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CLASSIFICATION OF THE ORDER CNEMIDOLESTIDA (INSECTA: PERLIDEA) WITH DESCRIPTIONS OF NEW TAXA

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The order Cnemidolestida (Insecta: Perlidea) is revised. A total of 11 families from the Carboniferous and Permian of Eurasia, North America, and South America and from the Triassic of Europe are included in the order: Cnemidolestidae Handlirsch, 1906, Spanioderidae Handlirsch, 1906, Gerapompidae Handlirsch, 1906, Cymenophlebiidae Pruvost, 1919, Emphylopteridae Handlirsch, 1922, Tillyardembiidae G. Zalessky, 1938, Psoropteridae Carpenter, 1976, Sylvabestiidae Aristov, 2000, Prygidae Aristov et Rasnitsyn, 2014, Neraphidiidae Aristov, **fam. n.**, and Ctenoptiliidae Aristov, **fam. n.** New synonymies are established: Cnemidolestidae = Aetophlebiidae **syn. n.**, = Narkemidae **syn. n.**, = Narkeminidae **syn. n.**; Emphylopteridae = Guloidae **syn. n.**; and Spanioderidae = Anthraconeuridae **syn. n.**, = Carpenteropteridae **syn. n.** The family Cymenophlebiidae and genus *Dieconeurites* Handlirsch, 1906, previously considered synonyms, are re-established as valid. Two new genera (both from the Permian of Russia) are described in the family Sylvabestiidae: *Ivkinus* Aristov, **gen. n.** (type species *Mezenalicula conjucta* Aristov et Storozhenko, 2011 = *Ivkinus conjuctus* **comb. n.**) and *Kityakia* Aristov, **gen. n.** (type species *Kityakia attrita* Aristov, **sp. n.**); a new combination is proposed: *Permula edemskii* Aristov et Storozhenko, 2011 = *Sojanopermula edemskii* (Aristov et Storozhenko, 2011), **comb. n.** The new genus *Anarkemina* Aristov, **gen. n.** (type species *Narkemina win-*

sdoriensis Lewis, 1979 = *Anarkemina winsdoriensis* **comb. n.**) is described from the Carboniferous of the United States in the family Cnemidolestidae. Two new genera are included in the family Neraphidiidae Aristov, **fam. n.**: *Fodinopenna* Aristov, **gen. n.** (type species *Fodinopenna abakanica* Aristov, **sp. n.** from the Carboniferous of Russia) and *Yaria* Aristov, **gen. n.** (type species *Yaria arenaria* Aristov, **sp. n.** from the Permian of Russia). The family Ctenoptilidae Aristov, **fam. n.** includes a single genus, *Ctenoptilus* Lameere 1917 from the Upper Carboniferous of France.

KEY WORDS: Insecta, Cnemidolestida, taxonomy, Carboniferous, Permian.

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Проведена ревизия отряда Cnemidolestida, относящегося к веснянкообразным насекомым (Insecta: Perlidea). В отряд включено 11 семейств из карбона и перми Евразии, Северной и Южной Америки и триаса Европы: Cnemidolestidae Handlirsch, 1906, Spanioderidae Handlirsch, 1906, Gerapompidae Handlirsch, 1906, Cymenophlebiidae Pruvost, 1919, Emphylopteridae Handlirsch, 1922, Tillyardembiidae G.Zalessky, 1938; Psoropteridae Carpenter, 1976; Sylvabestiidae Aristov, 2000, Prygidae Aristov et Rasnitsyn, 2014, Neraphidiidae Aristov, **fam. n.** и Ctenoptilidae Aristov, **fam. n.** Установлена новая синонимия: Cnemidolestidae = Aetophlebiidae **syn. n.**, = Narkemidae **syn. n.**, = Narkeminidae **syn. n.**; Emphylopteridae = Guloidae **syn. n.**; Spanioderidae = Anthraconeuridae **syn. n.**, = Carpenteropteridae **syn. n.** Семейство Cymenophlebiidae и род *Dieconeurites* Handlirsch, 1906 восстановлены из синонимов. В семействе Sylvabestiidae описаны два новых рода (оба из перми России): *Ivkinus* **gen. n.** (типовой вид *Mezenalicula conjucta* Aristov et Storozhenko, 2011 = *Ivkinus conjuctus* **comb. n.**) и *Kityakia* **gen. n.** (типовой вид *Kityakia attrita* **sp. n.**), а также предложена новая комбинация: *Permula edemskii* Aristov et Storozhenko, 2011 = *Sojanopermula edemskii* (Aristov et Storozhenko, 2011), **comb. n.** Из карбона США в семействе Cnemidolestidae описан новый род *Anarkemina* **gen. n.** (типовой вид *Narkemina winsdoriensis* Lewis, 1979 = *Anarkemina winsdoriensis* **comb. n.**). В семейство Neraphidiidae **fam. n.** включены два новых рода: *Fodinopenna abakanica* Aristov, **gen. n.** (типовой вид *Fodinopenna abakanica* Aristov, **sp. n.** из карбона России) и *Yaria arenaria* Aristov, **gen. n.** (типовой вид *Yaria arenaria* Aristov, **sp. n.** из перми России). Семейство Ctenoptilidae Aristov, **fam. n.** включает единственный род *Ctenoptilus* Lameere 1917 из верхнего карбона Франции.

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INTRODUCTION

The superorder Perlidea (= Plecopteroidea) is represented in the recent fauna by the orders Perlida (= Plecoptera), Forficulida (= Dermaptera), Embiida (= Embioptera), and Grylloblattida (= Grylloblattodea). The numbers of species and values of biomass of these orders make up extremely small proportions of the total number of species and biomass of extant insects. The total number of known extant species of Perlidea is about 6500, while the total number of known insect species is about one million. In the Paleozoic, the pattern was quite different. The orders that make up the majority of the recent insect diversity (Coleoptera, Hymenoptera, Diptera, and Lepidoptera) were either absent or scant, whereas Perlidea made up a large proportion of insects. There is no controversy about the limits and size of the Paleozoic Plecoptera and Protelytroptera (primitive suborder of Dermaptera). Plecopterans and protelytropterans, with a few exceptions, played no considerable role in the insect fauna of the Lower Permian and later periods, and play no such role in the recent fauna. The earliest Embioptera are known from as late as the Jurassic (Huang & Nel, 2009). The remaining Perlidea are a large group of families, mainly Paleozoic; their division into orders has long been debated. These families are placed either in a single order, Protorthoptera (Carpenter, 1992; Grimaldi & Engel, 2005), or in several: Protoblattoidea, Paraplecoptera, and Protoperlaria (Martynov, 1938); Protoblattodea and Paraplecoptera (Sharov, 1962); or Eoblattida and Grylloblattida (Rasnitsyn & Quick, 2002).

One of the orders that were recognized within this superorder is Cnemidolestodea Handlirsch, 1937. Handlirsch (1937) established this order to include the family Cnemidolestidae, in which he placed the genera *Cnemidolestes* Handlirsch, 1906, *Protodiamphipnoa* Brongniart, 1893, and *Bouleites* Lameere, 1917. Martynov (1938) placed the family Cnemidolestidae in the group Cnemidolestoidea of the order Paraplecoptera. Sharov (1962) transferred Cnemidolestidae to the superfamily Geraridea of the same order. Rasnitsyn (1980) placed it in the order Gerarida; Carpenter (1992), in the order Protorthoptera. Subsequently the genera I include in Cnemidolestidae were placed in the order Eoblattida (Rasnitsyn, 2002). The order that includes only the nominate family was re-established by Hamilton (2003). Cnemidolestodea were considered close to Caloneurodea, Titanoptera, and Mantophasmatodea (Hamilton, 2003). Béthoux (2005) places this order in the superorder Archaeorthoptera and includes in this order, in addition to the genera listed above, the following genera, which are not placed in any particular family: *Ischnoneura* Brongniart, 1893, *Narkemina* Martynov, 1930, *Narkeminospis* Whalley, 1979, *Aetophlebia* Scudder, 1885, *Amphiboliacridites* Langiaux et Parriat, 1974, *Paranarkemina* Pinto et Pinto de Ornellas, 1980, and *Narkema* Handlirsch, 1911. MP weak, joining CuA, or absent and enlarged forelegs were given as the principal diagnostic characters of the order (Béthoux, 2005). I place all these genera in the family Cnemidolestidae. In the above-mentioned study, the independence of the orders Caloneurodea, Titanoptera, and Mantophasmatodea is shown; these orders were previously considered close to Cnemidolestodea (Hamilton, 2003). Subsequently, the family Tococladidae Carpenter, 1966 was also placed in Cnemidolestodea (Béthoux, 2007); I place it in the order Hypoperlida (Rasnitsyn & Aristov, 2013).

In this study, Cnemidolestodea are treated as belonging to the superorder Perlidea and ranked as a separate order, Cnemidolestida. It comprises 11 families known from the Carboniferous to Middle Triassic. Diagnoses of the order and families are provided below, their compositions are specified, new synonymies are established, an identification key to families is given, and new taxa are described.

MATERIAL

The type material used in this study is stored in the following institutions: A.A. Borissiak Paleontological Institute, Russian Academy of Sciences (PIN); Chicago Natural History Museum, Chicago, United States (CNHM); Science Museum of Minnesota, St. Paul, Minnesota, United States (SMM); National Museum of Natural History, Smithsonian Institution, Washington, United States (USNM); Museum Comparative Zoology, Cambridge, United States (MCZ); Muséum national d’histoire naturelle, Paris, France (MNHN); Musée d'histoire naturelle, de géologie et d'ethnographie de Lille, Lille, France (ML); and Sammlung Mainfränkische Trias, Euerdorf, Lower Franconia, Germany (SMTE).

The notation of veins and typified names of orders and superorders are given according to Rasnitsyn & Quicke (2002). The vein symbols are as follows: C, costa; “C”, false costa (= subcosta anterior; short vein at the base of the costal space); SC, subcosta (= subcosta posterior); R, radius; RS, radius sector (= radius posterior); M, stem of media; MA, media anterior; MP, media posterior; M_5, strong oblique vein between stems of media and cubitus; Cu, stem of cubitus; CuA, cubitus anterior; CuA_1, first cubitus anterior; CuA_2, second cubitus anterior; CuP, cubitus posterior; A_1, first anal; and A_2, second anal vein. CuA_1 and CuA_2 are recognized if CuA distinctly divides in the basal quarter into two branches (the posterior branch is in most cases simple), diverging from the stem of CuA at an angle. The posterior branches of CuA are defined here as the branches of CuA in the intercubital space (stronger than crossveins), ending blindly or reaching CuP. The precostal space is the basal part of the costal space (between C and SC) separated by “C”; the costal lobe is the basal part of the costal space separated by a fold and situated anterior to the curved and swollen segment of SC. The subcostal space is the space between SC and R; interradial space, between R and RS; median space, between MP and CuA; intercubital space, between CuA and CuP. The clavus is the distinct anal area, often more or less lanceolate, separated by a deep fold along which CuP runs.

The number of studied imprints is given as the number of specimens examined (the positive and negative imprints of the same insect are considered here as one specimen).

The material was studied under a Leica M 165C stereomicroscope, using a Leica DFC 420 digital camera.

Since continental deposits are difficult to correlate, in descriptions of the distribution of taxa I indicate regional stages. The Western European stages Namurian B and C and Westphalian A and B correspond to the Bashkirian Stage; Westphalian C and D, to Moscovian; Cantabrian and Stephanian A and B, to Kasimovian; Stephanian C and Kuzel, to Gzhelian. The North American Morrowan Stage corresponds to the lower Bashkirian; Atokan, to upper Bashkirian and lower Moscovian; Desmoinesian, to upper Moscovian; Missurian and Virgillian, to Kasimovian and Gzhelian, respectively (Davydov *et al*., 2012). Namurian, Westphalian, Morrowan, Atokan, and Desmoinesian stages are placed here in the Upper Carboniferous (Pennsylvanian) of the Global Stratigraphic Scale. The term “Middle Carboniferous” (Bashkirian and

Moscovian Stages) is used only in Russia and some other countries (Alexeev, 2006); no Cnemidolestida have been found in Russia in localities dated to these stages. Thus, all Carboniferous localities discussed below belong to the Upper Carboniferous. The North American Wolfcampian Stage corresponds to the Asselian–Artinskian Stages, and Leonardian corresponds to the Kungurian Stage of the Lower Permian (Sawin *et al.,* 2008). The Kazanian Stage of Russia corresponds to the Roadian; Urzhumian, to Wordian and lower Capitanian; Severodvinian, to Capitanian; and Lower and Upper Vyatkian, to Wuchiapingian and Changhsingian Stages, respectively (Newell *et al.,* 2010).

TAXONOMY

Class Insecta Linné, 1758
Subclass Scarabaeona Laicharting, 1781 (= Pterygota Lang, 1888)
Infraclass Gryllones Laicharting, 1781 (= Polyneoptera Martynov, 1923)
Superorder Perlidea Latreille, 1802 (= Plecopteroidea Martynov, 1934)

Order Cnemidolestida Handlirsch, 1937, nom. transl.

Cnemidolestodea Handlirsch, 1937: 63; Hamilton, 2003: 22; Béthoux, 2005: 405; 2007: 3; Gu *et al*., 2011: 310; Prokop *et al*., 2013b: 8.
Cnemidolestoidea: Martynov, 1938: 101.

Type family: Cnemidolestidae Handlirsch, 1906.

DIAGNOSIS. Pronotum without paranotalia, hind legs not saltatorial. Forewing not elytrized, in most cases with oligomerized venation, not folded longitudinally at rest. “C” usually absent, RS without sharp curves at points where it is joined by crossveins, strong r-rs and rs-m absent. M_5 joining CuA proximal to its division into branches or base of M fused with CuA. M starting branching at some distance distal to M_5. First bifurcations of M and CuA not closely set. CuA in most cases without posterior branches in intercubital space, not divided into CuA_1 and CuA_2, dividing rather distally, usually pectinate posteriad. Clavus in most cases absent. Hindwing at rest not bent transversely, venation of remigium in fore- and hindwings not homonomous. Ovipositor fully developed, male genitalia symmetrical, cerci segmented.

DESCRIPTION. Head prognathous with long filiform antennae, usually with large eyes (in Prygidae eyes small), without ocelli (in Ctenoptilidae one median and two lateral ocelli are present). Pronotum in most cases elongate. Basisterna of all three thoracic segments with longitudinal sternal suture (known in Tillyardembiidae, Sylvabestiidae, and Neraphidiidae), without invagination of sternites (as in Scarabaeones). Legs clinging or cursorial, fore legs or hind legs sometimes enlarged, coxae set apart (in some Neraphidiidae metacoxae contiguous), tarsi five-segmented (in Emphylopteridae tarsus possibly three-segmented). Wings folding flatly, not fully overlapping. Forewing membranous. “C” and precostal space developed only in Ctenoptilidae and some species of *Narkemina* (Cnemidolestidae), costal lobe in most cases developed. SC concave over its entire length (in Tillyardembiidae and Emphylopteridae, SC concave only basally), ending on C or R (sometimes forming apical bifurcation) in distal half of wing. Base of RS in most cases situated in basal half of wing (except in Prygidae, some Cnemidolestidae, and *Izykhia* Aristov, 2013 of family Spanioderidae, in which RS begins at the middle of the wing or distal to the middle). M usually starting branching in basal half of wing (in Prygidae, M sometimes starts dividing in the distal third of the wing), MP sometimes not reaching wing margin. Base of M free only in some Sylvabestiidae. CuA with posterior branches in intercubital space only in Ctenoptilidae. CuA starting branching distal to its basal third (in Spanioderidae, Gerapompidae, and Psoropteridae, CuA starts branching in the basal quarter or third of the wing), pectinate posteriad (comb sometimes reduced or absent in Sylvabestiidae and Prygidae) or forming two combs directed towards each other. CuP usually concave (in *Yaria* **gen. n.** of the family Neraphidiidae, convex; in Tillyardembiidae and Prygidae, changes from concave to convex) and simple (in some *Miamia* Dana, 1864 and *Chenxiella* Liu, Ren et Prokop, 2009 of the family Spanioderidae, with simple bifurcation). Apex of A_2 often fused with A_1.

COMPOSITION. 11 families from the Carboniferous and Permian of North and South America, Eurasia, and Madagascar, and the Triassic of Europe: Cnemidolestidae Handlirsch, 1906, Spanioderidae Handlirsch, 1906, Gerapompidae Handlirsch, 1906, Cymenophlebiidae Pruvost, 1919, Emphylopteridae Handlirsch, 1922, Tillyardembiidae G. Zalessky, 1938, Psoropteridae Carpenter, 1976, Sylvabestiidae Aristov, 2000, Prygidae Aristov et Rasnitsyn, 2014, Neraphidiidae Aristov, **fam. n.,** and Ctenoptilidae Aristov, **fam. n.**

COMPARISON. In the absence of paranotalia on the pronotum and in the general venation pattern, Cnemidolestida are especially similar, among Perlidea, to the order Perlida. The differences from the Permian Perlida in morphology of the body common to all families of Cnemidolestida are the presence of the sternal suture on all thoracic segments, three-segmented tarsus (possibly except in Emphylopteridae), and fully developed ovipositor. In Perlida, the sternal suture is absent, the tarsus is three-segmented, and the ovipositor is lost. Folded wings in Cnemidolestida are not fully overlapping, whereas in Perlida they are fully overlapping. In the forewing of Cnemidolestida, there are no sharp curves of the stem of RS (characteristic of Perlida) at points where strong crossveins r-rs and rs-m join this stem, these crossveins are also absent, and the venation in most cases is more polymerized. Different families of Cnemidolestida show different degrees of similarity with Perlida. The families Gerapompidae, Cymenophlebiidae, and Sylvabestiidae, in addition to the characters mentioned above, are distinguished from Perlida by the apex of SC joining C. The families Cnemidolestidae, Spanioderidae, and especially Tillyardembiidae and Emphylopteridae are more similar to Perlida. In addition to the characters listed above, Tillyardembiidae are distinguished from the Permian Perlida in the venation of the forewing by SC convex distal to the middle of the wing, interradial space wide, veins with numerous apical bifurcations, comb of CuA branches long and dense, and apex of A_2 fused wtih A_1. Emphylopteridae are more similar to Perlida in morphology of the body and venation. Their forewing venation distinguishes them from Perlida by SC convex distal to its base, RS straight, and first bifurcation of M proximal, in basal third of wing, closer to the base of RS than to the apex of SC. In Perlida, SC is concave over its entire length, RS has sharp curves at the points where it is joined by the strong crossveins r-rs and rs-m, and M divides at the middle of the wing, at a considerable distance from M_5, in most cases closer to the apex of SC than to the base of RS (Sinitshenkova, 1987). In the structure of the hindwing, Emphylopteridae are closer to Cnemidolestida than to Perlida. RS in Emphylopteridae is free, without sharp curves, forming a posterior comb of branches, which transforms into an anterior comb at the apex of the wing (Béthoux *et al.,* 2011, fig. 2A). In Perlida (except Perlopseidae: Rasnitsyn, 1980, fig. 79) RS is fused with M, and the base of RS is reduced. The anterior branch of RS pectinate anteriad is typical of both fore- and hindwings in some Cnemidolestidae and forewigs in Spanioderidae and Tillyardembiidae, but not in Perlida. These differences, as well as the Carboniferous age of the Emphylopteridae (the earliest doubtless Perlida appear only at the end of the Lower Permian), are, in my opinion, sufficient to place Emphylopteridae in Cnemidolestida, rather than in Perlida. In morphology of the body, no considerable differences are found between Emphylopteridae and Perlida. The families Prygidae and, to a smaller extent, Psoropteridae are similar to earwigs (Forficulida) of the suborder Protelytrina. Both families are characterized by rather distally branching CuA, in most cases fused basally with M, and by the anal loop, formed by A_1 and A_2. Prygidae are similar to Protelytrina also in the distal shifts of the base of RS and apex of CuP. Psoropteridae are distinguished from Protelytrina by the absence of these characters. Psoropteridae and Prygidae are distinguished from Protelytrina by the non-elytrized forewing and anastomosis A_1+A_2 not fused with CuP. Prygidae also differ from Protelytrina in the absence of paranotalia and in the short hindwing (Aristov & Rasnitsyn, 2014).

