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A new basal osmylid neuropteran insect from the Middle Jurassic of China linking Osmylidae to the Permian–Triassic Archeosmylidae

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A new osmylid neuropteran insect *Archaeosmylidia fusca* gen. et sp. nov. is described from the Middle Jurassic locality of Daohugou (Inner Mongolia, China). Its forewing venation differs from that of other hitherto known osmylids by a set of plesiomorphic features. This genus is considered here as representing a basal group of Osmylidae. The Permian–Triassic family Archeosmylidae comprises the genera *Archeosmylus*, *Babykamenia*, and *Lithosmylidia*. *Archaeosmylidia* and Archeosmylidae share the few-branched CuP, the absence of zigzag vein pattern, and the scarcity of the crossveins in the radial space. We estimate that Osmylidae might have originated in the Triassic from some "archeosmylid-like" ancestor.

Key words: Neuroptera, Osmylidae, Archeosmylidae, Jurassic, Daohugou, China.

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Introduction

The family Osmylidae has a rich fossil history in comparison with other neuropteran families, going back to the Early Jurassic. These oldest osmylids are represented by four genera, *Mesosmylina* Bode, 1953, *Sogjuta* Martynova, 1958, *Petrushevskia* Martynova, 1958, and probably *Tetanoptilon* Bode, 1953 from Germany, Mongolia, and Kyrgyzstan (Bode 1953; Martynova 1958; Ponomarenko 1984, 1996; Lambkin 1988; Ansorge 1996). Their venation is quite typical for Osmylidae assuming an earlier divergence of the family from its ancestor.

The diversity of osmylids in the Middle–Upper Jurassic was probably highest than in any other period. The Chinese locality Daohugou being of this age has yielded numerous varied osmylids represented by more than one thousand known specimens (QY and VNM, unpublished data). Some of these are similar to extant taxa of different subfamilies (see e.g., Wang et al. 2009b, 2010), while some are very dissimilar, represented by taxa not crossing into the Cretaceous. For example, there were the large and extremely multi-veined species of the extinct subfamily Saucrosmylinae and of another yet undescribed extinct subfamily, as well as many species of the relict subfamily Gumillinae, some of which being minute species with peculiar and reduced venation (Ren and Yin 2003; Ren and Engel 2007; Wang et al. 2009a; Yang et al. 2010). Among this material, a new osmylid genus was discovered whose venation appears to be most "primitive" and somewhat similar to that of Archeosmylidae. Riek (1976: 788) argued that the Late Permian–Triassic family Archeosmylidae "is apparently directly ancestral to Osmylidae". The study of this new genus probably supports this supposition.

In the present paper, we describe a new genus and species of Osmylidae, discuss its systematic position and phylogenetic implications, analyze the composition of Archeosmylidae and provide its characteristics.

Institutional abbreviations.—CNUB, Capital Normal University, Beijing, China; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Other abbreviations.—Venation abbreviations: 1A–3A, anal veins; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media (M); ng, nygma; R1, first branch of radius (R); Rs, radial sector; Rs1, most proximal branch of Rs; Sc, subcosta.

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Material and methods

This study is based on one specimen collected near Daohugou Village (Shantou Township, Ningcheng County, Inner Mongolia, China). The insect-bearing beds are considered as belonging to the Jiulongshan Formation dated as Bathonian (Middle Jurassic) (Gao and Ren 2006). The map of the Daohugou locality is given in Wang et al. (2009a: fig. 1). The specimen was examined using an MZ12.5 dissecting microscope a Leica, illustrated with the aid of Adobe Photoshop, and photographed with a Nikon SMZ1000.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Osmylidae Leach, 1815

Genus *Archaeosmylidia* nov.

Type species: *Archaeosmylidia fusca* sp. nov., by monotypy; see below.

Etymology: From Greek *archaios*, old, primitive; and *Osmylidia*, an osmylid genus-group name, in reference to the primitive appearance. Gender feminine.

Diagnosis.—Differs from other osmylid genera by the combination of the following character states: subcostal crossveins numerous; all longitudinal veins not zigzagged; CuP few-branched, non-pectinate.

Archaeosmylidia fusca sp. nov.

Fig. 1.

Etymology: From Latin *fuscus*, dark; in reference to dark coloration of the wing.

Holotype: Specimen CNU-NEU-NN2009103. An excellently-preserved, nearly complete forewing.

Type locality: Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Type horizon: Jiulongshan Formation, Bathonian, Middle Jurassic (Gao and Ren 2006).

