), according to which mainly Mesozoic family Blattogryllidae arise directly from predominantly Paleozoic Megakhosaridae. Moreover, the living ice crawlers (Grylloblattidae) are found traceable down toward the Carboniferous Eoblattidae vie extinct Blattogryllidae – Megakhosaridae – Daldubidae – Cacurgidae (Aristov & Rasnitsyn, 2013). A sister-group relationship between Grylloblattidae and Blattogryllidae is based on the combination of a large number of apparently plesiomorphic features (e.g., filiform multi-segmented antennae, orthopteroid mouthparts, 5-segmented tarsi, multi-segmented cerci) with a complex of apomorphies linked to the enlarged coxae and highly derived asymmetric male genitalia (Rasnitsyn, 1976; Wipfler *et al.*, 2014).

## TAXONOMY

### Order Grylloblattida Walker, 1914

### Family Megakhosaridae Sharov, 1961

Megakhosaridae Sharov, 1961: 178.

Type genus: *Megakhosara* Martynov, 1937.

REVISED DIAGNOSIS. Pronotum with broad lateral expansions (paranota); mid and hind tibia directed backward. Forewing: *Sc* concave and ending on the anterior wing margin; costal field narrower or as wide as subcostal field; *RS* arises in basal third of wing; interradial field not widened; the base of *M* distinctly separated from *CuA* and in this case *M*<sub>5</sub> present, or in basal part of wing *M* anastomose with *CuA*, but in this case *M* arises from *CuA* as single branch (before dividing into *MA* and *MP*); main fork of *M* situated in basal quarter of wing before the origin of *RS*; *CuA* not divided in *CuA*<sub>1</sub> and *CuA*<sub>2</sub>; intercubital field crossed by posterior branches of *CuA*; *CuP* simple, concave; clavus absent.

COMPOSITION. Family consists of 20 genera, beside them 14 genera are known from the Lower, Middle and Upper Permian only, two genera known from the Middle Permian to the Middle Triassic, and fore genera known from the Middle Triassic only.

NOTES. Genera *Madygenocephalus*, *Mesoblattogryllus*, *Protoblattogryllus* and *Megablattogryllus* are characterized by *M* arise from *CuA* as single branch before dividing in *MA* and *MP*, and transferred herein from Blattogryllidae to Megakhosaridae. One new genus is also described below.

#### List of the genera and species of Megakhosaridae with description of new taxa

##### Genus *Abbrevikhosara* Aristov, 2013

Type species: *Abbrevikhosara ovoidea* Aristov, 2013, by original designation.

COMPOSITION. One species from the Upper Permian of Europe.

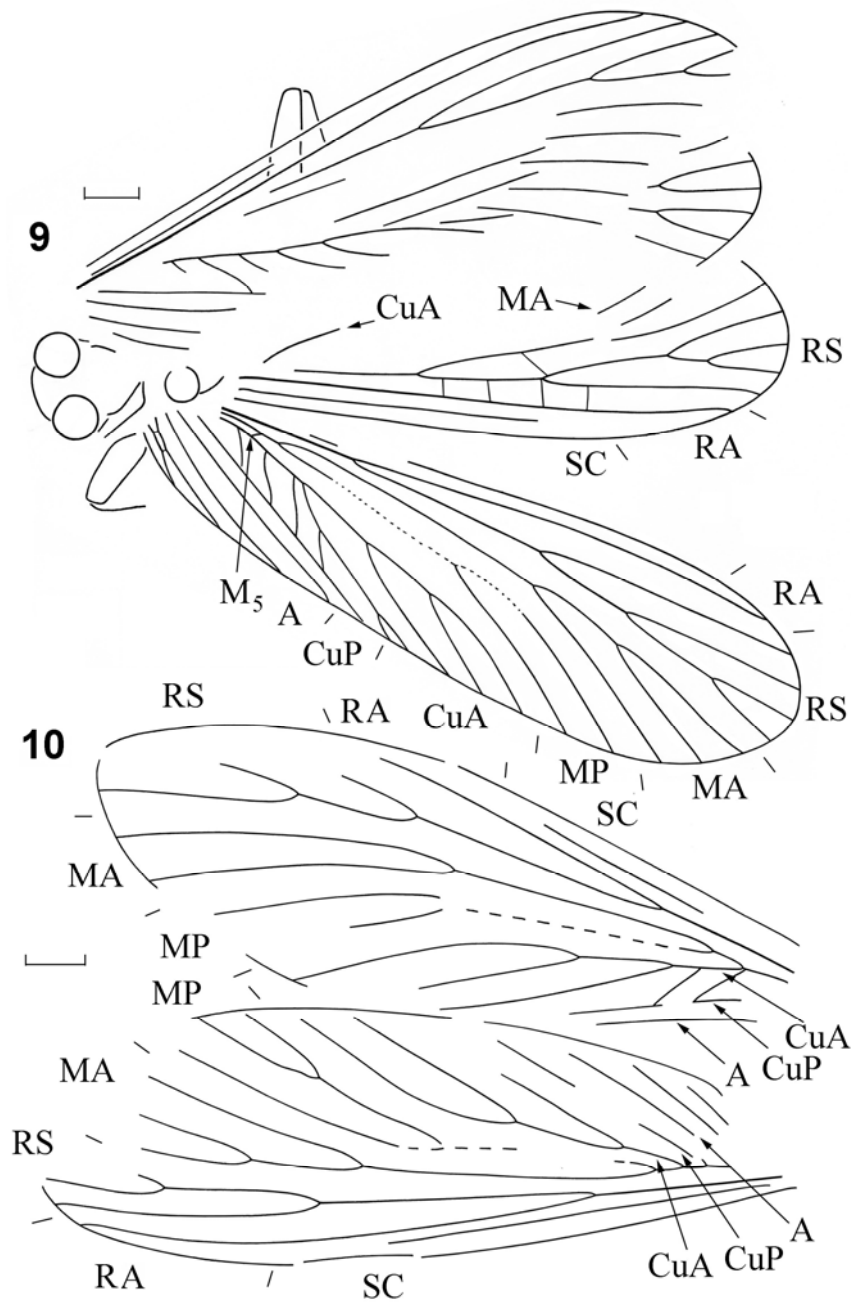
##### *Abbrevikhosara ovoidea* Aristov, 2013

LOCALITY. The Upper Permian Isady locality in European Russia (Aristov, 2013b).

