

Position and taxonomy of the Permian fossil insect family Permembiiidae (Insecta: Palaeomanteida = Miomoptera)

Положение и систематика пермского ископаемого семейства насекомых Permembiiidae (Insecta: Palaeomanteida = Miomoptera)

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КЛЮЧЕВЫЕ СЛОВА: Ископаемые насекомые, Palaeomanteida, Permembiiidae, Sheimiidae, Letopalopteridae, Visheriferidae, пермь.

ABSTRACT. Taxonomy and position among the insects of family Permembiiidae (Insecta; Palaeomanteida = Miomoptera) is examined. Described *Soyanembia sharovi* gen. et sp.n., *Soyania logica* gen. et sp.n., *Pseudosheimia alligans* sp.n., *Pseudosheimia caudissima* sp.n., *Parasheimia kazanica* sp.n.; *Visherifera camura* Novokshonov, Ivanov, Aristov, 2002, is re-described; family Visheriferidae is synonymized under Sheimiidae; families Sheimiidae and Letopalopteridae are regraded as separate subfamilies under Permembiiidae; *Kungurmica sojanensis* Aristov, 1998 is transferred to Tshekarcephalidae (incertae sedis) as *Tshekarcephalus sojanensis* (Aristov, 1998), **comb.n.**

РЕЗЮМЕ. Рассмотрены систематика и положение среди насекомых семейства Permembiiidae (Insecta; Palaeomanteida = Miomoptera). Описаны *Soyanembia sharovi* gen. et sp.n., *Soyania logica* gen. et sp.n., *Pseudosheimia alligans* sp.n., *Pseudosheimia caudissima* sp.n., *Parasheimia kazanica* sp.n.; переопирана *Visherifera camura* Novokshonov, Ivanov, Aristov, 2002, семейство Visheriferidae сведено в синонимы к Sheimiidae; статус семейств Sheimiidae и Letopalopteridae понижен до подсемейств в пределах Permembiiidae; *Kungurmica sojanensis* Aristov, 1998 перенесена в Tshekarcephalidae (incertae sedis) и предложена новая комбинация *Tshekarcephalus sojanensis* (Aristov, 1998), **comb. n.**

Introduction

Permembia delicatula Tillyard, 1928 has been described from the Artinsk (Lower Permian) locality Elmo in Kansas, USA in the family Delopteridae [Order Protorthoptera; Tillyard, 1928]. Later [Tillyard, 1937]

the new, monotypical family Permembiiidae has been erected attributed along with Delopteridae to the new suborder Embiopsocidae within the order Copeognatha = Psocoptera. O.M. Martynova [1962] has included the family with doubts into the order Miomoptera [now Palaeomanteida: Ponomarenko, 1980; Rasnitsyn, 2002] and synonymised Delopteridae under Palaeomanteidae. J. Kukulová [1963] and E.F. Riek [1973, 1976] considered the family as a member of Miomoptera as well. Carpenter [1976] has re-described the genus and the family and treated them as unplaced within Neoptera [cf. Carpenter, 1992]. Storozhenko [1998] transferred the family to the order Grylloblattida. One more fossil has been ascribed to Permembiiidae, viz., *Kungurmica tshekardensis* Novokshonov, 1998 from the Lower Permian (Kungurian) of Tshekarda in Urals [Novokshonov, 1998]. *Kungurmica* Novokshonov, 1998 is insufficiently known for wing venation including the basal wing half as well as SC apex preventing us to confirm its close relation to *Permembia*. Until more information about the genus is accumulated we prefer to consider the genus as unplaced within Permembiiidae s.l. as defined below.

The family Sheimiidae and the monotypical suborder Sheimoidea have been described by Martynova [1958, 1962] within the order Embioptera based on the unique holotype of *Sheimia sojanensis* Martynova, 1958 from the Middle Permian (Lower Kazanian) locality Soyana in the Arkhangel'sk Region (northern European Russia). Later [Storozhenko, 1997] the family has been also transferred to the order Grylloblattida. Additionally to the type genus and species, 5 more sheimiid species has been described from Soyana, viz., two in the genus *Pseudosheimia* Aristov, 2004 and one each in *Parasheimia* Aristov, 2004 and in monotypical genera *Soya-*

noembia Aristov et Rasnitsyn, **gen.n.** and *Soyania* Aristov et Rasnitsyn, **gen.n.** Further four species have been described from the Kungurian Tshekarda (one in each *Sheimia* Martynova, 1958 and *Pseudosheimia* and two in *Parasheimia*, Aristov, 2004 [Aristov, 2004]). Wing venation of Sheimiidae is essentially similar to that of Permembaliidae, as well as the available body characters. That is why we lower the rank of the former up to the subfamily Sheimiinae Martynova, 1958, **stat.n.** within Permembaliidae. Accordingly *Permembia* is considered representing the monotypical subfamily Permembaliinae **stat.n.** there.

The family Letopalopteridae Martynova, 1961 has been originally established within the order Raphidioptera [Martynova, 1961; 1962]. This attribution has been discussing at length by Ponomarenko [1980]. Carpenter [1992] has missed this taxon. Besides the type genus *Letopaloptera* Martynova, 1961 with its constituent two species from the Lower Kazanian of Soyana, the genus *Permindigena* Novokshonov, 1998 has been described based on the new species from the Kungurian of Tshekarda, and the family was moved to the order Hypoperlida [Novokshonov, 1998; Rasnitsyn, 2002]. Herein we re-describe both species of *Letopaloptera* and re-interpret the family Letopalopteridae as the subfamily Letopalopterinae Martynova, 1961, **stat.n.** of the family Permembaliidae within the order Paleomantiida.

The monotypical family Visheriferidae Novokshonov, Ivanov, Aristov, 2002 has been described in the order Grylloblattida from the Ufimian (Middle Permian) of Mogil'nikov in the Permian Region [Novokshonov et al., 2002]. Later [Aristov, 2004] the second species of *Visherifera* Novokshonov, Ivanov, Aristov, 2002 has been described from the Kungurian of Tshekarda. The family rank has been assigned to *Visherifera* based on the pronotum with paranota, even though the respective structures were narrow and so not characteristic of Grylloblattida: that time similar paranota have not been known yet present in some Sheimiinae. Additional information of Sheimiidae and the present re-description of the type species of *Visherifera* shows that Visheriferidae merits no formal distinction from Sheimiinae. Thus, the new synonymy is established: Sheimiidae Martynova, 1958 (= Visheriferidae Novokshonov, Ivanov, Aristov, 2002, **syn.n.**)

The insects under above discussion apparently form a tight group distinct venationally, and with body morphology inconsistent with that of Grylloblattida and Gryllones (= Polyneoptera) in general. In the wing morphology, the above group can be diagnosed after essentially homonomous wings (with hind pair lacking expanded anal lobe and with more or less similar venation), narrow preradial space, RS with at most two branches, MA, MP, CuA, and CuP simple, M lacking its own base and starting from CuA, so as the M+Cu system forms a standard 4-branched posterior comb, and only one or two anal veins.

