

## New Axymyiidae (Insecta: Diptera) from the Mesozoic of East Siberia

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**ABSTRACT.** The new species of Axymyiidae *Juraxymyia krzeminskii* sp. n. and *Sinaxymyia szadziewskii* sp. n. from the Lower Cretaceous beds of Transbaikalia and *Juraxymyia evae* sp. n. from the Lower Cretaceous beds (Upper Jurassic not excluded) of Yakutia are described.

**KEY WORDS:** Axymyiidae, new species, Upper Jurassic, Lower Cretaceous.

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### INTRODUCTION

Axymyiidae is a small relict enigmatic family of nematoceros flies with uncertain phylogenetic placement. For a long time the single known genus *Axymyia* MCATEE, 1921 was placed as a member of various families (Anisopodidae, Bibionidae, Pachyneuridae; details in MAMAEV & KRIVOSHEINA 1966). Now most authors agree with a separate family status suggested by MAMAEV & KRIVOSHEINA; its infraorder position is debatable, however: Tipulomorpha (ROHDENDORF 1946), Bibionomorpha (HENNIG 1968, SHCHERBAKOV et al. 1995, WIEGMANN et al. 2011) or Axymyiomorpha (WOOD & BORKENT 1989, KOVALEV 1989, KRZEMIŃSKA et al. 1993, KRZEMIŃSKI & KRZEMIŃSKA 2003). Recently, axymyiids became a focus of attention as the subject of studies on morphology, life history and fossils (ZHANG 2004, 2010, WIHLM & COURTNEY 2011, BORKENT & SINCLAIR 2012, WIHLM et al. 2012, SINCLAIR 2013, SCHNEEBERG et al. 2013). The family has been used as example taxa in recent phylogenetic studies, but the results of

these provide no definite evidence for phylogenetic relationships of Axymyiidae to the other nematocerous families (BERTONE et al. 2008, SCHNEEBERG et al. 2013).

Currently, the Axymyiidae include four extant genera (*Axymyia*, *Mesaxymyia* MAMAEV, 1968, *Protaxymyia* MAMAEV & KRIVOSHEINA, 1966, *Plesioaxymyia* SINCLAIR, 2013) with eight described species, known from the Holarctic Region, Taiwan and southern China (ISHIDA 1953, MAMAEV & KRIVOSHEINA 1966, MAMAEV 1968, YANG 1993, PAPP 2007, SINCLAIR 2013). In addition, three monotypic genera are known from the Jurassic of Asia (*Psocites* (HONG), *Juraxymyia* ZHANG, and *Sinaxymyia* ZHANG, ZHANG 2010).

In this paper three new fossil species of two extinct genera *Juraxymyia* and *Sinaxymyia* are described from the Khasurty and Kempendyay localities. Recently, a large amount of fossil insect material, including over 3000 specimens, was collected in mudstones at Khasurty (50° 21'N 103° 37'E, Buryatia, Early Cretaceous). Aquatic insects are numerically dominant there, although their diversity is markedly lower than that of terrestrial insects (SINITSHENKOVA 2011). In mudstones at Kempendyay (62° 02'N 118° 39'E; Yakutia-Sakha; Late Jurassic or Early Cretaceous) about 1200 insect impressions were collected; only 152 of them are members of Diptera, and most of them are badly damaged. The beds are undoubtedly fluvial (SINITSHENKOVA 1992).

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#### MATERIAL AND METHODS

All the fossil specimens described are housed in the Borissiak Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN). All recent specimens illustrated are housed in the Hungarian Museum of Natural History, Budapest (HMNH). Photographs were taken using a Zeiss AxioZoom microscope with an AxioCam HRC3 digital camera, with further correction done with Adobe Photoshop SC6 software. The drawings were prepared in Adobe Illustrator SC6.

Morphological terms mainly follow CUMMING & WOOD (2009), except the wing venation, where the terms of WOTTON & ENNOS (1989) are used. The nomenclature of the wing venation and system of Bibionomorpha used in this study are those accepted by the authors earlier (SHCHERBAKOV et al. 1995, BLAGODEROV et al. 2002).

