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New Eoblattida from the Permian of Russia and the United States and the Origin of Earwigs (Insecta: Eoblattida, Forficulida)

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Abstract—New taxa of the order Eoblattida are described from the Lower Permian of the United States and Russia. *Pryg absurdus* gen. et sp. nov. of the family *Prygidae* fam. nov. is described from the Leonardian of Elmo (Kansas, United States). *Parapryg alogus* gen. et sp. nov. of the same family is described from the Vyatkian of Nedubrovo (Vologda Region, Russia). *Kamamica promota* gen. et sp. nov. of the family Tillyardembiidae is described from the Ufimian of Tyul'kino (Perm Region, Russia). The similarity of the new family with Tillyardembiidae and with basal earwigs, especially Bardacoleidae, is discussed. A hypothesis is proposed about the monophyletic origin of all three groups from spanioderids or other eoblattids close to them.

Keywords: Insecta, Eoblattida, Forficulida, Permian, new taxa

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INTRODUCTION

In this study we describe new taxa of the order Eoblattida from the Permian of the United States and Russia. The earliest members of this order are known from the Bashkirian (Namurian B-C) age of the Carboniferous (Gu et al., 2011). The diversity of this order was rather high in the Carboniferous (Rasnitsyn, 2002) and in the Late Kungurian to Early Roadian (Kazanian) ages of the Permian. Asselian to Lower Kungurian (Leonaridan) and the latest, Wuchiapingian (Severodvinian) representatives of the order display rather low diversity (Aristov and Rasnitsyn, 2012). The very latest, Changhsingian (Vyatkian) representative of the order is described here. We also describe here the new monotypic family Prygidae from the Leonardian locality Elmo in the United States and from the Vyatkian locality Nedubrovo in Russia. In addition, we describe here a new genus of the family Tillyardembiidae from Tyul'kino, Ufimian Stage of Russia.

The earliest representative of the family Prygidae, *Pryg absurdus* gen. et sp. nov., is known from the famous localiy Elmo, Dickinson County, Kansas, United States. Insects have been collected in this locality in deposits of the Wellington Formation (Sumner Group, Lower Leonardian), considered corresponding to the Lower Kungurian deposits of the Lower Permian (Sawin et al., 2008). The localities of the Wellington Formation (Elmo and Midco in Oklahoma) are the richest fossil insect localities of the Paleozoic. A total of over 23 000 insect fossils have been collected in these localities (Beckemeyer, 2000). Representatives of 21 orders, 53 families, 106 genera, and 194 species have been described from materials collected there (Beckemeyer and Hall, 2007). The place of Eoblattida in this diversity is quite modest. This order is represented only by *Protembia permiana* (Protembiidae) and "*Aibolitus*" *minutus* Béthoux et Beckemeyer, 2007 (Eoblattida incertae sedis), known from unique specimens. For comparison, in the later localities Chekarda (Upper Kungurian of Perm Region, Russia) and Soyana (Lower Kazanian of Arkhangelsk Region, Russia) eoblattids account for up to 5% of all insect fossils. Although the number of specimens collected in Elmo and Midco is much greater, materials from Chekarda include representatives of 12 genera and 16 species of Eoblattida, and materials from Soyana include members of seven genera and eight species, in both cases belonging to four families of Eoblattida (Aristov and Rasnitsyn, 2012). The low diversity of eoblattids in deposits of the Wellington Formation can be explained by the low latitudes (in the Paleozoic) and arid climate of the localities. Elmo and Midco were situated at 4.7° and 2.6° N, respectively, whereas Chekarda and Soyana were situated at 30.6° and 33.5° N, respectively (*Paleobiology...*, 2012). Elmo and Midco were situated in summer-wet (arid) climate zone, whereas Chekarda and Soyana were situated in winter moist (semiarid) zone (Shcherbakov, 2008).