Among other Gryllones, similarity with Cnemidolestida is displayed by the orders Eoblattida and Grylloblattida of the superorder Blattidea and by some primitive Gryllidea. Among Cnemidolestida, the most primitive venation is found in the Namurian genera *Ctenoptilus* Lameere, 1917 of the family Ctenoptilidae and *Sinopteron* Prokop et Ren, 2007 and *Chenxiella* of the family Spanioderidae (Béthoux & Nel, 2005; Prokop & Ren, 2007; Liu *et al.,* 2009), similar in venation of the forewing to the family Eoblattidae of the order Eoblattida (Aristov, 2012b). They are characterized by the strongly narrowed interradial space and very large CuA, which in Ctenoptilidae has posterior branches in the intercubital space. The latter character is typical of many Eoblattida and not known in other Cnemidolestida. However, because of the absence of paranotalia on the pronotum and because of CuA pectinate posteriad, I treat Ctenoptilidae and Spanioderidae as primitive Cnemidolestida. In Eoblattidae, the pronotum has paranotalia, and CuA divides irregularly. Ctenoptilidae also differ from Eoblattidae in the presence of "C." Normally developed "C" (ending on C) is typical neither of the other Cnemidolestida (except some *Narkemina* of the family Cnemidolestidae, in which "C" is rudimentary and does not reach the anterior margin of the wing), nor of Perlidea in general. There are some features of similarity between some families of Cnemidolestida and representatives of the order Grylloblattida. Cnemidolestida of the families Cymenophlebiidae, Emphylopteridae, Tillyardembiidae, and Neraphidiidae are characterized by CuA dividing rather distally (distal to its middle) and forming a posterior comb of branches. The same character is also known in Protoblattinidae, Camptoneuritidae, Demopteridae, and Telactinopterigidae of the order Grylloblattida. Emphylopteridae, Tillyardembiidae, and Neraphidiidae are distinguished from Grylloblattida by SC ending on R and by the absence of paranotalia (Aristov & Rasnitsyn, 2009; Aristov & Storozhenko, 2011; Béthoux *et al.,* 2011). The family Cymenophlebiidae is distinguished by M dividing distal to the base of RS, and by the base of M fused with CuA (Fig. 7). In Protoblattinidae, Camptoneuritidae, and Telactinopterigidae, SC ends on C, the base of M is not fused with CuA, and M starts branching distal to the base of RS. The pronotum in Protoblattinidae and Telactinopterigidae has paranotalia (Aristov *et al.,* 2010; Aristov & Rasnitsyn, 2011; Prokop *et al.,* 2013a). The family Ctenoptilidae is very similar to Cheliphlebiidae, which is probably a primitive representative of the superorder Gryllidea (see Discussion). The family Ctenoptilidae differs from Cheliphlebiidae in SC ending on R, in more proximal (in the basal quarter of the wing) origin of RS, in M_5 joining CuA considerably proximal to its division into branches, and in CuA not dividing into CuA_1 and CuA_2. This structure of M_5 and CuA is a difference from Gryllidea common to all Cnemidolestida.

Among Scarabaeones, Cnemidolestida are similar in venation of the forewing to the family Ishnoneuridae (suborder Strephocladina, order Hypoperlida). The genera *Ishnoneura* Brongniart, 1893 from Commentry (Carboniferous of France) and *Strephoptilus* Rasnitsyn et Aristov, 2013 from Isady (Permian of Russia) are very similar to representatives of Cnemidolestidae in the fusion of MP with CuA. Detailed differences of these genera from Cnemidolestidae were provided earlier (Rasnitsyn & Aristov, 2013). On the whole, Ishnoneuridae fully comply in forewing venation with the above-given diagnosis of Cnemidolestida. The hindwing of Ishnoneuridae has a bent anal lobe. Ishnoneuridae are distinguished from Cnemidolestida mainly by CuA dividing rather proximally and pectinate anteriad, in most cases having fewer branches than RS. The structure of the mouthparts of Ishnoneuridae and roof-shaped folding of the wings in some members of this family does not allow placing it in Cnemidolestida, which have chewing mouthparts of generalized structure and flatly folding wings. In Ishnoneuridae the head is beak-like elongate, and the mouthparts have narrow and long mandibles and maxillae. Based on these characters, Ishnoneuridae were placed in the order Hypoperlida (Rasnitsyn & Quicke, 2002). According to an alternative view, Ishnoneuridae belong to Gryllones (Sharov, 1962; Carpenter, 1992; Béthoux & Wieland, 2009). The family Tococladidae Carpenter, 1976 (Béthoux, 2007) was also considered close to Cnemidolestidae. It is distinguished from Cnemidolestida in forewing venation by the presence of posterior branches of CuA, which has rather few branches, in combination with SC ending on R. The forewings of the genera *Hadentomum* Handlirsch, 1906 (Carpenter, 1992), *Palaeocarria* Cockerell, 1917 (Rasnitsyn, 2002), *Endoiasmus* Handlirsch, 1906 (A.P. Rasnitsyn, personal communication) from the Mazon Creek locality (Desmoinesian Stage of the

Upper Carboniferous of the United States) and *Permetator* Novokshonov, 1999 (Novokshonov, 1999) from the Chekarda locality (Kungurian Stage of the Lower Permian of Russia) also comply with the diagnosis of Cnemidolestida. *Hadentomum* is similar in forewing venation to Tillyardembiidae; the other genera are similar in forewing venation to Sylvabestiidae. All these genera are distinguished from Cnemidolestida by the homonomous fore- and hindwings, which make them similar to Hypoperlida. The families Omaliaidae Handlirsch, 1904 (Ross *et al.,* 2013) and Herbstialidae Schmidt, 1953 (Schmidt, 1953) display no principal differences in forewing venation from the Cnemidolestida family Spanioderidae. However, similar venation patterns are also characteristic of the genera *Heterologopsis* Brauckmann et Koch, 1982 (Dictyoneuridea incertae sedis; Sinitshenkova, 2002) and *Kochopteron* Brauckmann, 1984 (Cacurgidae, Eoblattida). Both genera are characterized by paranotalia on the pronotum, and therefore cannot belong to Cnemidolestida. In addition, the mouthparts of *Heterologopsis* are of the sucking type, which means that this genus cannot belong to Gryllones. The morphology of the body is not known either in Omaliaidae or in Herbstialidae, and it is impossible to predict which order (Dictyoneuridea, Eoblattida, or Cnemidolestida) representatives of each of these families resembled. Thus, until the morphology of the body is known, it is difficult to place Omaliaidae or Herbstialidae in any order or even infraclass.

Key to families of the order Cnemidolestida

1 (2) MP weak, ending on CuA or MA, or absent ………………………………..
……………………………………………… Cnemidolestidae Handlirsch, 1906
2 (1) MP normally developed.
3 (4) CuA with posterior branches in intercubital space ..…………………………..
…………………………………………….... Ctenoptilidae Aristov, **fam. n.**
4 (3) CuA without posterior branches in intercubital space.
5 (16) CuA dividing proximal to basal third.
6 (13) SC ending on R.
7 (8) RS beginning at middle of wing, apex of A_2 fused with A_1 ………………….
…………………………………………..... Prygidae Aristov et Rasnitsyn, 2014
8 (7) RS beginning in basal third of wing, apex of A_2 not fused with A_1.
9 (10) M dividing proximal to base of RS ………… Neraphidiidae Aristov, **fam. n.**
10 (9) M dividing distal to base of RS.
11 (12) Interradial space narrow, CuA without dense comb of branches ..………….
……………………………………………… Emphylopteridae Handlirsch, 1922
12 (11) Interradial space wide, CuA with dense comb of branches …………………
……………………………………….… Tillyardembiidae G. Zalessky, 1938
13 (6) SC ending on C.
14 (15) Apex of CuA fused with MP ....………… Cymenophlebiidae Pruvost, 1919
15 (14) Apex of CuA not fused with MP …………..… Sylvabestiidae Aristov, 2000
16 (5) CuA starting branching in its basal third.
17 (18) SC ending on R ………………………..… Spanioderidae Handlirsch, 1906

18 (17) SC ending on C.
19 (20) RS beginning distal to basal quarter of wing ……………………………… ………………………………………….… Gerapompidae Handlirsch, 1906
20 (19) RS beginning in basal quarter of wing …… Psoropteridae Carpenter, 1976

Family Cnemidolestidae Handlirsch, 1906

Cnemidolestidae Handlirsch, 1906: 135; 1922: 90; Martynov, 1938: 101; Sharov, 1962: 124; Rasnitsyn, 1980: 165; Carpenter, 1992: 128; Aristov, 2013: 40; Rasnitsyn & Aristov, 2013: 682.

Ischnoneuridae Handlirsch, 1906: 133 (type genus: *Ischnoneura* Brongniart, 1893); Rasnitsyn, 2002: 258 (partim).

Aetophlebidae Handlirsch, 1906: 708 (type genus: *Aetophlebia* Handlirsch, 1906).

Aetophlebiidae Handlirsch, 1919: 52 (nom. transl.); 1922: 90; Sharov, 1962: 117; Rasnitsyn, 2002: 258; **syn. n.**

Narkemidae Handlirsch, 1911: 321 (type genus: *Narkema* Handlirsch, 1911); 1922: 90; Martynov, 1938: 100; Sharov, 1962: 122; Rasnitsyn, 1980: 134; Carpenter, 1992: 119; Storozhenko, 1996: 18; Nel & Béthoux, 2002: 17; Rasnitsyn, 2002: 258; **syn. n.**

Narkeminidae Pinto & Ornellas, 1991: 93 (nom. n. pro Narkemocacurgidae Pinto et Ornellas, 1978: 310) (type genus: *Narkemina* Martynov, 1930); Storozhenko, 1996: 18 (redescription); 1997: 4; 1998: 69; Rasnitsyn, 2002: 258; **syn. n.**

Type genus: *Cnemidolestes* Handlirsch, 1906.

DIAGNOSIS. Head rather small with large eyes, ocelli absent. Pronotum rather small, square or elongate rectangular. Fore legs strongly enlarged, usually much larger than midlegs (in *Bouletes* Lameere, 1917 somewhat smaller than midlegs), without armature, mid- and hind legs directed anteriad. Tarsus with arolium, without pulvilli. In forewing, precostal space with “C” in most cases absent (in *Narkemina angustata* Martynov, 1930, “C” short, not reaching anterior margin of wing, and precostal space open), costal lobe absent. SC concave or convex, without swelling basally, ending on R. RS beginning distal to basal third of wing, often fused with MA; interradial space not narrowed. M with M_5, dividing into MA and MP in basal third of wing, proximal to base of RS. MP weak, with sharp curves at points where it is joined by crossveins, joining MA or CuA, or absent. CuA S-shaped, starting branching in its basal half, dividing into two stems: anterior stem pectinate posteriad and posterior stem usually pectinate anteriad (in *Evenkiophlebia* Aristov, 2013, some *Narkeminopsis* Whalley, 1979 and *Narkemina,* posterior stem of CuA dichotomizing). Anterior stem of CuA directed in center of wing towards its anterior margin, in most cases not parallel to MA (except in *Narkema* and *Narkeminuta* Aristov, 2013). Anterior branch of CuA in most cases fused with MA (in *Narkeminuta* and some *Narkemina,* anterior branch of CuA free). CuP simple, concave, ending in basal third of wing. Clavus in most cases absent (present in *Aetophlebia* Scudder, 1885, *Bouleites* Lameere, 1917, *Narkemina,* and *Carbonokata* Aristov, 2013); apex of A_2 in most cases fused with A_1.

COMPOSTION. Eighteen genera: *Cnemidolestes* Handlirsch, 1906, *Protodiamphipnoa* Brongniart, 1885, and *Bouleites* Lameere, 1917 from Commentry (France, Allier; Upper Carboniferous, Stephanian Stage B–C); *Aetophlebia* Scudder, 1885 from Mazon Creek (United States, Illinois; Upper Carboniferous, Desmoinesian Stage); *Narkema* Handlirsch, 1911 from Mazon Creek and, possibly, Benson's Clay Mine (United States, Maryland; Upper Carboniferous, Desmoinesian Stage); *Narkemina* Martynov, 1930 from Kasimovian localities of the Upper Carboniferous of Russia: Verkhnetomskoe, Zheltyi Yar, Zav'yalovo (Russia, Kemerovo Region), Izykhskie Kopi (Russia, Republic of Khakassia), Chunya (Russia, Krasnoyarsk Region) and, possibly, Mavonono (Madagascar; Lower Permian, Asselian Stage); *Amphiboliacridites* Langiaux et Parriat, 1974 from Montceau-les-Mines (France, Burgundy; Upper Carboniferous, Stephanian Stage B); *Narkeminopsis* Whalley, 1979 from Radstock (United Kingdom, Somerset; Upper Carboniferous, Westphalian Stage D), Piesberg (Germany, Lower Saxony; Upper Carboniferous, Westphalian Stage D), and Chunya; *Paranarkemina* Pinto et Ornellas, 1980 from Bajo de Veliz and Boituva (Argentina, San Luis, and Brazil, São Paulo, respectively; Lower Permian, Sakmarian Stage); *Irajanarkemina* Martins-Neto, Gallego et Brauckmann, 2007 from Boituva; *Argentinonarkemina* Martins-Neto, Gallego et Brauckmann, 2007 and *Velizphlebia* Martins-Neto, Gallego et Brauckmann, 2007 from Bajo de Veliz; *Narkemulla* Aristov, 2013 from Chunya and Izykhskie Kopi (Russia, Krasnoyarsk Region and Khakassia, respectively; Upper Carboniferous, Kasimovian Stage); *Carbonokata* Aristov, 2013, *Tshunoptera* Aristov, 2013, and *Evenkiophlebia* Aristov, 2013 from Chunya; *Narkeminuta* Aristov, 2013 from Kedrovka (Russia, Kemerovo Region; Lower Permian, Kungurian Stage); and *Anarkemina* Aristov, **gen. n.** from the Windsor locality (United States, Missouri; Upper Carboniferous, Desmoinesian Stage).

NOTES. The families Aetophlebiidae and Narkeminidae were synonymized under Ishnoneuridae (Rasnitsyn, 2002). As noted above, Ishnoneuridae (Hypoperlida) differ from Cnemidolestida mainly in CuA rather proximally branching and pectinate anteriad, in most cases with fewer branches than RS. Based on these characters, the genus *Ishnoneura*, previously placed in Cnemidolestidae, was transferred to Hypoperlida (Rasnitsyn & Aristov, 2013). The genus *Aviocladus* Prokop, Roques et Nel, 2013 from the Carboniferous of France, described in Cnemidolestodea (Prokop *et al.,* 2013b), should also be placed in Ishnoneuridae. The type genera of the families Aetophlebiidae, Narkemidae, and Narkeminidae are transferred here to Cnemidolestidae; thus, these families are synonymized under Cnemidolestidae.

Genus *Anarkemina* Aristov, gen. n.

