Paleontological Journal, Vol. 38, Suppl. 2, 2004, pp. S150–S157.

Grylloblattids of the Family Liomopteridae (Insecta: Grylloblattida) of the Upper Half of the Upper Permian

D. S. Aristov

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

Received September 18, 2002

Abstract—New grylloblattid taxa are described: *Protomia proteus* gen. et sp. nov., *Miralioma monstrosa* gen. et sp. nov., *Liomopterella acuminata* sp. nov., and *L. kitiakensis* sp. nov. from the upper Kazanian Belebeevo Formation of the Kityak locality (Kirov region); *Paraliomopterum alium* sp. nov. from the locality of Karaungir (Kazakhstan, Upper Tatarian, Akkolka Formation); *P. rectum* sp. nov. from the locality of Galevo (Udmurtiya, Lower Tatarian); *Expartalioma hirta* gen. et sp. nov. from the locality of Aristovo (Vologda region, Upper Tatarian, Vyatka Horizon); and *Rigidilioma radialis* gen. et sp. nov., *Parapermula tatarica* sp. nov., and *Liomopterites novissimus* sp. nov. from the locality of Chepanikha (Udmurtiya, Lower Tatarian).

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 adunca* Storozhenko, 1992); the Lower Tatarian locality of Kargala in the Orenburg region (*Khosara permiakovi* Martynov, 1937); the Upper Tatarian locality of Karaungir in Kazakhstan (*Karaungiroptera maculosa* Storozhenko, 1991 and *Paraliomopterum karaungirense* 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 Grylloblattina Walker, 1914

Family Liomopteridae Sellards, 1909

Genus *Protomia* Aristov, gen. nov.

E t y m o l o g y. From Greek *pro* (before) and genus *Tomia*.