Indicative of the taxonomic position of the group are SC forming in *Permembia* an apical fork which is typical of many Scarabaeones (winged insects other

than Gryllones or Polyneoptera) but strictly different from all known in Grylloblattida. MP never with desclerotized portion as is characteristic of most Grylloblattida. Unfortunately the taxonomically indicative wing life position is never preserved as demonstrating either roof-like (unknown in Gryllones), or flat and widely overlapping (common in Gryllones), except *Permindigena lientericus* Novokshonov, 1998 with apparently roof-like wing position at rest. In contrast, the body structures demonstrate almost unequivocally the characters unusual for Grylloblattida and Gryllones in general and compatible with the features of Scarabaeones. These are pronotum with paranota either lacking or narrow, and particularly the male genital appendages (in *Pseudosheimia alligans* Aristov et Rasnitsyn, **sp.n.** (Fig. 9) which are two-segmented, forceps-like and so very similar to those in some holometabolous insects including miomopterans, e.g. *Delopterus rasnitsyni* Novokshonov [Novokshonov, 2000: Fig. 4].

The above combination of characters seems indicative. Indeed, the venational scheme of the group under consideration is similar to, and can be easily interpreted as further specialisation of, that of the order Palaeomanteida. In fact the ground plan venation of the permembiid-sheimiid-letopalopterid assemblage can be easily obtained from that of an advanced miomopteran like *Delopterus* Selderds, 1909 by simple loss of the fore (apical) RS fork and of CuA fork. This make us possible to consider the assemblage at hand as a member of the order Palaeomanteida possibly descending from an advanced member of Palaeomanteidae comparable with *Delopterus* or related genera as defined by Rasnitsyn et al. [2004].

The present decision to attribute the above assemblage treated as Permembaliidae s.l. to the order well distant from Grylloblattida raises similar question about the rest grylloblattideans lacking wide and circular pronotal paranota as well as M base fused with CuA, viz., Sojanoraphdiidae and Tshekardominidae. This question cannot be answered finally at present, but Sojanoraphdiidae and Tshekardominidae differs profoundly from the above assemblage venationally (all main vein systems richly branched), and with some body structures indicative of Gryllones rather than of Scarabaeones (contralateral pterothoracic coxae well distant in Sojanoraphdiidae but not in Tshekardominidae). This justifies position at least of Sojanoraphdiidae within the order Grylloblattida. Tillyardembiidae also has paranota lost, but it differs from Permembaliidae s.l. additionally in having M base free of CuA.

Concerning the taxonomic state of the above assemblage, the standard venational scheme in spite of considerable variations of the body form and general appearance (cf. Figs. 1–17) makes it possible to lump all of them into one family Permembaliidae Tillyard, 1937. The former families deserve their rank to be reduced down to the subfamily level, viz., Permembaliinae Tillyard, 1937, **stat.n.**, Sheimiinae Martynova, 1958, **stat.n.** and Letopalopterinae Martynova, 1961, **stat.n.**

REMARK. *Kungurmica sojanensis* Aristov, 1998 differs from the type species of that genus in having pronotum short and mandibles long, sickle-shaped. For the reasons explained by Novokshonov and Rasnitsyn [2000] it is transferred in the family Tshekarcephalidae (unplaced in the superorder Psocidea) as *Tshekarcephalus sojanensis* (Aristov, 1998), **comb.n.**

Taxonomy

Order Palaeomanteida Handlirsch, 1906

(= Miomoptera)

Family Permembiiidae Tillyard, 1937

— Permembiiidae: Tillyard, 1937: 92; Martynova, 1962: 140; Carpenter, 1976: 359; 1992: 205; Storozhenko, 1997: 9; 1998: 100; 2002: 280; Novokshonov, 1998: 41;
= Sheimiidae: Martynova, 1958: 69; 1962: 139; Carpenter, 1976: 363; Storozhenko, 1997: 9; 1998: 100; 2002: 280; Aristov, 2004: 120 (**syn.n.**);
= Letopalopteridae O. Martynova, 1962: Martynova, 1962: 270; Novokshonov, 1998: 44; Rasnitsyn, 2002: 112 (**syn. n.**);
= Visheriferidae Novokshonov, Ivanov et Aristov, 2002: Novokshonov, Ivanov, Aristov, 2002: 39; Aristov, 2004: 88 (**syn. n.**).

TYPE SUBFAMILY. Permembiiinae Tillyard, 1937, **stat.n.**

DIAGNOSIS. Size small to medium. Head more or less prognathous. Eyes large or moderately small, ocelli expressed or lost. Antennae short, moderately thick. Pronotum usually equal to head in size, sometimes transverse or elongate, with with paranotal ring narrow at best, or usually lost. Pterothoracic segments and wings roughly homonomous. Wing moderately or well elongate, with fore margin at most slightly convex, preradial space narrow, pterostigma absent, costal space wider than subcostal one. SC simple or with apical fork, short to very long; RS 1–2 branched, M 2-branched, starting from CuA, with fore branch often joining RS; CuA and CuP simple; anal veins one or two (possibly three in some Letopalopterinae); crossveins variable. Hind wing when known with similar venation, no enlarged anal area known. Abdomen not wide, not distinctly depressed, with ovipositor short, male genitalia at least in one case with articulated gonocoxa and gonostylus forming characteristic forceps; cerci sometimes long, segmented.

COMPOSITION. Three subfamilies: monotypical Permembiiinae, **stat.n.** from the Artinskian of USA (Fig. 1), Sheimiinae, **stat.n.** with six genera and 12 species from the Kunguria, Ufimian and Lower Kazanian of the European Russia (Figs 2–15); Letopalopterinae, **stat.n.** with two genera and three species also from the Kungurian and Lower Kazanian of the European Russia (Figs 16–18) and unplaced monotypical genus *Kungurmica* from the Kungurian of Urals (Fig. 4).