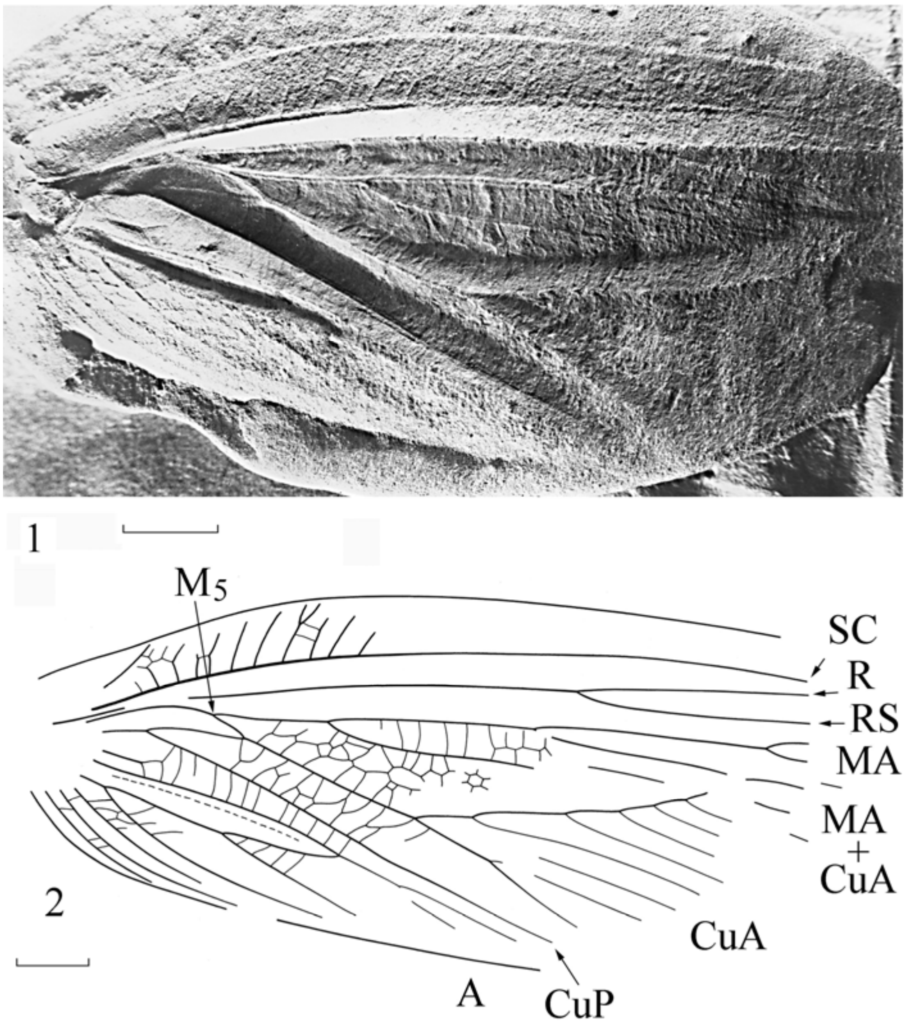
Type species: *Narkemina winsdoriensis* Lewis, 1979, here designated.

DIAGNOSIS. Costal space in middle of wing wider than subcostal space. Apex of SC joining R in distal third of wing, at some distance distal to base of RS. RS simple or distally branching, not fused with MA. M_5 short, MP fully developed, long, parallel to MA; MA starting branching proximal to base of RS. A_1 medially fused with apex of A_2.

SPECIES INCLUDED. Type species only.

COMPARISON. The new genus is especially similar to *Narkemulla* Aristov, 2013 from the Upper Carboniferous of Siberia (Aristov, 2013) and differs from it in the greater distance between the base of RS and apex of SC, in RS free, simple or distally branching, in MP long and parallel to MA, and in the rather proximal (at the middle of A_1) anastomosis A_1+A_2.

ETYMOLOGY. From the Greek negative prefix *a*- and the generic name *Narkemina* Martynov, 1930. Gender feminine.



Figs 1, 2. Forewing of *Anarkemina winsdoriensis* (Lewis, 1979), comb. n., holotype SMM, No W-1: 1 – original photograph by S.E. Lewis, 2 – drawing on photograph. Scale bar: 5 mm.

Anarkemina winsdoriensis (Lewis, 1979), comb. n.

Figs 1, 2

Narkemina winsdoriensis Lewis, 1979: 754, figs 1, 2.

MATERIAL. Holotype SMM, No W-1, positive imprint of forewing fragment; United States, Missouri, Henry County, Winsdor Quadrangle, spoil dump in 3.5 km northwest of Winsdor; Pennsylvanian, Desmoinesian (Westphalian C) Stage, Verdigris Fm; in Science Museum of Minnesota, St. Paul, Minnesota, United States. Holotype not examined.

LOCALITY AND HORIZON. United States: Winsdor locality; the Upper Carboniferous, Lower Desmoinesian (Westphalian) Stage.

REDESCRIPTION. RS until distal quarter wing simple. Free branch of MA dividing in distal quarter of wing, MP simple. Anterior branch of CuA with six ends; posterior branch with three ends. A_2 with three or more branches. Crossveins simple and, in most cases, forming rows of cells.

MEASUREMENTS. Forewing length about 70 mm.

Family Spanioderidae Handlirsch, 1906

Spanioderidae Handlirsch, 1906: 695; 1922: 70; Martynov, 1938: 98; Sharov, 1962: 124; Rasnitsyn, 1980: 165; Burnham, 1986: 117; Carpenter, 1992: 122; Kukalová-Peck & Brauckmann, 1992: 2463; Nel & Béthoux, 2002: 17; Rasnitsyn, 2002: 259; Aristov, 2013: 45.

Anthraconeuridae Laurentiaux & Laurentiaux-Vieira, 1980: 407 (type genus: *Anthraconeura* Laurentiaux et Laurentiaux-Vieira, 1980 = *Miamia* Dana, 1864); Carpenter 1992: 103; Nel & Béthoux, 2002: 25; **syn. n.**

Carpenteropteridae Pinto & Ornellas 1991: 93 (nom. n. pro Cacurgonarkemidae Pinto, 1990: 7) (type genus: *Carpenteroptera* Pinto, 1990); Nel & Béthoux, 2002: 24; Martins-Neto, 2007: 98; **syn. n.**

Type genus: *Miamia* Dana, 1864 (= *Spaniodera* Handlirch, 1906).

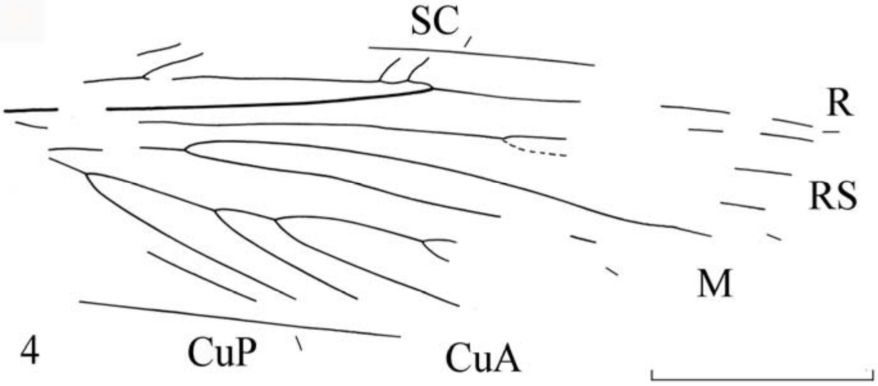
DIAGNOSIS. Head rather small with large eyes, ocelli absent. Pronotum elongate, longer than head. Fore legs not enlarged, not armed (in *Miamia maimai* Béthoux, Gu, Yue et Ren, 2012 apices of femora with spines), hind tibiae sometimes directed anteriad, tarsus five-segmented with arolium and pulvilli. Forewing: costal lobe in most cases absent (present only in *M. bronsoni* Dana, 1864; *M. sylvatica* Laurentiaux et Laurentiaux-Vieira, 1980 and *Longzhua* Gu, Béthoux et Ren, 2011), “C” absent. SC concave only basally, joining R. RS beginning in basal third of wing, often fused with MA, interradial space narrowed basally. Base of M with M_5 or fused with CuA over short distance; M dividing in basal half of wing distal to base of RS; MP fully developed. CuA starting branching in its basal third, forming posterior comb of branches. CuA distal to its division into branches more or less parallel to M (except in *Dieconeura* Scudder, 1885 and *Longzhua*). Anterior branch of CuA not fused with MA, posterior branch usually simple (in *Carpenteroptera* Pinto, 1990, *Etotabla* Béthoux et Jarzembowski, 2010, and *Izykhia* with two or three ends). CuP in most cases simple (in *Chenxiella*, *Miamia rossorum* Béthoux et Jarzembowski, 2010 and

M. maimai, CuP with bifurcation) and concave (in *Sinopteron* Prokop et Ren, 2007 and *Chenxiella,* CuP convex), ending in basal third of wing. Clavus usually absent (present only in *M. bronsoni* Dana, 1864, *Longzhua* and *Izykhia*), apex of A_2 not fused with A_1 (in *Carpenteroptera* and *Izykhia* apex of A_2 free). Ovipositor not protruding beyond abdominal apex.

COMPOSITION. 10 genera: *Miamia* Dana, 1864 from Mazon Creek (United States, Illinois; Upper Carboniferous, Desmoinesian Stage), Writhlington (United Kingdom, Somerset; Upper Carboniferous, upper Westphalian Stage D), Bruay-en-Artois (France, Pas-de-Calais; Upper Carboniferous, Westphalian Stage C), Xiaheyan (China, Ningxia; Upper Carboniferous, Namurian Stage B-C), and, possibly, Benson's Clay Mine (United States, Maryland; Upper Carboniferous, Desmoinesian Stage); *Dieconeura* Scudder, 1885 from Mazon Creek; *Dieconeurites* Handlirsch, 1906 from Pittston (United States, Pennsylvania; Upper Carboniferous, Desmoinesian Stage); *Carpenteroptera* Pinto, 1990 from the localities Anitápolis (Brazil, Santa Catarina; Lower Permian, Sakmarian Stage) and Durasnal (Brazil, Rio Grande do Sul; Lower Permian, Sakmarian Stage); *Carrizocladus* Rasnitsyn, 2004 from the Carrizo Arroyo locality (New-Mexoco, United States; Lower Permian, Wolfcampian Stage); *Sinopteron* Prokop et Ren, 2007, *Chenxiella* Liu, Ren et Prokop, 2009, and *Longzhua* Gu, Béthoux et Ren, 2011 from Xiaheyan; *Etotabla* Béthoux et Jarzembowski, 2010 from Writhlington; and *Izykhia* Aristov, 2013 from Izykhskie Kopi (Russia, Khakassia; Upper Carboniferous, Kasimovian Stage).

NOTES. Since the type genus of the family Anthraconeuridae, *Anthraconeura* Laurentiaux et Laurentiaux-Vieira, 1980, was synonymized under *Miamia* (Béthoux, 2008), this family is synonymized here under Spanioderidae. The type genus of the monotypic family Carpenteropteridae was erroneously attributed to Cnemidolestidae (Aristov, 2012a). *Carpenteroptera* is distinguished from Cnemidolestida in the media parallel to CuA distal of the division point of the latter. In this character, the small number of branches of CuA, and short bifurcation of the posterior branch of CuA, *Carpenteroptera* is similar to Spanioderidae. This genus is especially similar to *Miamia* and differs from it in M not fused with CuA and in the posterior branch of CuA that has several ends. These differences appear insufficient for preserving the separate family Carpenteropteridae, which is therefore synonymized here under Spanioderidae. The genera *Sinopteron*, *Chenxiella*, *Longzhua,* and *Etotabla* were described in the order Archaeorthoptera without specifying the family (Prokop & Ren, 2007; Liu *et al.,* 2009; Béthoux & Jarzembowski, 2010; Gu *et al.,* 2011). These genera were transferred to Spanioderidae because of their similarity with *Miamia*, *Dieconeurites,* and *Dieconeura* (Burham, 1986; Béthoux, 2008). The genus *Carrizocladus* Rasnitsyn, 2004 from the Carrizo Arroyo locality (lower Wolfcampian Stage, Lower Permian; New-Mexico, United States) was described in Hypoperlida (Rasnitsyn *et al.,* 2004). *C. arroyo* Rasnitsyn, 2004 is characterized by the posterior comb of CuA, which, in addition to its similarity to *Sinopteron* Prokop et Ren, 2007, allows placing it in Spanioderidae. In *Carrizocladus deter* Rasnitsyn, 2004, CuA probably branches anteriad, which does not contradict its placement in Ishnoneuridae. Thus, *"Carrizocladus" deter* is probably a member of a separate genus, which remains to be described.

3



4

Figs 3, 4. Forewing of *Dieconeurites rigidus* (Scudder, 1885), holotype UNSM, No 38156: 3 – original photograph by A.P. Rasnitsyn, 4 – drawing on photograph. Scale bar: 5 mm.

Genus *Dieconeurites* Handlirsch, 1906, nom. ressur.

Dieconeurites Handlirsch, 1906: 133.
Miamia: Béthoux, 2008: 158 (partim).

Type species: *Dieconeura rigida* Scudder, 1885, by subsequent designation.

SPECIES INCLUDED. Type species only.

NOTES. The monotypic genus *Dieconeurites* was synonymized under *Miamia*, and the species *D. rigidus* Handlirsch, 1906 was synonymized under *M. bronsoni* Dana, 1864 (Béthoux, 2008). The differences between these species were explained by post-sedimentation distortion of the rock containing the holotype of *D. rigidus*. However, *D. rigidus* (Figs 3, 4) is distinguished from *M. bronsoni* not only in the proportions of the wing, but also in the wider costal space at the level of the base of

RS, in R curved at the point where it is joined by SC, in the median space dilated in the middle of the wing, and in the denser branches of CuA, which occupies less than half of the width of the wing at the level of the apex of SC. In *M. bronsoni,* the costal space at the level of the base of RS is narrower than the subcostal space; R at the point where it is joined by SC is straight, the branches of CuA are sparser, and CuA at the level of the apex of SC occupies half of the width of the wing. In addition, the Pittston locality (Pennsylvania, United States), from which *D. rigidus* was described (Pottsville Fm., Westphalian C), is earlier than the Mazon Creek locality (Carbondale Fm., Westphalian D), from which *M. bronsoni* was described. In view of the above-said, *Dieconeurites* is treated here as a separate genus, not as a synonym of *Miamia*.

Family Gerapompidae Handlirsch, 1906

Gerapompidae Handlirsch, 1906: 711; 1922: 105; Sharov, 1962: 117; Rasnitsyn, 1980: 138; Rasnitsyn, 2002: 259.

Type genus: *Gerapompus* Scudder, 1885.

DIAGNOSIS. Head small, pronotum large, elongate, fore legs slender, hind tibiae directed anteriad. Forewing: costal space at base of RS in most cases equal in width to subcostal space. SC concave, ending on C. RS beginning at middle of wing (in *Gerapompus blattinoides* Scudder, 1885, in its basal third), in most cases not fused with MA, intercubital space not narrowed. M starting branching at middle of wing near base of RS (in *G. blattinoides,* in basal third of wing); MP fully developed. CuA starting dividing in basal quarter, pectinate posteriad, in basal third of wing occupying half or more of its width.

COMPOSITION. Two genera: *Gerapompus* Scudder, 1885 from Mazon Creek (United States, Illinois; Upper Carboniferous, Desmoinesian Stage; Figs 5, 6) and *Aenigmatella* Sharov, 1961 from Zheltyi Yar (Russia, Kemerovo Region; Upper Carboniferous, Kasimovian Stage).

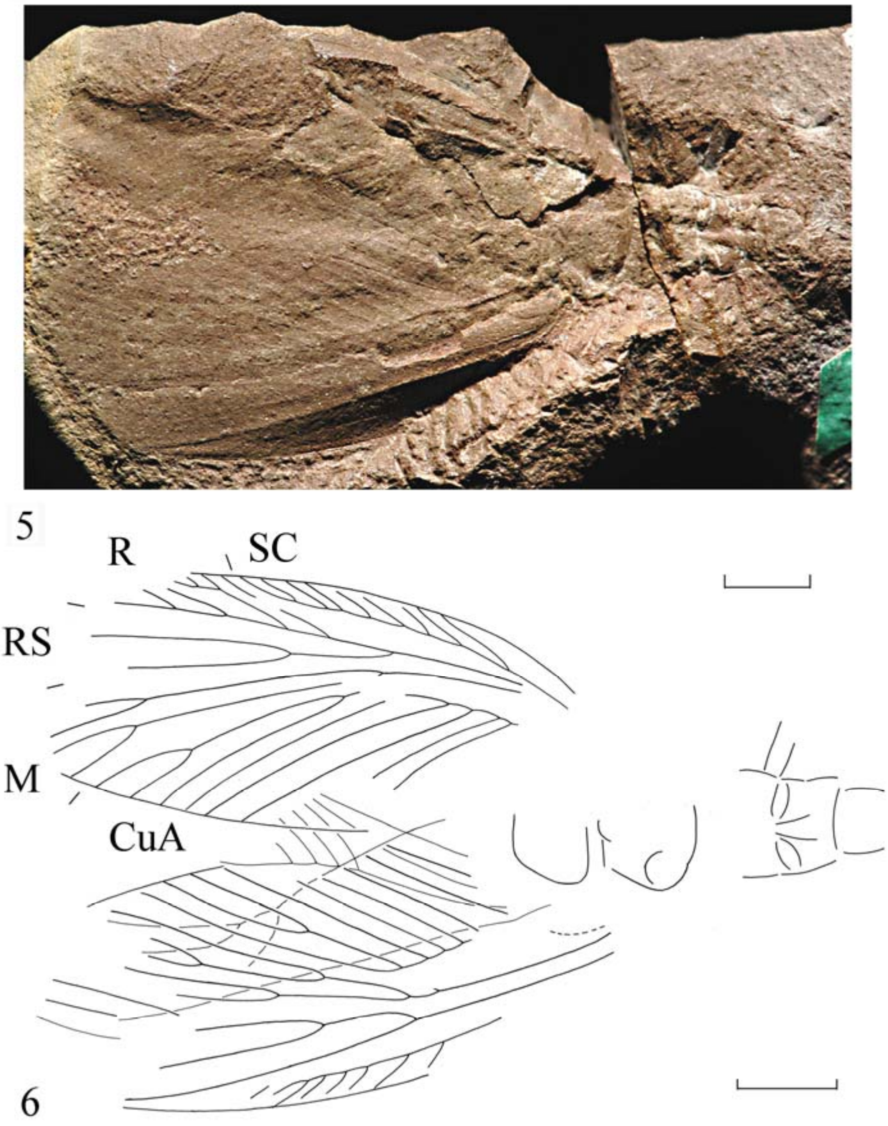
Family Cymenophlebiidae Pruvost, 1919, nom. ressur.

Cymenophlebidae Pruvost, 1919: 128.

Cymenophlebiidae Handlirsch, 1922: 99; Sharov, 1962: 122; Carpenter, 1992: 124.

Type genus: *Cymenophlebia* Pruvost, 1919.

DIAGNOSIS. Forewing with costal lobe; costal space at base of RS wider than subcostal space. SC concave, without swelling basally, ending on C in distal quarter of wing. RS beginning in basal third of wing, free, abundantly branching distal to middle of wing; ends of RS occupying all wing apex; interradial space wide. Base of M fused with CuA. M dividing proximal to middle of wing distal to base of RS; posterior branch M fully developed. RS and M sharply concave. CuA in distal quarter curved parallel to posterior margin of wing, forming there dense comb of slender branches, almost perpendicular to posterior margin of wing. Apex of CuA fused with posterior branch of M. CuP simple, ending at middle of wing; clavus present.