Description.—Forewing about 15.0 mm long (as preserved; estimated complete length about 15.5 mm), 5.7 mm wide. Costa anteriorly thick, especially basally. Trichosors prominent along hind margin, hardly visible along anterior apical margin, absent proximally. Costal space typical for Osmylidae, moderately dilated. Subcostal veinlets simple (two forked near costal margin); three basal-most markedly stouter than rest; strongly curved in medial part of costal space; closely spaced, especially in pterostigmal region. No crossveins between subcostal veinlets. Pterostigma barely evident. Subcostal space relatively broad, especially in distal portion; with 16 crossveins detected, of these three basal-most stouter, distal ones weak, poorly-discernible. Stem of Rs smooth, not zigzagged. R1 space very narrow, comparable in width with subcostal space. Proximal nygma clearly visible, located distal to origin of Rs1; distal nygma not detected. Ten crossveins, more or less regularly spaced in R1 space (between R1 and Rs); all well proximal to fusion of Sc and R1, no crossveins distal to this fusion detected. Crossveins between branches of Rs scarce, mostly form three irregular gradate series. Rs with 15 branches, not forked before outer gradate series; distal branches nearly straight, only slightly smoothly curved, not sinuous. Origin of M appears to originate from R at wing base. M deeply forked, slightly distal to origin of Rs1. MA and MP parallel before marginal dichotomous branching. Cu dividing into CuA and CuP near wing base; CuA and CuP sub-parallel before branching of CuP. CuA pectinate, with six oblique branches, mostly once forked. CuP relatively short, few-branched with two very oblique branches. 1A long, pectinate, with eight simple oblique branches. 2A pectinate, with seven simple oblique branches. 3A not preserved. Wing membrane fuscous, costal space slightly lighter except near costa.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion and conclusions

Characters of *Archaeosmylidia* forewing.—The forewing *Archaeosmylidia* differs from ones of other hitherto known osmylid genera by its "primitive" appearance. This is exhibited in particular by some venational details more characteristic of other families with generalized venation (e.g., Ithonidae and Nevrorthidae) than Osmylidae: (i) the entire absence of zigzag pattern characteristic of most other osmylids including the oldest, Early Jurassic (i.e., the longitudinal veins in *Archaeosmylidia* are smooth, not zigzagged); (ii) the pectinate branching of CuA, 1A and 2A are somewhat more oblique than in most other osmylids; (iii) some subcostal veinlets are markedly curved (straight or only slightly curved in other osmylids); (iv) the non-pectinate CuP (strongly pectinate in most other osmylids); (v) the crossveins in the radial to medial spaces are scarce. All these features taken together make the forewing venation of this species "primitive".

The important forewing characters are considered below.

Subcostal crossveins.—Osmylidae have normally one basal crossvein between Sc and R. The numerous subcostal crossveins as found in *Archaeosmylidia* occur very rarely in this family. The monotypic Australian subfamily Porismidae, with *Porismus strigatus* (Burmeister, 1839), is probably the only exception among the extant taxa. Also, there are two fossil genera, *Osmylochrysa* Jepson, Makarkin, and Coram, 2012 from the English Purbeck having widely spaced subcostal crossveins (Jepson et al. 2012), and an undescribed genus from Daohugou which has many closely spaced crossveins between Sc and R/R1 (Chaofan Shi, VNM, QY, and DR, unpublished data). No subcostal crossveins are detected in Archeosmylidae. We presume that the presence of numerous crossveins between Sc and R/R1 is autapomorphic of these four genera because their venation is strongly dissimilar to each other and they likely represent different lineages.

