

The Fauna of Grylloblattid Insects (Grylloblattida) from the End of the Late Permian to the First Half of the Triassic

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Abstract—The grylloblattid fauna that existed from the Late Permian to the first half of the Triassic is reviewed. Two new species of the family Geinitziidae, *Stegopterum anteanatalis* sp. nov. (Lek-Vorkuta Formation, Pechora Basin) and *Shurabia annosa* sp. nov. (Mal'tseva Formation, Kuznetsk Basin), are described. *Stegopterum hirtum* Shar., *Megakhosara fasciipennis* Mart., and *Syndesmopha composita* Mart. are redescribed. The family Stegopteridae becomes a subfamily of the family Geinitziidae. *Alicula asiatica* is transferred to the genus *Metidelia* of the family Ideliidae.

INTRODUCTION

This paper deals with the grylloblattid fauna described from the end of the Late Permian and the beginning of the Triassic. The review is based on data by Storozhenko (1998) and the author (Aristov, 2000b, 2004a).

Approximately 70% of families present in the Lower Kazanian became extinct at the Lower–Upper Kazanian boundary; thus, only four families are known from the Upper Kazanian and Lower Tatarian. Ideliidae, Megakhosaridae, and the dominant Liomopteridae have been recorded from the locality of Kityak (Kirov Region, Upper Kazanian), Liomopteridae have also been recorded from the locality of Bor-Tolgoy (Mongolia, Kazanian or Lower Tatarian, Tsanhin Formation). The family Tologopteridae, which was described from deposits of the Tsanhin Formation, has been transferred to the order Miomoptera (Storozhenko and Novokshonov, 1999).

In the locality of Kargala (Orenburg Region, Lower Tatarian), Ideliidae are represented by a monotypic genus known from a single impression, Chaulioditidae are also scarce. Megakhosaridae (Fig. 1) and Liomopteridae are dominant; however, in this fauna, the Liomopteridae are taxonomically less diverse than the Megakhosaridae, which is atypical for Permian faunas. A similar situation exists only in the locality of Natal (South Africa, Natal Province, Mooi River; Upper Permian, Tatarian, middle part of the Beaufort Series), where both families are equally diverse. Another feature shared by these two localities is the large size of the megakhosarids.

The other two localities of this age, Chepanikha and Galevo (Udmurtiya, Lower Tatarian), have yielded only isolated liomopterids. The fauna of Chepanikha is closer to that of the Ufimian, the liomopterids of Galevo are closer to those of the Upper Tatarian. One of the

impressions is indistinguishable from *Paraliomopterum karaungirense* Storozhenko, 1991 from the locality of Karaungir, but this is probably the result of incomplete preservation.

Thus, the Lower Tatarian fauna is typical of the Permian in that the Liomopteridae are dominant. The difference is in the small number of families, which declined as early as the mid-Kazanian, and in the relatively high diversity of Megakhosaridae.

The diversity and abundance of grylloblattids increased throughout the Upper Tatarian. The number of families and impressions is double that of the Lower Tatarian. The order is represented here by seven families. These are the numerically and taxonomically dominant Liomopteridae; the less abundant Megakhosaridae and Ideliidae; the rare Geinitziidae; and three newly appearing families, the Blattogryllidae, Chaulioditidae, and Tunguskapteridae, which in the Permian are represented by isolated specimens.

The most important locality of this age is Karaungir (Kazakhstan, East Kazakhstan Region; Upper Tatarian). Half of the impressions from this locality belong to *P. karaungirense* (Liomopteridae); the two other recorded liomopterids, as well as representatives of the Megakhosaridae, Ideliidae, and Blattogryllidae, are rare. The liomopterids present are taxa typical of the Permian (the genus *Paraliomopterum* is known from the Kazanian, and the genus *Karaungiroptera* is close to the genus *Ornaticosta* from the same stage).

Karaungirella minuta Storozhenko, 1991 was described from this locality as a member of the Lemmatophoridae and has subsequently been transferred to the Euryptilonidae (Storozhenko, 1998). *K. minuta* has the distal anterior branches of SC strongly inclined forward, and M and CuA late branching. These characters do not fit either Lemmatophoridae or Euryptilonidae but, along with a pectinate RS, and M and CuA with