The second member of Prygidae was found in the locality Nedubrovo, Kichgododetskii District, Vologda Region, Russia. The material was collected in the Nedubrovo Member, Lower Vokhma Formation, Vokhmian Horizon. The age of this member is controversial; we consider it Upper Vyatkian (Aristov et al., 2013). A rather small collection of insects (about 200 specimens) is available from Nedubrovo; it

includes the single forewing of *Parapryg alogus* gen. et sp. nov. This species is the latest known representative not only of the family, but also of the entire order Eoblattida. Like Chekarda and Soyana, Nedubrovo was situated in the winter-wet climate zone (33.6° N: *Paleobiology...*, 2012).

The new family shows similarity with the orders Eoblattida and Forficulida (suborder Protelytrina). In the structure of the body, *Pryg absurdus* is especially similar to the Kungurian–Kazanian family Tillyardembiidae, particularly to *Kungurembia pallida* Aristov, 2004 from Chekarda. Both species have a body length of less than 1 cm, large head, rather small pronotum without paranotalia, forelegs half as long as hindlegs, metacoxae set widely apart, strong and long ovipositor, and long cerci (Aristov, 2004). *P. absurdus* is distinguished from this species in the thicker antennae, small eyes, and strong metafemora, probably saltatorial. Judging by the position of the metafemora, the metatibiae of prygids were directed forward. Although the first two characters are known in some other eoblattids (Protembiidae; Aristov and Rasnitsyn, 2011), the dilated metafemora are a unique character among members of this order. The structure of the body of Protelytrina is less well studied than that of Eoblattida; it is known in members of the families Archelytridae, Protelytridae, and Blattelytridae (Carpenter and Kukalová, 1964; Kukalová, 1965) and Bardacoleidae (Shcherbakov, 2002). The system of the suborder is given according to Shcherbakov (2002).

Prygidae are distinguished from Protelytrina by the absence of paranotalia (Pl. 9, fig. 4) and elytra; otherwise they are similar to Bardacoleidae from Chekarda. The metatibiae of Bardacoleidae are directed in the impression forward and outward (Shcherbakov, 2002, fig. 421; Pl. 9, fig. 6). This position of the tibiae indicates either pulling (as in rheophiles and specialized phytophiles) or saltatorial legs. Hind tibiae directed behind and inward are typical of ambulatorial or cursorial insect legs. In Bardacoleidae, as well as in Prygidae, the function of the hindlegs was probably clinging or even leaping, although the metafemora were not typically saltatorial. In Bardacoleidae, strong and rather long ovipositor has also been recorded (Pl. 9, fig. 5).

In the venation of the forewing, Prygidae are similar to both Eoblattida and Protelytrina. Among Eoblattida, the family most similar to Prygidae is Tillyardembiidae, especially *Kamamica promota* gen. et sp. nov., described below from Tyul'kino (Ufimian Stage of Perm Region, Russia). This species differs in venation from the other tillyardembiids in CuA fused with the base of M, a character that makes it similar to some prygids. Otherwise Prygidae differ from Tillyardembiidae mainly in the more strongly oligomerized venation, base of RS shifted towards the middle of the wing, and apices of CuP and anal veins shifted to the distal third of the wing (Figs. 2d, 2e).

Some characters of Prygidae are known in Cnemidolestidae: the base of RS shifted distal, developed clavus, and apices of A_1 and A_2 fused (Aristov, 2012). Following Gorochov (2004), we use the term "clavus" for the anal area of the wing raised above the deep claval fold so as to provide for maximum mobility of this area relative to the remigium, needed during movements of the insect in crevices in the substrate. Prygidae are distinguished from Cnemidolestidae by the oligomerized venation, fused bases of M and CuA, and very long clavus.

Among Protelytrina, prygids are similar, in addition to Bardacoleidae, also to Archelytridae (in SC joining R and in branching RS and CuA), and especially to the genus *Megelytron* Tillyard, 1931 from Elmo, in fused bases of M and CuA (Fig. 2b). *Pryg* differs from *Megelytron* in the non-elytrized wing, short ambient vein (not reaching CuP) along posterior margin of the wing, and smaller number of anal branches. It has to be noted that the venation of the forewing in *Pryg* is more specalized in some details than in the most basal archelytrid, *Apachelytron* Carpenter et Kukalova, 1964 from the Sakmarian locality Obora in the Czech Republic (Fig. 2a). In *Apachelytron* the bases of M and CuA are not fused, but connected by M_5, the number of anal veins is five, and the areas between them are not dilated.