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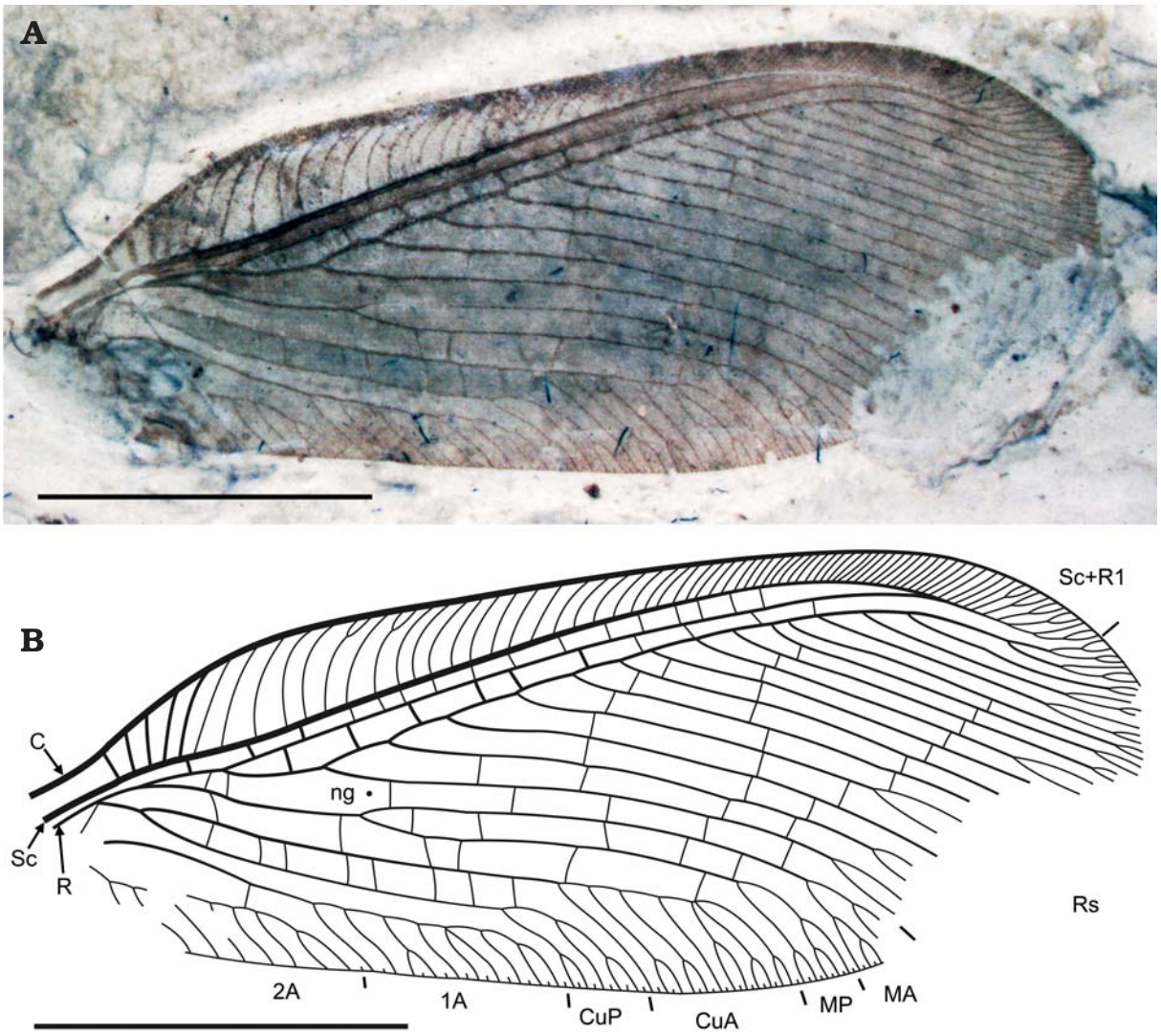


Fig. 1. Forewing of osmylid neuropteran insect *Archaeosmylidia fusca* gen. et sp. nov. (Osmylidae) from the Jiulongshan Formation of Daohugou, China. Holotype CNU-NEU-NN2009103. Photograph (**A**) and line drawing of venation (**B**). Scale bars 5 mm. Abbreviations: 1A, 2A, anal veins; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media (M); ng, nygma; R1, first branch of radius (R); Rs, radial sector; Sc, subcosta.

The subcostal/R1 spaces ratio.—In the majority of the osmylid genera the subcostal space is narrow, narrower (sometimes much narrower) than the R1 space (between R1 and Rs). In *Archaeosmylidia*, these spaces are nearly equal in width, as the subcostal space is dilated as compared with that of other osmylids, and the R1 space is narrow. The ratio of these spaces of *Archaeosmylidia* is similar to that of Archeosmylidae (Fig. 2).

Distal branches of Rs.—These branches in *Archaeosmylidia* are nearly straight for most of their length or slightly curved. This condition is plesiomorphic as it occurs in the majority of other families, including ones known from the Permian. The distal branches of Rs of the most extant osmylids are sinuous, more or less expressed.

Radial crossveins.—In the vast majority of the extant and extinct Osmylidae, the crossveins in the radial space are numerous and not arranged in gradate series except one outer. The arrangement of the crossveins in the genera of Mesosmylininae and Protosmylinae is rather similar to that of *Archaeosmylidia*, i.e., relatively scarce and arranged mainly in few gradate series.

