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Grylloblattids of the Family Chaulioditidae (= Tomiidae syn. nov.) (Insecta: Grylloblattida) from the Upper Permian of the Orenburg Region

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Abstract—A new representative of the family Chaulioditidae (Insecta: Grylloblattida), *Kargalella gibbosa* sp. nov., is described from the Lower Tatarian locality of Kargala (Orenburg region), and the species *K. subcostalis* Martynov, 1937 is redescribed. A new subfamily, Kargalellinae subfam. nov., is created for the genus *Kargalella.* The family Tomiidae is synonymized under Chaulioditidae.

INTRODUCTION

The first collection from the locality of Kargala (Orenburg region, Sakmara district, dumps of the Kargala copper mines; Upper Permian, Lower Tatarian, Amanak Formation) was made by Permyakova in 1931. On the basis of seven impressions of grylloblattids from this collection, Martynov (1937) described the monotypic genera *Metidelia, Khosara*, and *Megakhosara* (families Ideliidae, Liomopteridae, and Megakhosaridae, respectively). Additionally, two monotypic grylloblattid genera of unclear systematic position, *Kargalella* and *Kargalodes* (the latter being later synonymized), and the genus *Syndesmorpha*, which was classified by Martynov into Insecta incertae sedis, was later synonymized under *Megakhosara* (Sharov, 1961), and has now been reinstated as a separate genus of the family Megakhosaridae (Aristov, 2004), were described.

The next collection, which was taken by Martynova and Sviridov from this locality in 1938, contains 79 grylloblattid impressions. Preparation of this collection showed that, in addition to the listed taxa, Kargala fauna includes two undescribed liomopterid genera, two megakhosarid genera, and a new species of the genus *Kargalella*, which is described below. Complete wings of *Kargalella* have been found, thus allowing this genus to be placed into the family Chaulioditidae.

Kargala is the richest (86 fossil specimens) and the most diverse Lower Tatarian locality of grylloblattids (four families with nine genera). In other Lower Tatarian localities, grylloblattids are known in Chepanikha and Galevo (Udmurtiya) and are represented by rare liomopterids.

Chauliodites picteti Heer, 1864 and *Ch. zinkeni* Heer, 1864 have been described in the locality of Gödewitz in Germany (Lower or Middle Bundsandstein, Triassic). Later, this genus was enriched with two more species, *Ch. minor* Blake, 1876 (Hatham, England; Upper Lias) and *Ch. helveticus* Heer, 1877 (Mitten Berg, Switzerland; Keuper, Upper Lias). In 1908, Handlirsch created new genera (*Triadosialis* and *Pseudochauliodites*) for *Ch. zinkeni* and *Ch. helveticus*, respectively and put them alongside the type species in a new family (Chaulioditidae) of the order Megaloptera. *Ch. minor* was classified by him in the group of insects of unclear systematic position. Judging from the available illustrations of *Ch. picteti, Ch. zinkeni*, and *Ch. helveticus*, only the first species can be said to belong to grylloblattids without a doubt. When revising the order Paraplecoptera (= Grylloblattida), Sharov (1962) placed Chaulioditidae into it with reservations. In the course of subsequent revisions (Carpenter, 1992; Storozhenko, 1998), chaulioditids were not included in this order. However, comparison of *Ch. picteti* with grylloblattids demonstrates its clear resemblance to representatives of the family Tomiidae and to the genus *Tomia* in particular. *Ch. picteti* (Fig. 1a) possesses a set of features that is typical of tomiids: the anterior margin of the wing is convex, the wide costal field is crossed by simple and straight branches of SC, the media bifurcates beyond the RS base, and CuA_1 is simple and S-shaped (Aristov, 2003). Thus, *Chauliodites* does not differ from the genus *Tomia* and is considered here as a senior subjective synonym of the latter genus. The family Chaulioditidae is accordingly treated as a senior synonym of the family Tomiidae. *Tomia costalis* (Martynov, 1937) has been described from the Lower Triassic of the Kuznetsk Basin. One more representative each of the genus *Tomia* and the genus *Nivopteria* Lin have been described from the Middle Triassic of China (Lin, 1978). Recently, this family has been supplemented by one more genera of *Paratomia*, four species of *Tomia* from the Lower Triassic of the Kemerovo Region, and one *Tomia* species from the Upper Permian (Upper Tatarian) of the Vologda region. In addition, one