COMPARISON. Differs from all other Palaeomanteida in having simple CuA.

IDENTIFICATION KEY TO FAMILY PERMEMBIIIDAE TILLYARD, 1937

1 (32). Eyes small to medium sizes, flagellomeres not mushroom-like. Fore legs shortest, hind legs longest.
2 (27). Legs short, SC reaching at least near wing midlength, RS simple or forked not basad of its midlength.
3 (4) SC ending with apical fork near wing midlength. M branching distal of RS base. Cu split into CuA and CuP near basal third of wing. Permembiiinae Tillyard, 1937, **stat.n.**: *Permembia delicatula* Tillyard, 1928

4 (3). SC lacking characteristic apical fork, well surpassing wing midlength. M branched before RS base. Cu split into CuA and CuP near basal quarter of wing
..... Sheimiinae Martynova, 1958, **stat.n.**
5 (26) Antennae long, with more than with seven segments. Pronotum not elongate. Length of wing 2–3 times more than width
6 (25) Costal space not expanded basally, lacking numerous SC branches. MP not fused with CuA. Interradial crossveins not forming double row of cells.
7 (16) RS fused with M or MA.
8 (11) Pronotum trapezoid, narrowing behind, of equal length and width. *Sheimia* Martynova, 1958
9 (10) Eyes small. RS fused with M
..... *Sh. sojanensis* Martynova, 1958
10 (9) Eyes medium sized. RS fused with MA
..... *Sh. tshekardensis* Aristov, 2004
11 (8) Pronotum square or transverse
..... *Pseudosheimia* Aristov, 2004
12 (15) Scape ordinary. Pronotum transverse. CuA convex
13 (14) CuA and CuP parallel *P. caudata* Aristov, 2004
14 (13) CuA and CuP not parallel
..... *P. caudissima* Aristov et Rasnitsyn, **sp.n.**
15 (12) Scape unusually large. Pronotum square. CuA straight
..... *P. alligans* Aristov et Rasnitsyn, **sp.n.**
16 (7) RS not fused with M or MA.
17 (20) SC reaching near wing apex. RS starting at wing midlength, forking at its midlength. Space between RS and MA with double row of cells
..... *Visherifera* Novokshonov, Ivanov, Aristov, 2002
18 (19) Forewing fore margin slightly concave
..... *V. camura* Novokshonov, Ivanov, Aristov, 2002
19 (18) Forewing fore margin slightly convex
..... *V. sylvaensis* Aristov, 2004
20 (17) SC reaching apical third of wing. RS starting at basal third of wing, simple or with short fork. Space between RS and MA with simple crossveins
..... *Parasheimia* Aristov, 2004
21 (24) Fore pronotal margin not rounded
22 (23) Apex of R not parallel to apex of wing. RS simple, M with three branches *P. truncata* Aristov, 2004
23 (22) Apex of R parallel to apex of wing. RS and M with two branches *P. rotundata* Aristov, 2004
24 (21) Fore pronotal margin rounded
..... *P. kazanica* Aristov et Rasnitsyn, **sp.n.**
25 (6) Costal space expanded at base, with dense SC branches. MP fused with CuA. Interradial crossveins forming double row of cells *Soyanembia* Aristov et Rasnitsyn, **gen.n.**
(*Soyanembia sharovi* Aristov et Rasnitsyn, **sp.n.**)
26 (5) Antennae short with seven members. Pronotum elongate. Length of wing 4 times more than width
..... *Soyania* Aristov et Rasnitsyn, **gen.n.**
(*Soyania logica* Aristov et Rasnitsyn, **sp.n.**)
27 (2). Legs strongly elongate. SC reaching basal third of wing. RS forking well before its midlength
..... Letopalopterinae Martynova, 1961
28 (31) Pronotum elongate. Length of forewing 9.5–11 mm. R straight, not approaching wing fore margin. Forefemur longer than meso- and metanotum combined
..... *Letopaloptera* Martynova, 1961
29 (30) RS starting near midlength of wing. Apex of CuP not parallel to posterior wing margin
..... *L. albardiana* Martynova, 1961
30 (29) RS starting at basal third of wing. Apex of CuP parallel to posterior wing margin
..... *L. carpenteriana* Martynova, 1961

- 31 (28) Pronotum not elongate. Length of forewing 19–24 mm.
R bent at wing basal third, closely approaching wing anterior margin. Forefemuras long as meso- and metanotum combined
..... *Permindigena lienterocus* Novokshonov, 1998
- 32 (1) Eyes large, flagellomeres mushroom-like pedunculate.
All. legs of equal length
..... *Kungurmica tshekardensis* Novokshonov, 1998

Subfamily Permembiiinae Tillyard, 1937, **stat.n.**

Permembiiidae: Tillyard, 1937: 92

TYPE GENUS. *Permembia* Tillyard, 1928.

DESCRIPTION (Fig. 1). Small insects: forewing length 2.3–2.8 mm, body length 3 mm. Eyes small, ocelli lost. Antennae moderately long. Pronotum smaller than head, transverse, without paranota. Legs short. Wing with fore margin slightly convex, costal space expanded at base, about 2 time as wide as subcostal one. SC with apical fork near midlength; R straight, not approaching anterior wing margin; RS simple as preserved, M starting from CuA, forked after RS base, with free fore branch; CuA and CuP simple; anal veins two. Hind wing when known with similar venation. Abdomen not wide; cerci short.

COMPOSITION. Single species *Permembia delicatula* Tillyard, 1928 (Fig. 1) from the Artinskian of Elmo in the Kansas, USA [redescribed by Carpenter, 1976].

Subfamily Sheimiinae Martynova, 1958, **stat.n.**

Sheimiidae: Martynova, 1958: 69;

Visheriferidae: Novokshonov, Ivanov, Aristov, 39.

TYPE GENUS. *Sheimia* Martynova, 1958

DESCRIPTION (Figs 2–15). Size small to medium, forewing length 3–11 mm, body length 3–7 mm. Eyes large or moderately small, ocelli present or lost. Antennae short or long, moderately thick. Pronotum usually subequal to head in size, transverse or square, rarely elongate, with paranotal ring narrow or, usually, lost. Legs short, first pair shortest, hind longest. Wing with fore margin slightly convex, straight or concave, costal space not expanded at base, about 2–3 times as wide as subcostal one. SC simple, reaching wing distal third or beyond. R straight, not approaching anterior wing margin; RS simple or with fork not longer than stem. M forking before RS base, with 2–3 branches, starting from CuA, with fore branch often joining RS; CuA and CuP simple; anal veins one or two; crossveins variable. Hind wing when known with similar venation, no enlarged anal area known. Ovipositor short, male genitalia at least in one case with articulated gonocoxa and gonostylus forming characteristic forceps; cerci long or short.