## SYSTEMATIC PALAEOLOGY

**Family Axymyiidae SHANNON, 1921**

All the specimens described earlier (ZHANG 2010) and herein possess Rs with a kink at mid-length – one of the family-level synapomorphies of Axymyiidae (SINCLAIR 2013).

**Genus *Juraxymyia* ZHANG, 2010****Type species**

*Juraxymyia fossilis* (ZHANG, 2004): 692.

The genus is based on a single species from the uppermost Middle Jurassic–lowermost Upper Jurassic beds of China (Daohugou locality). Now several impressions of both sexes from this locality are known. A partly preserved male from the uppermost Middle Jurassic–lowermost Upper Jurassic beds of Kazakhstan (Karabastau Formation, Karatau locality; BLAGODEROV et al. 2002) has also been assigned to this species (ZHANG 2004).

The specimens under description are assigned to this genus based on the following characters of the wing venation: relatively long Sc, ending far distad of level of Rs bifurcation,  $R_{3+4}$  furcates at an obtuse angle,  $R_3$  ending at  $R_1$ ,  $bR_5$  long (much longer than r-m), r-m drifted distally, oblique and much shorter than  $dM_{1+2}$ , Rs fork distad of level of M fork,  $bM_{1+2}$  longer than  $dM_{1+2}$ , CuP free, ending far from hind wing margin. Moreover, haltere relatively short (stem twice as long as knob).

ZHANG believed that  $bM_{1+2}$  less than 1.5 times longer than  $dM_{1+2}$  forms a part of the generic diagnosis, but we suggest that the character is diagnostic for a species and thus include one of the new species with relatively long  $bM_{1+2}$  in the same genus (for the genus we presume that  $bM_{1+2}$  no more than twice as long as  $dM_{1+2}$ ).

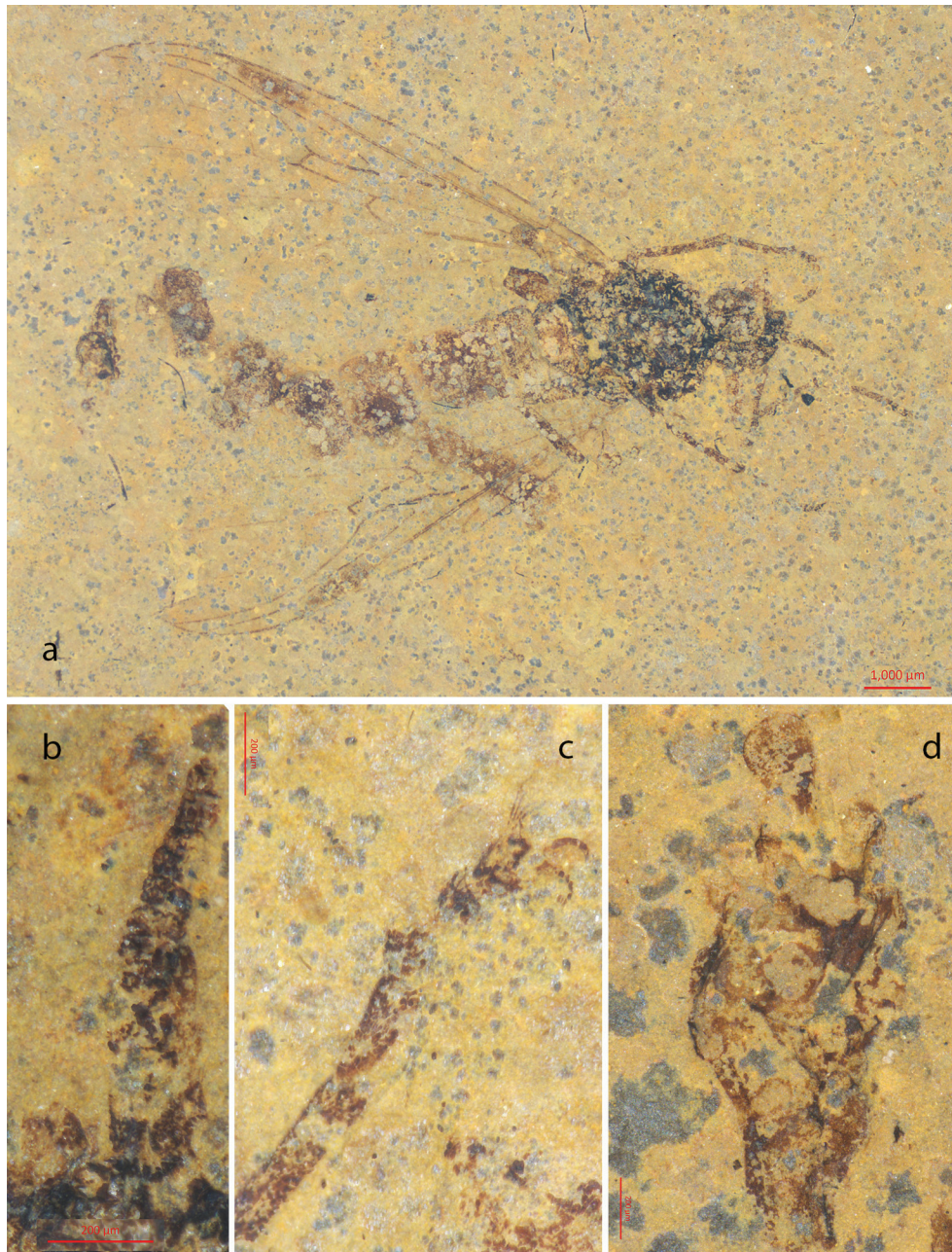
Eyes of the type species from China are holoptic in males and dichoptic in females (ZHANG 2010: fig. 2F, HAO et al. 2009: fig. 5), as in males of recent genera of Axymyiidae. In the species described herein, each eye is divided longitudinally into upper and lower hemispheres as in recent members, but the eyes appear separated in the male owing to the preservation of the head in the postero-ventral aspect.