It has to be noted that some signs of the transformation of the forewing into elytron (elytrization), so typical of earwigs (including Protelytrina), can already be found in Tillyardembiidae and Prygidae. For instance, they have weakened wing corrugation caused by gradual transition of SC and CuP from concave to convex. In Tillyardembiidae and Prygidae at least the apex of CuP is convex, and in Tillyardembiidae, in addition, SC is convex distal to the basal third of the wing. In Spanioderidae SC and CuP are concave.

On the whole, in spite of the similarity to some Protelytrina, we place the new family in Eoblattidae based on the absence of paranotalia, non-elytrized forewings, and short hindwings (no longer than the forewings). Prygidae differ from all other families of the order, especially the closest family Tillyardembiidae, mainly in the combination of the rather distally beginning RS, very long clavus, and saltatorial hindlegs. The presence of paranotalia in Protelytrina is a secondary character, resulting from adaptation to living in the litter, since the most basal winged insects, the order Paoliida, as well as some Eoblattida, which evolved from Paoliida, had no paranotalia on the pronotum (Rasnitsyn, 2002). The venation of Prygidae can be derived from the venation of Tillyardembiidae by reducing the number of ends of RS, M, and CuA, and shifting the base of RS, apices of CuP, and anal veins distal. However, taking into account the younger age of Tillyardembiidae, it is more likely that Prygidae and Tillyardembiidae evolved in parallel from a common ancestor. This ancestral group could have been the family Spanioderidae, ancestral to Tillyardembiidae (Aristov and Rasnitsyn, 2009), or forms close to Spanioderidae.

The similarity between Prygidae and primitive Forficulida makes it possible to say a few things about the origin of earwigs. There are several different views on this problem. According to one of them, the basal earwig suborder Protelytrina evolved from members of the order Grylloblattida close to the family Lemmatophoridae (Shcherbakov, 2002). However, the similarity between Lemmatophoridae and Archelytrydae is limited to the rather small size, presence of paranotalia, and oligomerized venation. In Lemmatophoridae, as in the rest of Grylloblattida, SC ends on C, the base of RS is situated in the basal half of the wing, the first bifurcations of M and CuA and the apex of CuP are situated in the basal third of the wing, the anal area is not transformed into clavus, and the anal veins are not fused. In Archelytrydae SC ends on R, the base of RS and the first bifurcation of CuA are situated in the distal half of the wing, M is simple, CuP reaches near the middle of the wing or distal to the middle, the anal area is transformed into clavus, and the apices of M, Cu, and A form an ambient vein. At least the metacoxae of Lemmatophoridae are situated close to the middle line of the body (Aristov, 2004), whereas in Archelytrydae and Tillyardembiidae (and possibly in Prygidae) they are set widely apart.

According to another view, Forficulida and Grylloblattida evolved independently (Gorochov, 2004; Grimaldi and Engel, 2005), which is correct in our opinion. The comparison of Prygidae and Tillyardembiidae with Archelytrydae in the above-listed characters of venation makes it possible to suggest that Archelytrydae evolved from Eoblattida in parallel with Grylloblattida. Either Prygidae or Tillyardembiidae or both probably constitute the sister group of earwigs, and they all probably originated from some Upper Carboniferous or Lower Permian group of Eoblattida, possibly close to Spanioderidae.

MATERIAL

The type material is stored in the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN), and in the Museum of Comparative Zoology, Cambridge, Massachusetts, United States (MCZ).

SYSTEMATIC PALEONTOLOGY

Order Eoblattida

Family Prygidae Aristov et Rasnitsyn, fam. nov.

Type genus. *Pryg* gen. nov.