COMPOSITION. 6 genera and 12 species: *Sheimia* with two species, the type *Sh. sojanensis* O. Martynova, 1958 from the Lower Kazanian of Soyana in North Russia (Fig. 2), and *Sh. tshekardensis* Aristov, 2004 from the Kungurian of Tshekarda in Urals (Fig. 3); *Visherifera* with two species (the type *V. camura* Novokshonov, Ivanov, Aristov, 2002 from the Ufimian of Mogil'nikov in Urals (Fig. 5), and *V. sylvaensis* Aristov, 2004 from the Kungurian of Tshekarda in Urals (Fig. 6); *Parasheimia* with three species, the type *P. truncata* Aristov, 2004 (Fig. 11) and *P. rotundata* Aristov, 2004 (Fig. 10) from the Kungurian of Tshekarda in Urals, and *P. kazanica* Aristov et Rasnitsyn, **sp.n.**, from the Lower Kazanian of Soyana in North Russia (Fig. 12); *Pseudosheimia* also with three species, the type *P. caudata* Aristov, 2004 (Fig. 7), from the Kungurian of Tshekarda in Urals, and *P. caudissima* Aristov et Rasnitsyn, **sp.n.** (Fig. 8), and *P. alligans* Aristov et Rasnitsyn, **sp.n.** (Fig.

9), from the Lower Kazanian of Soyana in North Russia). *Soyanembia* Aristov et Rasnitsyn, **gen.n.**, is monotypical (*S. sharovi* Aristov et Rasnitsyn, **sp.n.** (Figs 13–14), from the Lower Kazanian of Soyana in North Russia); and *Soyania* Aristov et Rasnitsyn, **gen.n.** (*S. logica* Aristov et Rasnitsyn, **sp.n.** (Fig. 15), from the Lower Kazanian of Soyana in North Russia). All new species are kept in collection of Paleontological Institute of Russian Academy of Science, Moscow [PIN].

Soyanembia sharovi Aristov et Rasnitsyn, **gen. et sp.n.** Figs 13–14

MATERIAL. Holotype imprint of head, thorax, and forewing PIN, no. 3353/540 (part and counterpart) — Soyana, right bank of Soyana River 56–60 km from mouth, Mezen' District, Arkhangel'sk Region; Iva-Gora Beds, Lower Kazanian Substage, Middle Permian. Paratype entire insects PIN, no. 3353/1120 (part and counterpart) from the same locality, A.G. Sharov leg. 1972 [PIN].

DIAGNOSIS. Length of body 8 mm, forewing 7.5–8 mm, hindwing 6.5–7 mm. Head large. Antenna filiform. Pronotum of equal length and width, slightly wider than head, narrowing backward. Mesonotum of equal length and width, scutum roundish trapezoid, with lateral lobes large and scutellum small. Metanotum similar except slightly smaller. Legs short, thin. Forewing with fore margin straight. Costal space wider than subcostal one. SC reaching beyond wing midlength. SC branchlets simple, straight. RS starting at wing basal third. M forking at about level of RS base, MP fused with CuA near wing midlength. MP+CuA apex sometimes lost among crossveins. CuA and CuP parallel. Crossveins simple or, in interradian space, forming double row of cells. Hindwing apex rounded. Abdomen almost reaching apex of folded wings, with cerci thin, short.

ETYMOLOGY. Genus name is after locality Soyana and genus *Embia*; gender feminine. The species is named after palaeoentomologist A.G. Sharov.

Soyania logica Aristov et Rasnitsyn, **gen. et sp.n.** Fig. 15

MATERIAL. Holotype almost entire insect PIN, no. 3353/350; (part and counterpart) — Soyana, right bank of Soyana River 56–60 km from mouth, Mezen' District, Arkhangel'sk Region; Iva-Gora Beds, Lower Kazanian Substage, Middle Permian. Paratypes almost entire insect PIN, no. 117/1314, 2759, 2803; 3353/175, 534, 536, 544 from the same locality, A.G. Sharov leg. 1972 [PIN].

DIAGNOSIS. Size small. Length of body 6–7 mm, fore wing 5.5–7 mm, hind wing 4.5–6 mm. Head small, acuminate. Antenna short, 7-segmented. Pronotum elongate trapezoid, with hind margin twice as wide as fore one. Fore leg short with tibia wide. Fore wing five times as long as wide, with fore margin straight, apex rounded. Costal space twice as wide as subcostal one. SC reaching beyond wing midlength. RS (or RS base) not apparent, might be lost. M forking near wing midlength. Vein representing either RS or MA or else RS+MA two-branched. MP and CuA visible. CuA nearly straight.

ETYMOLOGY. Genus name is after locality Soyana; dender feminine. Species name is the Latin for ordered.