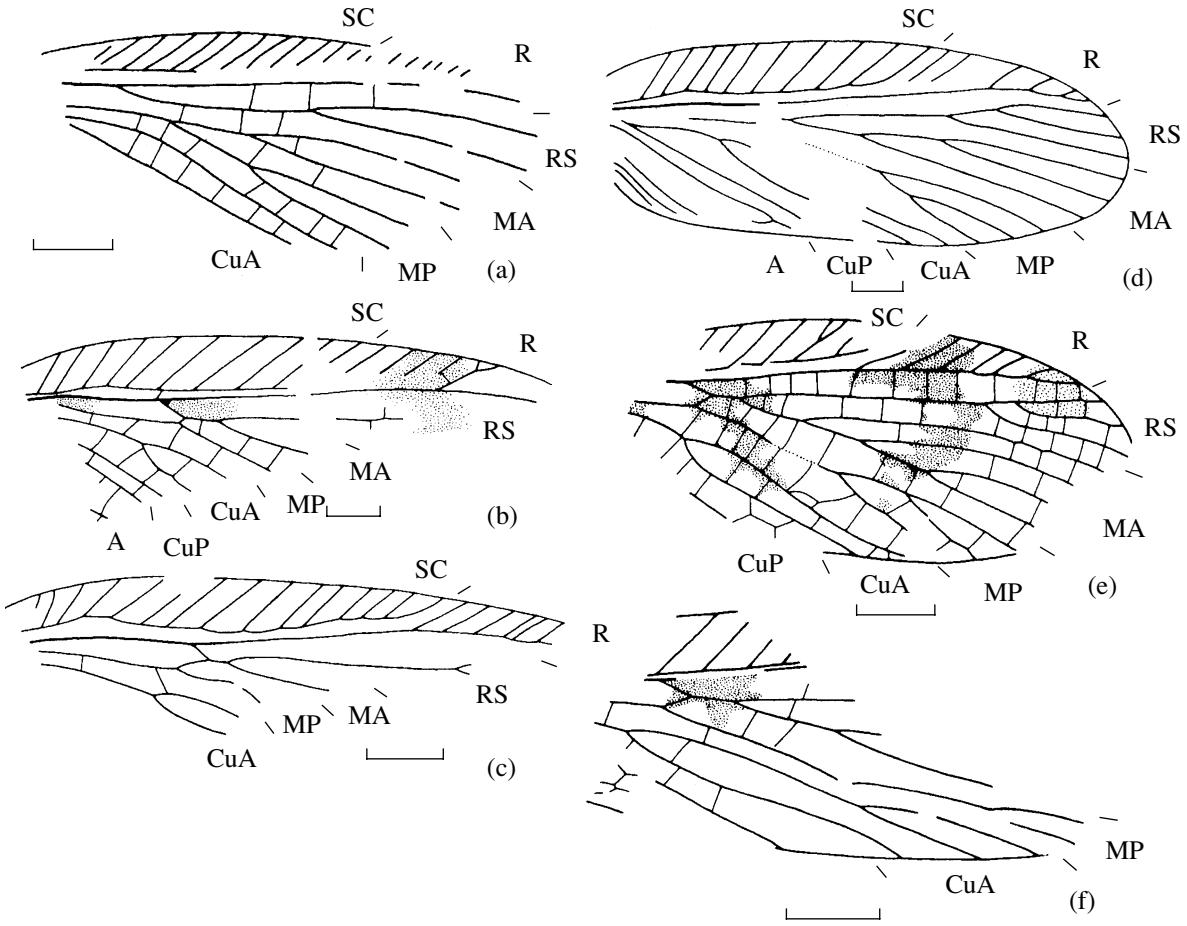

Fig. 1. Grylloblattids of the family Chauliodidae: (a) *Chauliodites picteti* Heer, 1864 (modified after Handlirsch, 1908), (b)–(f) *Kargalella subcostalis* Martynov, 1937: (b) holotype PIN, no. 100/10; (c) specimen PIN, no. 100/11 (holotype *Kargalodes incerta*); (d) specimen PIN, no. 199/122; (e) specimen PIN, no. 199/3; and (f) specimen PIN, no. 199/302. Scale bars 2 mm in Figs. 1 and 2.