Branching of CuA.—There is much variety in this branching observed across the osmylids. CuA is clearly (sometimes strongly) pectinate in the subfamilies Mesosmylininae, Protosmylinae, Saucrosmylinae (some), Gumillinae (many), Spilosmylinae, Porisminae, Osmylinae (some), and clearly not pectinate (sometimes simple with only marginal fork) in the subfamilies Saucrosmylinae (some), Eidoporisminae, Kempyninae, Stenosmylinae, Osmylinae (some). It should be noted that the pectinate branches of CuA originate at an obtuse angle (apomorphic state), differing from Archeosmylidae (see below). The non-pectinate branching of CuA in Osmylidae is probably secondary.

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Branching of CuP.—CuP is pectinate (often strongly) in the vast majority of known genera of Osmylidae; branches of CuP originate at obtuse angle. The only other known subfamily with the non-pectinate branching of CuP is the Middle Jurassic Saucrosmylinae. However, this taxon is now regarded as a distinct family, Saucrosmylidae (Wang et al. 2011).

Systematic position of *Archaeosmylidia*.—This genus can not be assigned to any of the ten known subfamilies of Osmylidae. It is very unlike Osmylinae, Kempyninae, Stenosmylinae, Porismimae, Eidoporismimae, and Spilosmylinae comprising the vast majority of the genera of the Recent fauna. Also, the fossil Saucrosmylinae and Gumillinae represented in Daohugou are very different from it by many derived features. *Archaeosmylidia* most resembles the genera of Protosmylinae and Mesosmylininae, but it cannot be assigned to any of them. These subfamilies have quite similar forewings (e.g., relatively small with the crossveins in the radial space are arranged mainly in few gradate series), and may be synonyms. The majority of the oldest osmylid genera (the Early Jurassic *Mesosmylina*, *Sogjuta*, and *Petrushevskia*) probably all belong to Mesosmylininae. Protosmylinae are known from the Middle Jurassic to today (Wang et al. 2010). Until the discovery of *Archaeosmylidia*, these two subfamilies possessed the most "primitive" wings. The protosmyline and mesosmylinine genera clearly differ from *Archaeosmylidia* in particular by the pectinate CuP and the zigzag vein pattern. It is obvious that this genus represents some basal group, but we refrain from establishing a new subfamily pending detailed phylogenetic analysis of entire group.

Archeosmylidae.—The forewing venation of *Archaeosmylidia* is rather similar to that of some species of the poorly-known Late Permian–Triassic family Archeosmylidae. This family was created by Riek (1953) for the monotypic genus *Archeosmylus* Riek, 1953 based on *A. pectinatus* Riek, 1953 from the Late Permian of Australian Belmont, Queensland. Later, three additional species of this genus have been identified from the Carnian (Late Triassic) of Australia (i.e., *A. stigmatus* Riek, 1955 and *A. costalis* Riek, 1955 from the Mount Crosby Formation of New South Wales, and an unnamed species from the Blackstone Formation of Denmark Hill, Queensland), and two species from the Rhaetian (Late Triassic)–earliest Jurassic of Gloucestershire, England (*A. complesus* Whalley, 1988 and *A. alysius* Whalley, 1988) (Riek 1955, 1956; Whalley 1988; Jarzembowski 1999). Ponomarenko (1996) subsequently transferred these two British species to the genus *Prohemerobius* Handlirsch, 1906, and therefore to Prohemerobiidae. Although their assignments to *Prohemerobius* are probably incorrect (judging from the examination of the type species of *Prohemerobius*), these two species are most probably not congeneric with *A. pectinatus*; their actual generic and family affinities will be clear only after the re-examination of their types. Actual generic affinities of "*Archeosmylus*" *stigmatus* and "*A.*" *costalis* are also not clear.

One unnamed species from the Middle Beaufort Series (Late Permian) of Natal (South African Republic) was assigned to Archeosmylidae based on a fragmentary wing (Riek 1976: pl. 6: 6).

The only other genus described in this family is the monotypic genus *Babykamenia* Ponomarenko and Shcherbakov, 2004 from the terminal Permian–basal Triassic Maltsevo Formation of Babii Kamen' in Siberia (Ponomarenko and Shcherbakov 2004). The single species is represented by a crumpled forewing.