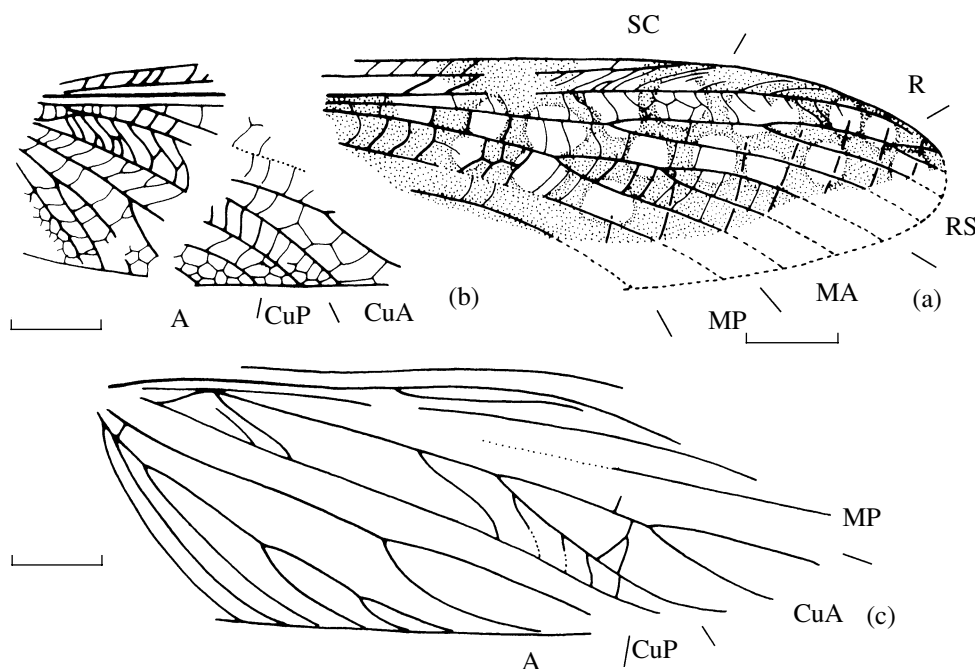


Fig. 1. Wings of members of the family Megakhosaridae: (a, b) *Megakhosara fasciipennis* Mart.: (a) holotype PIN, no. 100/9, (b) specimen PIN, no. 199/1; (c) *Syndesmorpha composita* Mart., holotype PIN, no. 100/19. Scale bar 5 mm.

their bases fused over a long distance, are clearly expressed in the genera *Tologoptera* Storozhenko, 1992 (Bor-Tolgoy) and *Sarbalopterodes* Storozhenko, 1991 (Karaungir). Both of these genera were originally described as grylloblattids and were subsequently transferred to the order Miomoptera (Storozhenko and Novokshonov, 1999). Apparently, *Karaungirella* is also a miomopteran of the family Permosialidae.

Another grylloblattid insect that was described from Karaungir is *Alicula asiatica* Storozhenko, 1997. This species was originally described in the family Aliculidae (Storozhenko, 1997a); however, this species differs strongly from other aliculids. The other three members of this family have a costal field that abruptly narrows to the wing base (the most distinctive feature of aliculids), a clearly S-shaped CuA with a backward comb of branches and the first fork of CuA distad of or at the same level as the M fork. In the holotype of *A. asiatica*, the basal part of the costal field is destroyed, CuA is not S-shaped, and branches considerably earlier than the M fork to form a comb of branches, the first portion of which runs forward and the second backward. This set of characters is characteristic of the family Ideliidae; thus, *A. asiatica* is here included in this family. Taking into account the similarity between *A. asiatica* and the Lower Tatarian ideliid species *Metidelia kargalensis* Mart. (Martynov, 1937), the former species is transferred to the genus *Metidelia*. *M. asiatica* comb. nov. differs from the type species in the wider subcostal field, denser archdictyon, and, probably, in a greater number of the CuA branches.

The impoverished fauna of the locality of Aristovo (Vologda Region, Upper Tatarian) is represented by liomopterids and chaulioditids. One tunguskapterid impression has been described from the locality of Nizhnyaya Tunguska (Krasnoyarsk Territory, Upper Tatarian), and one geinitziid impression, which cannot be identified further, is known from the locality of Novo-Aleksandrovka (Orenburg Region, Upper Tatarian) (Fig. 4b).

These Upper Tatarian faunas are similar to Lower Tatarian and Upper Kazanian faunas in the dominance of liomopterids, otherwise they closely resemble Triassic faunas. Not only a substantial number of families, but even three genera, *Megakhosarodes* (Megakhosaridae), *Protoblattogryllus* (Blattogryllidae), and *Chauliodites* (Chaulioditidae), survived into the Triassic.