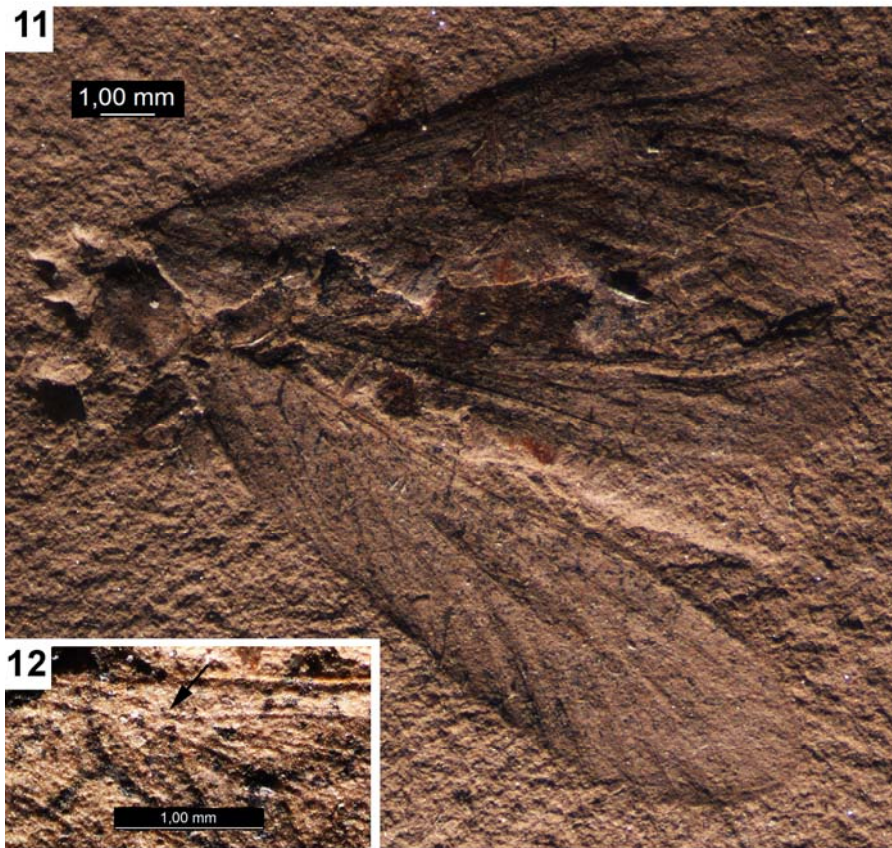
##### Genus *Blattokhosara* Storozhenko et Aristov, gen. n.

Type species: *Megakhosarina minuscula* Aristov, 2008, here designated.

DESCRIPTION. Forewing: *Sc* reaching apical third of wing, but not ending on *C*; *RS* originate in basal quarter of wing, pectinate upward, with 3-6 branches; the base of *M* connected with *CuA* by oblique vein (*M*<sub>5</sub>) or anastomose with *CuA* at short distance; *MA* with 2-4 branches; *MP* desclerotized near the middle, simple or with 2-3 branches; *CuA* with 3-4 branches; *CuP* simple, concave; intercubital area relatively narrow and crossed by few simple or Y-shaped veins; *A*<sub>1</sub> simple; *A*<sub>2</sub> with 3 branches.



Figs 9–10. *Blattokhosara minuscula* (Aristov, 2008), comb. n.: 9 – holotype PIN, No 117/86; 10 – specimen PIN, No 117/820. Scale bar = 1mm.



Figs 11–12. *Blattokhosara minuscula* (Aristov, 2008), comb. n., holotype PIN, No 117/86: 11 – body and wings; 12 – basal part of right forewing (arrow show  $M_3$ ). Scale bar = 1mm.

DIAGNOSIS. New genus is similar to *Megakhosarina*, but differs by *Sc* not reaching the anterior margin of forewing, by variability of the  $M+CuA$  anastomose in forewing, and by small size (in *Megakhosarina* *Sc* ending on anterior margin of forewing, the base of *M* always separate from *CuA*, and length of forewing is 30–44 mm).

SPECIES INCLUDED. Type species only.

ETYMOLOGY. From genera *Blattogryllus* and *Megakhosara*. Gender feminine.

***Blattokhosara minuscula* (Aristov, 2008), comb. n.**

Figs 9–22

*Megakhosarina minuscula* Aristov, 2008a: 270, fig. 2.