The genus *Lithosmylidia* Riek, 1955 from the Middle to Upper Triassic of Australia most likely can be assigned to Archeosmylidae as well. It is heterogeneous genus, and each species (*L. lineata* Riek, 1955, *L. barrone* Lambkin, 1988, and *L. parvula* Lambkin, 1988) might be generically distinct. Lambkin (1988: 457) determined family affinities of known species to be "species similar to Osmylidae or Polystoechotidae, but not able to be placed in either" for *L. barrone* and *L. parvula*, and "probable Polystoechotidae" (Lambkin 1988: 457) for *L. lineata*. The latter species is the type of the genus; it was subsequently removed from Polystoechotidae (Archibald and Makarkin 2006) and was not included in Ithonidae sensu lato (Winterton and Makarkin 2010). We believe that all three species may belong to the family Archeosmylidae. This implies from the examination of numerous undescribed wings having similar venation from Middle–Upper Triassic of the Madygen Formation, Kyrgyzstan in Central Asia (Fig. 2) (see Shcherbakov 2008 for characteristics of the locality). The venation of these wings is very similar to that of *Lithosmylidia* (especially to *L. lineata*) and *Babykamenia*; these taxa certainly belong to the same family (compare Fig. 2 with Lambkin 1988: fig. 1, and Ponomarenko and Shcherbakov 2004: fig. 3). However, the association of these Triassic taxa with the Late Permian *Archeosmulus pectinatus* (the type of Archeosmylidae) is not obvious. The main problem is that the holotype of *A. pectinatus* is represented by an incomplete forewing. Nevertheless, its preserved venation has all main features in common with that of *Lithosmylidia*, *Babykamenia* and undescribed taxa from the Madygen Formation (see Riek 1953: fig. 66; Jell 2004: two upper figures on p. 81).

We consider the following described genera as confamilial and belonging to Archeosmylidae: *Archeosmylus* (only type species *A. pectinatus*), *Babykamenia* (one species, *Babykamenia eskovi* Ponomarenko and Shcherbakov, 2004), and *Lithosmylidia* (three species: *L. lineata*, *L. barrone*, and *L. parvula*). The forewing of this family is preliminarily characterized as follows: The costal space is similarly constructed to that of Osmylidae, with mainly simple subcostal veinlets; the subcostal crossveins are not detected; Sc and R1 are fused distally; Sc+R1 is smoothly curved running nearly parallel to the costal margin, entering wing margin well before apex; M is forked distal to the origin of Rs; Cu is divided into CuA and CuP near to the wing base; CuA, CuP and 1A are few-branched, often pectinate, but their branches are very oblique and not as strongly pectinate as in Osmylidae; the crossveins in the radial space are scarce, often very rare. The

