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 Goede-witz in Germany (Lower or Middle Bundesstein, 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. helveti-cus, 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; Storzhenko, 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 tomids: 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 CuA1 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 of the type 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 Paratoma, 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
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 Kargalodes 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 CuA₁, 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...
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.)

**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. Kargalella Martynov, 1937.

**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, CuA₁ is simple in all complete specimens except for the paratype PIN, no. 199/302 (Fig. 1f), in which CuA₁ bifurcates. The absence of this characteristic in all the othe 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 CuA₁.

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 CuA₁ 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**


**Type species.** K. subcostalis.
Diagnosis. 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 CuA₁ and CuA₂ approximately at RS base level, and CuA₁ is simple, with both branches of CuA₂ being S-shaped. CuP is straight and A₁ 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.

Species composition. Type species and K. gibbosa sp. nov.

Kargarella subcostalis Martynov, 1937


Holotype. PIN, no. 100/10, forewing fragment; Kargala locality; Upper Permian, Lower Tatarian, Amanak Formation.

Description (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 does not broaden basally. A₂ is two-branched. Crossveins are simple or form a double row of cells in the fields between R and RS and A₁ and A₂. The color pattern consists of small spots at the wing base, around the pterostigma, and in the middle of the costal margin of the wing.

Measurements, mm. Forewing midlength, 11.5.

Comparison. It differs from the type species in its simple RS, double row of cells between R and RS, straight CuA₁, and two-branched A₂.

Material. In addition to the holotype, paratype PIN, no. 199/3a from the same locality.

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