The most distinctive feature of Lower Triassic faunas is the transformation of the chaulioditids into a taxonomically and numerically dominant group. Representatives of only two families, Chaulioditidae and Geinitziidae, have been found in the Lower Triassic. Since the family Chaulioditidae was revised elsewhere (Aristov, 2003, 2004b), it need not be considered in detail here. Judging from the fact that Permian Megakhosaridae, Blattogryllidae, and Ideliidae survived into the Middle–Upper Triassic but have not been found in the Lower Triassic, they apparently decreased in abundance during that time. By contrast, the abundance of Geinitziidae, which appeared in the Kazanian (see below), increased and they reappeared in oryctocenoses being represented by the nominal subfamily rather than by stegopterins.

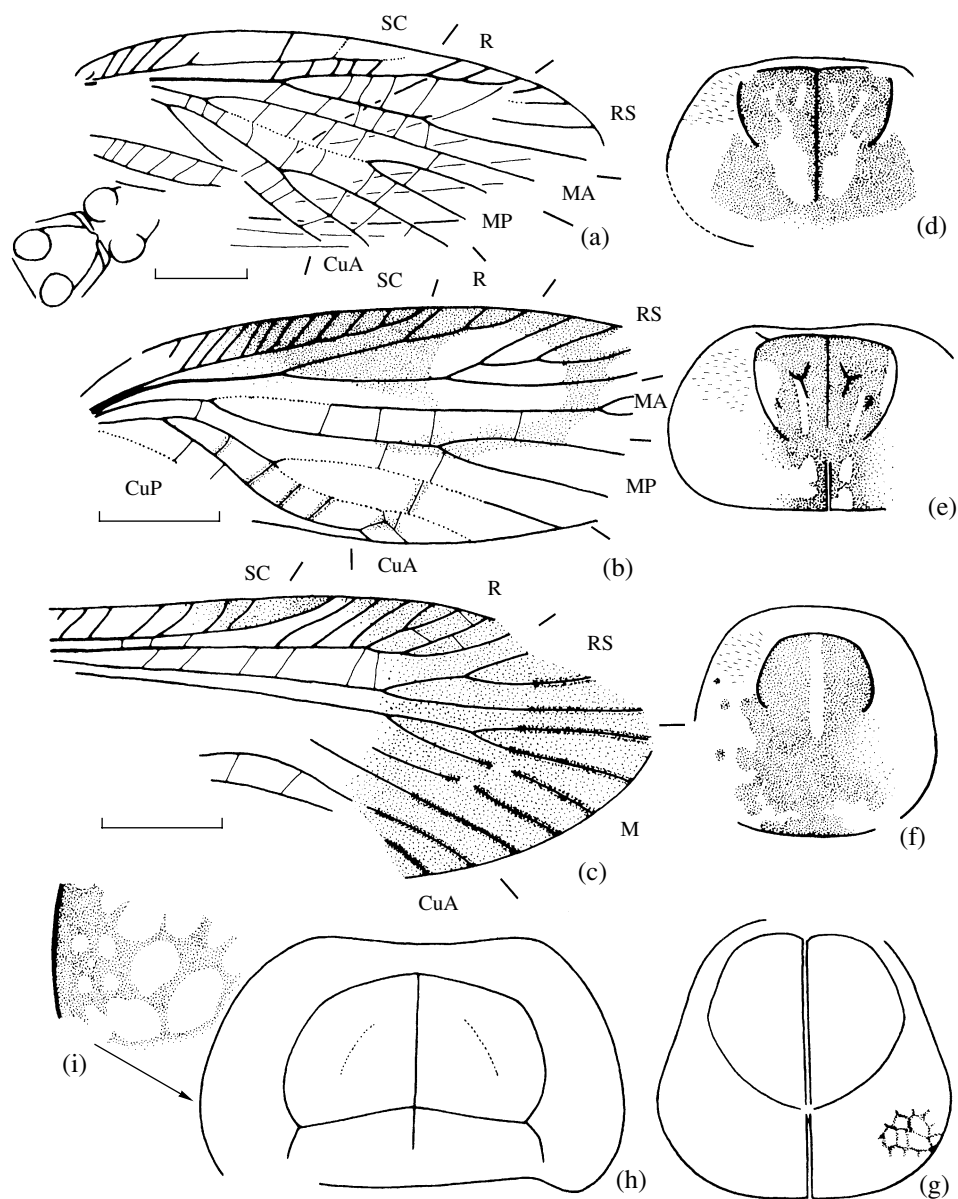


Fig. 2. Representatives of the order Grylloblattida: (a) *Stegopterum hirtum* Sharov, holotype PIN, no. 1197/318, (b) *Shurabia annosa* sp. nov., holotype PIN, no. 4887/28, (c) *Shurabia* sp. specimen PIN, no. 4887/11, locality of Babii Kamen'; (d) pronotum, specimen PIN, no. 4048/12, locality of Tikhvinskoe; (e) pronotum, specimen PIN, no. 4887/25, locality of Babii Kamen'; (f) *Shurabia parvula* A. Rasn., fragment of holotype PIN, no. 1873/18; (g) pronotum, specimen PIN, no. 4887/1, (h, i) specimen PIN, no. 4887/13: (h) pronotum, (i) fragments of paranotalia, locality of Babii Kamen'. Scale bar 2 mm in Figs. 2a–2c; Figs. 2d–2i out of scale.