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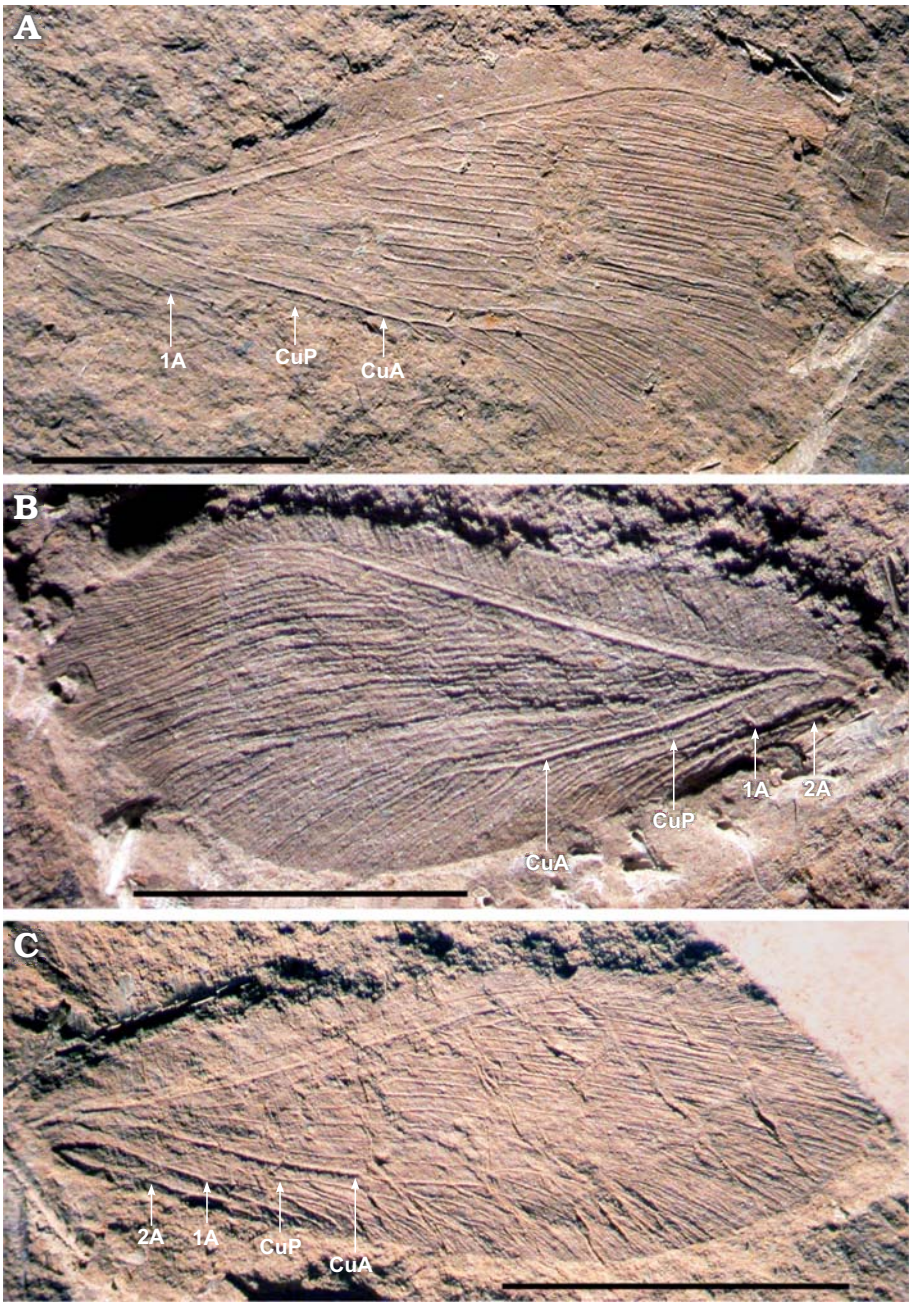


Fig. 2. Forewings of undescribed archeosmylid insects from the Madygen Formation, Middle to Upper Triassic, Kyrgyzstan, Central Asia. **A**. PIN 2785/4081. **B**. PIN 2555/ 2096. **C**. PIN 2069/3604. Scale bars 5 mm. Abbreviations: 1A, 2A, anal veins; CuA, anterior cubitus; CuP, posterior cubitus.

known temporal range of the family is from the Late Permian to Late Triassic.

Archeosmylidae are sometimes considered a synonym of Permithonidae (Whalley 1988; Makarkin and Archibald 2003; Engel and Grimaldi 2008), but its validity (as treated here) is unquestioned. Permithonidae is easily differentiated from Archeosmylidae by R1 (or Sc+R1) being distally straight, not running parallel to the costal margin, M profusely branched, often proximad the origin of Rs, and CuP simple or at most with a marginal shallow fork.

Phylogenetic implications.—Osmylidae and Archeosmylidae (as treated herein) are probably closely related families. Their known temporal ranges are not overlapping: Late Permian to the Late Triassic for Archeosmylidae, and the Early Jurassic to today for Osmylidae. They have generally similar venation, but conspicuously differ by the forewing configuration of CuP and/or CuA. These are strongly pectinate with branches that originate at obtuse angle in the vast majority of the osmylid genera and are never strongly pectinate with branches that originate at acute angle in Archeosmylidae. Differing from most other osmylids, *Archaeosmylidia* and Archeosmylidae share the few-branched CuP, the absence of zigzag vein pattern, and the scarcity of the crossveins in the radial space. It is quite possible that *Archaeosmylidia* represents a relict of the Triassic–Early Jurassic osmylids that survived into the Middle–Upper Jurassic fauna retaining these and some other "primitive" features. Osmylidae might have originated in the Triassic from some "archeosmylid-like" ancestor,

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as predicted by Riek (1976). One contradiction to this hypothesis is that the nygmata are not detected yet in Archeosmylidae, but these are present in all osmylids, including *Archaeosmylidia*. It is possible, however, that the state of preservation of known archeosmylids is not good enough to preserve the nygmata. The presence of these structures is a plesiomorphic state in the order, and their reformation from the membrane is very unlikely. Therefore, a hypothetic ancestor of Osmylidae had to possess the nygmata.

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