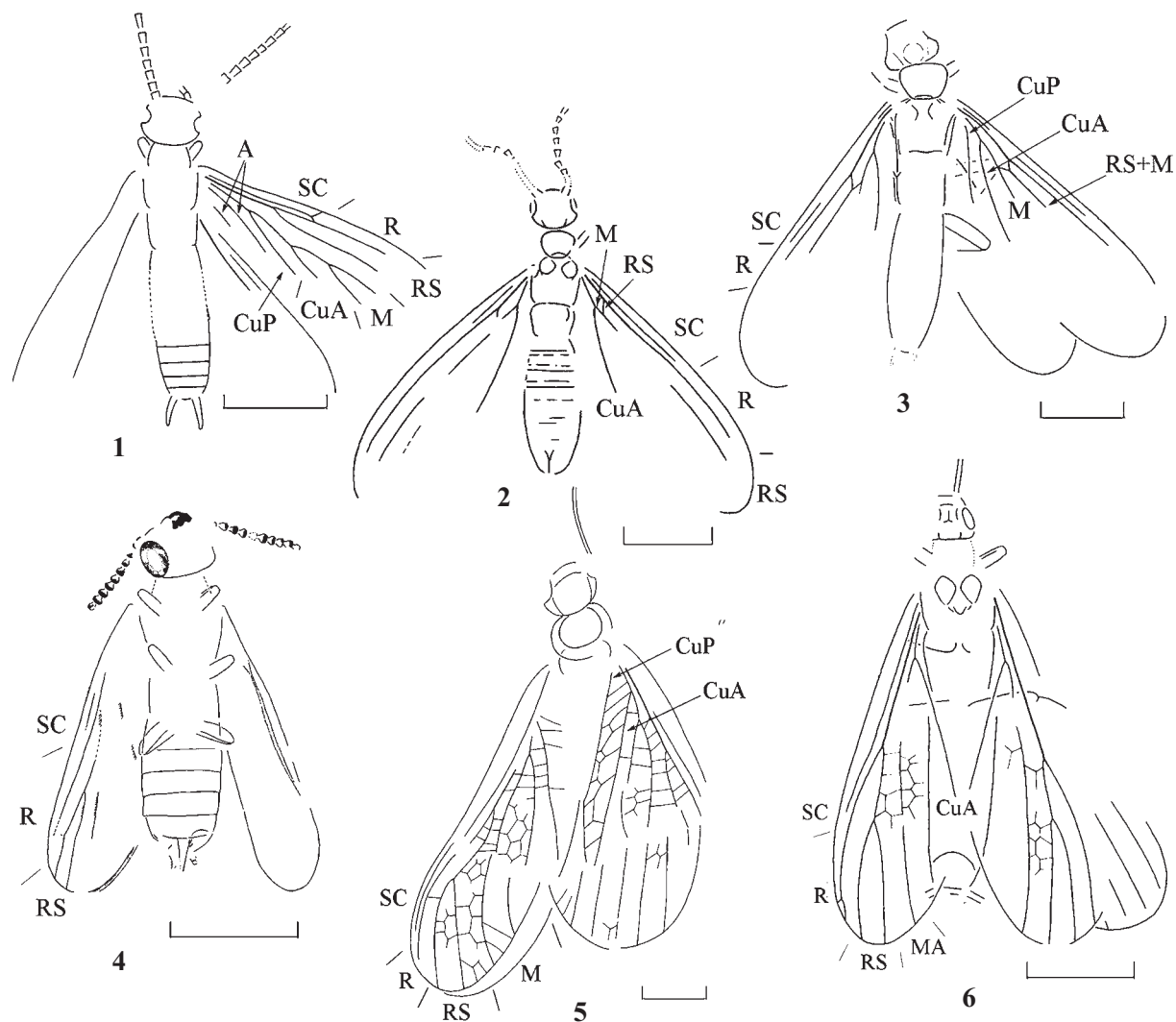
Genus *Pseudosheimia* Aristov, 2004

Pseudosheimia alligans Aristov et Rasnitsyn, **sp.n.** Fig. 9

MATERIAL. Holotype entire insect PIN, no. 3353/447 (part and counterpart of) — Soyana, right bank of Soyana River 56–60 km from mouth, Mezen' District, Arkhangel'sk Region; Iva-Gora Beds, Lower Kazanian Substage, Middle Permian, A.G. Sharov leg. 1972 [PIN].

DIAGNOSIS. Size small. Length of body 5.5 mm, fore wing 6 mm, hind wing 5 mm. Head large with eyes rather small. Antenna filiform, with scape very large. Pronotum quadrate, of less size than head. Mesonotum of equal length and width, scutum roundish, with lateral lobes large,

metanotum transverse. Legs short. Fore wing with fore margin straight. Costal space wider than subcostal one before wing midlength, equal to that beyond midlength. SC reaching beyond wing midlength. RS starting at basal wing third, fused with MA. RS+MA simple. CuA straight. Hind wing with



Figs 1–6. Members of subfamilies Permembiiinae, Sheimiidae, and unplaced, general appearance: 1 — *Pernembia delicatula* (Permembiiinae), original drawing based on the photograph of holotype, PMYU, no. 5403 [Carpenter, 1976: Fig. 14a]; Lower Permian (Artinskian) of Elmo (Kansas, USA); 2 — *Sheimia sojanensis* (Sheimiinae), holotype, PIN, no. 117/1145; Middle Permian (Lower Kazanian) of Soyana (Arkhangelsk Region, Russia) [from Aristov, 2004]; 3 — *Sb. tshekardensis* (Sheimiinae), holotype, PIN, no. 4987/25; Lower Permian (Kungurian) of Tshekarda (Perm Region, Russia) [from Aristov, 2004]; 4 — *Kungurmica tshekardensis* (Sheimiidae), holotype, PIN, no. 1700/3185; Lower Permian (Kungurian) of Tshekarda (Perm Region, Russia) [from Novokshonov, 1998]; 5 — *Visberifera camura* (Sheimiinae), holotype, PIN, no. 3473/7; Lower Permian (Ufimian) of Mogil'nikovo (Perm Region, Russia) (orig.); 6 — *V. sylvanensis* (Sheimiinae), holotype, PIN, no. 1700/983; Lower Permian (Kungurian) of Tshekarda (Perm Region, Russia) [from Aristov, 2004]. Scale bar in Figs. 1–5 — 1mm, in Fig. 6 — 3mm.

Рис. 1–6. Представители подсемейств Permembiiinae, Sheimiinae и incertae subfamiliae, общий вид: 1 — *Pernembia delicatula* (Permembiiinae), оригинальный рисунок по фотографии голотипа, РМУУ, № 5403 [Carpenter, 1976, Fig. 14a]; нижняя пермь (артинский ярус), местонахождение Эльмо (Канзас, США); 2 — *Sheimia sojanensis* (Sheimiinae), голотип, ПИН, № 117/1145, средняя пермь (казанский ярус, нижнеказанский подъярус), местонахождение Сояна (Архангельская обл., Россия); 3 — *Sheimia tshekardensis* (Sheimiinae), голотип, ПИН, № 4987/25; нижняя пермь (кунгурский ярус), местонахождение Чекарда (Пермская обл., Россия) [из Aristov, 2004]; 4 — *Kungurmica tshekardensis* (Sheimiidae), голотип ПИН, № 1700/3185, нижняя пермь (кунгурский ярус), местонахождение Чекарда (Пермская обл., Россия) [из Novokshonov, 1998]; 5 — *Visberifera camura* (Sheimiinae), голотип, ПИН, № 3473/7; нижняя пермь (уфимский ярус), местонахождение Могильниково (Пермская обл., Россия) (ориг.); 6 — *V. sylvanensis* (Sheimiinae), голотип, ПИН, № 1700/983; нижняя пермь (кунгурский ярус), местонахождение Чекарда (Пермская обл., Россия) [из Aristov, 2004]. Длина масштабной линейки на рис. 1–5 соответствует 1мм, на рис. 6 — 3мм.

costal space slightly wider than subcostal one. SC reaching beyond wing midlength. R bent at base. Abdomen not narrowed toward apex, not reaching apices of folded wings. Gonocoxa and gonostylus large, elongate.