Diagnosis. Small insects with elongate body and large prognathous head. Pronotum without paranotalia, smaller than head. Forelegs of medium length; metafemur swollen, almost twice as long and twice as wide as profemur. Forewing membranous, rather small, narrow, with all veins except SC (and probably base of CuP) convex. Base of costal space dilated; SC parallel to C, ending in bifurcation on C and R. R short, S-shaped, ending at beginning of distal quarter of wing. RS beginning immediately distal to middle of wing, free (not fused with R or MA), reaching anterior margin of wing. M simple or with short bifurcation. CuA beginning branching distal to its basal third, straight until branching point. CuP very long, ending at beginning of distal third of wing. Anal area forming long and narrow lanceolate clavus. A_1 and A_2 forming anal loop. Base of A_1 arcuate, A_2 parallel to posterior margin of wing, fused with A_1 at middle of wing, $A_1 + A_2$ continuing A_2, ending at boundary of distal third of wing, and thus forming small ambient vein not reaching apex of CuP. Hindwing shorter than forewing; RS beginning proximal to middle of wing; M and CuA simple. Anal area long, ending in distal quarter of wing; CuP reaching posterior margin of wing. Ovipositor strong and long; cerci longer than ovipositor.

Generic composition. *Pryg* gen. nov. from the Lower Permian of the United States and *Parapryg* gen. nov. from the Upper Permian of Russia.

Comparison. The new family is especially similar to Tillyardembiidae from the Lower and Middle Permian of Russia. In the structure of the body, Prygidae are distinguished by the strongly enlarged metafemora; in the venation of the forewing, by the distal beginning of RS, simple or distally branching M, and apices of CuP and anal veins ending distal to the middle of the wing. In Tillyardembiidae the metafemora are similar in size to the profemora, base of RS is situated in the basal third of the wing, M branches near the middle of the wing, and the anal veins end proximal to the middle of the wing (Aristov and Rasnitsyn, 2009; Rasnitsyn and Aristov, 2010; Fig. 2e).

Genus *Pryg* Aristov et Rasnitsyn, gen. nov.

Etymology. Allusion to the Russian *prygat'* (to leap). Gender masculine.

Type species. *P. absurdus* sp. nov.

Diagnosis. Head large with small eyes. Mandible pointed; maxillary palpus of moderate length. Antenna thick, with scape and pedicel enlarged, flagellomeres elongate, narrowing towards base. Pronotum trapezoid, with posterior margin convex, longer than mesonotum. Forewing four times as long as its maximum width. Anterior margin of forewing convex, in basal half of wing costal space half as wide as maximum width of subcostal space. SC ending proximal to distal third of wing; RS pectinate posteriad. M simple, straight, fused with CuA at base. M and CuA diverging distal to basal third of wing; both stems straight distal to anastomosis; CuA branching in distal third. Apices of CuP and $A_1 + A_2$ closely set and curved towards posterior margin of wing. Space between A_1 and A_2 dilated, with double row of cells. Clavus separated by sharply concave fold near bases of CuP and A_1. Hindwing with costal space at base of RS approximately as wide as subcostal space. RS beginning branching proximal to distal third of wing and pectinate anteriad.