***Juraxymyia krzeminskii* sp. n.**

(Figs 1, 2a-d)

**Material**

Holotype: PIN 5026/197±, male.



**Fig. 1.** *Juraxymyia krzeminskii* sp. n., holotype PIN 5026/197: a – habitus, b – antenna, c – tarsus, d – male genitalia.

**Type locality**

Khasurty; Western Transbaikalia, Buryatia, Zakamensk District, in the middle reaches of the River Khasurty 10 km south of the village of Tsakir (50° 21'N 103° 37'E); Gusinoe Ozero Group, Lower Cretaceous.

**Etymology**

Named after the eminent dipterologist Dr Wiesław Krzemiński, to commemorate his contribution to the study of fossil insects.

**Diagnosis**

Large fly, wing with anterior margin of costal area straight, basal portion of  $R_5$  longer than  $dM_{1+2}$ , CuP relatively long, ending clearly distad of m-cu level.

**Description**

Male. Large fly, body length about 10 mm, wing length 8.7 mm. Antenna robust, shorter than head, flagellomeres wider than long; maxillary palp robust. Wings large, slightly longer than the abdomen, with distinct pterostigma. Costa greatly reduced just at  $R_5$  apex, anterior margin of costal area straight, Sc relatively long, ending before midwing, distad of  $R_s$  kink, sc-r rather basal; pterostigma dark,  $R_3$  reaching  $R_1$  just at apex, basal portion of  $R_5$  longer than  $dM_{1+2}$ , M stem weak and desclerotised except for distal portion,  $bM_{1+2}$  1.8 times longer than  $dM_{1+2}$ , CuP relatively long, ending clearly distad of m-cu level, longer than bm cell. Stem of haltere bare. Legs fairly short, lacking spurs; first tarsomere the longest; t3 and t4 shorter than the remaining tarsomeres, subequal; pretarsus with prominent claws and pulvilli; pulvillus shorter than claw; a bunch of long setae on dorsal surface at the apex of t5. Hypandrial lobe long, relatively wide, spoon-shaped, gonostyli much shorter and narrower, other parts of male genitalia unclear.

***Juraxymyia evae* sp. n.**

(Figs 2e, 3)

**Material**

Holotype: PIN 923/1075±, isolated wing. Paratype: PIN 923/1076±, isolated wing.