The faunas of the localities of Tikhvinskoe (Yaroslavl' Region, Lower Triassic, Rybinsk Formation), Nedubrovo (Vologda Region, Lower Triassic, Nedubrovo Member of the Vokhminsk Formation), Anakit and Tura (Krasnoyarsk Territory, Lower Triassic or terminal Permian, Bugarikta Formation) are represented by isolated members of the genus *Chauliodites*. The fauna of the locality of Babii Kamen' (Kemerovo Region, Lower Triassic, Mal'tseva Formation) is more diverse. In addition to relatively abundant Chaulioditidae (four species in two genera), there are two species

of Geinitziidae, *Sh. annosa* sp. nov. and an undescribed hindwing (Fig. 2c), which cannot belong to the new species because of its size.

In addition to wings, the locality of Babii Kamen' has yielded grylloblattid body fragments, including pronota (Figs. 2d, 2e, 2g–2i). Very similar pronota have been found in the Lower Kazanian locality of Kaltan (Kemerovo Region). In particular, specimens PIN, nos. 1197/879 (Sharov, 1961, pl. 13, fig. 72), 1197/889, 1197/896, 1197/900, 1197/903, and others are similar to the pronotum illustrated in Fig. 2e. Specimens PIN,

nos. 1197/928 (Sharov, 1961, pl. 13, fig. 74), 1197/908, and 1197/933 are almost identical to the pronotum depicted in Fig. 2h. The pronotum of specimen PIN, no. 1197/885 and that depicted in Fig. 2g are also similar in appearance. Although these two localities have only one family (Geinitziidae) in common, it is quite unlikely that all these pronota belong to this family. Indeed, these pronota are numerous in Kaltan, where geinitziids are represented by only two impressions among nearly 600 grylloblattid remains. Apparently, these pronota belonged to Liomopteridae, which were dominant in Kaltan. In Babii Kamen', similar pronota may be attributable to the families Chaulioditidae and Geinitziidae, which are closely related to the Liomopteridae; however, it is difficult confidently assign them to a family. On the one hand, the pronota illustrated in Figs. 2d and 2e are similar to the pronotum of *Shurabia parvula* (Fig. 2f) in the shape of their paranotalia, colored nota with a pale pattern, and specific color pattern and hairs on the paranotalia; moreover, one pronotum (Fig. 2e) was found near the wing of *Sh. annosa* sp. nov. On the other hand, geinitziids are rare in Babii Kamen' as well, whereas pronota are relatively abundant, and most probably belong to chaulioditids.

Chaulioditidae are known from the Middle Triassic of China (Lin, 1978). Undescribed Blattogryllidae (Fig. 4c) and Chaulioditidae are known from the Anisian of France (Vosges) (Aristov, 2003). Chaulioditids have not been recorded in the Upper Triassic. The nymph of *Triaseurypylon accostai* from the Middle Triassic of Argentina was originally described as a miomopteran nymph and subsequently transferred to the family Atactophlebiidae (Storozhenko, 1997b). To date, two atactophlebiid nymphs are known, *Guriano-vella silphidoides* G. Zalessky, 1939 and *Atactophlebia termitoides* Martynov, 1928 from the Kungurian and Lower Kazanian, respectively. These nymphs share a number of characters that are absent in *Triaseurypylon*. These include a relatively short body, paranotalia, short abdomen, and middle and hind legs buried in a position characteristic of grylloblattids, i.e., with the tibiofemoral joint directed outwards. By contrast, *Triaseurypylon* has an elongate body with the tibiofemoral joint directed inwards, toward the body, as in stoneflies. Thus, it cannot be assigned to Atactophlebiidae, and its assignment to Grylloblattida remains questionable.

The fauna of Madygen (Ladinian or Carnian of central Asia), in which grylloblattids were again abundant and diverse, is younger and considerably richer. Four new families appeared and brought the total number of families to nine, only two of which survived into the Jurassic.