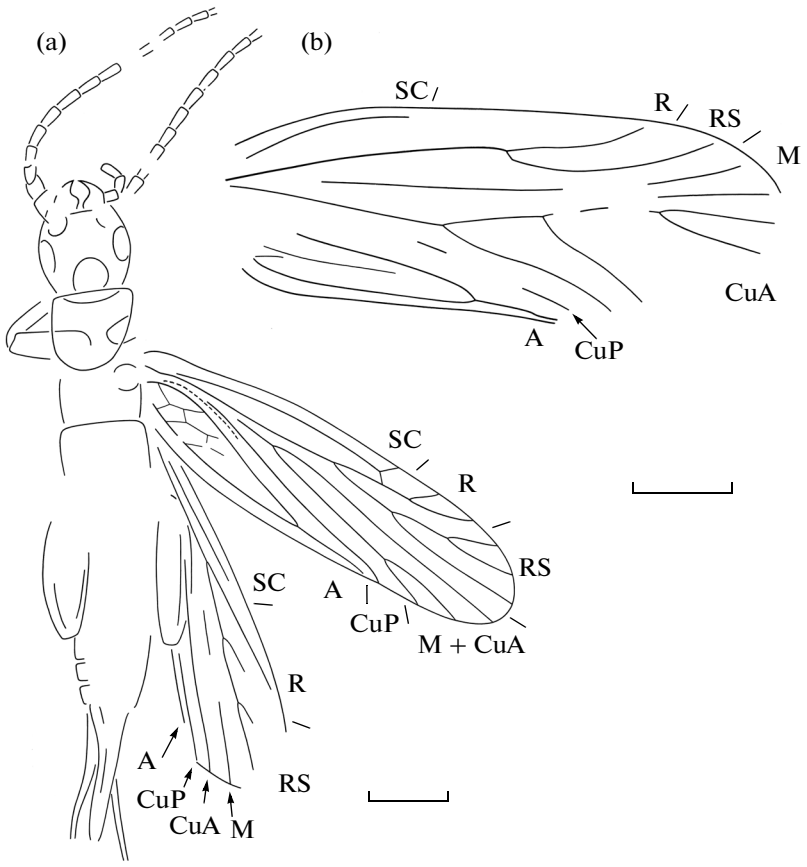


Fig. 1. Species of the family Prygidae: (a) *Pryg absurdus* sp. nov., holotype MCZ, no. 31156, habitus; Elmo, Leondardian Stage of Kansas, United States; (b) *Paraprygalogus* sp. nov., holotype PIN, no. 4811/263, forewing; Nedubrovo, Vyatkian Stage of Vologda Region, Russia. In Figs. 1 and 2, scale bar 1 mm.

Species composition. Type species.

***Pryg absurdus* Aristov et Rasnitsyn, sp. nov.**

Plate 9, fig. 1

Etymology. From the Latin *absurdus* (awkward).

Holotype. MCZ, no. 31156; part and counterpart of complete insect; United States, Kansas, Dickinson County, Banner Township, 5 km southeast of Elmo town, Elmo locality; Lower Permian, Lower Leonardian, Sumner Group, Wellington Formation, Carlton Member.

Description (Figs. 1a; 2b). R has one anterior branch; RS begins branching in distal third of wing and has three ends. CuA is two-branched; its anterior branch ends closer to posterior margin of the wing. In the hindwing, SC reaches the middle of the wing; RS is three-branched; apices of CuP and A_1 are closely set.

Measurements, mm. Body length without antennae and ovipositor, 6.2; forewing length, 5.6; hindwing length, 4.7.

Material. Holotype.

Genus *Paraprygal* Aristov et Rasnitsyn, gen. nov.

Etymology. From the Latin *par* (suitable) and the generic name *Pryg*. Gender masculine.

Type species. *P. alogus* sp. nov.

Diagnosis. Forewing 2.7 times as long as its maximum width. Anterior margin in middle of wing straight; base of costal space slightly dilated. Costal space narrow; RS simple. Base of M not fused with CuA; M simple proximal to distal third of wing. CuA not angulated at base (M_5 probably absent), beginning branching near middle of wing, forming posterior comb of branches diverging from stem at angle and occupying half of wing width. Space between A_1 and A_2 narrow, with longitudinal veins.

Species composition. Type species.

Comparison. The new genus is distinguished from the type genus of the family by RS simple and not fused basally with M and by CuA proximally branching and forming wide comb of branches.

***Paraprygalogus* Aristov et Rasnitsyn, sp. nov.**

Plate 9, fig. 2

Etymology. From the Latin *alogus* (nonsensical).