MATERIAL EXAMINED. Holotype (PIN, No 117/86; negative imprint of forewing), paratype (PIN, No 94/131) and 3 additional specimens (PIN, No 117/820;





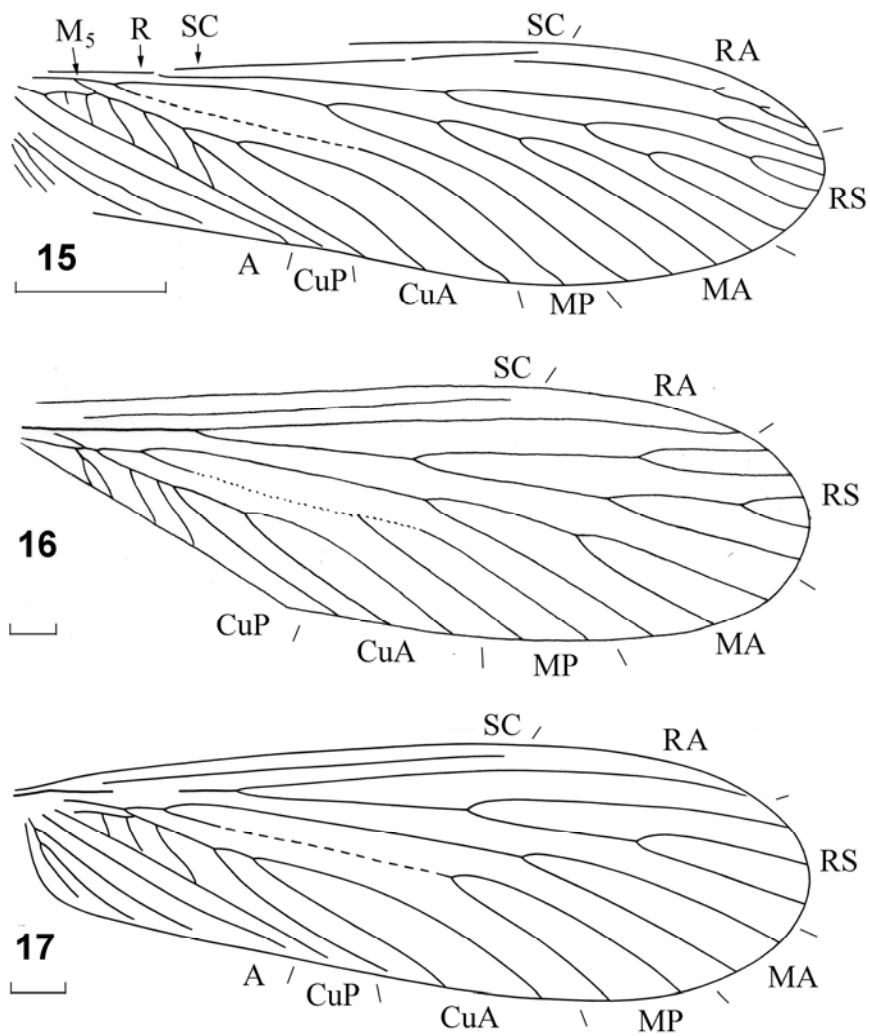
Figs 13–14. *Blattokhosara minuscula* (Aristov, 2008), comb. n., specimen PIN, No 117/820: 13 – forewing; 14 – basal part of right forewing (arrow show *M+CuA*). Scale bar = 1mm.

PIN, No 3353/396, PIN, No 94/238); all from the Soyana locality (European Russia: Arkhangelsk Region; the Middle Permian, Lower Kazanian Substage).

DESCRIPTION. Mesonotum triangular, rounded, with distinct and large lobes. Mid leg short. Forewing: anterior margin weakly convex; costal area near the origin of *RS* as wide as or slightly wider than subcostal area. Hind wing: anterior margin weakly convex; costal area near the origin of *RS* as wide as subcostal area; *Sc* reaching apical third of wing; *RA* straight, but indistinctly curved near the apex; *RS* originate in basal quarter of wing, pectinate backward, with 6 branches; first fork of *RS* situated before middle of wing.

MEASUREMENTS. Length of forewing 13.5-18 mm, or (specimen PIN, No 3353/369) 27 mm.

NOTES. The forewing of specimen PIN, No 3353/369 is about two times longer than forewings of other studied specimens, but differ from them only by *RS* with 6 branches and *MA* with 4 branches (in other specimens *RS* with 3-5 branches, *MA* simple or with 2-3 branches). Probably the small-sized specimens are males, and the large-sized specimen is female.

