INTRODUCTION

Liomopteridae is the largest family of the order Grylloblattida and today comprises no less than 35 genera (Storozhenko, 1998). Liomopterids are the most characteristic grylloblattids in Permian deposits, often taxonomically and quantitatively dominating with respect to other representatives of this order. The first members of this family have been recorded in the locality of Carrizo Arroia, which is Early Asselian. Within the Artinskian and Kungurian (localities of Elmo and Tshekarda, respectively), liomopterids are numerous but not dominating. Among all Kazanian and Tatarian localities, Liomopteridae do not appear to be dominating only in the locality of Soyana, where they are abundant but give way to Ideliidae, and in the locality of Tikhie Gory, which is characterized by the absolute domination of Atactophlebiidae, which are rare in other places.

The characteristic feature of the second half of the Upper Permian is the absolute domination of liomopterids in all localities (except for Kargala). During this time, the diversity of grylloblattids diminishes; in the upper Kazanian and Lower Tatarian, scarce Ideliidae and Megakhosaridae are known in addition to Liomopteridae; in addition to them, rare Chaulioditidae, Blattogryllidae, Geinitziidae, and Tunguskapteridae appear in the Upper Tatarian. Liomopterid diversity remains, however, at the same level, and, thus, they are the most characteristic grylloblattids in the time under consideration.

To date, representatives from the second half of the Upper Permian of the family Liomopteridae have been found in the Lower Tatarian (Kazanian, according to other data) locality of Bor-Tolgoy in Mongolia (Liomopterites exoticus Storozhenko, 1992, Micropermula mongolica Storozhenko, 1992, and Mongolopermula adunc Storozhenko, 1992); the Lower Tatarian locality of Kargala in the Orenburg region (Khosara permi-akovi Martynov, 1937); the Upper Tatarian locality of Karaungir in Kazakhstan (Karaungiroptera maculosa Storozhenko, 1991 and Paraliomopterum karaungi-rense Storozhenko, 1991); and the Tatarian locality of Natal in South Africa (Mioloptoides andrei Riek, 1976 and Mioloptera stuckenbergi Riek, 1973).

The present study of the collection at the Paleontological Institute (in Moscow) has resulted in the description of four more genera and ten new species of liomopterids from deposits of the upper half of the Upper Permian. Liomopterids are described for the first time from the localities of Kityak, Chepanikha, Galevo, and Aristovo.

The liomopterid faunas of localities of the second half of the Upper Permian show the closest similarity to the fauna of the Ufimian locality of Kaltan in the Kemerovo region, one-third of their genera having been recorded from Kaltan.

At the end of the Upper Tatarian, Liomopteridae disappeared from fossil assemblages, and Chaulioditidae became dominant during the first half of the Triassic.

MATERIAL

The material under study is stored in the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN).

SYSTEMATIC PALEONTOLOGY

Order Grylloblattida Walker, 1914
Suborder Grylloblatina Walker, 1914
Family Liomopteridae Sellards, 1909
Genus Protomia Aristov, gen. nov.

Etymology. From Greek pro (before) and genus Tomia.
**Type species.** *P. proteus* sp. nov.

**Diagnosis.** Forewing elongate, anterior margin weakly convex, apex acuminate. Costal field comparable to subcostal field in its width, SC terminating near wing midlength, RS starting in basal third of wing. M branching beyond RS base or at the same level. Apices of basal branches of CuA terminating either on proximal cubital branches or on posterior margin of wing. CuP terminates on CuA, $A_1$ simple, $A_2$ has three branches.

**Species composition.** Type species.

**Comparison.** M branching beyond the RS base is unique to liomopterids. Apices of CuA branches that
terminate on each other are known in *Liomopterites* (Sharov, 1961), and this character is still more strongly expressed in *Expartalioma* gen. nov. *Protomia* gen. nov. differs from both in the CuP apex terminating on CuA.