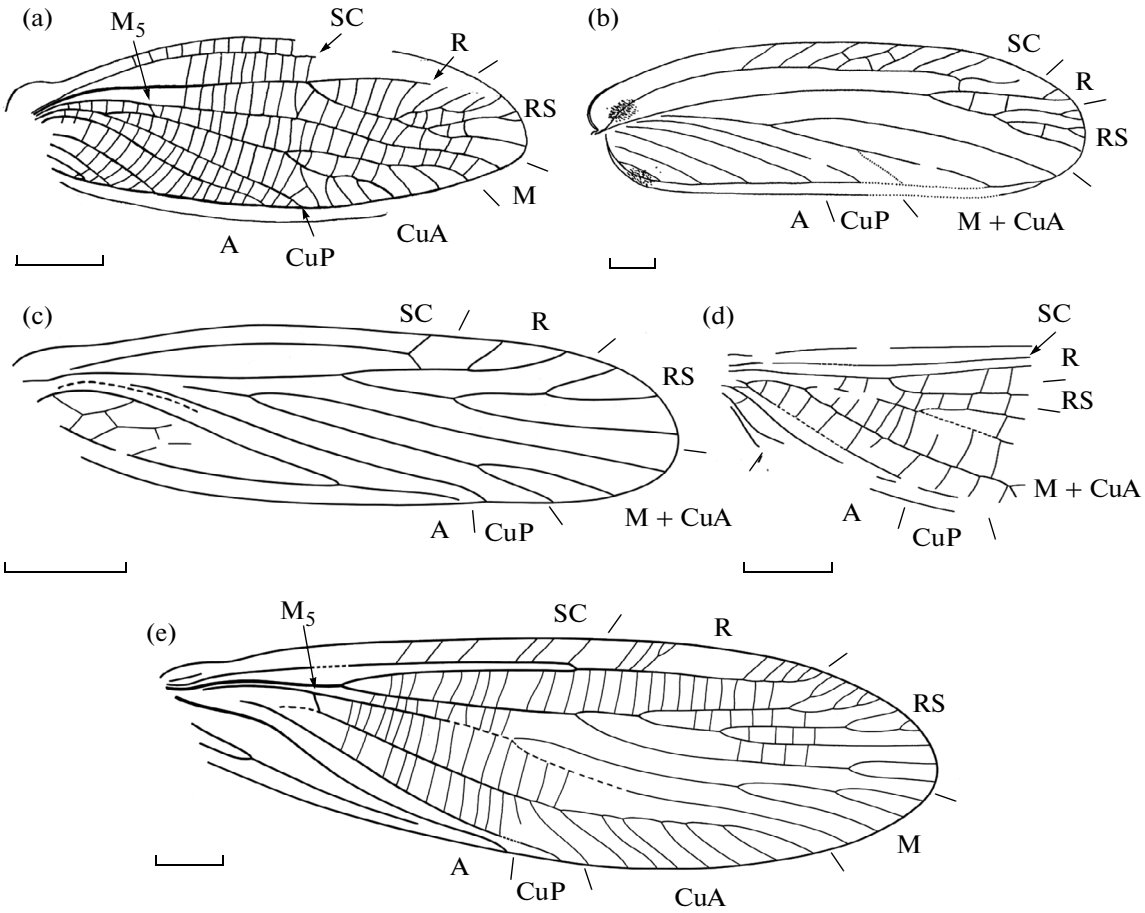


Fig. 2. Forewings of Protelytrina and Eoblattida: (a) *Apachelytron transversum* Carpenter et Kukalová, 1964, holotype DPCU, no. 47/1964; Obora, Sakmarian Stage of Moravia, Czech Republic; (b) *Megelytron robustum* Tillyard, 1931, holotype YPM, no. 5406 (modified from Carpenter and Kukalová, 1964); (c) *Pryg absurdus* sp. nov., holotype MCZ, no. 31156; Elmo, Leondardian Stage of Kansas, United States; (d) *Kamamica promota* sp. nov., holotype PIN, no. 3474/339; Tyul'kino, Ufimian Stage of Perm Region, Russia; (e) *Tillyardembia antennaeplana* G. Zalessky, 1937, reconstruction; Chekarda, Kungurian Stage of Perm Region (modified from Aristov and Rasnitsyn, 2009).