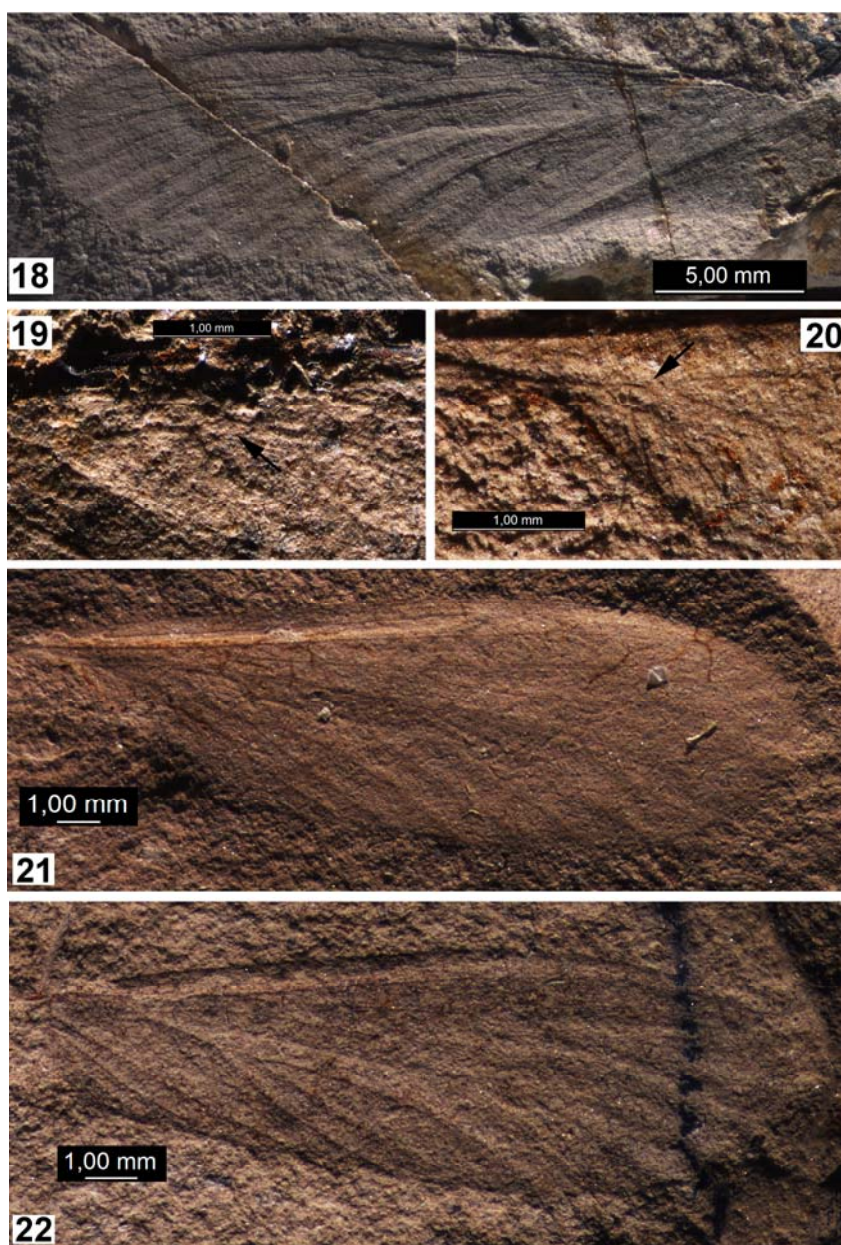


Figs 15–17. *Blattokhosara minuscula* (Aristov, 2008), comb. n., forewing: 15 – specimen PIN, No 3353/396; 16 – paratype PIN, No 94/131; 17 – specimen PIN, No 94/238. Scale bars Fig. 15 = 5 mm, Figs 16, 17 = 1 mm.

**Genus *Ivakhosara* Aristov, 2008**

Type species: *Ivakhosara pectinimedia* Aristov, 2008, by original designation.

COMPOSITION. Two species from the Lower and Middle Permian of Europe.



Figs 18–22. *Blattokhosara minuscula* (Aristov, 2008), comb. n.: 18, 19 – specimen PIN, No 3353/396: 18 – forewing, 19 – basal part of forewing (arrow show  $M_5$ ); 20, 21 – paratype PIN, No 94/131: – basal part of right forewing (arrow show  $M+CuA$ ); 21 – forewing; 22 – specimen PIN, No 94/238, forewing. Scale bars Fig. 18 = 5 mm, Figs 19–22 = 1 mm.

***Ivakhosara pectinimedia* Aristov, 2008**

LOCALITY. The Middle Permian Soyana locality in European Russia (Aristov, 2008a).

***Ivakhosara prima* Aristov, 2010**

LOCALITY. The Lower Permian Tyulkino locality in European Russia (Aristov, 2010).

**Genus *Kargalokhosara* Aristov, 2008**

Type species: *Kargalokhosara terraefossa* Aristov, 2008, by original designation.

COMPOSITION. One species from the Middle Permian of Europe.

***Kargalokhosara terraefossa* Aristov, 2008**

LOCALITY. The Middle Permian Kargala locality in European Russia (Aristov, 2008a).

**Genus *Liomopterina* Riek, 1973**

Type species: *Liomopterina clara* Riek, 1973, by original designation.

COMPOSITION. One species from the Upper Permian of Africa.

***Liomopterina clara* Riek, 1973**

LOCALITY. The Upper Permian Mooi River locality in South Africa: (Kwazulu-Natal) (Riek, 1973).

**Genus *Madygenocephalus* Aristov, 2011**

Type species: *Madygenocephalus micropteron* Aristov, 2011, by original designation.

COMPOSITION. One species from the Middle Triassic of Asia.

NOTES. Herein this genus is transferred from Blatto Gryllidae to Megakhosaridae.

***Madygenocephalus micropteron* Aristov, 2011**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Aristov, 2011a).

**Genus *Megablattogryllus* Storozhenko, 1990**

Type species: *Megablattogryllus magister* Storozhenko, 1990, by original designation.

COMPOSITION. Three species from the Middle Triassic of Asia.

NOTES. Herein this genus is transferred from Blatto Gryllidae to Megakhosaridae.

***Megablattogryllus austerus* Storozhenko, 1990**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

***Megablattogryllus magister* Storozhenko, 1990**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

***Megablattogryllus pinguis* Storozhenko, 1990**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

**Genus *Megakhosara* Martynov, 1937**

Type species: *Megakhosara fasciipennis* Martynov, 1937, by original designation.

COMPOSITION. Two species from the Middle Permian of Europe.

***Megakhosara fasciipennis* Martynov, 1937**

LOCALITY. The Middle Permian Kargala locality in European Russia (Martynov, 1937; Aristov, 2004a).

***Megakhosara nana* Aristov, 2009**

LOCALITY. The Middle Permian Kargala locality in European Russia (Aristov, 2009a).

**Genus *Megakhosarella* Sharov, 1961**

Type species: *Megakhosarella regressa* Sharov, 1961, by original designation.

COMPOSITION. Two species from the Lower Permian of Europe and the Middle Permian of Asia.

***Megakhosarella prisca* Aristov, 2010**

LOCALITY. The Lower Permian Tyulkino locality in European Russia (Aristov, 2010).

***Megakhosarella regressa* Sharov, 1961**

LOCALITY. The Middle Permian Suriekova locality in Russia (West Siberia) (Sharov, 1961).

**Genus *Megakhosarina* Storozhenko, 1993**

Type species: *Megakhosarina explicata* Sharov, 1961, by original designation.

COMPOSITION. Six species from the Middle and Upper Permian of Europe and Asia.

***Megakhosarina delucida* (Sharov, 1961)**

LOCALITY. The Middle Permian Kaltan locality in Russia (West Siberia) (Sharov, 1961; Storozhenko, 1993).