Tomia from the Middle Triassic (Anisian) of France remains undescribed (Aristov, 2003).

Thus, after synonymizing tomiids under Chaulioditidae, the subfamily Chaulioditinae includes ten species of three genera: *Ch. picteti* Heer, 1864 from the Triassic of Germany; *Ch. costalis* (Martynov, 1937) from the Lower Triassic of the Kuznetsk Basin; *Ch. fuyuanensis* and *Nivopteria nanshenghuensis* (Lin, 1978) from the Middle Triassic of China; *Ch. cancellatus, Ch. ramosus, Ch. sennikovi, Ch. durus*, and *Paratomia pectinata* from the Lower Triassic of the Kemerovo region; and *Ch. antiquus* from the Upper Permian of the Vologda region (Aristov, 2003).

The genus *Lemmatophoropsis* G. Zalessky, 1935, which was described on the basis of a wing fragment from the Lower Triassic of Russia, is most likely to be a junior synonym of *Chauliodites* (Zalessky, 1935; Aristov, 2003).

Another grylloblattid belonging to the family Chaulioditidae is *K. subcostalis.* Originally, Martynov (1937) described two insects assigned to Paraplecoptera incertae sedis from Kargala, *K. subcostalis* and *Kargalodes incerta.* Subsequently, Sharov (1962) transferred the genus *Kargalella* to the family Tomiidae, whereas the second genus was retained in Paraplecoptera incertae sedis. The genus *Kargalodes* was synonymized with the genus *Kargalella* (Rasnitsyn, 1980), which was again assigned to Grylloblattida incertae sedis, where it remains (Storozhenko, 1998). Comparison of the holotypes of *K. subcostalis* (Fig. 1b) and *K. inserta* (Fig. 1c) with additional material from the same locality (Figs. 1d–1f) shows that these wings are conspecific.

Of all grylloblattids, *K. subcostalis* shows the greatest similarity to the family Chaulioditidae in that it shares the following characters: the wide costal field that is crossed by straight anterior branches of SC, branches of RS, MA, and MP changing their position in relation of the wing membrane from convex to concave, simple CuA_1, a narrow field between CuA and CuP, hairs on the wing membrane, and the specific color pattern. At the same time, *K. subcostalis* has a number of characters that have not been met in chaulioditids, these are SC that is basally angled, anastomosis between RS