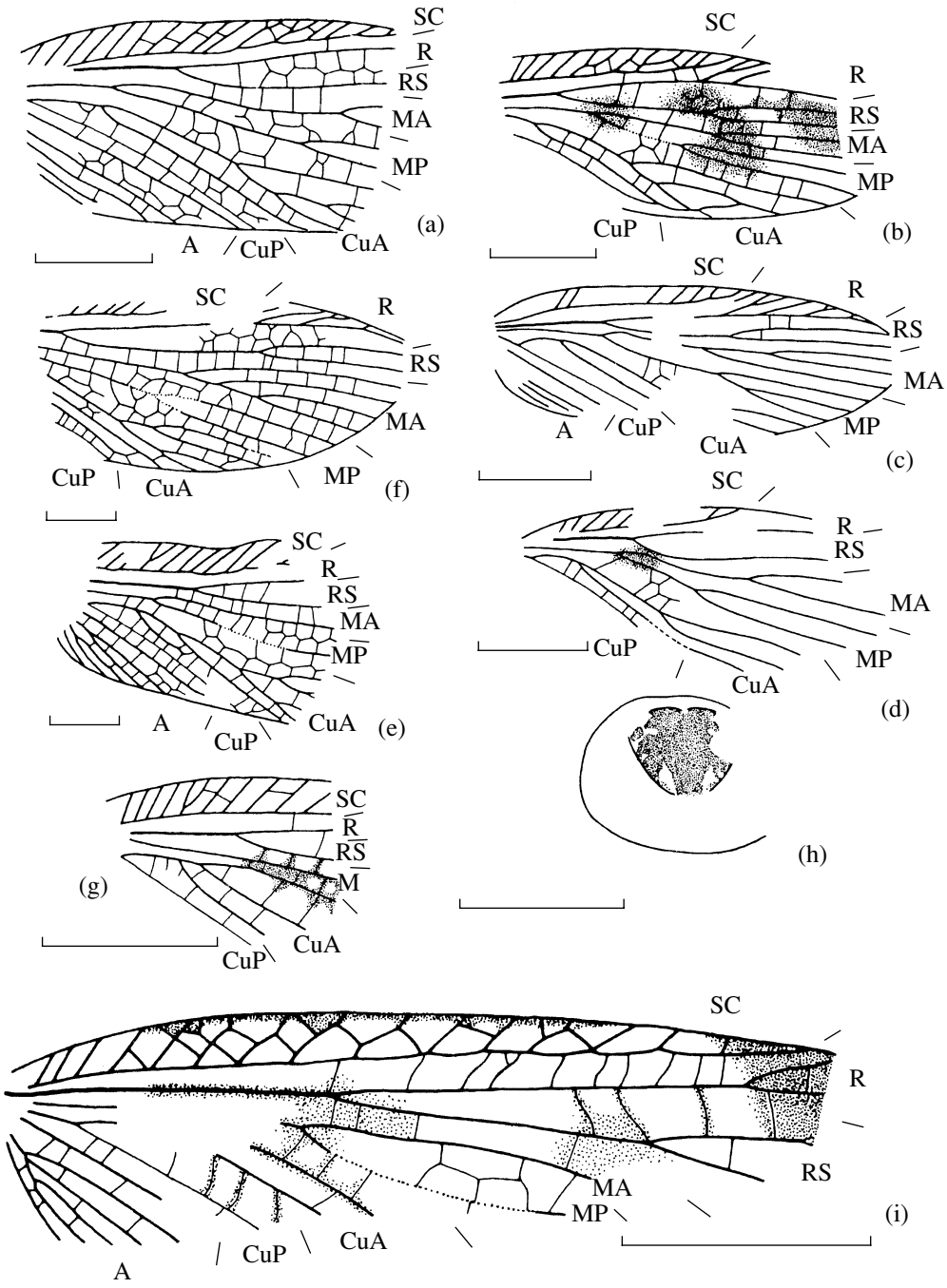

Fig. 1. Representatives of the family Liomopteridae: (a) *Liomopterella kitiakensis* sp. nov., holotype PIN, no. 1366/121; (b)–(d) *Protomia proteus* gen. et sp. nov.: (b) holotype PIN, no. 1366/226, (c) paratype PIN, no. 1366/184, (d) paratype PIN, no. 1366/124; (e) and (f) *Liomopterella acuminata* sp. nov.: (e) holotype PIN, no. 1366/260, (f) paratype PIN, no. 1366/177; (g) *Miralioma monstrosa* gen. et sp. nov., holotype PIN, no. 1366/152; (h) Liomopteridae gen. sp., specimen PIN, no. 1366/222, pronotum; (i) *Paraliomopterum alium* sp. nov., holotype PIN, no. 2781/228. Scale bar 5 mm in Figs. 1–3.