***Megakhosarina explicata* (Sharov, 1961)**

LOCALITY. The Middle Permian Kaltan locality in Russia (West Siberia) (Sharov, 1961; Storozhenko, 1993).

***Megakhosarina magna* Aristov, 2008**

LOCALITY. The Middle Permian Chepanikha locality in European Russia (Aristov, 2008a).

***Megakhosarina simplex* (Sharov, 1961)**

LOCALITY. The Middle Permian Kaltan locality in Russia (West Siberia) (Sharov, 1961; Storozhenko, 1993).

***Megakhosarina tshepanikhensis* Aristov, 2008**

LOCALITY. The Middle Permian Chepanikha locality in European Russia (Aristov, 2008b).

***Megakhosarina vyaznikensis* Aristov, 2009**

LOCALITY. The Upper Permian Balymotikha locality in European Russia (Aristov, 2009b).

**Genus *Megakhosarodes* Storozhenko, 1993**

Type species: *Megakhosarodes zajsanicus* Storozhenko, 1993, by original designation.

COMPOSITION. Seven species from the Middle and Upper Permian and the Middle Triassic of Europe and Asia.

***Megakhosarodes borealis* Aristov, 2013**

LOCALITY. The Upper Permian Balymotikha locality in European Russia (Aristov, 2013a).

***Megakhosarodes obtusus* Storozhenko, 1993**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1993).

***Megakhosarodes paulovenosus* Storozhenko, 1993**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

***Megakhosarodes shcherbakovi* Aristov, 2011**

LOCALITY. The Upper Permian Anakit locality in Russia (West Siberia) (Aristov, 2011b).

***Megakhosarodes tensilis* Aristov, 2013**

LOCALITY. The Upper Permian Isady locality in European Russia (Aristov, 2013a).

***Megakhosarodes vosgesicus* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).

***Megakhosarodes zajsanicus* Storozhenko, 1993**

LOCALITY. The Middle Permian Karaungir I locality in Kazakhstan (Storozhenko, 1993).

**Genus *Mesoblattogryllus* Storozhenko, 1990**

Type species: *Mesoblattogryllus intermedius* Storozhenko, 1990, by original designation.

COMPOSITION. Originally *Mesoblattogryllus* includes only the type species from Madygen locality. Later *M. conjunctus* and *M. longipennis* was described from the same locality (Storozhenko, 1992), but herein both are placed in the genus *Costatoviblasta* (Blattogryllidae) by the branches *MA* and *MP* arisen from *CuA* separately one from another. Finally, *Protoblattogryllus abruptus* described from Madygen (Storozhenko, 1990) was transferred to *Mesoblattogryllus* (Aristov, 2011a). Thus, now the genus *Mesoblattogryllus* consists of two species from the Middle Triassic of Asia.

NOTES. Herein this genus is transferred from Blattogryllidae to Megakhosaridae.

***Mesoblattogryllus abruptus* (Storozhenko, 1990)**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990; Aristov, 2011a).

***Mesoblattogryllus intermedius* Storozhenko, 1990**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

**Genus *Metakhosara* Storozhenko, 1993**

Type species: *Metakhosara sharovi* Storozhenko, 1993, by original designation.

COMPOSITION. One species from the Middle Triassic of Asia.

***Metakhosara sharovi* Storozhenko, 1993**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1993).

**Genus *Microkhosara* Storozhenko, 1993**

Type species: *Microkhosara fragilis* Storozhenko, 1993, by original designation.

COMPOSITION. One species from the Middle Permian of Europe.

***Microkhosara fragilis* Storozhenko, 1993**

LOCALITY. The Middle Permian Kityak locality in European Russia (Storozhenko, 1993).

**Genus *Miolopterina* Riek, 1976**

Type species: *Miolopterina tenuipennis* Riek, 1976, by original designation.

COMPOSITION. One species from the Upper Permian of Africa.

***Miolopterina tenuipennis* Riek, 1976**

LOCALITY. The Upper Permian Mooi River locality in South Africa (Kwazulu-Natal) (Riek, 1976).

**Genus *Parakhosara* Storozhenko, 1993**

Type species: *Parakhosara nasuta* Storozhenko, 1993, by original designation.

COMPOSITION. Ten species from the Permian of Europe.

***Parakhosara amoena* Storozhenko, 1993**

LOCALITY. The Middle Permian Soyana locality in European Russia (Storozhenko, 1993).

***Parakhosara coalita* Aristov, 2004**

LOCALITY. The Lower Permian Tshékarda locality in European Russia (Aristov, 2004b).

***Parakhosara incommoda* Storozhenko, 1993**

LOCALITY. The Lower Permian Vorkuta locality in European Russia (Storozhenko, 1993).

***Parakhosara kopylovi* Aristov, 2009**

LOCALITY. The Upper Permian Isady locality in European Russia (Aristov, 2009c).



***Parakhosara magna* Storozhenko, 1994**

LOCALITY. The Middle Permian Soyana locality in European Russia (Storozhenko, 1994a).

***Parakhosara martynovi* (Storozhenko, 1993)**

LOCALITY. The Lower Permian Tshekarda locality in European Russia (Aristov, 2000).

***Parakhosara mutoviensis* Aristov, 2009**

LOCALITY. The Upper Permian Isady locality in European Russia (Aristov, 2009c).

***Parakhosara nasuta* Storozhenko, 1993**

LOCALITY. The Middle Permian Soyana locality in European Russia (Storozhenko, 1993).

***Parakhosara proxima* Storozhenko, 1993**

LOCALITY. The Middle Permian Soyana locality in European Russia (Storozhenko, 1993).

***Parakhosara reticulata* Aristov, 2013**

LOCALITY. The Upper Permian Isady locality in European Russia (Aristov, 2013b).

**Genus *Pectinokhosara* Aristov, 2004**

Type species: *Pectinokhosara sylvardembioides* Aristov, 2004, by original designation.