ETYMOLOGY. Species name is the Latin for clinging.

Pseudosheimia caudissima Aristov et Rasnitsyn, **sp.n.**

Fig. 8

MATERIAL. Holotype entire insect PIN, no. 3353/535 (part and counterpart) - Soyana, right bank of Soyana River 56–60 km from mouth, Mezen' District, Arkhangel'sk Region; Iva-Gora Beds, Lower Kazanian Substage, Middle Permian, A.G. Sharov leg. 1972 [PIN]

DIAGNOSIS. Size small. Length of body 4 mm, fore wing 4.5 mm, hind wing 4 mm. Head large. Antenna filiform. Pronotum trapezoid, slightly narrowed backward, subequal to head in size. Mesonotum of equal length and width, metanotum transverse. Legs short. Fore wing with fore margin straight. Costal space wider than subcostal one before wing midlength. SC reaching beyond wing midlength. RS starting at basal wing quarter, fused with MA. CuA curved. Abdomen short, reaching fore wing midlength. Cercus as long as body.

ETYMOLOGY. Species name is the Latin for 'the most caudate'.

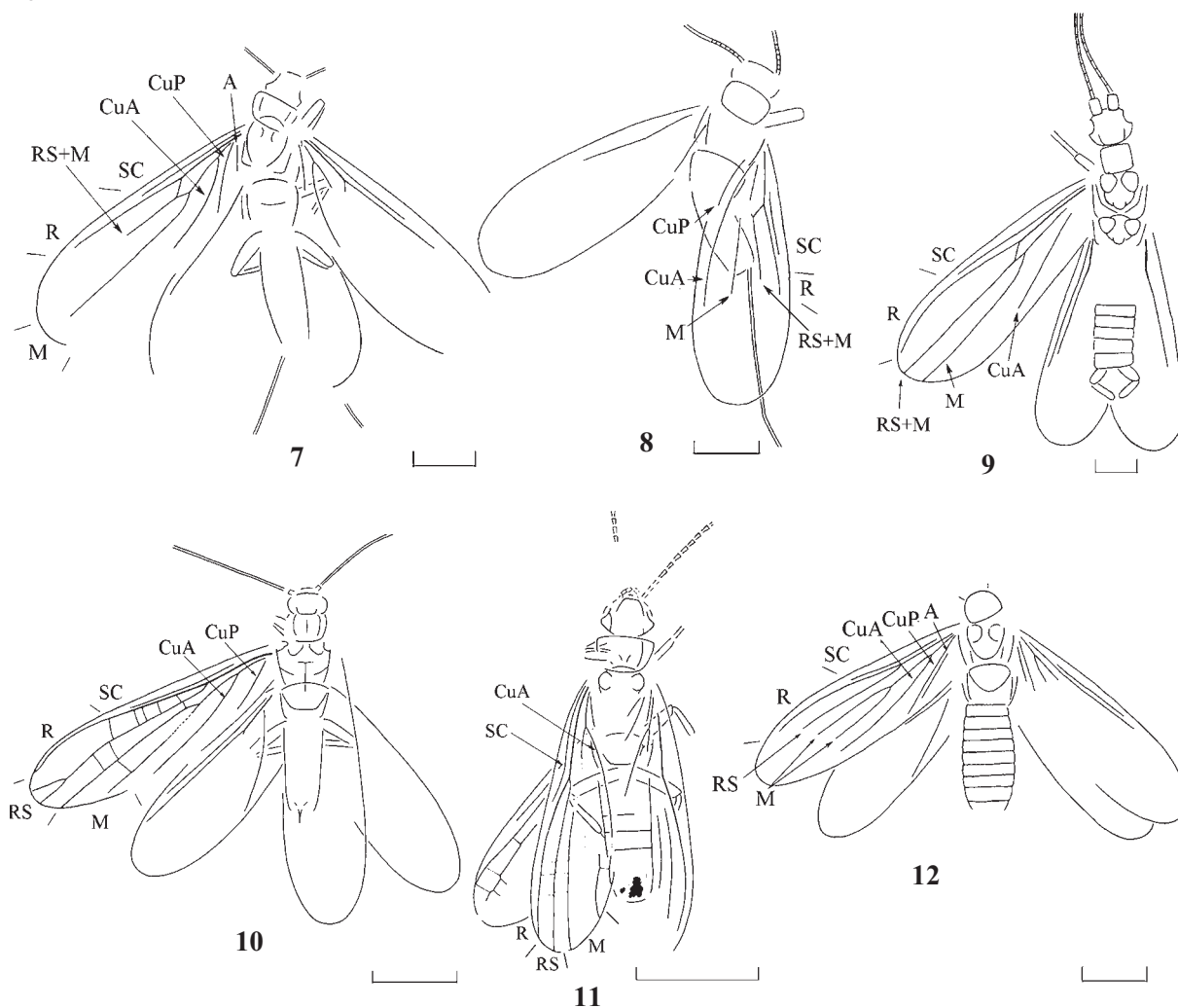


Fig. 7–12. Members of subfamily Sheimiinae, general appearance: 7 — *Pseudosheimia caudata* (Sheimiinae), holotype, PIN no. 1700/1167; Lower Permian (Kungurian) of Tsherkarda (Perm Region, Russia) [from Aristov, 2004]; 8 — *P. caudissima* **sp.n.**, holotype, PIN no. 3353/535; 9 — *P. alligans* **sp.n.**, holotype, PIN, no. 3353/447; Middle Permian (Lower Kazanian) of Soyana (Arkhangel'sk Region, Russia); 10 — *Parasheimia rotundata*, reconstruction based on holotype, PIN, no. 4987/30, and paratype, PIN, no. 4987/32, (orig.); 11 — *P. truncata*, holotype, PIN, no. 4987/27; Lower Permian (Kungurian) of Tsherkarda (Perm Region, Russia) [from Aristov, 2004]; 12 — *P. kazanica* **sp.n.**, holotype, PIN, no. 3353/420, Middle Permian (Lower Kazanian) of Soyana (Arkhangel'sk Region, Russia) (orig.). Scale bar in Figs. 7, 10, 11 — 2 mm, in Figs. 8, 9, 11 — 1 mm.