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

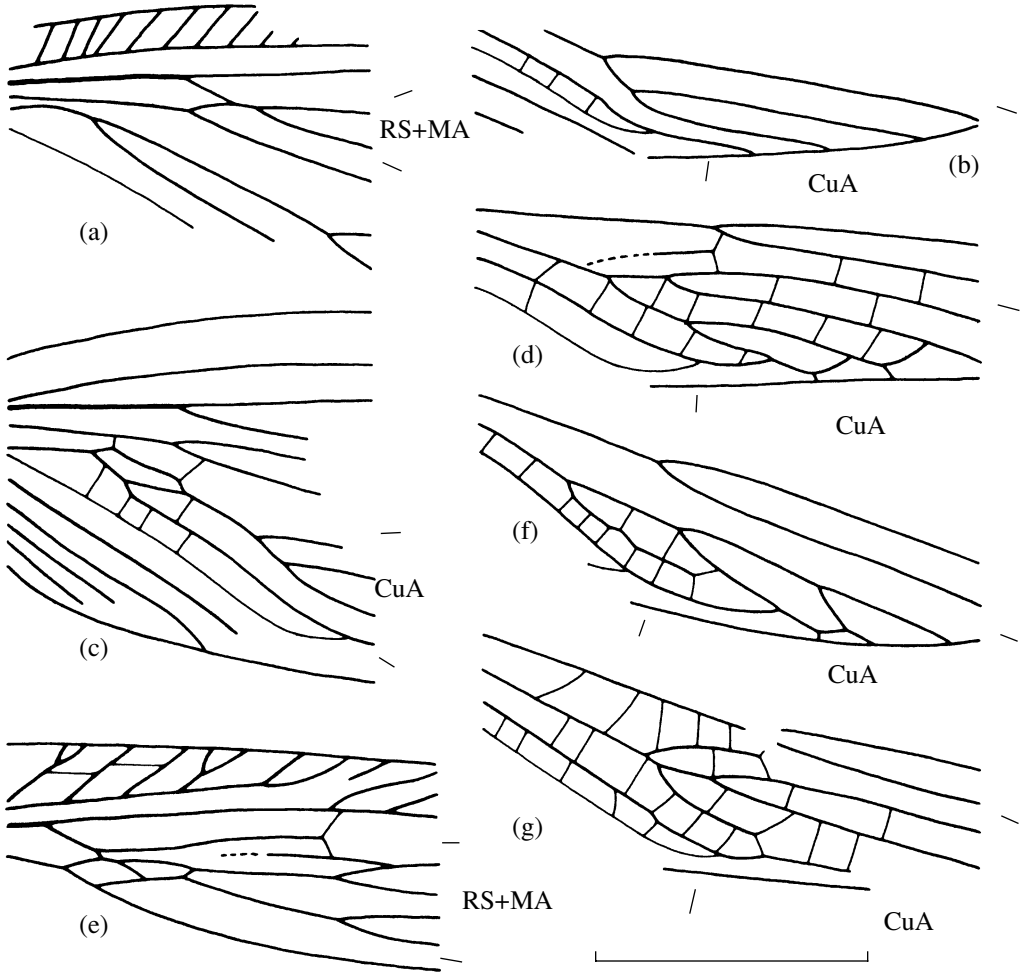

Fig. 2. *Protomia proteus* gen. et sp. nov. (a) paratype PIN, no. 1366/250, (b) paratype PIN, no. 1366/171, (c) paratype PIN, no. 1366/245, (d) paratype PIN, no. 1366/153, (e) paratype PIN, no. 1366/266, (f) paratype PIN, no. 1366/161, (g) paratype PIN, no. 1366/155.

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'shoi 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). CuA_1 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). CuA_2 terminates either on CuA_1 (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 *Megakhosarodes zajsanicus* (Megakhosaridae) from the locality of Karaungir. This character is known in Late Permian 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 CuA_1 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 CuA_1 branches very early. M branching beyond the RS base combined with a simple CuA_1 is characteristic of chaulioditids. It seems to be the case that Chaulioditidae arose from liomopterids close to *Protomia* gen. nov. through the reduction of CuA_1 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.

Material. In addition to the holotype, paratypes PIN, nos. 165/171, 165/178, 165/184, 165/189, 165/201, 165/202, 165/203, 165/207, 165/208, 165/218, 165/245, 165/250, 165/261, 165/266, 1366/124, 1366/153, 1366/155, 1366/156, and 1366/161 from the same locality.

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. CuA_1 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 CuA_1.

Miralioma monstrosa Aristov, sp. nov.

Etymology. From Latin *monstrosa* (monstrous).

Holotype. PIN, no. 1366/152, impression of forewing fragment; Kirov region, Malmyzha district, basin of the Vyatka River, left bank of the Kityak River opposite the village of Kityak, locality of Kityak; Upper Permian, upper Kazanian, Belebeevo Formation.

Description (Fig. 1g). The anterior branches of SC are simple or forked and connected by crossveins. The distal branch of CuA_1 forks late. The color pattern is developed as darkening along parts of M, CuA, and crossveins connected to them.

Measurements, mm: presumed forewing, about 15.

Material. Holotype.

Genus *Liomopterella* Sharov, 1961

Liomopterella acuminata Aristov, sp. nov.

Etymology. From Latin *acuminata* (acuminate).

Holotype. PIN, no. 1366/260, forewing part and counterpart; Kirov region, Malmyzha district, Vyatka River basin, left bank of the Kityak River opposite the village of Bol'shoi Kityak, locality of Kityak; Upper Permian, upper Kazanian, Belebeevo Formation.

Description (Figs. 1e, 1f). The forewing apex is acuminate. The anterior margin is weakly convex, the costal field is twice as broad as the subcostal field. SC has simple or forked anterior branches and reaches the distal half of the wing. RS has three branches and starts in the basal third of the wing. MA and MP branch late, MA has four branches and is pectinate frontward, MP is two-branched. CuA_1 divides near the point of separation of M into MA and MP and subsequently dichotomizes twice near the posterior margin of the wing. CuA_2 is weak and does not reach the posterior margin of the wing, disappearing amid crossveins. A_1 is simple, A_2 has five branches. The crossveins are simple or form a double row of cells.