COMPOSITION. One species from the Lower Permian of Europe.

***Pectinokhosara sylvardembioides* Aristov, 2004**

LOCALITY. The Lower Permian Tshekarda locality in European Russia (Aristov, 2004b).

**Genus *Protoblattogryllus* Storozhenko, 1990**

Type species: *Protoblattogryllus zajsanicus* Storozhenko, 1990, by original designation.

COMPOSITION. Five species from the Middle and Upper Permian of Europe and Asia and the Middle Triassic of Asia.

NOTES. Herein this genus is transferred from Blattogryllidae to Megakhosaridae. The genus *Microblattogryllus* Storozhenko, 1990 from the Middle Triassic of Kyrgyzstan (Storozhenko, 1990) was synonymized with *Protoblattogryllus* (Aristov, 2011a).

***Protoblattogryllus asiaticus* Storozhenko, 1990**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

***Protoblattogryllus nedubrovensis* Aristov, 2011**

LOCALITY. The Upper Permian Nedubrovo locality in European Russia (Aristov, 2011a).

***Protoblattogryllus variabilis* (Storozhenko, 1990)**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990; Aristov, 2011a).

***Protoblattogryllus vittatus* Aristov, 2011**

LOCALITY. The Upper Permian Anakit locality in European Russia (Aristov, 2011b).

***Protoblattogryllus zajsanicus* Storozhenko, 1990**

LOCALITY. The Middle Permian Karaungir II locality in Kazakhstan (Storozhenko, 1990).

**Genus *Syndesmophora* Martynov, 1937**

Type species: *Syndesmophora composita* Martynov, 1937, by original designation.

COMPOSITION. One species from the Middle Permian of Europe.

NOTES. This genus was synonymized under genus *Megakhosara* (Sharov, 1961), but later was considered as separate genus (Aristov, 2004a).

***Syndesmophora composita* Martynov, 1937**

LOCALITY. The Middle Permian Kargala locality in European Russia (Martynov, 1937; Aristov, 2004a).

**Genus *Tshekhosara* Novokshonov, 1998**

Type species: *Tshekhosara improvida* Novokshonov, 1998, by original designation.

COMPOSITION. One species from the Lower Permian of Europe.

***Tshekhosara improvida* Novokshonov, 1998**

LOCALITY. The Lower Permian Tshekarda locality in European Russia (Novokshonov, 1998).

### Taxa erroneously placed in Megakhosaridae

The genus *Ideliopsis* Carpenter, 1948 from the Lower Permian of USA, which was placed in the family Megakhosaridae (Storozhenko, 1998), is recently transferred to the family Cacurgidae (Aristov, 2012). The genus *Alekhosara* Aristov, 2008 described in Megakhosaridae from the Upper Permian of European Russia (Aristov, 2008a) is transferred to the family Liomopteridae (Aristov, 2013c). *Megakhosarina intricata* Aristov, 2008 from the Upper Permian of European Russia (Aristov, 2008a) is transferred to the family Mesorthopteridae (Aristov, in press).

### Family Blattogryllidae Rasnitsyn, 1976

Blattogryllidae Rasnitsyn, 1976: 503.

Plesioblattogryllidae Huang, Nel & Petrulevicius, 2008: 18; **syn. nov.**

Type genus: *Blattogryllus* Rasnitsyn, 1976.

REVISED DIAGNOSIS. Pronotum with broad lateral expansions (paranota); mid and hind tibia directed backward. Forewing: *Sc* concave and ending on the anterior wing margin; costal field narrower or as wide as subcostal field; *RS* arises in basal half of wing; interrarial field not widened; the base of *M* completely integrate with *CuA*; *MA* and *MP* arise from *CuA* as separate branches; *CuA* not divided in *CuA*<sub>1</sub> and *CuA*<sub>2</sub>; intercubital field crossed by posterior branches of *CuA*; *CuP* simple, concave; clavus absent.

COMPOSITION. Family consists of 13 genera, beside them one genus is known from the Middle Permian only, one genus is known from the Upper Permian to the Middle Triassic, fore genera are known from the Triassic only, three genera are known from the Triassic to Jurassic, and fore genera are known from the Jurassic only.

NOTES. The genus *Duoduo* was described as Grylloblattida incertae sedis (Gui, 2012). Herein it is placed in Blattogryllidae based on separated origin of *MA* and *MP* from *CuA* in forewing. Herein Plesioblattogryllidae is synonymized under Blattogryllidae, therefore the genus *Plesioblattogryllus* is transferred in the latter family. Two species of the genus *Mesoblattogryllus* are placed below in the genus *Costatoviblatta*.

### List of the genera and species of Blattogryllidae with taxonomic notes

#### Genus *Anoblattogryllus* Storozhenko, 1990

*Anoblattogryllus* Storozhenko, 1990: 62.

*Anablattogryllus* (sic!): Storozhenko, 1998: 172.

Type species: *Anoblattogryllus fundatus* Storozhenko, 1990, by original designation.

COMPOSITION. One species from the Middle Triassic of Asia.

***Anoblattogryllus fundatus* Storozhenko, 1990**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

**Genus *Baharellinus* Storozhenko, 1992**

Type species: *Baharellinus dimidiatus* Storozhenko, 1992, by original designation.

COMPOSITION. Five species from the Upper Permian of Europe and the Middle Triassic of Europe and Asia.

***Baharellinus dilaceratus* Aristov, 2013**

LOCALITY. The Upper Permian Isady locality in European Russia (Aristov, 2013b).

***Baharellinus dimidiatus* Storozhenko, 1992**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

***Baharellinus pectinatus* Storozhenko, 1992**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1990).

***Baharellinus porrectus* Aristov, 2013**

LOCALITY. The Upper Permian Isady locality in European Russia (Aristov, 2013b).