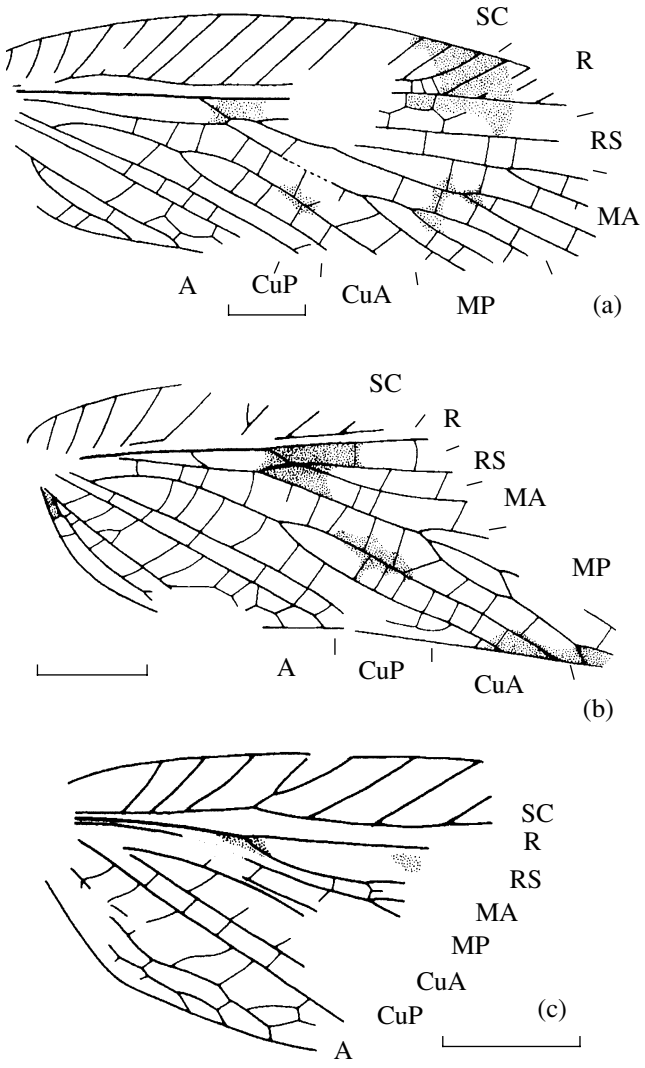

Fig. 2. Grylloblattids of the subfamily Kargalellinae and Grylloblattida incertae sedis: (a, b) *Kargalella gibbosa* sp. nov.: (a) holotype PIN, no. 199/127; (b) paratype PIN, no. 199/3a; and (c) Grylloblattida incertae sedis, specimen PIN, no. 199/308.

and MA, a media bifurcation at the level of the RS base, and a change of CuA position in relation to the membrane. These characteristics are sufficient for the placing the genus *Kargalella* into a separate subfamily. Thus, the nominative subfamily Chaulioditinae that comprises the above-listed genera and is characterized by a straight or gently curved SC, the media bifurcation beyond the RS base, free MA, and convex CuA and the monotypic subfamily Kargalellinae subfam. nov. are recognized as lying in the family Chaulioditidae.

Accordingly, the genus *Kargalella* is the most ancient representative of the family Chaulioditidae; the earliest (Upper Tatarian) representative of the nominative subfamily is *Ch. antiquus*, which was recorded from the Vyatka Horizon of the Vologda region.

MATERIAL

The material being studied (including type material) is housed at the Paleontological Institute of the Russian Academy of Sciences (PIN).

SYSTEMATIC PALEONTOLOGY

Order Grylloblattida

Suborder Grylloblattina

Family Chaulioditidae Handlirsch, 1908

Subfamily Kargalellinae Aristov, subfam. nov.

Tomiidae: Martynov, 1936, p. 1254 (syn. nov.)

Type genus. *Kargalella* Martynov, 1937.

Diagnosis. SC with an angle in the basal quarter of the wing, with its anterior branches not being connected to crossveins. RS forming anastomosis with MA. Media branching at the RS base level. CuA changing from concavity to convexity in relation to the wing membrane immediately after separation into branches.

Composition. Type genus.

Remarks. The specimen PIN, no. 199/308 from the Kuz'minovskie dumps of the same locality (Fig. 2c) may also belong to Kargalellinae. However, despite its superficial resemblance (first of all, due to the SC shape and coloration), it differs from the latter in the absence of anastomosis and in the closely spaced MP and CuA. Additionally, CuA branches have not been preserved in this specimen, thus preventing its description.

In 11 impressions of *K. subcostalis*, CuA_1 is simple in all complete specimens except for the paratype PIN, no. 199/302 (Fig. 1f), in which CuA_1 bifurcates. The absence of this characteristic in all the other Chaulioditidae and the shape of MP in the specimen in question suggest that we deal with an aberration such that the posterior branch of MP shifted onto CuA_1.

One of the distinctive features of the subfamily Kargalellinae is the change in the position of CuA relative to the wing membrane, which is unknown not only in the nominative subfamily but in all other grylloblattids. The change in the positions of RS, MA, MP, and the distal branch of CuA_1 is quite common in grylloblattids (in particular, RS, MA, and MP change their position relative to the membrane in Chaulioditinae), but the change in the entire CuA almost immediately after its bifurcation is described for the first time. The neutral position of RS ahead of the anastomosis with MA is also very unusual.