Figs 5, 6. General appearance of *Gerapompus extensus* Scudder, 1885, holotype UNSM, No 38141: 5 – original photograph by A.P. Rasnitsyn, 6 – drawing on photograph. Scale bar: 5 mm.

COMPOSITION. One genus, *Cymenophlebia* Pruvost, 1919 from Lens (France, Nord-Pas-de-Calais; Upper Carboniferous, Westphalian Stage D).

NOTE. The family Cymenophlebiidae was considered synonymous with Epideigmatidae (Carpenter, 1992), which belongs to Grylloblattida (Aristov, 2011) or to Scarabaeona incertae sedis (Rasnitsyn & Quick 2002). *Cymenophlebia* is distinguished from Epideigmatidae by M, branching distal to the base of RS, the base of M fused with CuA, and CuA not dividing into CuA_1 and CuA_2 (Fig. 7). In Epideigmatidae, M branches proximal to the base of RS, the base of M is free, and CuA divides into CuA_1 and CuA_2 (Aristov, 2011). Based on these differences, the family Cymenophlebiidae is re-established here. It is similar in the pectinate RS and distally branching M and CuA with the family Tillyardembiidae and differs from it in the wide preradial space, in SC ending on C, and in the anastomosis CuA+MP. On the other hand, in the wide preradial space sharply narrowing at the middle of the wing, in RS with a large posterior comb and one branch ending on R, and in M distally branching and fused basally with CuA, Cymenophlebiidae are similar to some Permosialidae of the order Palaeomanteida, especially to the Permian genus *Epimastax* Martynov, 1928. *Cymenophlebia* is distinguished from Palaeomanteida by the bifurcation of MP and by the dense comb of slender branches formed by CuA. These two characters are typical of Tillyardembiidae; the family Cymenophlebiidae is therefore placed here in Cnemidolestida.

Family Emphylopteridae Handlirsch, 1922

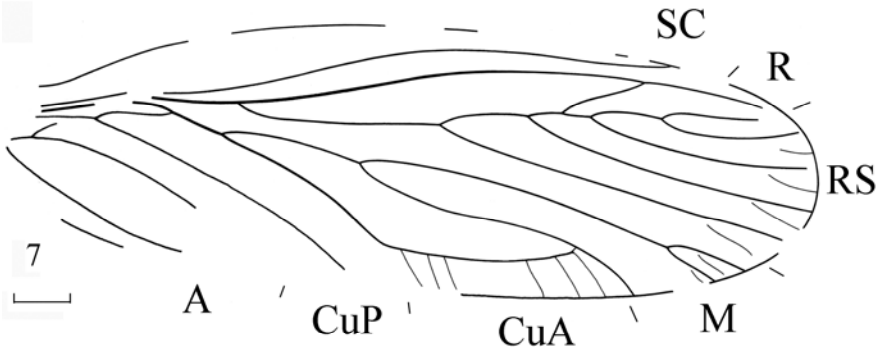
Emphylopteridae Handlirsch, 1922: 69; 1937: 63; Sharov, 1961: 122; Béthoux & Nel, 2002: 26.

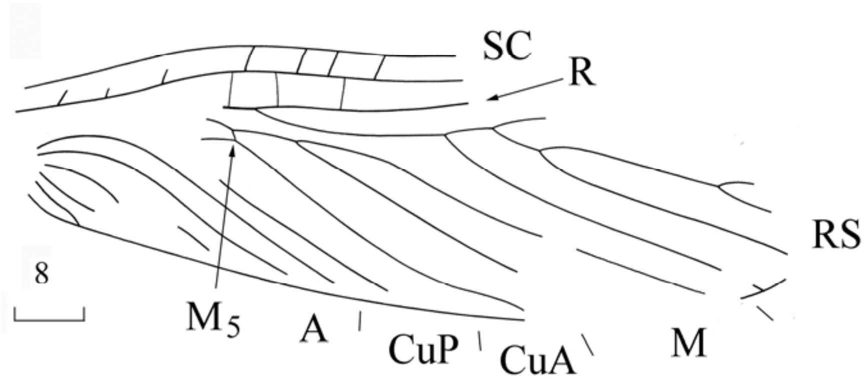
Guloidae Béthoux, Cui, Kondratieff, Stark & Ren, 2011: 2 (type genus *Gulou* Béthoux, Cui, Kondratieff, Stark et Ren, 2011); **syn. n.**

Type genus: *Emphyloptera* Pruvost, 1919.

DIAGNOSIS. Head large, with large eyes; pronotum square, smaller than head; fore legs slender, short, without armature, mid- and hind legs medium-sized, with tibiae directed anteriad; tarsus probably three-segmented. Forewing without costal lobe and without “C”. Costal space at base of RS equal in width to or narrower than subcostal space. SC without swelling basally, concave at base, convex more distally, ending on R. RS beginning in basal third of wing, abundantly branching distal to middle of wing; ends of RS occupying all wing apex, interradial space narrow. RS without sharp curves medially; strong crossveins r-rs and rs-m absent. M_5 present, M dividing proximal to middle of wing, distal to base of RS; first bifurcation of M situated closer to base of RS than to apex of SC. CuA dividing in distal quarter, with several slender branches. CuP concave, ending in basal third of wing. Clavus possibly present only in *Emphyloptera*; apex of A_1 not fused with A_2.

COMPOSITION. Two genera: *Emphyloptera* Pruvost, 1919 from the Lens locality (France, Pas-de-Calais; Upper Carboniferous, Westphalian Stage D; Fig. 8) and *Gulou* Béthoux, Cui, Kondratieff, Stark et Ren, 2011 from Xiaheyan (China, Ningxia; Upper Carboniferous, Namurian Stage B-C).





Figs. 7, 8. Forewings. 7 – *Cymenophlebia carpenteri* (Pruvost, 1914), holotype ML, No 1756, original figure after Pruvost, 1919: Tabl. V, figs. 5, 6; 8 – *Emphyloptera lecrivaini* Pruvost, 1919, holotype ML, No 1755, original figure after Pruvost, 1919: Tabl. V, fig. 3. Scale bar: 1 mm.

NOTE. In recent publications the type genus of the family was placed in Caloneurida (Rasnitsyn & Quick, 2002) or Archaeorthoptera (Béthoux & Nel, 2002). Comparison of Emphylopteridae with Tylliardembiidae shows that the principal differences of the former are limited to the narrow interradial space, more proximal branching of M, and less developed comb of CuA. This similarity allows placing Emphylopteridae in Cnemidolestida. *Emphyloptera* is similar to the genus *Gulou*, which is distinguished from *Emphyloptera* by the regular comb of RS, sharp curve of CuA at the point where it is joined by M_5, and more strongly curved bases of the anal veins. In my opinion, these differences are insufficient for retaining the separate family Guloidae, which was described in the order Plecoptera (Béthoux *et al.,* 2011); this family is therefore synonymized here under Emphylopteridae.

Family Tillyardembiidae G. Zalessky, 1938

Tillyardembiidae G.Zalessky, 1938: 64; Sharov, 1962: 124; Rasnitsyn, 1980: 152; Carpenter, 1992: 123; Storozhenko, 1997: 8; 1998: 91; 2002: 279; Aristov & Rasnitsyn, 2009: 263; 2012: 48.

Permocapniidae Martynov, 1940: 20 (type genus *Permocapnia* Martynov, 1940); synonimized by G. Zalessky, 1950: 41-60.

Type genus: *Tillyardembia* G. Zalessky, 1937.

DIAGNOSIS. Head large, with large eyes, without ocelli. Pronotum comparable in size to or smaller than head, square or elongate. Body elongate with short or medium-sized legs. Sternal suture developed on all three thoracic segments. Coxae set widely apart. Fore legs without armature, male profemora sometimes strongly enlarged. Meso- and metatibiae directed posteriad; tarsus five-segmented, with arolium and without pulvilli. Forewing with costal lobe; costal space at base of RS somewhat wider than subcostal space. SC with swelling basally, changing from concave to convex, ending on R. RS beginning in basal third of wing, straight, free, abundantly dividing, occupying part of anterior margin and part of apex of wing; interradial space wide. M with M_5, starting branching at middle of wing, distal to base of RS, with posterior branch fully developed. CuA starting branching distal to middle, forming dense regular posterior comb of slender branches along posterior margin of wing. CuP simple, changing from concave to convex, ending at middle of wing. Clavus present; apex of A_2 approaching A_1. Ovipositor strong, long; cerci long.

COMPOSITION. Two genera: *Tillyardembia* G. Zalessky, 1937 from Chekarda, Barda, and Kishert' (Russia, Perm Region; Lower Permian, Kungurian Stage) and *Kungurembia* Aristov, 2004 from Chekarda and Soyana (Russia, Arkhangelsk Region; Middle Permian, Kazanian Stage).

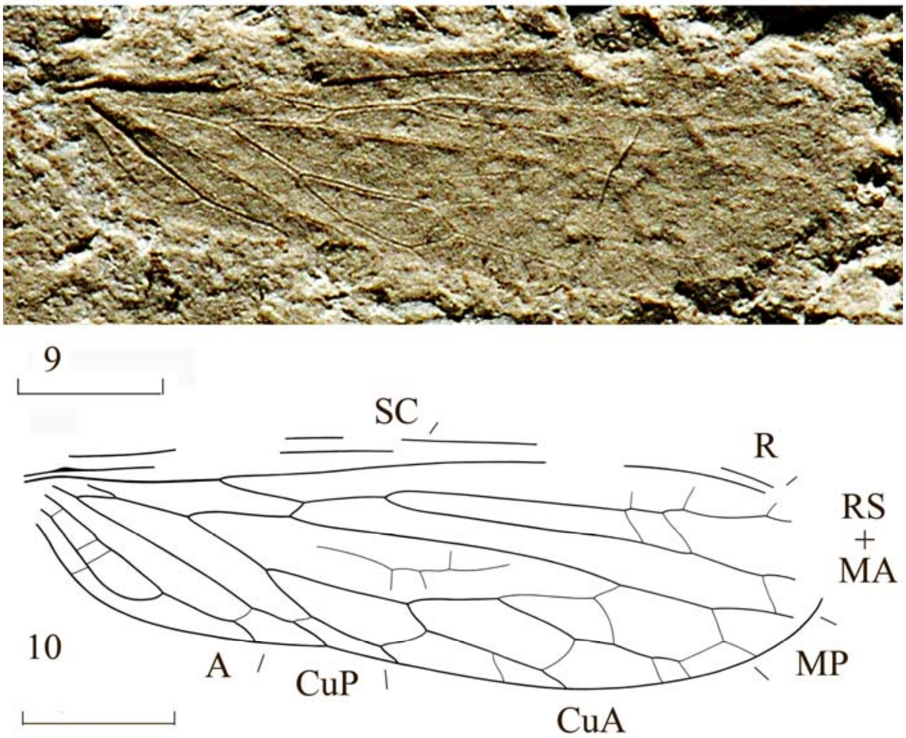
Family Psoropteridae Carpenter, 1976

Psoropteridae Carpenter, 1976: 345; 1992: 126.

Type genus: *Psoroptera* Carpenter, 1976.

DIAGNOSIS. Forewing with costal lobe probably only in *Psoroptera*; "C" absent. Costal space at base of RS slightly wider than subcostal space, SC concave, ending on C. RS beginning in basal quarter of wing, interradial space not narrowed, fused with MA. Base of M fused with CuA; M starting branching in basal third of wing distal to base of RS; posterior branch M fully developed. Space between RS and MA or median space strongly dilated. CuA starting branching in basal third, forming sparse posterior comb of branches; anterior branch fused with MP. CuP simple, concave, ending in basal third of wing. Clavus absent; apex of A_2 fused with A_1.

COMPOSITION. Two genera: *Psoroptera* Carpenter, 1976 from Elmo (United States, Kansas; Leonardian Stage; Fig. 9, 10) and *Hammelburgia* **gen. n.** from Hammelburg (Germany, Lower Franconia; Middle Triassic, Anisian Stage).



Figs 9, 10. Forewing of *Psoroptera cubitalia* Carpenter, 1976, holotype MCZ, No 5840: 9 – original photograph by A.P. Rasnitsyn, 10 – drawing on photograph. Scale bar: 1 mm.

NOTE. The type genus of the family was previously placed in Hypoperlida (Rasnitsyn & Quick 2002). I place this family in Cnemidolestida because of its similarities with Cymenophlebiidae (M that starts dividing distal to base of RS, the long anastomosis of the base of M and CuA, and the fusion of the anterior branch of CuA with MP).

Genus *Hammelburgia* Aristov, gen. n.

Type species: *Hammelburgia selli* sp. n., here designated.

DIAGNOSIS. Costal space at base of RS somewhat wider than subcostal space. SC ending on C distal to middle of wing. RS beginning in basal quarter of wing, fused with MA. Space between branches of RS+MA dilated. M diverging from CuA and dividing into MA and MP in basal third of wing, distal to base of RS. Median space narrowed. Anastomosis M+CuA curved towards anterior margin of wing, CuA starting branching in basal quarter of wing, proximal to middle of this vein. First bifurcation CuA at middle of wing width.

SPECIES INCLUDED. Type species only.

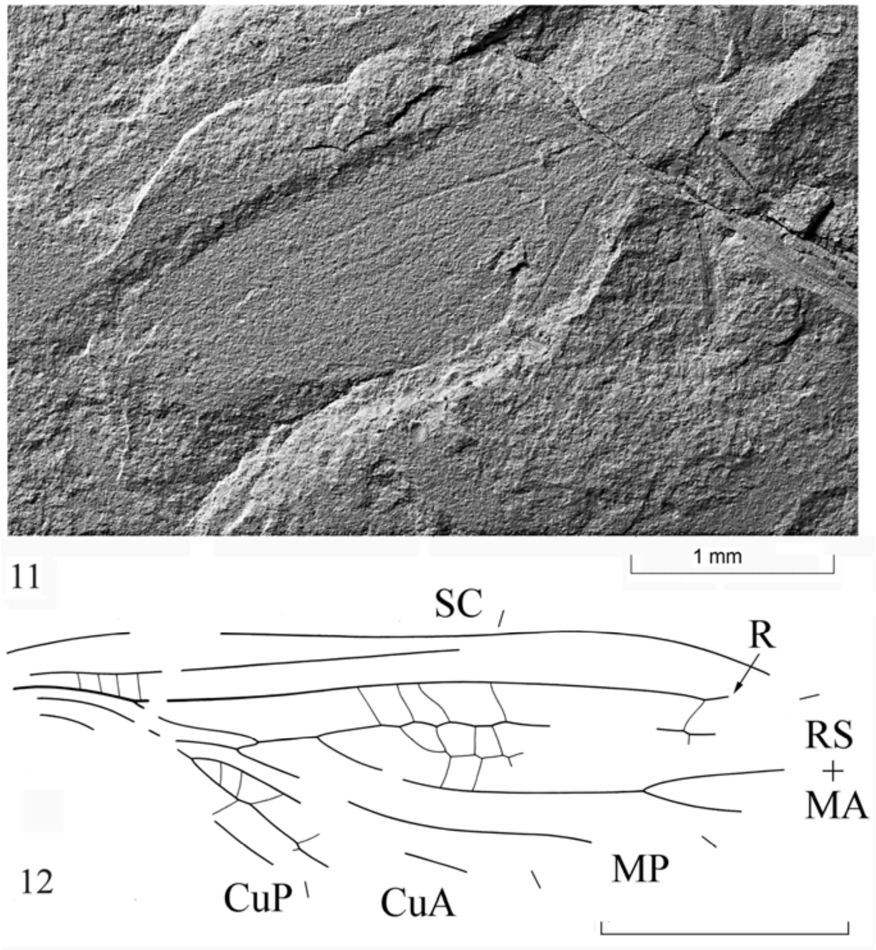
COMPARISON. The new genus is especially similar to *Psoroptera* and differs from it in the dilated space between branches of RS+MA, the narrowed median space, and the first bifurcation of CuA situated at the middle of the width of the wing.

ETYMOLOGY. From Hammelburg locality. Gender feminine.

Hammelburgia selli **Aristov, sp. n.**

Figs 11, 12

MATERIAL. Holotype: SMTE, No 5825/2-584; imprint of forewing; Germany, Lower Franconia, Hammelburg; Middle Triassic, Bythinian, Early Anisian, Röt Fm, *Myophoria* beds ("Obere Dendritenschichten"), Hammelburg locality; stored in Sammlung Mainfränkische Trias, Euerdorf, Lower Franconia (SMTE).



Figs 11, 12. Forewing of *Hammelburgia selli* gen. et sp. n., holotype SMTE, No 5825/2-584: 11 – original photograph by R.A. Rakitov, 12 – reconstruction. Scale bar: 1 mm.

DESCRIPTION. Anterior margin of wing convex in basal and distal thirds of wing, convex in its middle. RS+MA three-branched; MP probably simple; CuA two-branched. Crossveins simple, in space between branches of RS+MA forming double row of cells.

MEASUREMENTS. Length of forewing about 2.8 mm.

ETYMOLOGY. In honor of J. Sell.

Family Sylvabestiidae Aristov, 2000

Sylvabestiidae Aristov, 2000: 2; Storozhenko, 2002: 279; Aristov, 2004: 85; 2009: 41.

Type genus: *Sylvabestia* Aristov, 2000.

DIAGNOSIS. Head and pronotum rather small; eyes large; ocelli absent. Meso- and metathorax with sternal suture. Legs long; fore legs strongly enlarged, without armature, meso- and metatibiae directed posteriad. Forewing: "C" absent; costal lobe present only in *Sylvabestia* and *Cerasopterum* Kukalová, 1964. SC concave, ending on C. RS beginning in basal half of wing, in most cases not fused with MA, interradial space wide (in *Kityakia* **gen. n.,** strongly narrowed). Base of M in most cases free (in *Sylvabestia,* M_5 present; in *Neprotembia* Aristov, 2004 and *Ivkinus* **gen. n.,** base of M fused with CuA). M dividing into MA and MP in basal third of wing, proximal to base of RS or at its level; MP fully developed. CuA starting branching distal to its middle (in *Neprotembia,* in its basal third), with one to four ends, in most cases two or three. CuP simple, concave, ending between basal third and middle of wing. Clavus absent; apex of A_2 not fused with A_1.