***Baharellinus umbrosus* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).

**Genus *Baharellus* Storozhenko, 1988**

Type species: *Baharellus lineatus* Storozhenko, 1988, by original designation.

COMPOSITION. Two species from the Middle Triassic and the Middle or Upper Jurassic of Asia.

***Baharellus lineatus* Storozhenko, 1988**

LOCALITY. The Middle or Upper Jurassic Bakhar locality in Mongolia (Storozhenko, 1988).

***Baharellus madygensis* Storozhenko, 1992**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1992).

### **Genus *Blattogryllus* Rasnitsyn, 1976**

Type species: *Blattogryllus karatavicus* Rasnitsyn, 1976, by original designation.

COMPOSITION. Two species from the Lower and Upper Jurassic of Asia.

#### ***Blattogryllus karatavicus* Rasnitsyn, 1976**

LOCALITY. The Upper Jurassic Karatau locality in Kazakhstan (Rasnitsyn, 1976).

#### ***Blattogryllus rasnitsyni* Storozhenko, 1990**

LOCALITY. The Lower Jurassic Sogyuty locality in Kyrgyzstan (Storozhenko, 1990).

### **Genus *Costatoviblatia* Storozhenko, 1992**

*Costatoviblatia* Storozhenko, 1992: 70.

*Costatoviblatia* (sic!): Storozhenko, 1998: 172.

Type species: *Costatoviblatia aenigmatosa* Storozhenko, 1992, by original designation.

REVISED DIAGNOSIS. Forewing: *Sc* ending on *C* and reaching apical third or quarter of wing; *RS* originate in basal third or quarter of wing, pectinate backward, with 4-8 branches; *MA* simple or with 2-4 branches; *MP* desclerotized near the middle, simple or with 2-3 branches; *CuA* with 2-4 branches; *CuP* simple, concave; intercubital area narrow and crossed by few simple S-shaped veins; *A<sub>1</sub>* with 2-6; *A<sub>2</sub>* with 2-4 branches.

SPECIES INCLUDED. Four species from the Middle Triassic and the Lower Jurassic of Kyrgyzstan, two of them are transferred herein from *Mesoblattogryllus* to *Costatoviblatia*.

#### ***Costatoviblatia aenigmatosa* Storozhenko, 1992**

*Costatoviblatia aenigmatosa* Storozhenko, 1992: 70, figs. 3, 4; Storozhenko, 1998: 172, figs. 422-424.

MATERIAL EXAMINED. Holotype (PIN, No 2240/1804; positive and negative imprints of head, pronotum, forewings and basal part of hind wings,) from the Middle Triassic Madygen locality in Kyrgyzstan and 59 paratypes from the same locality.

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan.

#### ***Costatoviblatia conjuncta* (Storozhenko, 1992), comb. n.**

*Mesoblattogryllus conjunctus* Storozhenko, 1992: 69, figs. 2a, 2b; Storozhenko, 1998: 172, fig. 427.

MATERIAL EXAMINED. Holotype (PIN, No 2785/2242; positive and negative imprints of forewings, head, pronotum and fore femora) from the Middle Triassic Madygen locality in Kyrgyzstan and two paratypes from the same locality.

NOTES. This species is transferred from *Mesoblattogryllus* to *Costatoviblatta* based on the follow combination of features: *MA* and *MP* arise from *CuA* as separate branches; *C* reaching apical third of wing, *RS* with 4-8 branches and the proximal branch of *CuA* almost straight.

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan.

***Costatoviblatta longipennis* (Storozhenko, 1992), comb. n.**

*Mesoblattogryllus longipennis* Storozhenko, 1992: 70, fig. 2c; Storozhenko, 1998: 172, fig. 428.

MATERIAL EXAMINED. Holotype (PIN, No 2389/159; positive imprint of hind wing) from the Lower Jurassic Sagul locality in Kyrgyzstan.

NOTES. This species is also transferred herein from *Mesoblattogryllus* to *Costatoviblatta*. It is a single Jurassic species of the genus *Costatoviblatta*.

LOCALITY. The Lower Jurassic Sagul locality in Kyrgyzstan.

***Costatoviblatta similis* Aristov, 2011**

*Costatoviblatta similis* Aristov, 2011a: 63, figs. 2b, 2c; Pl. 12, fig. 7.

MATERIAL EXAMINED. Holotype (PIN, No 2555/1280; positive and negative imprints of forewing) from Madygen locality, the Middle Triassic, Madygen Formation).

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan.

NOTES. This species closely related to *C. aenigmatosa*, but differs by the two-branched *A*<sub>1</sub> (in *C. aenigmatosa* *A*<sub>1</sub> with 3-5 branches).

**Genus *Dorniella* Bode, 1953**

Type species: *Dorniella pulchra* Bode, 1953, by original designation.

COMPOSITION. Six species from the Middle Triassic and the Lower Jurassic of Europe and Asia.

***Dorniella apectinata* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).

***Dorniella diluta* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).

***Dorniella elcanoides* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).

***Dorniella ovalis* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).

***Dorniella primitiva* Storozhenko, 1992**

LOCALITY. The Middle Triassic Madygen locality in Kyrgyzstan (Storozhenko, 1992).

***Dorniella pulchra* Bode, 1953**

LOCALITY. The Lower Jurassic Grassel and Beienrode localities in Germany (Bode, 1953).

NOTES. Described from same localities *Dorniella biramosa* Bode, 1953, *D. brunsvicensis* Bode, 1953, *D. multiramosa* Bode, 1953, *D. triramosa* Bode, 1953, and *D. violata* Bode, 1953 were synonymized with *D. pulchra* by Storozhenko (1988).

**Genus *Duoduo* Cui, 2012**

Type species: *Duoduo qianae* Cui, 2012, by original designation.

COMPOSITION. One species from the Middle Jurassic of Asia.