Рис. 7–12. Представители подсемейства Sheimiinae, общий вид: 7 — *Pseudosheimia caudata*, голотип ПИН, № 1700/1167; нижняя пермь (кунгурский ярус), местонахождение Чекарда (Пермская обл., Россия) [из Aristov, 2004]; 8 — *P. caudissima* **sp.n.**, голотип, ПИН, № 3353/535; 9 — *P. alligans* **sp.n.**, голотип, ПИН № 3353/447; средняя пермь (казанский ярус, нижнеказанский подъярус), местонахождение Сояна (Архангельская обл., Россия); 10 — *Parasheimia rotundata*, реконструкция на основе голотипа, ПИН, № 4987/30 и паратипа, ПИН, № 4987/32, (ориг.); 11 — *P. truncata*, голотип, ПИН, № 4987/27; нижняя пермь (кунгурский ярус), местонахождение Чекарда (Пермская обл., Россия) [из Aristov, 2004]; 12 — *P. kazanica* **sp.n.**, голотип, ПИН, № 3353/420; средняя пермь (казанский ярус, нижнеказанский подъярус), местонахождение Сояна (Архангельская обл., Россия) (ориг.). Длина масштабной линейки на рис. 7, 10, 11 соответствует 2 мм, на рис. 8, 9, 12 — 1 мм.

Genus *Parasheimia* Aristov, 2004*Parasheimia kazanica* Aristov et Rasnitsyn, **sp.n.**

Fig. 12

MATERIAL. Holotype entire insect PIN, no. 3353/420 (part and counterpart) - Soyana, right bank of Soyana River 56–60 km from mouth, Mezen' District, Arkhangel'sk Region; Iva-Gora Beds, Lower Kazanian Substage, Middle Permian, A.G. Sharov leg. 1972 [PIN].

DIAGNOSIS. Size small. Length of fore wing 5 mm, hind wing 4 mm. Pronotum trapezoid, rounded in front, larger than head. Mesonotum of equal length and width, scutum rounded triangular, with large lateral lobes, metanotum transverse. Fore wing with fore margin straight and apex acute. Costal space wider than subcostal one before wing midlength, of equal width after that. SC reaching beyond wing midlength. RS starting at basal wing quarter, free. CuA curved. CuP straight. 1A close to CuP. Hind wing with apex acute, CuA simple, curved.

ETYMOLOGY. Species name is after the Kazanian Stage.

Genus *Visherifera*

Novokshonov, Ivanov, Aristov, 2002

Visherifera camura

Novokshonov, Ivanov, Aristov, 2002

Fig. 5

MATERIAL. Holotype moderately preserved, incomplete insect PIN, no. 3473/7 (counterpart) — Mogil'nikovo, right bank of the Vishera River 1 km upstream from the village of Mogil'nikovo, Cherdyn' District, Perm Region, Russia; upper Solikamsk Formation, Solikamsk Horizon, Ufimian Stage, Lower Permian, V.V. Ivanov leg. 2001 [PIN].

DIAGNOSIS. Size small. Length of forewing about 10mm. Head large, eyes moderately large, antennae filiform. Pronotum smaller than head, rounded, with narrow complete ring of paranotalia. Mesonotum little larger than pronotum. Anterior margin of forewing slightly convex. In basal half of wing, costal space 2–3 times as wide as subcostal one, in distal half of equal width. SC long, reaching near wing apex. RS originating near wing midlength, with simple fork as long