COMPOSITION. Nine genera: *Sylvabestia* Aristov, 2000 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage); *Cerasopterum* Kukalová, 1964 from Obora (Czech Republic, South Moravian Region; Lower Permian, Sakmarian Stage); *Sojanopermula* Storozhenko, 1992 from Chekarda and Soyana (Russia, Arkhangelsk Region; Middle Permian, Kazanian Stage); *Neprotembia* Aristov, 2004 from Chekarda and Vorkuta (Russia, Perm Region; Lower Permian, Ufimian Stage); *Elmopterum* Béthoux et Beckemeyer, 2007 from Elmo (United States, Kansas; Lower Permian, Leonardian Stage); *Tshepanichoptera* Aristov, 2008 from Chepanikha (Russia, Udmurtia; Middle Permian, Urzhumian Stage); *Kazanalicula* Aristov et Storozhenko, 2011 from Soyana; *Kityakia* **gen. n.** from Kityak (Russia, Kirov Region; Middle Permian, Kazanian Stage); and *Ivkinus* **gen. n.** from Isady (Russia, Vologda Region; Upper Permian, Severodvinian Stage).

NOTES. The genera *Sojanopermula*, *Neprotembia*, *Elmopterum*, *Tshepanichoptera*, and *Kazanalicula* and species *Permula tshekardensis* (Aristov, 2004), *P. minor* (Aristov, 2004), *P. edemskii* Aristov et Storozhenko, 2011, and *Mezenalicula conjucta* Aristov et Storozhenko, 2011 were recently transferred to Sylvabestiidae of the family Permulidae, order Grylloblattida (Aristov & Storozhenko, 2011). The photograph of the holotype of the type species of *Permula*, *P. lebachensis* (Schlechtendal, 1913) provided by Gutörl (1934: Tafel 16, fig. 4) is of a better quality than the one provided in the original description (Schlechtendal, 1913: Tab. 2, figs.

10a, 10b) and shows CuA proximally and abundantly branching, pectinate posteriad, with posterior branches in the intercubital space, which is atypical either of the other species of this genus or of the other genera of Permulidae. Based on this observation, the family Permulidae, including the type species of the type genus, and *Mezenalicula connata* Aristov et Storozhenko, 2011 were retained in Grylloblattida, while all above-listed taxa were transferred to Sylvabestiidae. *P. tshekardensis*, *P. minor,* and *P. edemskii* are transferred below to the genus *Sojanopermula*, and the new genus *Ivkinus* is described for *Mezenalicula conjucta*. *Cerasopterum gracile* Kukalová, 1964 is transferred here from Liomopteridae (Grylloblattida: Kukalová, 1964) to Sylvabestiidae, based on CuA branching rather distally (distal to its middle and to the level of the base of RS) and general similarity to the genus *Elmopterum*. The other species of the genus *Cerasopterum* are provisionally transferred here to the genus *Tapopterum* Carpenter, 1950 of the family Liomopteridae. A more detailed revision of the family Permulidae and the genus *Tapopterum* is outside the scope of this study and will be published separately.

***Sojanopermula edemskii* (Aristov et Storozhenko, 2011), comb. n.**

Permula edemskii Aristov & Storozhenko, 2011: 118, figs 4, 15.

MATERIAL. Holotype PY 94/1027, positive and negative imprints of an incomplete forewing; Russia, Arkhangelsk Region, Mezen District, Soyana locality, right bank of the Soyana River 56–60 km upstream of the mouth; Middle Permian, Kazanian Stage, Lower Kazanian Substage, Iva-Gora Beds.

Genus *Ivkinus* Aristov, gen. n.

Type species: *Mezenalicula conjucta* Aristov et Storozhenko, 2011, here designated.

DIAGNOSIS. Anterior margin of forewing strongly convex. Costal space at base of RS wider than subcostal space, crossed by long, oblique anterior branches of SC. M fused basally with CuA; MA fused with RS; intermedian space strongly dilated. CuA starting branching distal to middle. A_1 simple; A_2 with three or more ends. Crossveins simple.

COMPOSITION. Type species from the Isady locality (Russia, Vologda Region; Upper Permian).

COMPARISON. The new genus is especially similar to *Neprotembia* and differs from it in the long, oblique branches of SC, dilated intermedian space, and distally branching CuA.

ETYMOLOGY. From the Ivkin Brook. Gender masculine.

***Ivkinus conjuctus* (Aristov et Storozhenko, 2011), comb. n.**
Fig. 13

Mezenalicula conjucta Aristov & Storozhenko, 2011: 124, figs 10, 19.

MATERIAL. Holotype PIN, No 3840/1243, negative imprint of forewing fragment; Russia, Vologda Region, Veliky Ustyug District, left bank of the Sukhona River 1 km upstream of Isady village, Isady locality; Upper Permian, Upper Severodvinian Substage, Poldarsa Fm.; in PIN.

DESCRIPTION. SC ending in distal third of wing. RS beginning in basal third of wing, simple until distal third of wing. Interradial space wide. Preserved parts of MA and MP simple. CuA pectinate anteriad, with three or more branches.

MEASUREMENTS. Forewing length about 20 mm.

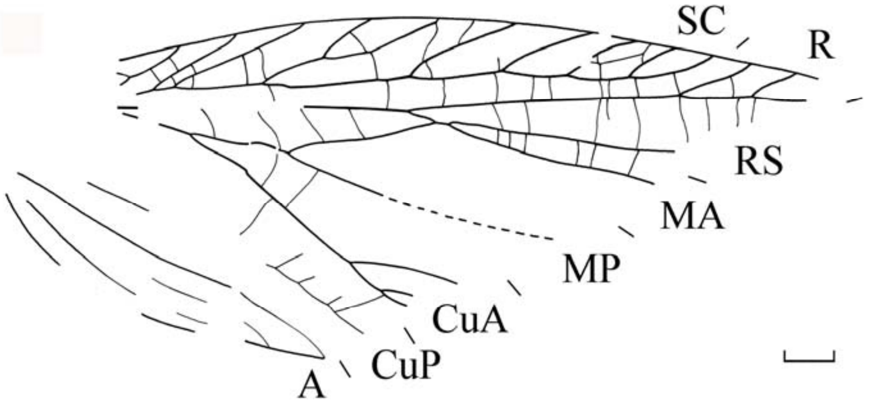


Fig. 13. Forewing of *Ivkinus conjuctus* (Aristov et Storozhenko, 2011), comb. n., holotype PIN, No 3840/1243, modified after Aristov & Storozhenko, 2011. Scale bar: 1 mm.

Genus *Kityakia* Aristov, gen. n.

Type species: *Kityakia attrita* sp. n., here designated.

DIAGNOSIS. Costal space at base of RS narrower than subcostal space. RS beginning in basal third of wing, simple. Interradial space narrow. Base of M not fused with CuA; M_5 absent; MA dividing; MP simple, without traces of desclerotization. CuA starting branching in distal quarter, three-branched; apex of CuA S-shaped. Intercubital space dilating towards posterior margin of wing. Apices of CuP and A_1 curved parallel to posterior margin of wing. Anal area rather small. R until distal third of wing, base of RS, M until division into branches, CuA, and A_1 swollen. MA and MP very weak.

COMPOSITION. Type species from the Kityak locality (Russia; Middle Permian).

COMPARISON. The new genus is distinguished from the other members of the family by the simple RS, narrow interradial space, and apices of CuP and A_1 curved parallel to the posterior margin of the wing.

ETYMOLOGY. From the Kityak locality. Gender feminine.

Kityakia attrita Aristov, sp. n.
Figs 14, 15

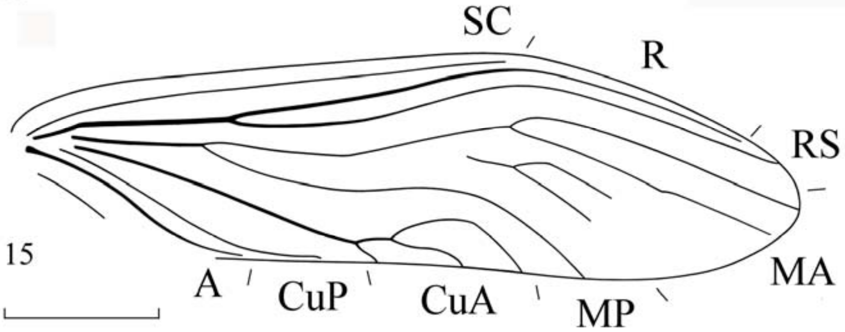
MATERIAL. Holotype PIN, No 1366/695, positive and negative imprints of forewing; Russia, Kirov Region, Malmyzh District, left bank of the Kityak River opposite Bol'shoy Kityak village, Kityak locality; Middle Permian, Upper Kazanian Substage, Belebeevo Fm.; in PIN. In addition to the holotype, paratypes PIN, Nos 1366/498 and 568 from the same locality.

DESCRIPTION. Anterior margin of forewing probably weakly convex. SC ending in distal third of wing. MA starting branching at middle of wing, with four or more branches; MP S-shaped. A_1 simple with swelling basally, A_2 simple or with several ends.

MEASUREMENTS. Forewing length 27-33 mm.

ETYMOLOGY. Feminine form of the Latin '*attritus*' (wasted).

14



15

Figs 14, 15. Forewing of *Kityakia attrita* sp. n., holotype PIN, No 1633/695: 14 – photograph, 15 – reconstruction. Scale bar: 5 mm.

Family Prygidae Aristov et Rasnitsyn, 2014

Prygidae Aristov & Rasnitsyn, 2014: 68.

Type genus: *Pryg* Aristov et Rasnitsyn, 2014

DIAGNOSIS. Head large with rather small eyes; ocelli absent; pronotum not elongate, slightly smaller than head. Fore legs short, without armature; procoxae closely set; metafemora strongly enlarged. Forewing with costal lobe; SC concave, parallel to C, ending on R. RS beginning distal to middle of wing, free; interradial space wide. Base of M free, without M_5, or fused with CuA. M simple or with short bifurcation in basal quarter of wing, distal to base of RS. CuA starting branching distal to middle, pectinate posteriad or with simple short bifurcation. CuP simple, concave only basally, ending in distal third of wing. Clavus present; apex of A_2 fused with A_1. Ovipositor strong, long, cerci longer than ovipositor.

COMPOSITION. Two genera: *Pryg* Aristov et Rasnitsyn, 2014 from Elmo (United States, Kansas; Lower Permian, Leonardian Stage) and *Parapryg* Aristov et Rasnitsyn, 2014 from Nedubrovo (Russia, Vologda Region; Upper Permian, Vyatkian Stage).

Family Neraphidiidae Aristov, fam. n.

Type genus: *Neraphidia* Novokshonov et Novokshonova, 1997.

DIAGNOSIS. Head medium-sized; eyes large; pronotum smaller than head. Meso- and metathorax with sternal suture. Legs slender, medium-sized, closely set coxae; fore legs without armature. Forewing: costal lobe preserved only in *Neraphidia*. SC concave, ending on R. RS beginning in basal half of wing, free, interradial space wide. M with short M_5, dividing into MA and MP in basal quarter of wing, proximal to base of RS, MP not reduced. CuA starting branching distal to middle, comb of branches sometimes shortened. CuP concave (in *Yaria* **gen. n.** convex over its entire length), simple, ending between basal third and middle of wing. Clavus absent; apex of A_2 not fused with A_1.

COMPOSITION. Three genera: *Neraphidia* Novokshonov et Novokshonova, 1997 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage); *Fodinopenna* **gen. n.** from Izykhskie Kopi (Russia, Khakassia; Upper Carboniferous, Kasimovian Stage); and *Yaria* **gen. n.** from Belyi Yar (Russia, Khakassia; Middle Permian, Urzhumian Stage).

Genus *Fodinopenna* Aristov, gen. n.

Type species: *Fodinopenna abakanica* Aristov, sp. n., here designated.

DIAGNOSIS. Venation polymerized. SC ending at middle of wing. RS beginning in basal third of wing; branches of RS reaching anterior margin of wing. MA dividing.

CuA starting branching in its middle, forming long, sparse comb; CuP concave, not S-shaped. Crossveins mostly simple, in interradial space forming double row of cells. Hindwing with SC ending distal to middle of wing.

COMPARISON. The new genus differs from *Neraphidia* in the rather proximally ending SC, rather proximal origin of RS, and sparse branches of CuA. In *Neraphidia,*

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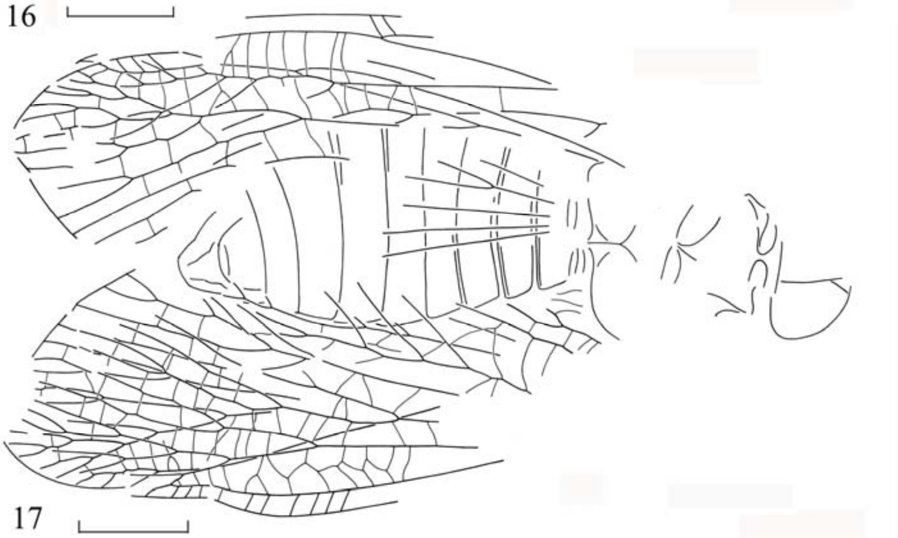


17

Figs 16, 17. General appearance of *Fodinopenna abakanica* sp. n. holotype PIN, No 5384/99, 16 – photograph, 17 – reconstruction as preserved. Scale bar: 3 mm.

SC ends in the distal quarter of the wing, RS begins in the middle of the wing, and CuA forms a dense comb of branches (Storozhenko & Aristov, 2011).

COMPOSITION. Type species from the Izykhskie Kopi locality (Russia; Upper Carboniferous).

ETYMOLOGY. From the Latin '*fodina'* (mine) and '*penna'* (wing). Gender feminine.

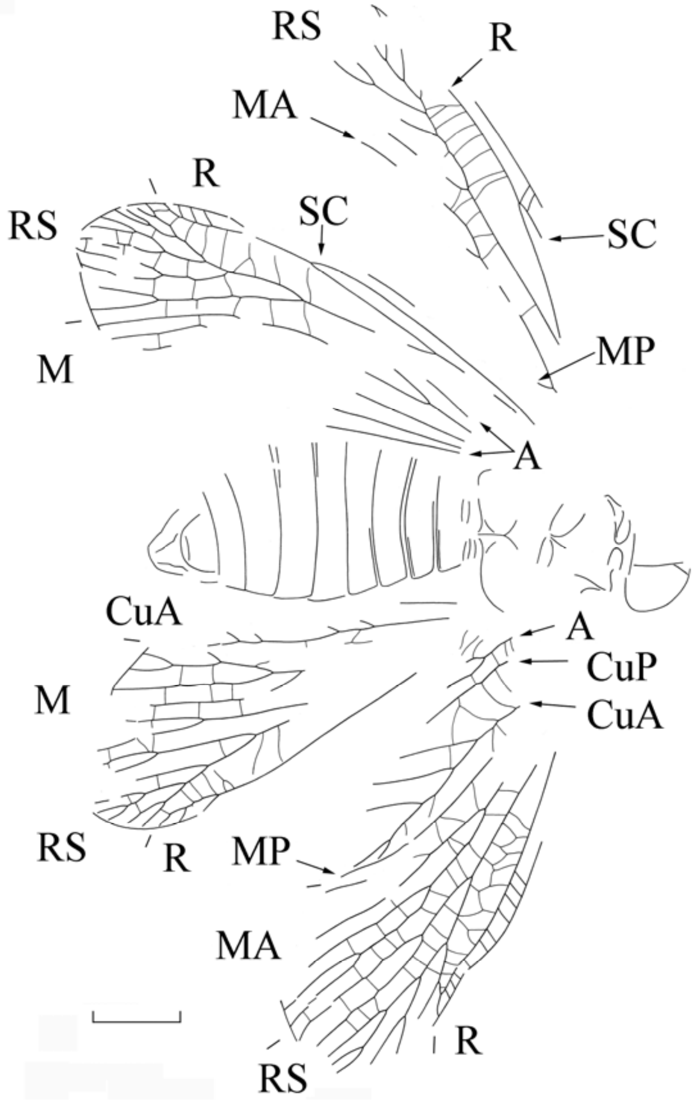


Fig. 18. General appearance of *Fodinopenna abakanica* sp. n. holotype PIN, No 5384/99, reconstruction. Scale bar: 3 mm.

Fodinopenna abakanica **Aristov, sp. n.**
Figs 16–18

MATERIAL. Holotype PIN, No 5384/99, positive and negative imprints of whole insect; Russia, Republic of Khakassia, Altay District, right bank of the Abakan River downstream of Izykhskie Kopi village, Izykhskie Kopi locality; Upper Carboniferous, Kasimovian or Gzhelian Stage, Khakassia Group, Belyi Yar Fm., Lower Belyi Yar Subfm.; in PIN.

DESCRIPTION. Forewing: anterior branches of SC and R simple and short. RS starting branching distal to middle of wing, with nine or more branches; its anterior branch fused with R. MA starting branching proximal to RS, four-branched. CuA with five or more branches. Hindwing: RS dividing distal to middle of wing, with 10 or 11 branches not reaching anterior margin of wing. M four-branched; anal fan rather small.

MEASUREMENTS. Forewing length about 20; hindwing length about 18; body length 22 mm.

ETYMOLOGY. From the Abakan River.