Thus, a period of stagnation started after the extinction of almost 70% of families at the end of the Early Kazanian and continued through the Late Kazanian and Early Tatarian. During that time, there were neither extinctions nor appearances, the diversity was low at the familial level, the fauna was represented by three generalized families, and one family disappeared temporarily from oryctocenoses. It is not inconceivable that

this decrease in diversity is an artifact. The Upper Permian faunas of Kaltan (Mitina Formation), Vorkuta (Lek-Vorkuta and Inta formations, which have essentially similar faunas), and some other localities are represented mainly by the families Liomopteridae, Ideliidae, and Megakhosaridae (other families are rare, represented by isolated impressions, and their presence can be explained by a large amount of material). Thus, the situation is similar to that in the Upper Kazanian and Lower Tatarian, in which the apparent low diversity can be misleading, since localities of that time are few and poor. In addition to the above families, the Upper Tatarian localities—except for Soyana (Lower Kazanian of the Arkhangelsk region), which exhibits an unusually high diversity—contain three other families typical for the Triassic; thus, their diversity rises to a level that is typical of the Permian. The most remarkable events of the terminal Permian and the first half of the Triassic are the change in the dominant taxa at the Permian–Triassic boundary (liomopterids were replaced by chaulioditids) and the low diversity of grylloblattids during the entire first half of the Triassic. Although these localities are numerous and widely distributed geographically, they have only yielded members of the Chauliodotidae, Geinitziidae and Blattogryllidae.

The available facts may be interpreted in terms of the hypothesis of a biocenotic crisis (Rasnitsyn, 1988, 1989; Zherikhin and Rautian, 1999). It turns out that the dramatic phase of the crisis (crisis itself) took place in the Late Tatarian, when an abrupt faunal change, which was due to an increased rate of extinction and appearance (the latter prevailed), and a change in the dominant taxa occurred.

MATERIAL

The material being studied, including types, is housed in the Paleontological Institute, Russian Academy of Sciences (PIN).

SYSTEMATIC PALEONTOLOGY

Family Megakhosaridae Sharov, 1961

Genus *Megakhosara* Martynov, 1937

Megakhosara fasciipennis Martynov, 1937

Holotype. PIN, no. 100/9, forewing fragment; Orenburg Region, Sakmara District, spoil heaps of the Kargala Copper Mines; Upper Permian, Lower Tatarian, Amanak Formation

Redescription (Figs. 1a, 1b). The forewing is elongate, its anterior margin is straight, the costal field is narrow and crossed with simple branches of SC, which reaches the distal third of the wing, R is straight, with the apical portion running along the wing apex, the anterior branches of R are thin and numerous. RS starts at the end of the basal third of the wing, pectinate, with four branches, MA is three-branched, MP is simple. CuA is probably three- or four-branched, becoming

convex from neutral after the fusion with M_5 . CuP is almost straight, A_1 is two-branched, A_2 is three-branched. Crossveins are simple or form a double row of cells within part of the radial field and between MA and MP and CuA and CuP. Crossveins form a fine net near the posterior margin of the basal part of the wing. The background of the wing is dark, with round pale spots.

Measurements. mm. Fragment length, 35; entire length, about 45.

Remarks. *M. fasciipennis* was described as a fragment of the hindwing of a member of the family Khosaridae (Martynov, 1937) and was subsequently included in the Liomopteridae, but the general pattern of its venation and the convexity of CuA after the fusion with M_5 leave no doubt that we are dealing with a forewing. Sharov (1961) established a separate family Megakhosaridae for *Megakhosara*. Later, the specimen PIN, no. 199/1 was identified as *M. fasciipennis*, and a reconstruction was made on the basis of this impression and the holotype (Storozhenko, 1998). Although these impressions belong to nonoverlapping fragments, they probably belong to the same species because of their similarity in size (another megakhosarid from Kargala, *S. composita*, is noticeably larger and has a longer RS).

Material. Besides the holotype, specimens PIN, nos. 199/1 and 100/17.

Genus *Syndesmorpha* Martynov, 1937

Syndesmorpha composita Martynov, 1937

Holotype. PIN, no. 100/19, fragment of a deformed forewing; Orenburg Region, Sakmara District, spoil heaps of the Kargala Copper Mines; Upper Permian, Lower Tatarian, Amanak Formation.

Redescription (Fig. 1c). The base of RS is at the level of the first anal vein bifurcation, the media bifurcates into MA and MP at the level of the RS base. CuA is three-branched, close to M at M_5 (this may be the result of deformation). CuP is straight, A_1 is two-branched, A_2 is pectinate with six branches. Crossveins are S- and Y-shaped.

Measurements. mm. Fragment length, 43; entire length, about 60.

Remarks. This species was originally described as *Insecta incertae sedis* (Martynov, 1937) and subsequently synonymized under *M. fasciipennis* (Sharov, 1961). Comparison of these insects demonstrates a number of differences (*S. composita* is larger, RS starts earlier, and A_2 has more branches), which prevent them from being treated as members of the same genus.