Measurements, mm: forewing length, about 35.

Comparison. This species is most similar to *L. vulgaris* Shar. in its venation pattern but is larger.

Material. In addition to holotype, paratype PIN, no. 1366/177 from the same locality.

Liomopterella kitiakensis Aristov, sp. nov.

Etymology. From the locality of Kityak.

Holotype. PIN, no. 1366/121, forewing impression; Kirov region, Malmyzha district, Vyatka River basin, left bank of the Kityak River opposite the village of Bol'shoi Kityak, locality of Kityak; Upper Permian, upper Kazanian, Belebeevo Formation.

Description (Fig. 1a). The anterior margin of the wing is weakly convex, the costal field is broad. SC reaches the distal half of the wing, its anterior branches are simple or forked. R is straight, RS diverges in the basal third of the wing, MA and MP branch late. CuA_1 ramifies irregularly near its midlength, giving not less than four branches. The apical portion of CuA_2 is not

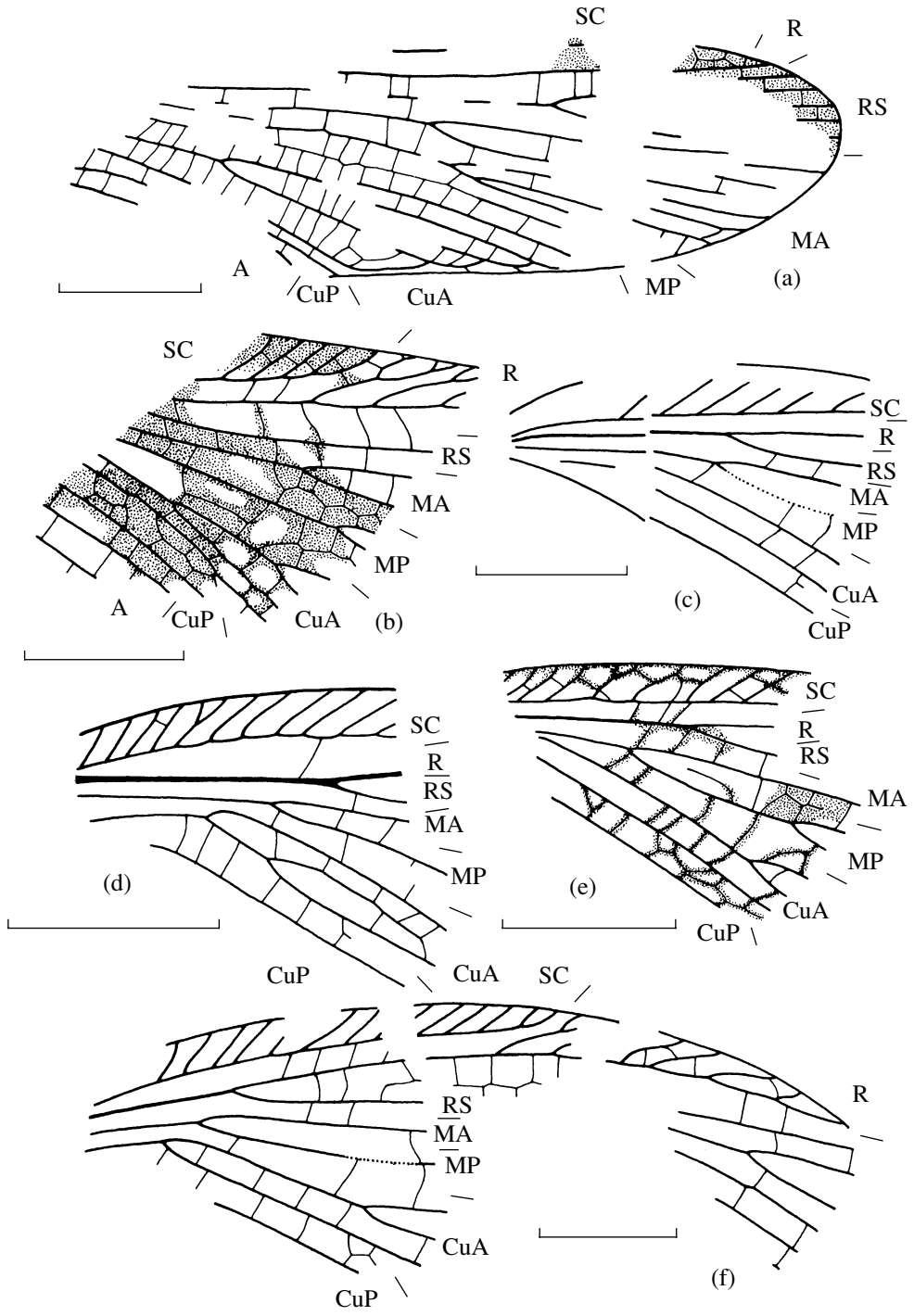

Fig. 3. Representatives of the family Liomopteridae: (a) *Expartalioma hirta* gen. et sp. nov., holotype PIN, no. 3446/7, (b) *Paraparmula tatarica* sp. nov., holotype PIN, no. 3286/10, (c) *Paraliomopterum karaungirense* Storozhenko, 1991, specimen PIN, no. 3695/2, (d) *Rigidilioma radialis* gen. et 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.

parallel to CuA_1, A_1 is simple, A_2 has four branches. The crossveins are simple or form a double row of cells.

M e a s u r e m e n t s, mm: forewing length, about 25.

C o m p a r i s o n. This species is most similar to *L. vulgaris* but differs in that its SC is longer and its branches of CuA_1 are more numerous. It differs from *L. acuminata* sp. nov. in being smaller, having a normal CuA_2, and having a CuA_1 that branches late.

M a t e r i a l. In addition to holotype, paratype PIN, no. 1366/259 from the same locality.

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 *Rigidilioma* 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 parallel to costal margin of wing in its basal half, costal field as broad as subcostal field. C and R thickened, crossveins forming strong intercalary vein in field between CuA branches. Field between CuA and CuP not broadened basally, without double row of cells.

Species composition. Type species.