Genus *Yaria* Aristov, gen. n.

Type species: *Yaria arenaria* sp. n., here designated.

DIAGNOSIS. Venation oligomerized. Costal space at base of RS narrower than subcostal space. SC ending at middle of wing. RS beginning in basal third of wing. MA simple. CuA dividing into two branches in distal third; CuP convex, S-shaped. Crossveins simple.

COMPARISON. The new genus is distinguished from all other genera of the family by the two-branched CuA and convex CuP. In *Neraphidia* (Storozhenko & Aristov, 2011) and *Fodinopenna,* CuA is pectinate posteriad, and CuP is concave.

COMPOSITION. Type species from the Belyi Yar locality (Russia; Middle Permian).

ETYMOLOGY. From the Belyi Yar locality. Gender feminine.

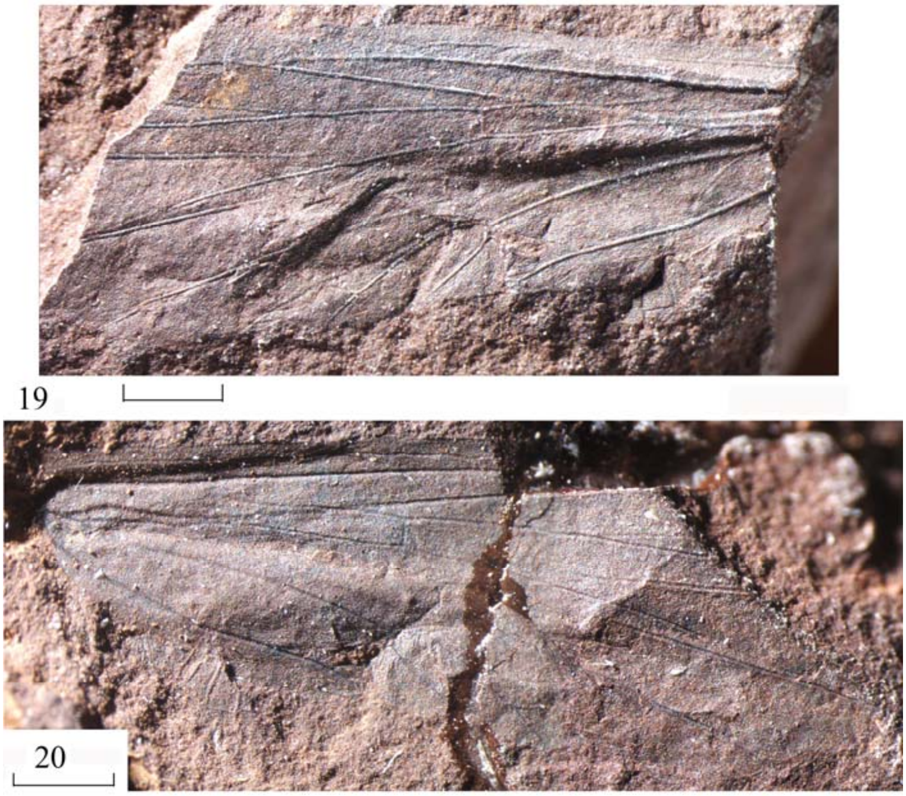
Yaria arenaria **Aristov, sp. n.**
Figs 19–23

MATERIAL. Holotype PIN, No 5386/49, positive and negative imprints of fore- and hindwing; Russia, Republic of Khakassia, Altay District, 4 km south of Belyi Yar village, Izykhsky Coal Mine, area No 1, Belyi Yar locality; Middle Permian, Urzhumian Stage, Arshanov Group, Izykh Fm.; in PIN.

DESCRIPTION. Anterior margin of forewing in its basal third slightly concave, more distally convex. Anterior branches of SC simple. RS and MA at middle of wing with sharp curves at points where it is joined by crossveins. Preserved parts of RS, MA, and MP simple. Hindwing: R S-shaped; RS, MA, MP, and possibly anterior branch of CuA simple.

MEASUREMENTS. Forewing length about 10; hindwing length 9 mm

ETYMOLOGY. The Latin *arenaria* (sandpit).

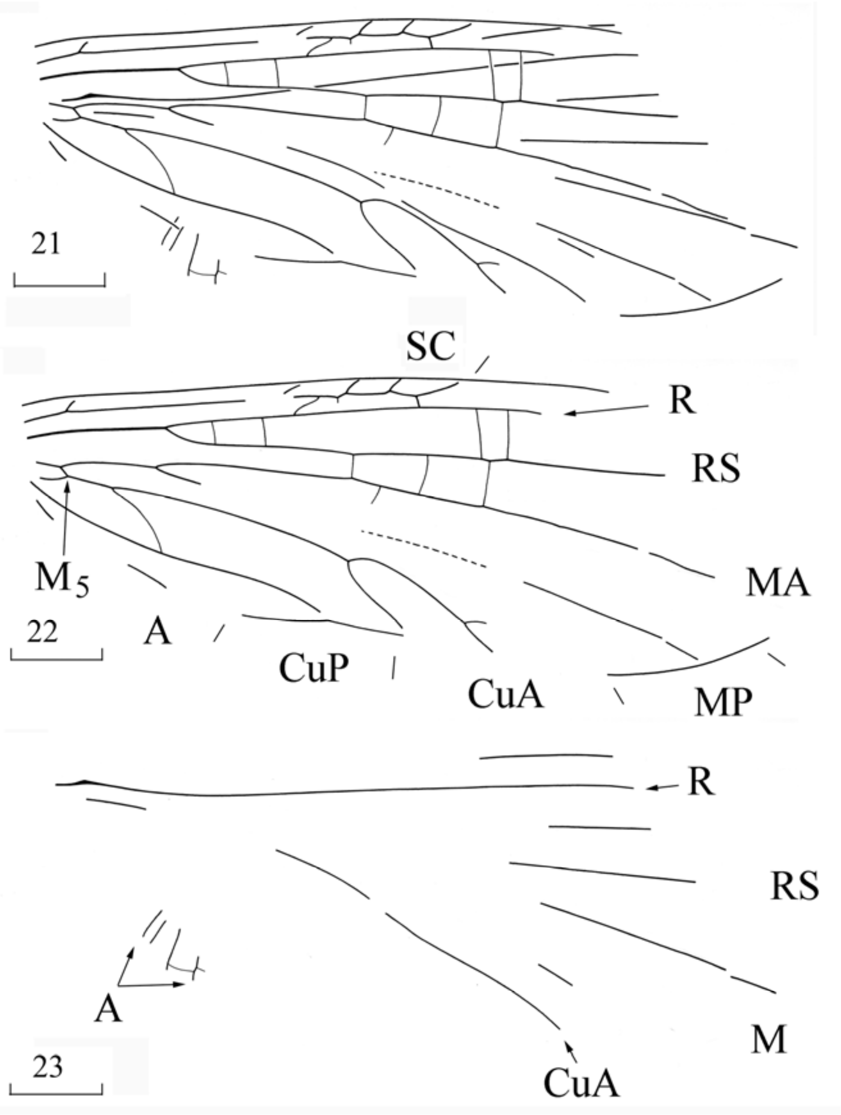


Figs 19, 20. General appearance of *Yaria arenaria* sp. n. holotype PIN, No 5386/49, 19 – photograph of positive imprint, 20 – photograph of negative imprint. Scale bar: 1 mm.

Family Ctenoptilidae Aristov, fam. n.

Type genus: *Ctenoptilus* Lameere 1917.

DIAGNOSIS. Head large with large eyes and ocelli. Pronotum rather small, elongate. Sternal suture probably present on mesothorax (Béthoux, 2009: fig. 2a). Protibiae with armature; meso- and metatibiae directed anteriad. Tarsus five-segmented with arolium and pulvilli. Forewing: precostal space present; “C” ending on C; costal space at base of RS wider than subcostal space. SC without swelling basally, concave, ending on R proximal to distal third of wing. RS beginning in basal quarter of wing, intercubital space narrowed. M_5 joining CuA near its base; M dividing into MA and MP proximal to middle of wing, distal to base of RS. CuA with posterior branches, not divided into CuA_1 and CuA_2, pectinate posteriad. CuP simple, concave, ending in basal third of wing. Clavus present; apex of A_2 not fused with A_1.



Figs 21-23. Reconstruction of *Yaria arenaria* sp. n. holotype PIN, No 5386/49, 21 – general appearance, 22 – forewing, 23 – hindwing. Scale bar: 1 mm.

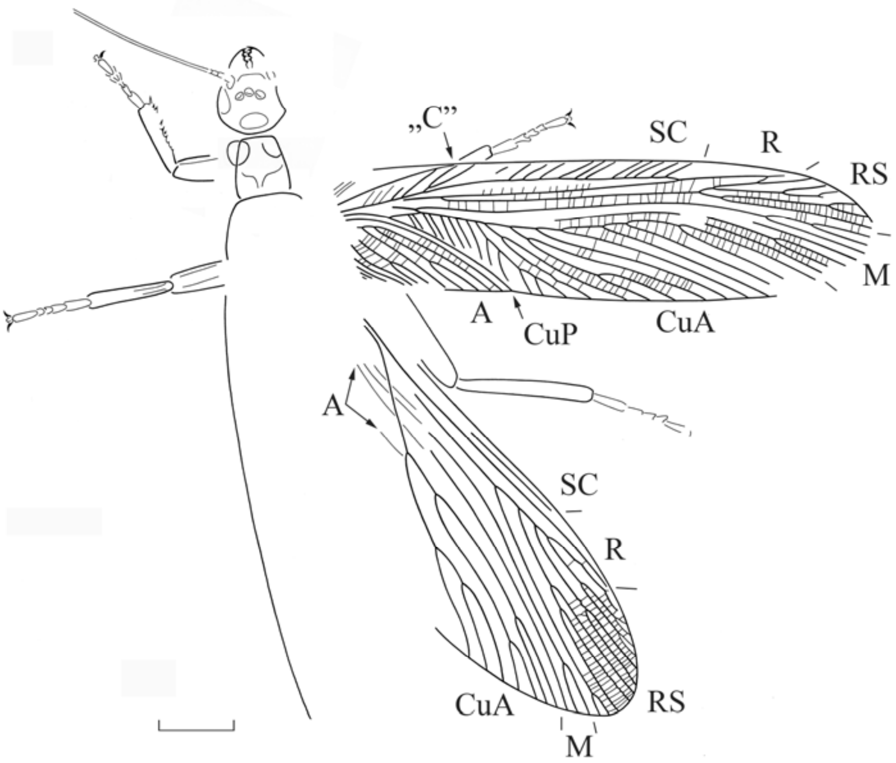


Fig. 24. Reconstruction of general appearance of *Ctenoptilus elongatus* (Brongniart, 1893) based on original drawing by A.P. Rasnitsyn of spec. MNHN-DHT-R51392 and photographs in Béthoux, 2009: figs 1, 2. Scale bar: 5 mm.

COMPOSITION. One genus, *Ctenoptilus* Lameere 1917 from Commentry (France, Allier; Upper Carboniferous, Stephanian Stage B-C; Fig. 24).

NOTE. The genus *Ctenoptilus* was placed in the family Ischnoneuridae *sensu* Rasnitsyn, 2002 (= Cnemidolestidae), but this genus does not have MP reduced and CuA divided into two combs, which is characteristic of Cnemidolestidae. The new family is described based on the unique combination of the absence of paranotalia, presence of "C," and CuA not divided into CuA_1 and CuA_2 and having posterior branches in the intercubital space (see above).

DISCUSSION

The order Cnemidolestida in the sense accepted here is rather small, comprising 11 families, 54 genera, and 76 species. Table 1 shows the distribution of families from the Upper Carboniferous to Middle Triassic. Carboniferous Cnemidolestida are known from the United States, England, France, Germany, Russia, and China.

Table 1. Distribution of families of the order Cnemidolestida in Carboniferous, Permian and Triassic.

Epoch	Upper Carboniferous								Lower Permian					Middle Permian					Upper Permian		Middle Triassic
Stage	Namurian B-C	Westphalian C	Atokan / Desmoines.	Desmoinesian	Westphalian D	Stephanian B	Kassinovian	Stephanian B-C	Wolfcampian	Sakmarian		Leonardian	Kungurian	Ufimian		Kazanian		Urzhumian	Severodvinian	Vyatkian	Anisian
Locality	Xiaheyan	Bruay-en-Artois	Pittston, Winsdor	Mazon Creek	Piesberg et al.	Montceau-les-Mines	Chunya et al.	Commentry	Carrizo Arroio	Obora	Boituva et al.	Elmo, Midco	Chekarda	Vorkuta	Tyulkino	Soyana	Kityak	Chepanikha	Isady	Nedubrovo	**Hammelburg**
Cnemidolestidae			x	x	x	x	x	x			x		+								
Spanioderidae	x	x	x	x	x		x		x		x										
Gerapompidae				x			x														
Cymenophlebiidae					x																
Emphylopteridae	x				x																
Tillyardembiidae													x		x	x					
Psoropteridae												x									x
Sylvabestiidae										x		x	x	x		x	x	x	x		
Prygidae												x								x	
Neraphidiidae							x						x					+			
Ctenoptilidae								x													

Localities: **Xiaheyan** – China, Ningxia Hui Autonomous Region; Upper Carboniferous, Namurian B-C, Tupo Fm.; **Bruay-en-Artois** – France, Nord-Pas-de-Calais, Pas-de-Calais**;** Upper Carboniferous, Westphalian C; **Pittston** – United States Pennsylvania, Luzerne County; Upper Carboniferous, Westphalian C, Pottsville Fm.; **Wisdor** – United States, Missouri, Henry County; Upper Carboniferous, Lower Desmoinesian, Verdigris Fm.; **Mazon Creek** – United States, Illinois, Grundy County; Upper Carboniferous, Desmoinesian, Carbondale Fm.; **Piesberg et al.:** Piesberg – Germany, Lower Saxony; Upper Carboniferous, Westphalian D, Flöz Zweibänke Fm.; Radstock**,** Writhlington – United Kingdom, Somerset; Upper Carboniferous, Westphalian D, Radstock Fm.; Lens – France, Nord-Pas-de-Calais, Pas-de-Calais; Upper Carboniferous, Westphalian D, Faisceau d'Olympe, Faisceau de Dusouich; **Montceau-les-Mines** – France, Burgundy; Upper Carboniferous, Stephanian B, Montceau Fm.; **Chunya etc.:** Chunya – Russia, Krasnoyarsk Region, Evenkia District; Upper Carboniferous, Kasimovian Stage, Kata Fm.; Verkhotomskoe – Russia, Kemerovo Region, Kemerovo District; Zheltyi Yar – Russia, Kemerovo Region, Krapivinsky District; Zav'yalovo – Russia, Novosibirsk Region, Toguchin District; Upper Carboniferous, Kasimovian Stage, Alykaeva Fm.; Izykhskie Kopi – Russia, Khakassia, Abakan District; Upper Carboniferous, Kasimovian Stage, Belyi Yar Fm.; **Commentry** – France, Allier; Upper Carboniferous, Stephanian B-C, Upper Coal Measures of the Commentry Basin; **Carrizo Arroyo** – United States, New Mexico; Lower Permian, Wolfcampian, Burzum Fm.; **Obora –** Czech Republic, South Moravian Region, Blansko District; Lower Permian, Sakmarian, Letovice Fm.; **Boituva et al.:** Boituva – Brasil, São Paulo State, Boituva; Lower Permian, Sakmarian, Boituva Fm.; Durasnal – Brasil, Rio Grande do Sul State, Caçapava do Sul; Lower Permian, Sakmarian, Budó Fm.; Anitápolis – Brazil, Santa Catarina State, Anitápolis; Lower Permian, Sakmarian, Anitápolis Fm.; Bajo de Veliz – Argentina, Rio Negro, San Antonio; Lower Permian, Sakmarian, Bajo de Veliz Fm.; **Elmo** – United States, Kansas, Dickinson County; Lower Permian, Lower Leonardian, Wellington Fm.; **Midco** – United States, Oklahoma, Noble County, Midco Mb.; Lower Permian, Lower Leonardian, Wellington Fm.; **Chekarda** – Russia, Perm Region, Suksun District; Lower Permian, Kungurian Stage, Koshelevka Fm.; **Vorkuta** – Russia, Perm Region, Pechora Coal Basin; Lower Permian, Ufimian Stage, Lek-Vorkuta and Inta Fms; **Tyulkino** – Russia, Perm Region, Solikamsk District; Lower Permian, Ufimian Stage, Solikamsk Fm.; **Soyana** – Russia, Arkhangelsk Region, Mezen District; Middle Permian, Lower Kazanian Substage, Iva-Gora Beds; **Kityak** – Russia, Kirov Region, Malmyzha District; Middle Permian, Upper Kazanian Substage, Belebei Fm.; **Chepanikha**– Russia, Udmurtia, Sarapul District; Middle Permian, Urzhumian Stage; **Isady** – Russia, Vologda Region, Velikoustyugskii District; Upper Permian, Upper Severodvinian Substage, Poldarsa Formation; Nedubrovo – Russia, Vologda Region, Kichgorodetskii District; Upper Permian, Upper Vyatkian Substage, Vokhma Fm.; **Hammelburg** – Germany, Lower Franconia; Middle Triassic, Early Anisian Stage, Röt Fm. In family Cnemidolestidae "+" designates Kedrovka locality, Russia, Kemerovo Region; Lower Permian, Kungurian Stage, Ishanovian Horizon. In Neraphidiidae "+"designates Belyi Yar locality, Russia, Khakassia, Abakan District; Middle Permian, Urzumian Stage, Izykh Fm.

The family-level diversity of Cnemidolestida in the Carboniferous was relatively modest. The generic diversity and abundance of this order were also rather low, with the exception of the Kasimovian localities Chunya and Izykhskie Kopi in Russia, where Cnemidolestida is one of the dominant insect taxa. A total of seven families of Cnemidolestida are known from the Carboniferous; three of these are also known from the Permian. Permian Cnemidolestida are known from Asselian to Vyatkian deposits of the United States, Czech Republic, Russia, Brazil, Argentina, and possibly Madagascar. The total diversity in the Permian remained at the same level as in the Carboniferous (six families), but the composition, especially beginning with the Kungurian, changed considerably. The highest diversity of this order during this period is found at the end of the Lower Permian (Chekarda) and at the beginning of the Middle Permian (Soyana), but even in these two localities Cnemidolestida make up only 5–6% of all insect families. The highest abundance of this order is also found in Chekarda, where it accounts for 5% of all insect fossils. In the other Permian localities, Cnemidolestida are sporadic. They are not known from the Lower Triassic; the latest unique representative of the order is known from the Middle Triassic of Germany.