Material. Holotype.

Family Geinitziidae Handlirsch, 1906

Subfamily Stegopterinae Sharov, 1961, stat. nov.

Stegopteridae: Sharov, 1961, p. 220–221.

Diagnosis. Forewing with finely tuberculate structure. RS regularly pectinate, media with three

branches, CuA_2 not parallel to posterior margin of wing. In hindwing, stem CuA noticeably thicker than branches.

Composition. One genus from the Upper Permian of the Kuznetsk and Pechora basins.

Remarks. *Stegopteron hirtum* was described as the only representative of the family Stegopteridae, the diagnostic features of which included the tuberculate sculpture of the wing, the absence of hairs from the wing membrane, and the R stem and RS branches being bent toward the anterior margin of the wing. The above features (except for the tuberculate sculpture of the wing) are equally characteristic of the family Geinitziidae; comparison of *S. hirtum* with geinitziids and, especially, with the genus *Shurabia* demonstrates that it differs in the combination of a regularly pectinate RS and straight posterior branch of CuA. These features are quite common in members of *Shurabia*, and their combination does not seem sufficient for keeping the family Stegopteridae; thus, it is included in the family Geinitziidae as a subfamily.

The inclusion of Stegopteridae into Geinitziidae raises the question of the origin of the family Geinitziidae. Geinitziidae were considered to be descended from Ideliidae; and Stegopteridae from Liomopteridae (Storozhenko, 1998). The most typical character of geinitziids, RS directed toward the anterior margin of the wing, appears independently in both liomopterids (genera *Parasylyviodes* and *Tyrannopterum* from the Lower Permian) and ideliids (genus *Pseudoshurabia* from the Middle or Upper Triassic). In the latter, however, this character shows individual variation; this fact, along with their younger age, polymerized CuA, and the presence of the archdictyon, makes Liomopteridae the most probable forbear of Geinitziidae.

Genus *Stegopteron* Sharov, 1961

Stegopteron hirtum Sharov, 1961

Holotype. PIN, no. 1197/318, positive impression of a fragment of the thorax and fore- and hindwings; Kemerovo Region, Kuznetsk District, locality of Kaltan; Upper Permian, Kazanian, Mitina Formation.

Redescription (Figs. 2a, 3a). The mesonotum is approximately as long as wide, the scutum is rounded triangular, and the scutal lobes are distinct and separated. The metanotum is similar but slightly shorter. The forewing has finely tuberculate sculpture. The anterior margin of the wing is weakly convex, the costal field is wider than the subcostal one and narrows toward the apex. SC has straight anterior branches and terminates in the distal third of the wing. R has two anterior branches and terminates at the anterior margin of the wing, RS starts at the wing midlength and ends in a regular comb of four branches at the anterior margin and apex of the wing. M bifurcates closer to the RS base than to the first CuA fork, MA is simple, MP is two-branched. CuA is three-branched, the posterior branch