Genus *Kargalella* Martynov, 1937

Kargarella: Martynov, 1937, p. 32; Sharov, 1962, p. 131; Carpenter, 1992, p. 128; Storozhenko, 1998, p. 187.

Kargalodes: Martynov, 1937, p. 33; Rasnitsyn, 1980, p. 154; Sharov, 1962, p. 132.

Type species. *K. subcostalis.*

D i a g n o s i s. Medium-sized insects. Anterior margin of forewing convex. Costal field broad, approximately four times as wide as the subcostal field. SC angled in its basal quarter and terminates in the distal third of the wing. More than ten anterior branches of SC are straight, poorly dichotomizing, and not connected by crossveins. Anterior branches of R similar to SC branches. The RS base is situated in the basal third of the wing, and RS is fused with MA for a short distance. Media dichotomizing at the RS base level. CuA separates into CuA_1 and CuA_2 approximately at RS base level, and CuA_1 is simple, with both branches of CuA_2 being S-shaped. CuP is straight and A_1 simple. Wing membrane is covered with fine hairs. RS, MA, MP, and CuA change from concavity to convexity in relation to wing membrane. RS is neutral ahead of its anastomosis with MA, then concave, and later convex.

S p e c i e s c o m p o s i t i o n. Type species and *K. gibbosa* sp. nov.

Kargalella subcostalis Martynov, 1937

Kargarella subcostalis: Martynov, 1937, p. 32, text-fig. 12; Sharov, 1962, p. 131, text-fig. 329; Carpenter, 1992, p. 128, text-fig. 74 (4); Storozhenko, 1998, p. 187.

Kargalodes incerta: Martynov, 1937, p. 33, text-fig. 13; Rasnitsyn, 1980, p. 154; Sharov, 1962, p. 132, text-fig. 334.

H o l o t y p e. PIN, no. 100/10, forewing fragment; Kargala locality; Upper Permian, Lower Tatarian, Amanak Formation.

D e s c r i p t i o n (Figs. 1b–1f). Wing apex is slightly acuminate, the anterior margin being more convex than the posterior margin. RS has two or three branches, MA has three or four branches, and MP has two or three branches. The field between CuA and CuP slightly broadens basally. A_2 has four branches, the most anterior of which is fused with the A_1 tip. Crossveins are mainly simple, rarely Y- or H-shaped. The color pattern is developed as spots at the wing base and near the pterostigma and as vertical bands at the RS base and near the SC tip.

M e a s u r e m e n t s, mm. Forewing length, 14–17.

M a t e r i a l. In addition to the holotype, specimens PIN, nos. 100/11 (Dmitrievskaya shaft mine, *Kargalodes incerta* holotype), 199/10, 11, 117 (Nikolaevskie dumps), 141, 299, 302 (Kuz'minovskie dumps), 3, 14, and 112.

Kargalella gibbosa Aristov, sp. nov.

E t y m o l o g y. From Latin *gibbosa* (humpbacked).

H o l o t y p e. PIN, no. 199/127, forewing; Kargala locality; Upper Permian, Lower Tatarian, Amanak Formation.

D e s c r i p t i o n (Figs. 2a, 2b). The anterior margin of the wing is strongly convex, and the posterior margin is almost straight. RS is simple, MA has four branches, and MP has three or four branches (in the latter case, two posterior branches form an anastomosis). CuA_1 is simple and almost straight, and the field between CuA and CuP does not broaden basally. A_2 is two-branched. Crossveins are simple or form a double row of cells in the fields between R and RS and A_1 and A_2. The color pattern consists of small spots at the wing base, around the anastomosis between RS and MA, near the pterostigma, and in the middle of the costal margin of the wing.

M e a s u r e m e n t s, mm. Forewing midlength, about 14.

C o m p a r i s o n. It differs from the type species in its simple RS, double row of cells between R and RS, straight CuA_1, and two-branched A_2.

M a t e r i a l. In addition to the holotype, paratype PIN, no. 199/3a from the same locality.

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