Cnemidolestida are distinguished among Paleozoic Gryllones by a set of adaptations associated with facultative phytophilous mode of life and switch to active predation. Originally Cnemidolestida were probably predators that found their prey on plants and were capable of sheltering in the litter when in danger. This mode of life is characteristic of primitive Orthoptera (Gorochov, 1995), from which Cnemidolestida differed in the absence of the set of adaptations to jumping (Gorochov, 2004). Ecologically they were somewhat similar to the recent mantids, although the majority of Cnemidolestida were less specialized predators. Ctenoptilidae and Spanioderidae, which had the most primitive venation, were ambush predators, mainly phytophilous. Their predatory mode of life is indicated by the prognathous head with large eyes, mandibles with long teeth on the cutting edge, absence of paranotalia (which provide for greater motility of the head) on the often elongate pronotum, and prehensile fore legs, sometimes with spines on internal surfaces of femora and tibiae. The most highly specialized (mantid-like) predators were representatives of the family Cnemidolestidae; they had strongly enlarged prehensile fore legs (Aristov, 2012a). Prehensile armature on non-enlarged fore legs has been described in *Ctenoptilus elongatus* (Brongniat, 1893) of the family Ctenoptilidae (Béthoux, 2009) and *Miamia maimai* of the family Spanioderidae (Béthoux *et al.,* 2012). In the other Carboniferous Cnemidolestida, the legs show no adaptations to grasping the prey.

The presence of the arolium and pulvilli on the tarsi and the clinging mid- and hind legs (with tibiae directed anteriad) are adaptations to living on plants. Such legs allow phytophilous insects to perform pulling movements, rather than supporting movements typical of herpetobionts. The anteriad shift of the coxae (at least the procoxae) in Ctenoptilidae and Cnemidolestidae is also an adaptation to this type of movement. Judging by the shape of the mid- and hind legs, specialized phytophilous Cnemidolestida included Ctenoptilidae, Cnemidolestidae, Emphylopteridae, and the genus *Miamia* of the family Spanioderidae. Phytophilous mode of life is also indicated by the presence of cryptic (disruptive) coloration in some Cnemidolestidae and Spanioderidae (Aristov, 2012a; Béthoux *et al.,* 2012; Gu *et al.,* in press).

In Ctenoptelidae, in the genus *Longzhua* of the family Spanioderidae (Gu *et al.,* 2011), and in several other Carboniferous Cnemidolestida, e.g., *Aetophlebia* or *Carbonokata* of the family Cnemidolestidae (Aristov, 2013; Gu *et al.,* in press), the anal area of the forewing is transformed into the clavus. This structure facilitates the bending of strengthened wings during crawling in narrow crevices (Gorochov, 2004) and helps keeping folded wings in a fixed position. Another adaptation to movement in substrates with large crevices is the precostal space or the analogous costal lobe. Adaptation to the stratobiont mode of life results either in flattening or in downward bending of the convex base of the costal space. In the latter case, the point of the bend forms an extra stiffener and can be strengthened by an additional convex vein, the so-called false costa ("C," or ScA). This structure of the precostal space is typical mainly of the superorder Gryllidea (Gorochov, 2004). In some other Gryllones, "C" is absent, and the dilated area at the base of the costal space is separated from the rest of this space by a fold, which forms the costal lobe. The base of SC, situated below this lobe, is often curved and swollen. The precostal space and costal lobe perform the same function as the paranotalia, protecting the wings during movement within litter. Modifications of the base of the costal space are known in some Carboniferous and all Permian families of Cnemidolestida.

This combination of characters suggests that primitive Cnemidolestida were phytophilous predators capable of sheltering from danger in the large-sized plant litter (the *macrolitter*) considerably raised above the ground, typical of the Carboniferous. Large crevices under the deciduous bark of Paleozoic plants could also be used as shelter. In Ctenoptilidae (Fig. 24) and in the spanioderid *Miamia bronsoni* Dana, 1864, clinging legs were combined with the precostal space (costal lobe in *Miamia*) and clavus (Béthoux & Nel, 2005; Béthoux, 2008). Some Cnemidolestidae and Spanioderidae had a more phytophilous mode of life. This is indicated by the absence of modifications of the costal space or clavus. The cryptic coloration of these insects allowed them to hide among vegetation without using shelters. As for the majority of Carboniferous Cnemidolestida, their mode of life was similar to that of *Ctenoptilus*. Others, such as spanioderids of the genus *Longzhua*, judging by the shape of their head and pronotum, were also predators, but their mid- and hind legs were not of the clinging type (their tibiae were directed posteriad), and they had the costal lobe and clavus. Such forms were less strongly associated with plants or entirely stratobiont.

In the Permian, the evolution of Cnemidolestida followed two different paths. Some of them (Sylvabestiidae) remained phytophilous predators. *Sylvabestia* is characterized by strongly enlarged prehensile fore legs and slender and long mid- and, especially, hind legs (Aristov, 2000), adapted to moving on plants. Other families (Tillyardembiidae, Prygidae, and Neraphidiidae) have elongate, flexible bodies with shortened legs, adapted to living in litter or under bark. Psoropteridae should probably also be included in this group, because of their small size (5-6 mm). Prygidae were predators, judging by their strong mandibles with a long tooth on the cutting edge. Tillyardembiidae had curved mandibles, narrow distally and pointed apically; they could be strictly predaceous or polyphagous (Vilesov & Novokshonov, 1993). Facultative feeding on pollen is also known in Tillyardembiidae (Krasilov & Rasnitsyn, 1999), although they were probably not specialized in palynophagy, since pollen has been found only in a few specimens among a total of over 300. They could feed, for instance, on pollen accumulated on the surface of pools, like some extant insects.

Thus, two rather clearly delineated phases can be recognized in the evolution of the order Cnemidolestida: the Carboniferous phase and the Permian phase (the latter prolonged into the very beginning of the Triassic). The Carboniferous assemblage included six families (Cnemidolestidae, Spanioderidae, Gerapompidae, Cymenophlebiidae, Emphylopteridae, and Ctenoptilidae), comprising mainly large insects, which lived mostly on plants and/or, sometimes, in accumulations of large-sized

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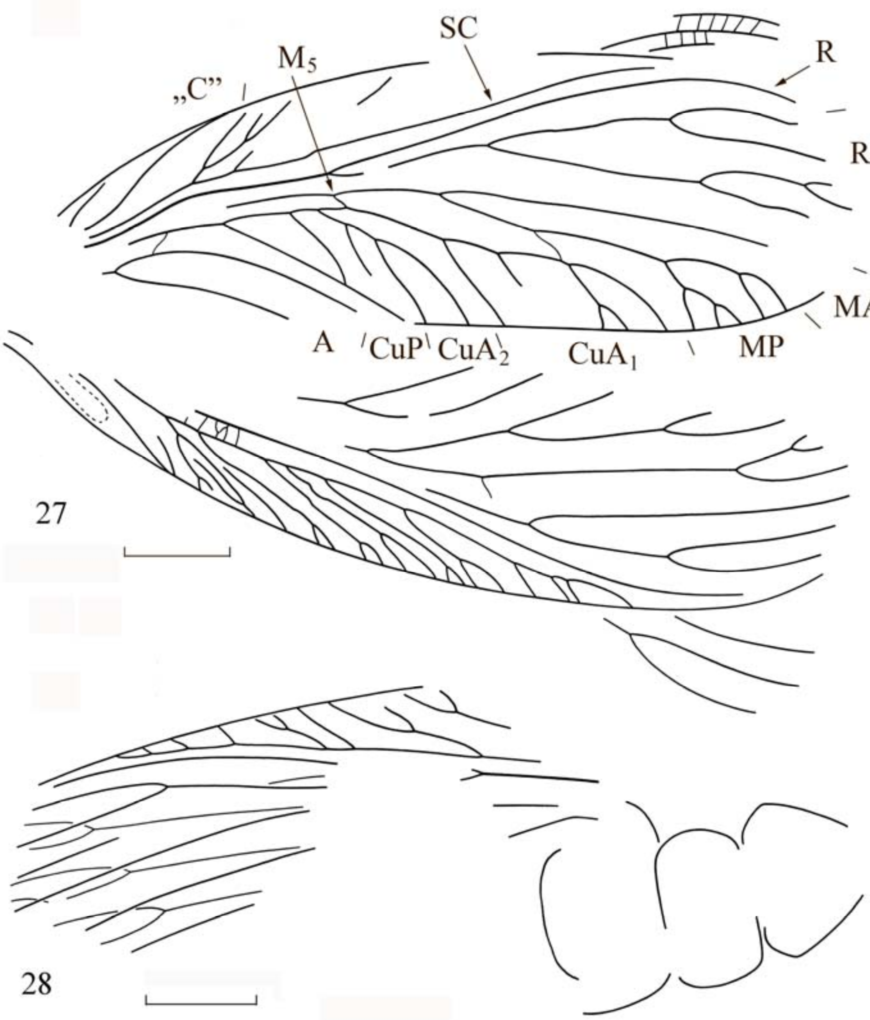
Figs. 25, 26. General appearance of *Cheliphlebia carbonaria* Scudder, 1885, holotype USNM, No 38149, original photo by A.P. Rasnitsyn.

plant remains (the macrolitter) and had adaptations typical of predators of the ambush type and, possibly, of the active type. Only two of these families, Cnemidolestidae and Spanioderidae, survived into the Permian as relicts. The Permian assemblage proper (Tillyardembiidae, Psoropteridae, Sylvabestiidae, Prygidae, and Neraphidiidae) started emerging in the Carboniferous (Neraphidiidae) and comprised almost exclusively relatively small insects living in the litter and displaying appropriate adaptations. Only Sylvabestiidae retained the relatively large size and characteristic mode of life of their Carboniferous ancestors, ambush predators living on plants.

The subsequent specialization of Cnemidolestida of the family Prygidae or similar forms into stratobionts resulted in the emergence of primitive Forficulida of the suborder Protelytrina (Aristov & Rasnitsyn, 2014). This specialization manifested itself in the appearance of the paranotalia, elytrization of the forewing accompanied with minor changes in venation (oligomerization, shift of the apex of SC from R to C, elongation of the ambient vein, etc.) and enlargement of the hindwing, which becomes characteristically transversely bent.

It was shown earlier that the Permian Tillyardembiidae are the sister group of Perlida and that both evolved from Spanioderidae (Aristov & Rasnitsyn, 2009). The Carboniferous genus *Gulou* described later (Béthoux *et al.,* 2011) should, in my opinion, be placed in Emphylopteridae; the morphological reasons for this placement are given above. In addition, Emphylopteridae probably lack one of the principal synapomorphies of Perlida, the aquatic nymphal stage. The earliest doubtless Perlida, both adults and aquatic nymphs, are known from the Kungurian age of the Lower Permian. In later deposits aquatic nymphs of Perlida are constantly found (Sinitshenkova, 1987). No aquatic nymphs that could have belonged to Perlida are known from deposits of the Upper Carboniferous to Kungurian. Until such nymphs are found, it is preferable to include Emphylopteridae in Cnemidolestida. In all likelihood, Perlida evolved in the Lower Permian from Cnemidosterida nymphs similar to Emphylopteridae and Tillyardembiidae as a result of adaptation to living in water.

I have discussed above the similarity of Ctenoptilidae with Cheliphlebiidae. The latter and some related families (Tshekardominidae, Pinideliidae, Juraperlidae, and possibly some others) form a taxon of unclear placement (the "cheliphlebiid complex"). In members of this taxon, the forewing has the precostal space and "C" that separates it or the costal lobe, CuA divided into CuA_1 and CuA_2, M_5 that joins CuA near its division into branches or joins CuA_1, and simple CuP (my unpublished data). The precostal space and the described structure of CuA are the characters of the forewing especially typical of the superorder Gryllidea (Orthopteroidea: Gorochov, 2004). Another character in which these families are similar to Gryllidea is the close position of the first bifurcations of M and CuA. This combination of characters does not allow placing the "cheliphlebiid complex" either in Blattidea or Perlidea. However, these families cannot be placed in any order of Gryllidea either. The "cheliphlebiid complex" is distinguished from all Gryllidea by the presence of posterior branches of CuA in the intercubital space or by SC ending in a bifurcation. Families of this complex are distinguished from the order Orthoptera, in addition to



Figs. 27, 28. General appearance of *Cheliphlebia*: 27 – *C. carbonaria* Scudder, 1885, holotype USNM, No 38149, reconstruction after original photo by A.P. Rasnitsyn; 28 – *C. mazona* Handlirsch, 1911, holotype YPM, No 046, original reconstruction by A.P. Rasnitsyn. Scale bar 5 mm.

these characters, in the absence of paranotalia and in the absence of the set of adaptations to jumping (Gorochov, 2004). They are distinguished from the primitive Mesotitanida (Titanoptera: Gorochov, 2004) also by the simple CuP. A more detailed revision of this group of Gryllones will be published separately. Cheliphlebiidae (*Cheliphlebia* Scudder, 1885 and *Arthrakoris* Richardson, 1956) (Figs 25-29) are similar to Geraridae, especially *Osnogerarus* Kukalová-Peck et

Brauckmann, 1992 (Kukalová-Peck & Brauckmann, 1992). This family was placed in the primitive monotypic suborder Gerarina of the order Mesotitatida and is considered ancestral to the other Gryllidea (Gorochov, 2004). The characters shared by Cheliphlebiidae and Geraridae are the absence of paranotalia, developed “C,” SC ending on C, base of RS shifted to the middle of the wing, M that has M$_5$ joining CuA$_1$ and starts branching in the middle of wing, distal to the base of RS (in *Cheliphlebia*), and CuA divided into CuA$_1$ and CuA$_2$. Cheliphlebiidae are distinguished from Geraridae by the absence of the anastomosis RS+MA, present in the majority of Geraridae, by the presence of the plesiomorphic posterior branches of CuA, absent in Geradidae, and by the simple CuP.

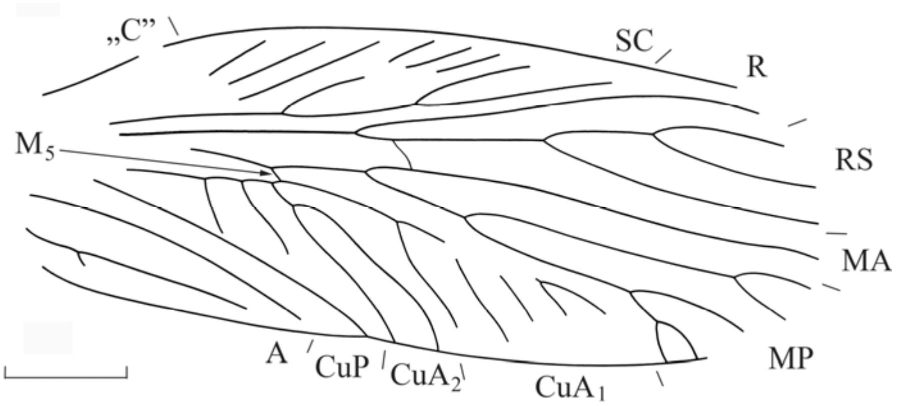


Fig. 29. Forewing of *Anthrakoris aethernus* Richardson, 1956, holotype CNHM no PE, No 145, original reconstruction after Richardson, 1956: fig. 17. Scale bar 5 mm.

Namurian or Early Westphalian forms similar to Ctenoptilidae were most probably the ancestors of Cheliphlebiidae, which separated from Ctenoptilidae with the shift of the apex of SC onto C, shift of the base of RS to the middle of the wing (in *Arthrakoris*), appearance of the division of CuA into CuA$_1$ and CuA$_2$, and shift of M$_5$ onto CuA$_1$. Geraridae, in turn, could have separated from Cheliphlebiidae with the disappearance of posterior branches of CuA in the intercubital space and appearance of the second bifurcation of CuP.

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REFERENCES

Alexeev, A.S. 2006. Dvuchlennoe delenie kamennougol’noi sistemy [Binomial division of the Carboniferous system] P. 527-539. *In*: S.V. Rozhnov (ed.). *Evolyutsiya biosfery i bioraznoobraziya. K 70-letiyu A. Y. Rozanova* [Evolution of the biosphere and biodiversity. Towards the 70th anniversary of A.Y. Rozanov]. Moscow, 600 pp. [In Russian].

Aristov, D.S. 2000. A new family of Early Permian grylloblattids (Insecta: Grylloblattida) from Ural Moutains. *Far Eastern Entomologist*, 85: 1–4.

Aristov, D.S. 2004. The Fauna of Grylloblattid Insects (Grylloblattida) of the Lower Permian Locality of Tshekarda. *Paleontological Journal*, 38 (Suppl.2): 80–145.

Aristov, D.S. 2009. Review of the Stratigraphic Distribution of Permian Grylloblattida (Insecta), with Descriptions of New Taxa. *Paleontologicheskii Zhurnal*, 6: 37–45. [In Russian, English translation *Paleontological Journal*, 43(6): 643–651].

Aristov, D.S. 2011. Revision of the Family Epideigmatidae (Insecta: Grylloblattida). *Paleontologicheskii Zhurnal*, 4: 41–48. [In Russian, English translation *Paleontological Journal*, 45(4): 397–405.]

Aristov, D.S. 2012a. Predstaviteli roda *Narkemina* Martynov (Insecta; Eoblattida: Cnemidolestidae) iz karbona Sibiri [Members of genus *Narkemina* Martynov (Insecta; Eoblattida: Cnemidolestidae) from the Carboniferous of Siberia]. *Modern Paleontology: classical and new methods*. PIN RAS, 37–48 [In Russian].

Aristov, D.S. 2012b. Composition and Distribution of the Family Cacurgidae (Insecta; Grylloblattida). *Paleontologicheskii Zhurnal*, 3: 29–36. [In Russian, English translation *Paleontological Journal*, 46(3): 250–257].