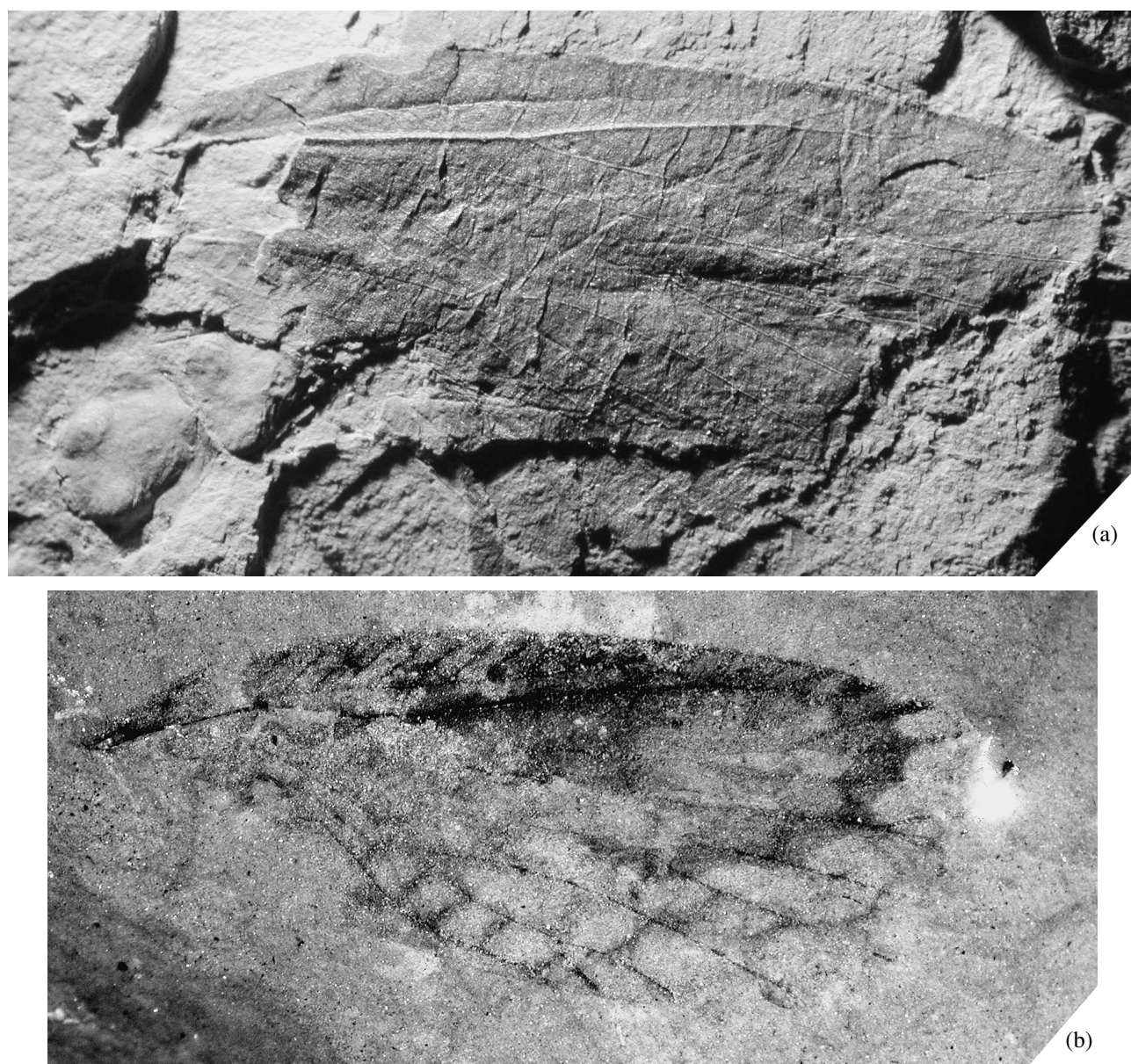


Fig. 3. Representatives of Geinitziidae: (a) *Stegopterum hirtum* Sharov, holotype PIN, no. 1197/318, (b) *Shurabia annosa* sp. nov., holotype PIN, no. 4887/28.

of CuA is straight, CuA₁ bifurcates near its midlength. A₁ and A₂ are simple. Crossveins are simple. In the hindwing, the costal field is as wide as the subcostal one. RS and M form three or four branches, CuA is two-branched.

Measurements, mm. Forewing length, 11.

Remarks. The forewing of the holotype (but not the fragment of the thorax nor the hindwing) and an isolated hindwing (specimen no. 1197/155), which was assigned to the same species, were figured in the original description (Sharov, 1961). Comparison of the isolated hindwing with the hindwing of the holotype reveals that it has a larger number of RS and M

branches and simple CuA and, thus, seems to belong to another species.

Material. Holotype and specimen PIN, no. 676/14.

Stegopterum anteanatalis Aristov sp. nov.

Etymology. From Latin *antea* (before) and *natalis* (referring to birth).

Holotype. PIN, no. 1631/206, impression of a forewing fragment; Komi, Nenets Autonomous Area, Bol'shezemel'skaya tundra, Chernyshev Range, Adz'va River; Upper Permian, Ufimian, Lek-Vorkuta Formation, Rudnitsy Subformation.