H o l o t y p e. PIN, no. 4811/263; part and counterpart of forewing; Russia, Vologda Region, Kichgorodetskii District, left bank of the Kichmenga River near Nedubrovo village, Nedubrovo locality; Upper Permian, Upper Vyatkian Substage, Vokhmian Horizon, Lower Vokhma Formation, Nedubrovo Member.

D e s c r i p t i o n (Fig. 1b). M in distal third of the wing is simple or has a simple short bifurcation. CuA is six- or seven-branched; its anterior branch reaches wing apex.

M e a s u r e m e n t s, mm. Forewing length, 6.

M a t e r i a l. Holotype.

Family Tillyardembiidae Zalessky, 1938

Genus *Kamamica* Aristov et Rasnitsyn, gen. nov.

E t y m o l o g y. From the Kama River and the Latin *mica* (particle). Gender feminine.

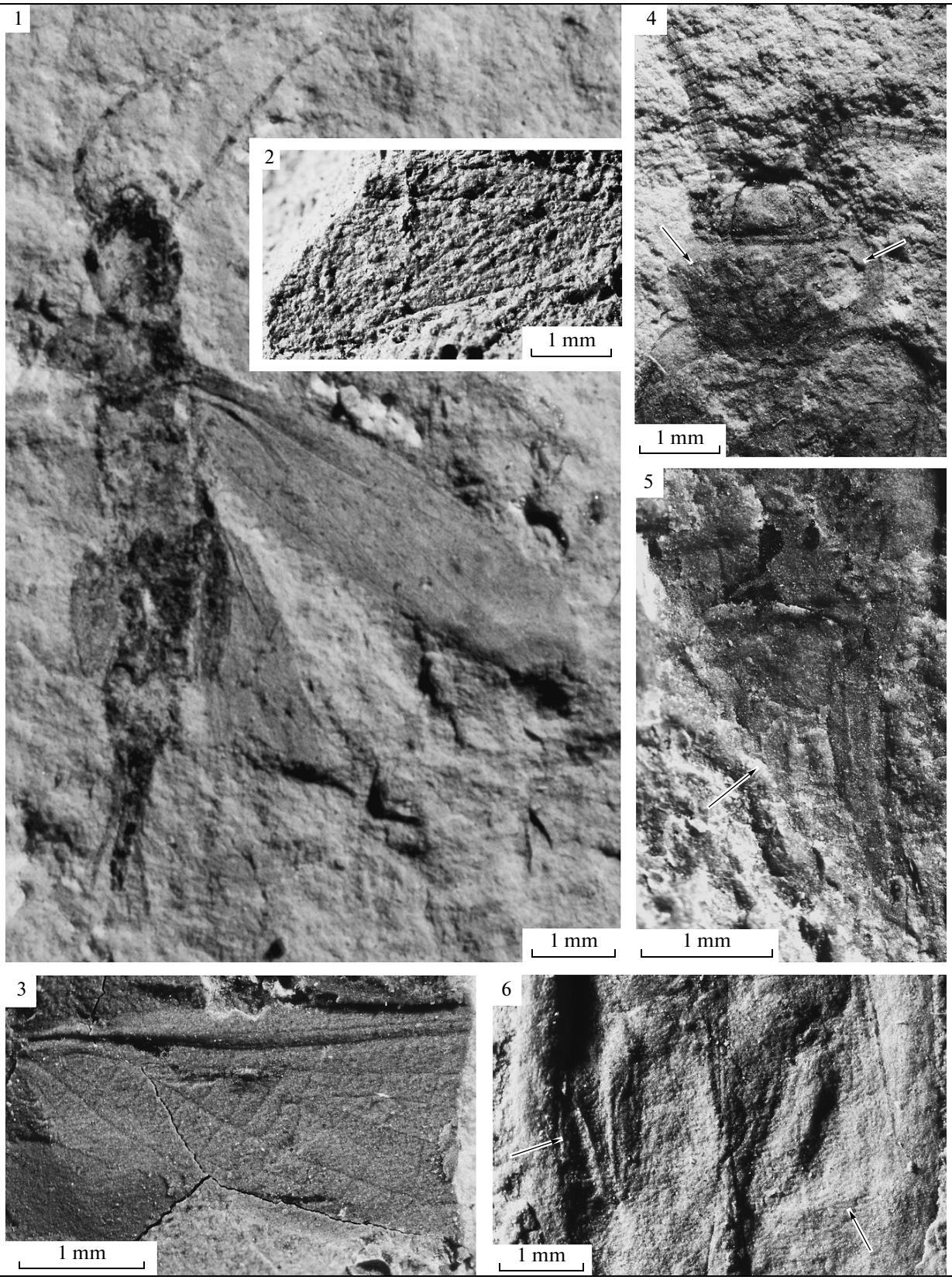
T y p e s p e c i e s. *K. promota* sp. nov.