**Protomia proteus** Aristov, sp. nov.

**Etymology.** From Latin *proteus* (changeable nature).

**Holotype.** PIN, no. 1366/226, forewing impression; Kirov region, Malmyzha district, Vyatka River basin, left bank of the Kityak River opposite the village of Bol’shoy Kityak, locality of Kityak; Upper Permian, upper Kazanian, Belebeevo Formation.

**Description** (Figs. 1b–1d, 2). The anterior branches of SC and R are simple or forked and linked by crossveins. R is straight, the radial field is broad or relatively narrow. The total number of RS, MA, and MP branches is usually six, but may increase up to eight (Fig. 1c). The number of RS branches is two or three, the first bifurcation of RS may occur both near its base and near its tip. MA has one to four branches, MP has one to three branches, but both MA and MP are more often two-branched. RS and MA may run independently, be fused for a small distance (Fig. 2a), or form a complex anastomosis (Fig. 2e). CuA has two to five branches and may be pectinate forward (Fig. 2b), rearward (Fig. 2f), or dichotomized (Fig. 2d). CuA₁ apices may terminate on the posterior margin of the wing (Fig. 2b), fuse with each other (Fig. 2d), or be lost amid crossveins (Fig. 2g). CuA₂ terminates either on CuA₁ (Fig. 1b) or on the posterior margin of the wing (Fig. 1d). The crossveins are simple and form a double row of cells in the radial and medial fields. The color pattern is expressed as small dark spots.

**Measurements**, mm: forewing length, 16–18.

**Remarks.** For CuA apices to fuse with each other is not usual for grylloblattids. In addition to *Protomia* gen. nov., such a CuA structure is only known in *Expar-
talioma gen. nov. (Aristovo locality) and Megahosarodes zajasnicus (Megahosaridae) from the locality of Karaungir. This character is known in Late Permain grylloblattids only.

Liomopteridae is one of those rare grylloblattid families in which individual variation of venation is more or less well known. Comparison of the variation of P. proteus sp. nov. with that of liomopterids from the localities of Kaltan (Sharov, 1961) and Tshekarda (Storozhenko and Aristov, 1999) shows that the venation of P. proteus sp. nov. is probably the most inconstant amongst known liomopterids. One of the most variable features of P. proteus sp. nov. is the CuA; structure; however, this is not the case for other liomopterids.

The structure of M, which divides beyond the RS base in some individuals of P. proteus sp. nov., and the late bifurcation of CuA1 give reasons for classifying this insect closer to the ancestors of the family Chaulioditidae. Representatives of the genus Miralioma gen. nov. have a similar media, but their CuA1 branches very early. M branching beyond the RS base combined with a simple CuA2 is characteristic of chaulioditids. It seems to be the case that Chaulioditidae arose from liomopterids close to Protomia gen. nov. through the reduction of CuA1 branches and stabilization of the late fork of M. The origin of Chaulioditidae has been discussed in detail elsewhere (Aristov, 2003). In addition to wings, a pronotum has been found in the locality of Kityak (Fig. 1h), the shape of which does not differ from that of pronota found in the locality of Babii Kamen’ (Lower Triassic of the Kemerovo region) and possibly belonging to chaulioditids. The pronotum from Kityak differs only in the absence of coloration on paranotalia.


**Genus Miralioma Aristov, gen. nov.**

**Etymology.** From Latin mira (strange) and the genus Lioma.

**Type species.** M. monstrosa sp. nov.

**Diagnosis.** Anterior margin of wing convex, costal field twice as wide as subcostal one. RS starting in basal third of wing, M branching far beyond RS base. CuA1 branching very early and forming wide fork. Crossveins simple.

**Comparison.** This new genus is most similar to the genus Protomia gen. nov. but differs from the latter primarily in the wider costal field, late branching of M, and in early branching of CuA1.