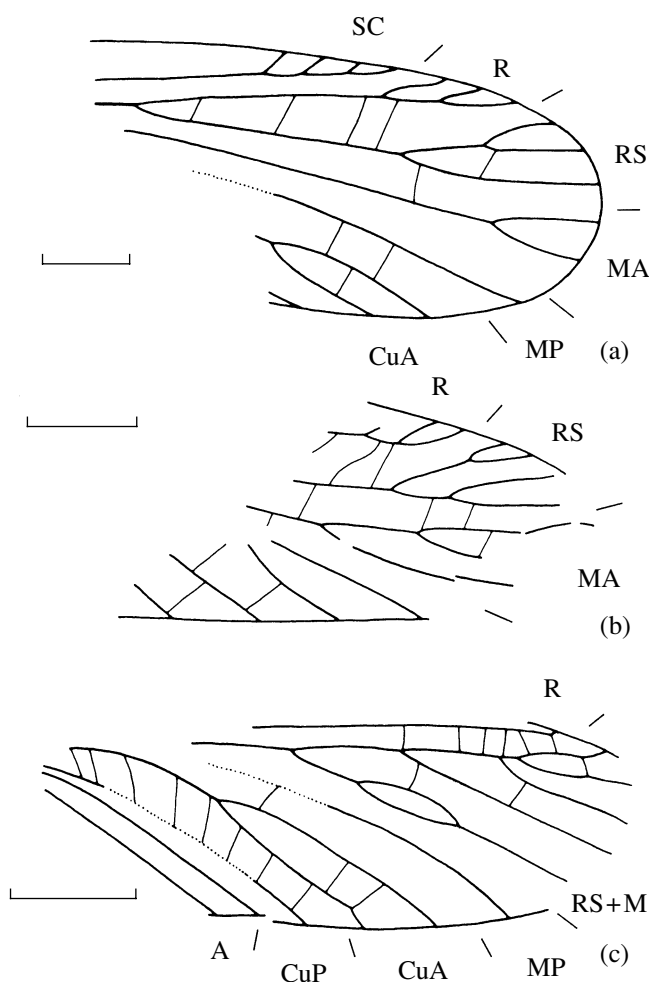


Fig. 4. Representatives of the order Grylloblattida: (a) *Stegopterus anteanatalis* sp. nov., holotype PIN, no. 1631/206, (b) Geinitziidae gen. et sp. indet., specimen PIN, no. 3700/32 from the locality of Novo-Aleksandrovka, Upper Tatarian; (c) Blattogryllidae gen. et sp. indet., specimen no. 5739-5740 (Arzviller, Moselle) (after Gall *et al.*, 1996, pl. 9, fig. 3). Scale bar 2 mm.

Description (Fig. 4a). The forewing has finely tuberculate sculpture. The anterior margin of the wing is weakly convex, the costal broader than the subcostal. SC runs into the distal third of the wing, R is straight, with two anterior branches. RS starts near the wing midlength, forms a backward comb of three branches, MA has one short fork, MP is simple. CuA_1 bifurcates once near the apex. Crossveins are simple and straight.

Comparison. This species differs from the types species in having fewer RS branches, simple MP, and CuA_1 that branches later.

Measurements, mm. Forewing length, about 12.

Material. Holotype.

Subfamily Geinitziinae Handlirsch, 1906

Diagnosis. Forewing membranous. RS irregularly pectinate or spontaneously branching, media with

more than three branches, CuA_2 parallel to posterior margin of wing. In hindwing, stem CuA approximately as wide as branches.

Composition. *Geinitzia* Handlirsch, 1906 from the Jurassic of Europe and Asia; *Shurabia* from the Triassic and Jurassic of Siberia, central Asia, Mongolia, China, and Australia; and *Fletchizia* Riek, 1976 from the Triassic of South Africa.

Genus *Shurabia* Martynov, 1937

Shurabia annosa Aristov, sp. nov.

Etymology. From Latin *annosa* (ancient).

Holotype. PIN, no. 4887/28, forewing; Kemerovo Region, Novokuznetsk District, right bank of the Tom' River, 10 km downstream of the village of Ust'-Naryk, locality of Babii Kamen'; Lower Triassic, Mal'tseva Formation.

Description (Figs. 2b, 3b). Both the anterior and posterior margins of the wing are convex, the costal field is wider than the subcostal one. SC is straight and terminates near the wing midlength, its anterior branches are simple, straight, and closely spaced. R is S-shaped, with two anterior branches, RS starts near the wing midlength and forms an irregular comb of four branches. M bifurcates closer to the first fork of CuA than to the RS base, its both branches bifurcate. CuA is three-branched, CuA_1 bifurcates early, its distal branch terminates in the distal quarter of the wing, CuA_2 is sinuous, the field between CuA and CuP is narrow. Crossveins are simple, bordered with a color pattern in the rear half of the wing; the fore half is dark, with a round pale spot. MA and CuA_1 are partially changing their position in relation to the wing membrane from convex to neutral (these sections are dotted in Fig. 2b).

Measurements, mm. Forewing length, 10.

Comparison. *Sh. annosa* sp. nov. has a three-branched CuA , which is typical of the genus, and oligomerized venation, being most similar to *Sh. parvula* A. Rasnitsyn, 1982, from which it differs in having a narrower costal field, early bifurcation of M, and larger number of the SC, R, and RS branches.

Remark. The situation when veins change their position, which has been recorded in several grylloblattid families (Ideliidae, Euremisciidae, and Protembidiidae), is recorded for the first time in geinitziids.

Material. Holotype.

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