D i a g n o s i s. Costal space near base of RS slightly wider than subcostal space. SC in basal third of wing changing from concave to convex. RS beginning at end of basal third of wing; interradial space not narrowed. M fused at base with CuA and beginning branching immediately distal to base of RS. CuA curved towards posterior margin of wing; CuP changing from concave to convex, with apex fused with A_1. Anastomosis CuP+ A_1 reaching beyond basal third of wing. Anal area narrow and long; A_1 and A_2 simple. Crossveins simple, dense at base of median space.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. *Kamamica* is placed in Tillyardembiidae because of M branching distal to the base of RS, CuA branching near posterior margin of the wing, and characteristic dense crossveins in the median space. The new genus differs from all other members of this family in the base of M fused with CuA. It differs from *Tillyardembia* G. Zalessky, 1937 also in the anastomosis CuP+ A_1. In *Tillyardembia* and *Kungurembia* Aristov, 2004, M is connected with CuA by M_5; in *Tillyardembia* CuP is not fused with A_1 (Aristov and Rasnitsyn, 2009).

Plate 9



Explanation of Plate 9

Fig. 1. *Pryg absurdus* sp. nov., holotype MCZ, no. 31156, habitus; Elmo, Leondardian Stage of Kansas, United States.
Fig. 2. *Parapryg alogus* sp. nov., holotype PIN, no. 4811/263, forewing; Nedubrovo, Vyatkian Stage of Vologda Region, Russia.
Fig. 3. *Kamamica promota* sp. nov., holotype PIN, no. 3474/339; Tyul'kino, Ufimian Stage of Perm Region, Russia.
Figs. 4–6. *Bardacoleidae* gen. sp.; Chekarda, Kungurian Stage of Perm Region: (4) specimen PIN, no. 4987/822, head and pronotum (arrows indicate paranotalia); (5) specimen PIN, no. 1700/3377, apex of abdomen (arrow indicates cercus); (6) specimen PIN, no. 1700/498, hindlegs (arrows indicate tibiae).

***Kamamica promota* Aristov et Rasnitsyn, sp. nov.**

Plate 9, fig. 3

Etymology. Feminine form of the Latin *promotus* (advanced).

Holotype. PIN, no. 3474/339, part and counterpart of basal half of forewing; Russia, Perm Region, Solikamsk District, right bank of the Kama River 1 km above Tyul'kino village, Tyul'kino locality; Lower Permian, Ufimian Stage, Solikamskian Horizon, Solikamsk Formation, Upper Solikamsk Subformation.

Description (Fig. 2d). The anterior margin of the forewing is convex at the base, then straight. The costal space is dilated at the base; SC is S-shaped in the basal quarter of the wing and has a rather small desclerotized portion (shown as dotted line in the figure). The bifurcation of M and the base of its posterior branch are desclerotized. CuA is curved towards the posterior margin of the wing; CuP has a rather small desclerotized portion. A_2 is short, S-shaped, possibly with apex joining A_1 .

Measurements, mm. Forewing length, about 8.

Material. Holotype.

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