Comparison. In other liomopterids, the combination of a double row of cells between the CuA branches with SC running parallel to C is best expressed in the genus *Donopterum* Kukalová, 1964, from which the new genus differs in thickened C and R, strong intercalary vein between the CuA branches, and in a not broadened field between CuA and CuP lacking a double row of cells.

Rigilioma radialis Aristov sp. nov.

Plate 8, fig. 4

Etymology. From radial vein.

Holotype. PIN, no. 3286/9, forewing fragment; Udmurtiya, Sarapul district, Bakhilka River valley, left tributary of the Nechkhinka River, 1.2 km north of the village of Chepanikha, locality of Chepanikha; Upper Permian, Lower Tatarian.

Description (Fig. 3d). The anterior branches of SC are almost straight, poorly branching, and linked by crossveins. Beyond the RS base, R runs toward the anterior margin of the wing. MA is parallel to RS, CuA_2 forms an angle at the starting point of the intercalary vein. The crossveins are mainly simple and form a double row of cells in the medial field and between CuA_1 and CuA_2.

Measurements, mm: forewing length, about 26.

Material. Holotype.

Genus *Paraliomopterum* Sharov, 1961

Paraliomopterum alium Aristov, sp. nov.

Etymology. From Latin *alium* (other).

Holotype. PIN, no. 2781/228, part and counterpart of forewing fragment; Kazakhstan, Zaisan district, Saikan Mountain Ridge, Karaungir River, Kyuryul'tyu Ravine, locality of Karaungir; Upper Permian, Upper Tatarian, Akkolka Formation.

Description (Fig. 1h). The anterior margin of the wing is weakly convex; in the distal half, the costal field is as broad as the subcostal field. SC has curved anterior branches, which are connected by simple crossveins. R is nearly straight and has S-curved anterior branches. RS starts in the basal third of the wing and is pectinate. The radial field is devoid of a double row of cells. The branching of MA and MP does not occur before than that of RS, MP is curved toward the anterior margin of the wing. CuA_1 is curved, CuA_2 is straight, A_1 is simple, and A_2 is four-branched. The crossveins are mainly simple and form a double row of cells in the field between MA and MP. The color pattern is developed in the form of small spots along the anterior margin of the wing and the darkened area.

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.

Material. Holotype.