Aristov, D.S. 2013. New or little-known Eoblattida (Insecta) from the Paleozoic of Russia. *Paleontologicheskii Zhurnal*, 3: 39–48. [In Russian, English translation *Paleontological Journal,* 47(3): 272–282].

Aristov, D.S. & Rasnitsyn, A.P. 2009. The family Tillyardembiidae Zalessky, 1938 and the system of the plecopteroid insects. *Russian Entomological Journal*, 18(3): 257-264.

Aristov, D.S. & Rasnitsyn, A.P. 2011. A review of the family Protembiidae (Insecta: Eoblattida). *Russian Entomological Journal*, 20(2): 119–127.

Aristov, D.S. & Rasnitsyn, A.P. 2012. Revision of the Family Idelinellidae, with a Review of the Permian Eoblattida (Insecta). *Paleontologicheskii Zhurnal*, 1: 48–59. [In Russian, English translation *Paleontological Journal*, 46(1): 49–60].

Aristov, D.S. & Rasnitsyn, A.P. 2014. New Eoblattida from the Permian of Russia and USA and Origin of Earwigs (Insecta: Eoblattida, Forficulida). *Paleontologicheskii Zhurnal*, 4: 66-71 [In Russian, English translation *Paleontological Journal*, 48(4): 407–413].

Aristov, D.S. & Storozhenko, S.Yu. 2011. Review of the Permian family Permulidae nomen novum pro Aliculidae Storozhenko, 1997 (Grylloblattida). *In*: Shcherbakov, D.E., Engel, M.S., Sharkey, M.J. (Eds). *Advances in the Systematics of Fossil and Modern Insects: Honouring Alexandr Rasnitsyn*. *ZooKeys*, 130: 111–130.

Aristov, D.S., Storozhenko, S.Yu. & Cui, Y.Y. 2010. Review of the Permian Camptoneuritidae (Insecta: Grylloblattida). *Acta Geologica Sinica*, 84(4): 756–761.

Béthoux, O. 2005. Cnemidolestodea (Insecta): an ancient order reinstated. *Journal of Systematic Palaeontology*, 3(4): 403–408.

Béthoux, O. 2007. Original assignment of genus *Tococladus* Carpenter, 1966 (Insecta: Archaeorthoptera). *Alavesia*, 1: 3.

Béthoux, O. 2008. Revision and Phylogenetic Affinities of the Lobeattid Species *bronsoni* Dana, 1864 and *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980 (Pennsylvanian; Archaeorthoptera). *Arthropod Systematics & Phylogeny*, 66(2): 145–163.

Béthoux, O. 2009. Head and leg morphology of *elongata* Brongniart, 1893: 433 (Late Carboniferous, Archaeorthoptera): phylogenetic and palaeoecological implications. *Annales Zoologici (Warszawa)*, 59(2): 141–147.

Béthoux, O., Cui, Y., Kondratieff, B., Stark, B. & Ren, D. 2011. At last, a Pennsylvanian stem-stonefly (Plecoptera) discovered. *BMC Evolutionary Biology*, 11: 248.

Béthoux, O., Gu, J-J. & Ren, D. 2012. *Miamia maimai* n.sp., a new Pennsylvanian stem-orthopteran insect, and a case study on the application of cladotypic nomenclature. *Fossil Record*, 15(2): 103–113.

Béthoux, O. & Jarzembowski, E. 2010. New basal neopterans from Writhlington (UK, Pennsylvanian). *Alavesia*, 3: 87–96.

Béthoux, O. & Nel, A. 2002. Venational pattern and revision of Orthoptera *sensu* nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa*, 96: 1–88.

Béthoux, O. & Nel, A. 2005. Some Palaeozoic 'Protorthoptera' are 'ancestral' Orthopteroids: major wing braces as clues to a new split among the 'Protorthoptera' (Insecta). *Journal of Systematic Palaeontology*, 2 (4): 285–309.

Béthoux, O. & Wieland, F. 2009. Evidence for Carboniferous origin of the order Mantodea (Insecta: Dictyoptera) gained from forewing morphology. *Zoological Journal of the Linnean Society*, 156: 79–113.

Burnham, L. 1986. Studies on Upper Carboniferous Insects: 2. The Spanioderidae (Order Protorthoptera). *Unpublished D. Phil. Thesis. Cornell University*, xi + 178 pp.

Carpenter, F.M. 1976. The Lower Permian insects of Kansas. Part 12. Protorthoptera (continued), Neuroptera, additional Palaeodictyoptera, and families of uncertain position. *Psyche*, 83: 336–376.

Carpenter, F.M. 1992. *Treatise on Invertebrate Paleontology. Part R. Arthropoda 4. Vol. 3: Superclass Hexapoda*. Boulder, Colorado and Lawrence Publishers, Kansas. 655 pp.

Davydov, V.I., Korn, D. & Schmitz, M.D. 2012. With contributions from F.M .Gradstein and O.Hammer. Chapter 23. The Carboniferous Period. P. 603-651. *In*: Gradstein F.M. et al. (Eds.). *The Geologic Time Scale*. Elsevier BV, xviii + 1144 pp.

Gorochov, A.V. 1995. *Sistema i evolyutsiya pryamokrylykh podotryada Ensifera* (*Orthoptera*) [System and Evolution of the Suborder Ensifera (Orthoptera)]. Pt. 1, 2. *Trudy Zoologicheskogo Instituta Rossiiskoi Akademii Nauk*, 260: 224 + 212 pp. [In Russian].

Gorochov, A.V. 2004. Primitivnye Titanoptera i rannyaya evoluciya Polyneoptera [Primitive Titanoptera and the Early Evolution of the Polyneoptera]. *Lectures in Memory of N.A. Kholodkovskii*, 57(1): 1–54. [In Russian].

Grimaldi, D. & Engel, M.S. 2005. *Evolution of the insects*. Cambridge university press. xv + 755 pp.

Gu, J-J., Béthoux, O. & Ren, D. 2011. *Longzhunia locustata* n. gen. n. sp. one of the most completely documented Pennsylvanian Archaeorthoptera (Insecta; Ningxia, China). *Journal of Paleontology*, 85(2): 303–314.

Gu, J., Béthoux, O. & Ren, D. 2013. A new cnemidolestodean stem-Orthoptera (Insecta, Archaeorthoptera) from the Late Carboniferous of China. *Acta Palaeontologica Polonica*. in press (doi: http://dx.doi.org/10.4202/app.2011.0045).

Gutörl, P. 1934. Die Arthropoden aus dem Carbon und Perm des Saar-Nahe-Pfalz-Gebietes. *Abhandlungen der koenigliche pressischen geologischen Landesanstalt*, 164: 1-219.

Hamilton, K.G.A. 2003. Cnemidolestodea: an ancient insect order resurrected. *Biodiversity*, 4(2): 22–24.

Handlirsch, A. 1906-1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen.* Wilhelm Engelmann, Leipzig, 1430 pp.

Handlirsch, A. 1922. *Fossilium Catalogus. I: Animalia. Pars 16: Insecta palaeozoica.* W. Junk, Berlin, 230 pp.

Handlirsch, A. 1937. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. I Teil. *Annalen des Naturhistorischen Museums in Wien*, 48: 1–140.

Huang, D-Y. & Nel, A. 2009. Oldest webspinners from the Middle Jurassic of Inner Mongolia, China (Insecta: Embiodea). *Zoological Journal of the Linnean Society*, 156: 889–895.

Krasilov, V.A. & Rasnitsyn, A.P. 1999. Plant remains from the guts of fossil insects: Evolutinary and Paleoecological inferences. *Proceeding of the first Palaeoentomological Conference*. Moscow, 1998: 65-72.

Kukalová, J. 1964. Permian insects of Moravia. Pt. 2. Liomopteridae. *Sborník geologických věd. Paleontologie*, 3: 39–118.

Kukalová-Peck, J. & Brauckmann, C. 1992. Most Paleozoic Protorthoptera are ancestral hemipteroids: major wing braces as clues to a new phylogeny of Neoptera (Insecta). *Canadian Journal of Zoology*, 70: 2452–2473.

Laurentiaux, D. & Laurentiaux-Vieira, F. 1980. Un type singulier d'Insecte protorthoptéroïde du Westphalien supérieur du Pas-de-Calais. *Annales de la Société Géologique du Nord*, 99: 407–413.

Lewis, S.E. 1979. A new specimen of Insect (Protorthoptera: Narkemidae) from the Verdigris Formation (Pennsylvanian) of the West Central Missouri. *Journal of Paleontology*, 53: 754–756.

Liu, Y., Ren, D. & Prokop, J. 2009. Discovery of a new Namurian archaeorthopterid from Ningxia, China (Insecta: Archaeorthoptera). *Zootaxa*, 2032: 63–68.

Martins-Neto, R.G., Gallego, O.F., Brauckmann, C. & Cruz, J.L. 2007. A review of the South American Palaeozoic entomofauna Part I: the Ischnoneuroidea and Cacurgoidea, with description of new taxa. *African Invertebrates*, 48(1): 87–101.

Martynov, A.V. 1938. An essay on the geological history and phylogeny of the insect orders (Pterygota). Pt. I. Palaeoptera and Neoptera-Polyneoptera. *Trudy Paleontologicheskogo Instituta AN SSSR*, 7(4): 148 p. [In Russian].

Martynov, A.V. 1940. Permskie iskopaemye nasekomye Chekardy [Permian Fossil Insects of Tshekarda]. *Trudy Paleontologicheskogo Instituta AN SSSR*, 11(1): 5–62. [In Russian].

Newell, A.J., Sennikov, A.G., Benton, M.J., Molostovskaya, I.I., Golubev, V.K., Minikh, A.V. & Minikh, M.G. 2010. Disruption of playa–lacustrine depositional systems at the Permo-Triassic boundary: evidence from Vyazniki and Gorokhovets on the Russian Platform. *Journal of the Geological Society*, 167: 695–716.

Novokshonov, V.G. 1999. New Fossil Insects (Insecta: Hypoperlida, Panorpida, Ordinis incertis) from the Chekarda Locality. *Paleontologicheskii Zhurnal*, 1: 54–58. [In Russian, Englisch translation *Paleontological Journal*, 33(1): 52–56].

Pinto, I.D. 1990. A new Upper Carboniferous paraplecopteran insect from South Brazil. *Pesquisas. Inst. Geociencias. U.F.R.G.P. Porto Alegre*, 17(1-2): 7–10.

Pinto, I.D. & Ornellas, L.P. 1978. Carboniferous insects (Protorthoptera and Paraplecoptera) from the Gondwana (South America, Africa and Asia). *Pesquisas. Inst. Geociencias. U.F.R.G.P. Porto Alegre*, 11: 305–321.

Pinto, I.D. & Ornellas, L.P. 1991. Substitute Names for the Extint Insecta Families Narkemocacurgidae Pinto & Ornellas, 1978 and Cacurgonarkemina Pinto, 1990. *Pesquisas. Inst. Geociencias. U.F.R.G.P. Porto Alegre*, 18(1): 93.

Prokop, J. & Ren, D. 2007. New significant fossil insects from the Upper Carboniferous of Ningxia in northern China (Palaeodictyoptera, Archaeorthoptera). *European Journal of Entomology*, 104: 267–275.

Prokop, J., Krzeminski, W., Krzeminska, E., Hörnschemeyer, T., Ilger, J.-M., Brauckmann, C., Grandcolas, P. & Nel, A. 2013a. Late Palaeozoic Paoliida is the sister group of Dictyoptera (Insecta: Neoptera). *Journal of Systematic Palaeontology*, doi: http://dx.doi.org/10.1080/ 14772019.2013.823468.

Prokop, J., Roques, P. & Nel, A. 2013b. New non-holometabolous insects from the Pennsylvanian of the Avion locality in Pas-de-Calais, France (Insecta:'Exopterygota'). *Alcheringa: An Australasian Journal of Palaeontology*, doi: 10.1080/03115518.2014.848620.

Pruvost, P. 1919. *La faune continentale du terrain houiller du Nord de la France*. Mémoires pour servir à l'explication de la carte géologique détaillée de la France, 584 pp.

Rasnitsyn, A.P. 1980. Infraklass Gryllones Laicharting, 1781; Otryad Gerarida Handlirsch, 1906 [Infraclass Gryllones Laicharting, 1781; Order Gerarida Handlirsch, 1906]. *In*: Rodendorf B.B. & Rasnitsyn A.P. (Eds.) Istorocheskoe razvitie klassa nasekomykh [Historical Development of the Class Insecta]. *Trudy Paleontologicheskogo Instituta AN SSSR*, 178: 134–135; 164–165. [in Russian].

Rasnitsyn, A.P. 2002. Infraclass Gryllones Laicharting, 1781. Order Eoblattida Handlirsch, 1906 Superorder Perlidea Latreille, 1802. P. 254-256; 256-260, 276-278. *In*: Rasnitsyn, A.P. & Quicke, D.L.Q. (Eds.) *History of Insects.* Dordrecht, Kluwer Academic Publishers, Dordrecht. 517 pp.

Rasnitsyn, A.P. & Aristov, D.S. 2013. 2.1. New Fossil Insects (Insecta: Caloneurida, Hypoperlida, Palaeomanteida, Jurinida) from the Middle and Upper Permian of European Russia. P. 678-704. *In*: Aristov, D.S. (ed.) Fossil Insects of the Middle and Upper Permian of European Russia. *Paleontological Journal*, 47(7): 641–832.

Rasnitsyn, A.P., Aristov, D.S., Gorochov, A.V., Rowland, J.M. & Sinitshenkova, N.D. 2004. Important new insect fossils from Carrizo Arroyo and the Permo-Carboniferous faunal boundary. P. 215-246. *In*: S. Lucas, G. & Zeigler, K.E. (Eds.). *Carboniferous–Permian transition at Carrizo Arroyo, Central New Mexico*. Bulletin of the New Mexico Museum of Natural History and Science, 25: 301 pp.

Rasnitsyn, A.P. & Quicke, D.L.J. (Eds.). *History of insects*. Kluwer Academic Publishers, Dordrecht. 517 pp.

Ross, A.J., Nicholson, D.B. & Jarzembowski, E.A. 2013. Omaliidae Handlirsch, 1904 (Insecta, Archaeorthoptera) and Xenopteridae Pinto, 1986 (Insecta, Megasecoptera): proposed emendation to Omaliidae and Xenopteridae respectively to remove homonymy with Omaliinae MacLeay, 1825 (Insecta, Coleoptera) and Xenopteridae Riek, 1955 (Insecta, Orthoptera). *Bulletin of Zoological Nomenclature*, 70(3): 166–170.

Sawin, R. S., Franseen, E. K., West, R. R., Ludvigson, G. A., & Watney, W. L. 2008. Clarification and changes in Permian stratigraphic nomenclature in Kansas. *In*: *Current Research in Earth Sciences: Kansas Geological Survey*, 254(2) [available online: http://www.kgs.ku.edu/Current/2008/Sawin/index.html].

Schlechtendal, D. 1913. Untersuchung über die karbonischen Insekten und Spinnen von Wettin unter Berücksichtigung verwandter Faunen. Erster Teil: Revision der Originale von Germar, Giebel und Goldenberg. *Nova Acta Leopoldina*, 98: 1–186.

Schmidt, W. 1953. *Herbstiala herbsti* n. g. et n. sp. (Herbstialidae n. fam., Protocicada), das erste Insekt aus dem Eckelenzer Karbon (Westfal A). *Paläontologische Zeitschrift*, 27, 149–168.

Sharov, A.G. 1962. Otryad Paraplecoptera [Order Paraplecoptera]. P. 119–134. *In*: Rohdendorf, B.B. (Ed.). *Osnovy paleontologii. Chlenistonogie, trakheinye i khelitserovye* [Fundamentals of Paleontology: Arthropods, Tracheates, and Chelicerates]. AN SSSR Publ., Moscow. 560 p. [In Russian].

Sinitshenkova, N.D. 1987. Istoricheskoe razvitie vesnyanok [Historical development of the stoneflies]. *Trudy Paleontologicheskogo Instituta AN SSSR*, 221: 144 pp. [In Russian].

Sinitshenkova, N.D. 2002. Superorder Dictyoneuridea Handlirsch, 1906. P. 115-116. *In*: Rasnitsyn, A.P. & Quicke, D.L.Q. (Eds.) *History of Insects.* Dordrecht, Kluwer Academic Publishers, Dordrecht. 517 pp.

Storozhenko, S.Yu. 1996. New Upper Carboniferous grylloblattids (Insecta: Grylloblattida) from Siberia. *Far Eastern Entomologist*, 26: 18–20.

Storozhenko, S.Yu. 1997. Classification of order Grylloblattida (Insecta) with description of new taxa. *Far Eastern Entomologist*, 42: 1–20.

Storozhenko, S.Yu. 1998. *Sistematika, filofeniya i evolyutsiya grilloblattidovykh nasekomykh* (*Insecta:Grylloblattida*) [Sistematics, phylogeny and evolution of the grylloblattids (Insecta:Grylloblattida)]. Dalnauka, Vladivostok. 207 pp. [In Russian].

Storozhenko, S.Yu. 2002. Order Grylloblattida Walker, 1914 (= Notoptera Crampton, 1915, = Grylloblattodea Brus et Melander, 1932, + Protorthoptera Handlirsch, 1906, = Paraplecoptera Martynov, 1925, + Protoperlaria Tillyard, 1928). P. 278–281. *In*: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds.). *History of insects*. Kluwer Academic Publishers, Dordrecht. 517 pp.

Vilesov, A.P. & Novokshonov, V.G. 1993. Permian Tillyardembiidae (Insecta, Grylloblattida). *Paleontologicheskii Zhurnal*, 3: 56–65. [In Russian, English translation *Paleontological Journal*, 27(3): 71–82].

Zalessky, G.M. 1938. Les nouveaux insects permiens de l'odre Emboidea. *Annales de la Société Géologique du Nord*, 63: 62–81.

Zalessky, G.M. 1950. Novye nasekomye basseina reki Sylva i voprosy evolyucii v klasse nasekomykh. IV. Novye predstaviteli gruppy Epiembioidea i evoluciya embii [Permian insects of the Sylva River basin and problems of evolution in the class Insecta. IV. New representatives of the group Epiembioidea and the webspinner evolution]. *Problemy paleontologii*, 1: 41–60. [In Russian].