**Miralioma monstrosa Aristov, sp. nov.**

**Etymology.** From Latin monstrosa (monstrous).
parallel to CuA₁, A₁ is simple, A₂ has four branches. The crossveins are simple or form a double row of cells.

Measurements, mm: forewing length, about 25.

Comparison. This species is most similar to L. vulgaris but differs in that its SC is longer and its branches of CuA₂ are more numerous. It differs from L. acuminata sp. nov. in being smaller, having a normal CuA₂, and having a CuA₁ that branches late.

Material. In addition to holotype, paratype PIN, no. 1366/259 from the same locality.

Fig. 3. Representatives of the family Liomopteridae: (a) Expartalioma hirta gen. et sp. nov., holotype PIN, no. 3446/7, (b) Papapermula tatarica sp. nov., holotype PIN, no. 3286/10, (c) Paraliomopterum karaungirense Storozhenko, 1991, specimen PIN, no. 3695/2, (d) Rigidioloma radialis gen. et sp. nov., holotype PIN, no. 3286/9, (e) Paraliomopterum rectum sp. nov., holotype PIN, no. 3695/1, (f) Liomopterites novissimus sp. nov., holotype PIN, no. 3286/8.
Genus *Expartalioma* Aristov, gen. nov.

**Etymology.** From Latin *exparta* (infertile) and the genus *Lioma*.

**Type species.** *E. hirta* sp. nov.

**Diagnosis.** Forewing elongated, with polymerized venation. SC terminating in distal quarter of wing; R straight, without anterior branches; RS starting in basal quarter of wing, branching for the first time in distal third of wing, radial field narrow. MA branching prior to CuP apex, MP simple. Apices of CuA parallel to posterior margin of wing with some terminating on one another, field between CuA and CuP narrow. Crossveins mainly simple. Wing membrane covered with fine hairs. Color pattern expressed in form of darkened anterior margin of wing.

**Species composition.** Type species.

**Comparison.** This new genus is similar to *Semopterum* Carpenter, 1950 and *Ornaticosta* Shar., 1961 in having a straight R, narrow radial field, and RS that starts early and ramifies late but differs from the above genera in its SC being longer, early branching of MA, and a simple MP. The latter character occurs in *Liomopterites* and *Khosara* Mart., 1937 species, from which *Expartalioma* gen. nov. differs in having polymerized venation and a long SC. Hairs on the wing membrane and apices of the CuA branches that are parallel to the posterior margin of the wing are unique to liomopterids.

*Expartalioma hirta* Aristov, sp. nov.

**Etymology.** From Latin *hirta* (covered with fur).

**Holotype.** PIN, no. 3446/7, forewing impression; Vologda Region, right bank of the Severnaya Dvina River near the Aristovo pier, locality of Aristovo; Upper Permian, Upper Tatarian, Vyatka Horizon.

**Description (Fig. 3a).** The forewing apex is acuminate, the subcostal field is broader than the radial field, RS has five terminations. MA ramifies in the basal third of the wing and has at least eight branches, CuA has five branches.

**Measurements.** mm: forewing length, about 35.

**Material.** Holotype.

Genus *Rigidioma* Aristov, gen. nov.

**Etymology.** From Latin *rigida* (inflexible) and the genus *Lioma*.

**Type species.** *R. radialis* sp. nov.

**Diagnosis.** Anterior margin of wing convex, SC terminating in distal quarter of wing; R straight, with anterior branches; MA branching for the first time in distal third of wing, radial field narrow. MA branching prior to CuP apex, MP simple. Apices of CuA parallel to posterior margin of wing with some terminating on one another, field between CuA and CuP narrow. Crossveins mainly simple. Wing membrane covered with fine hairs. Color pattern expressed in form of darkened anterior margin of wing.

**Species composition.** Type species.

**Comparison.** This species is closest to *P. karaungirense*, from which it differs in a straighter wing anterior margin, narrower costal field, and absence of a double row of cells in the radial field.

**Measurements.** mm: forewing length, about 19.