NOTES. Herein this genus is transferred from the formal cladotypic taxon Blattogrylloptera to Blattogryllidae.

***Duoduo qianae* Cui, 2012**

LOCALITY. The Middle Jurassic Daohugou locality in China (Inner Mongolia) (Cui, 2012).

**Genus *Embigryllus* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

Type species: *Embigryllus shcherbakovi* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011, by original designation.

COMPOSITION. One species from the Middle Triassic of Europe.

***Embigryllus shcherbakovi* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).

**Genus *Griphopteron* Handlirsch, 1939**

Type species: *Griphopteron molle* Handlirsch, 1939, by original designation.

COMPOSITION. One species from the Lower Jurassic of Europe.

***Griphopteron molle* Handlirsch, 1939**

LOCALITY. The Lower Jurassic Dobbertin locality in Germany (Mecklenburg) (Handlirsch, 1939).

**Genus *Mallorcagryllus* Aristov et Zessin, 2009**

Type species: *Mallorcagryllus hispanicus* Aristov et Zessin, 2009, by original designation.

COMPOSITION. One species from the Triassic of Europe.

***Mallorcagryllus hispanicus* Aristov et Zessin, 2009**

LOCALITY. The Triassic Mallorca locality in Spain (Port de Estellencs) (Aristov & Zessin, 2009).

**Genus *Permoblattogryllus* Aristov, 2011**

Type species: *Permoblattogryllus praecox* Aristov, 2011, by original designation.

COMPOSITION. One species from the Middle Permian of Europe.

***Permoblattogryllus praecox* Aristov, 2011**

LOCALITY. The Middle Permian Soyana locality in European Russia (Aristov, 2011a).

**Genus *Plesioblattogryllus* Huang, Nel et Petrulevičius, 2008**

Type species: *Plesioblattogryllus magnificus* Huang, Nel et Petrulevičius, 2008, by original designation.

COMPOSITION. Two species from the Middle Jurassic of Asia.

***Plesioblattogryllus magnificus* Huang, Nel et Petrulevičius, 2008**

LOCALITY. The Middle Jurassic Daohugou locality in China (Inner Mongolia) (Huang *et al.*, 2008).

***Plesioblattogryllus minor* Ren et Aristov, 2011**

LOCALITY. The Middle Jurassic Daohugou locality in China (Inner Mongolia) (Ren & Aristov, 2011).

**Genus *Vosgesopterum* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

Type species: *Vosgesopterum arzvillerensis* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011, by original designation.

COMPOSITION. One species from the Middle Triassic of Europe.

***Vosgesopterum arzvillerensis* Aristov, Grauvogel-Stamm et Marchal-Papier, 2011**

LOCALITY. The Middle Triassic Vosges locality in France (Aristov *et al.*, 2011).



### Taxa erroneously placed in Blattogryllidae

Described in Blattogryllidae genus *Parablattogryllus* Storozhenko, 1988 from the Lower Cretaceous locality Baissa in East Siberia was transferred to the infraclass Polyneoptera as the genus of uncertain systematic position (Aristov & Storozhenko, 2011). Described also in Blattogryllidae genus *Blattogryllulus* Storozhenko, 1988 with two species from the Upper Jurassic Houtiin-Hotgor locality in Mongolia (Storozhenko, 1988) is transferred herein to Grylloblattida incertae sedis because of lacking the main features of Blattogryllidae or Megakhosaridae.

### DISCUSSION

Thus, there are 50 described species in 20 genera of the family Mehakhosaridae and 28 species in 13 genera of Blattogryllidae. Majority of Mehakhosaridae (14 genera) are Permian, two genera (*Megakhosarodes* and *Protoblattogryllus*) are known from the Upper Permian to the Middle Triassic, and only four genera (*Madygenocephalus*, *Megablattogryllus*, *Mesoblattogryllus* and *Metakhosara*, totally with 7 species) are Triassic. On the contrary, Blattogryllidae is predominately Mesozoic insects. Only three species of this family (*Permoblattogryllus praecox*, *Baharellinus porrectus*, *B. dilaceratus*) are known from the Middle and Upper Permian. Other 25 species are Mesozoic: 16 species in 8 genera are known only from Triassic, nine species in 7 genera are Jurassic (4 species in 4 genera are found in the Lower Jurassic, 4 species in 2 genera in the Middle Jurassic, and only *Blattogryllus karatavicus* is known from the Upper Jurassic).

We believe that Mehakhosaridae, Blattogryllidae and Grylloblattidae forming a single stem traceable from Permian to nowadays. Therefore the formal cladotypic taxon Blattogryllopterida (Cui, 2012) is identical to the order Grylloblattida. The stem Mehakhosaridae + Blattogryllidae + Grylloblattidae is supported in having pterothoracic segments bearing the midsternal suture (an apomorphic condition), while in recent Plecoptera and related orders such sutures absent (plesiomorphy). The predominantly Mesozoic Blattogryllidae show distinct venational synapomorphies to mainly Paleozoic Mehakhosaridae. Both Grylloblattidae and Blattogryllidae are characterized by the distinctly prognathous head, which is very likely an apomorphic condition (Wipfler *et al.*, 2011). Prognathism, predaceous habits suggested by features of the mouthparts (Huang *et al.*, 2008), and highly derived asymmetric male genitalia tentatively support the hypothesized relationship of extinct forms with modern Grylloblattida (Wipfler *et al.*, 2014). Moreover, the habitus of Blattogryllidae and Grylloblattidae is an extremely similar, except the obvious differences between winged and apterous forms. If both taxa occurs in the same time, they probably be considered as only two subfamilies (Blattogryllinae and Grylloblattinae) of the family Grylloblattidae, but the long time hiatuses (extinct grylloblattids unknown from Cretaceous to nowadays) allows us attribute them to different families.

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