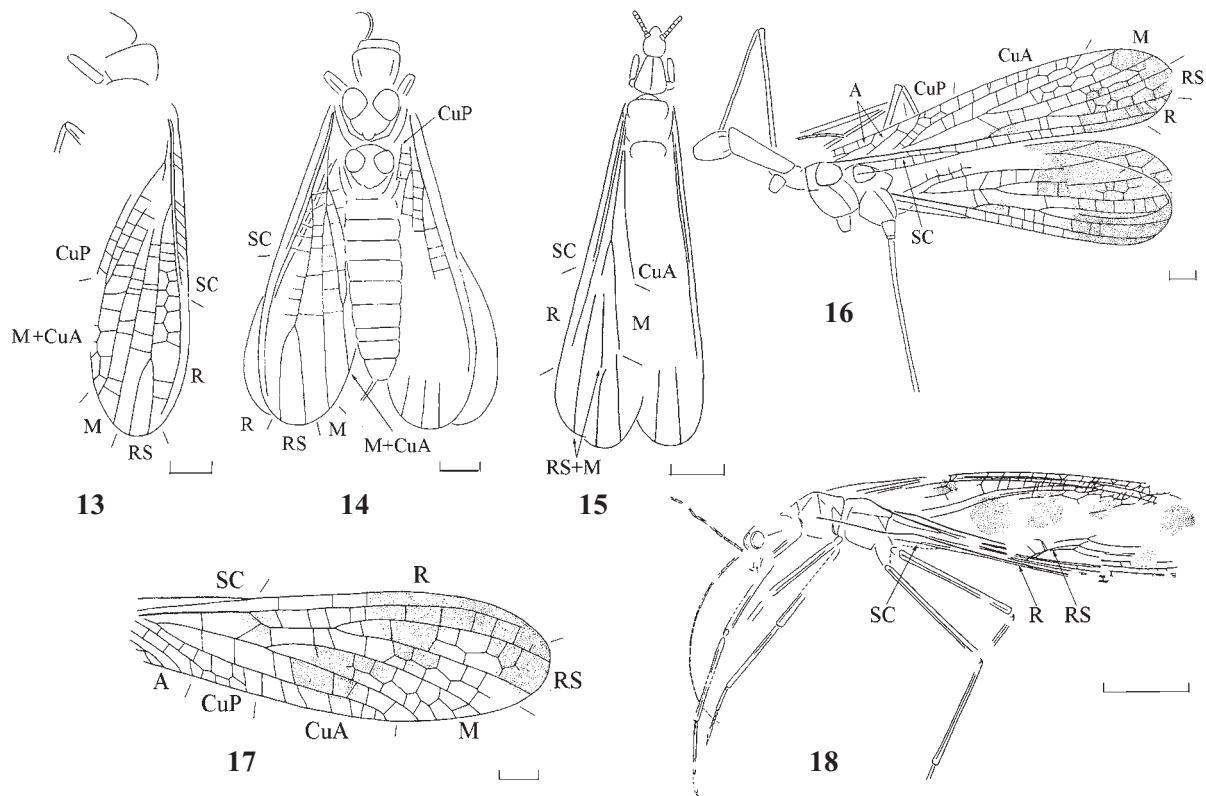


Fig. 13–18. Members of subfamilies Sheimiinae and Letopalopterinae: 13, 14 — *Soyanoembia sharovi*, **gen. et sp.n.** (Sheimiinae): 13 — holotype, PIN no. 3353/540, general appearance, 14 — paratype, PIN, no. 3353/1120, general appearance; 15 — *Soyania logica*, **gen. et sp.n.** (Sheimiinae), holotype, PIN, no. 3353/350, general appearance; 16 — *Letopaloptera albardiana* (Letopalopterinae), holotype, PIN, no. 117/2258, general appearance; 17 — *L. carpenteriana* (Letopalopterinae), holotype, PIN, no. 94/561, forewing; all Middle Permian (Lower Kazanian), of Soyana (Arkhangel'sk Region, Russia) (orig.); 18 — *Permindigena lienterocus* (Letopalopterinae), holotype, PIN, no. 1700/1666, general appearance; Lower Permian (Kungurian) of Tshekarda (Perm Region, Russia) [from Novokshonov, 1998]. Scale bar in Fig. 18 — 5 mm, in Fig. 13–17 — 1 mm.

Рис. 13–17. Представители подсемейств Sheimiinae и Letopalopterinae: 13, 14 — *Soyanoembia sharovi*, **gen. et sp.n.** (Sheimiinae): 13 — голотип, ПИН № 3353/540, общий вид, 14 — паратип, ПИН, № 3353/1120, общий вид; 15 — *Soyania logica*, **gen. et sp.n.** (Sheimiinae), голотип, ПИН № 3353/350; 16 — *Letopaloptera albardiana* (Letopalopterinae), голотип — ПИН, № 117/2258, общий вид; 17 — *L. carpenteriana* (Letopalopterinae), голотип — ПИН, № 94/561, переднее крыло; средняя пермь (казанский ярус, нижнеказанский подъярус), местонахождение Сояна (Архангельская обл., Россия) (ориг.); 18 — *Permindigena lienterocus* (Letopalopterinae), голотип, ПИН, №1700.1666; нижняя пермь (кунгурский ярус), местонахождение Чекарда (Пермская обл., Россия) [из Новокшенов, 1998]. Длина масштабной линейки на рис. 18 соответствует 5 мм, на рис. 13–17 — 1 мм.

as stem. M two-branched, forking before wing apical third. CuA fused with M basally, simple. CuP simple, weak. Crossveins simple and forming double rows of cells.

Subfamily Letopalopterinae O. Martynova, 1962,
stat.n.

Letopalopteridae O. Martynova, 1962: 270

TYPE GENUS. *Letopaloptera* O. Martynova, 1961

DIAGNOSIS. Size small to medium, forewing length 9.5–24 mm. Eyes moderately large, ocelli lost. Antennae short, moderately thick. Pronotum equal to head in size or elongate, paranota lost. Legs strongly elongate. Wing with fore margin straight, costal space lacking basal expansion, about 2–3 times as wide as subcostal one. SC simple, at most reaching wing basal third. R straight or bend at wing basal third, sometimes closely approaching anterior wing margin. RS fork 2–3 times as long as stem. M forking before RS base, with free fore branch; CuA and CuP simple. Anal veins two or three. crossveins variable.

COMPOSITION. Two genera with three species, viz., *Letopaloptera* O. Martynova, 1961 (the type *L. albardiana* Martynova, 1961, Fig. 16, and *L. carpenteriana* Martynova, 1961, Fig. 17, from the Lower Kazanian of Soyana in the northern European Russia), and monotypical *Permindigena* Novokshonov, 1998 (the type, *P. lientericus* Novokshonov, 1998; Fig. 18, from the Kungurian of Tsherkarda in Urals).

Genus *Letopaloptera* Martynova, 1961

Letopaloptera albardiana Martynova, 1961

Fig. 16

MATERIAL. Holotype entire insect PIN, no. 117/2258 (part and counterpart) — Soyana, right bank of Soyana River 56–60 km from mouth, Mezen' District, Arkhangel'sk Region; Iva-Gora Beds, Lower Kazanian Substage, Middle Permian. Paratypes PIN, no. 117/2369; 3353/42, 798 from the same locality. J.D. Zekkel leg. 1935 [PIN].

DIAGNOSIS. Size small. Length of body and fore wing 11 mm, hind wing 10 mm. Head of medium size, elongate. Pronotum length 3.4 times of maximum width, narrowing backwards. Legs very long and thin, coxae small, conical, femora expanded apical, slightly thicker than tibiae. Fore wing with fore margin weakly convex up to SC apex, farther straight, wing apex rounded. Costal space wider than subcostal basally. SC reaching basal wing third, with branchlets straight. RS starting near wing midlength, with two branches. M forking at level of RS base. CuA disappearing among crossveins apically. 1A and 2A simple. Crossveins simple or, in apical wing third, forming double cell rows (also in hind wing). Color pattern forming dark spots at RS base, M forking, and along wing apex.

Letopaloptera carpenteriana Martynova, 1961

Fig. 17

MATERIAL. Holotype fore wing PIN, no. 94/561 (part) — Soyana, right bank of Soyana River 56–60 km from mouth, Mezen' District, Arkhangel'sk Region; Iva-Gora Beds, Lower Kazanian Substage, Middle Permian. Paratypes PIN, no. 117/2369; 3353/42, 798 from the same locality. J.D. Zekkel leg. 1935 [PIN].

DIAGNOSIS. Fore wing length 9.5 mm. Fore wing with fore margin weakly convex up to SC apex, farther straight, wing apex rounded. Costal space wider than subcostal basally. SC reaching basal wing third, with branchlets straight. RS starting at wing basal third, with two branches. M forking distal of RS base. CuA distinct throughout. 1A simple, 2A with two branches. Crossveins simple or, in apical wing half, forming double cell rows. Color pattern forming dark spots at RS base, at M forking, and along wing apex.

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