**Type locality**

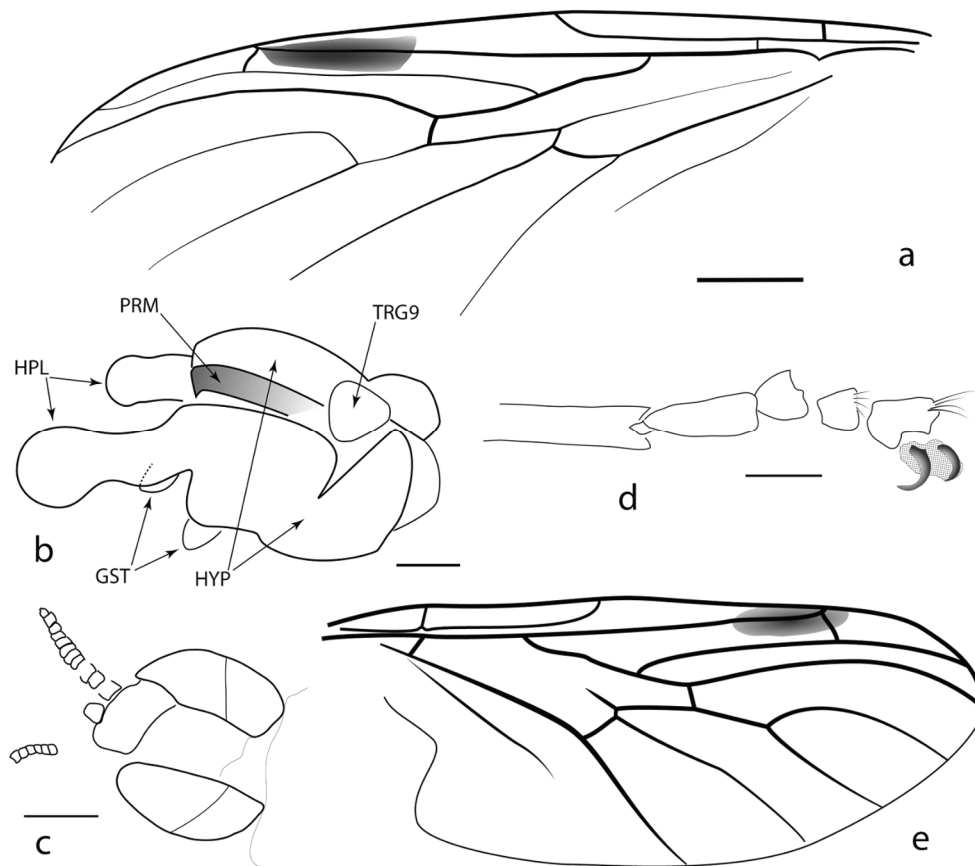
Kempendyay; Yakutia-Sakha, Suntar District, right bank of the River Kempendyay (tributary of the Vilyui), 40 km upstream from Kempendyay (62° 02'N 118° 39'E); Upper Jurassic–Lower Cretaceous.

**Etymology**

Named after the eminent dipterologist Dr Ewa Krzemińska, to commemorate her contribution to the study of fossil insects.

**Diagnosis**

Anterior margin of costal area convex, basal portion of  $R_5$  shorter than  $dM_{1+2}$ , CuP relatively long, ending clearly distad of m-cu level, anal lobe prominent.



**Fig. 2.** Holotypes of *Juraxymia krzeminskii* sp. n. (a-d) and *J. evae* sp. n. (e): a – wing, b – male terminalia (superposition of part and counterpart photographs), c – head, d – tarsus, e – wing.

Abbreviations: HPL – hypandrial lobes, HYP – hypandrium, GST – gonostyli, PRM – parameres, TRG9 – tergite 9. Scale a = 1 mm; b, d = 0.2 mm; c = 0.5 mm.

### Description

Isolated wing. Length: 4.5-5.2 mm. Costa greatly reduced slightly beyond  $R_5$  apex, anterior margin of costal area convex, Sc relatively long, ending before midwing, distad of  $R_s$  kink, sc-r rather basal; pterostigma pale,  $R_3$  reaching  $R_1$  clearly before apex, basal portion of  $R_5$  shorter than  $dM_{1+2}$ , M stem weak and desclerotised except for distal portion,  $bM_{1+2}$  1.1-1.4 times longer than  $dM_{1+2}$ ; CuP relatively long, ending clearly distad of m-cu level, longer than cell bm, anal lobe prominent.

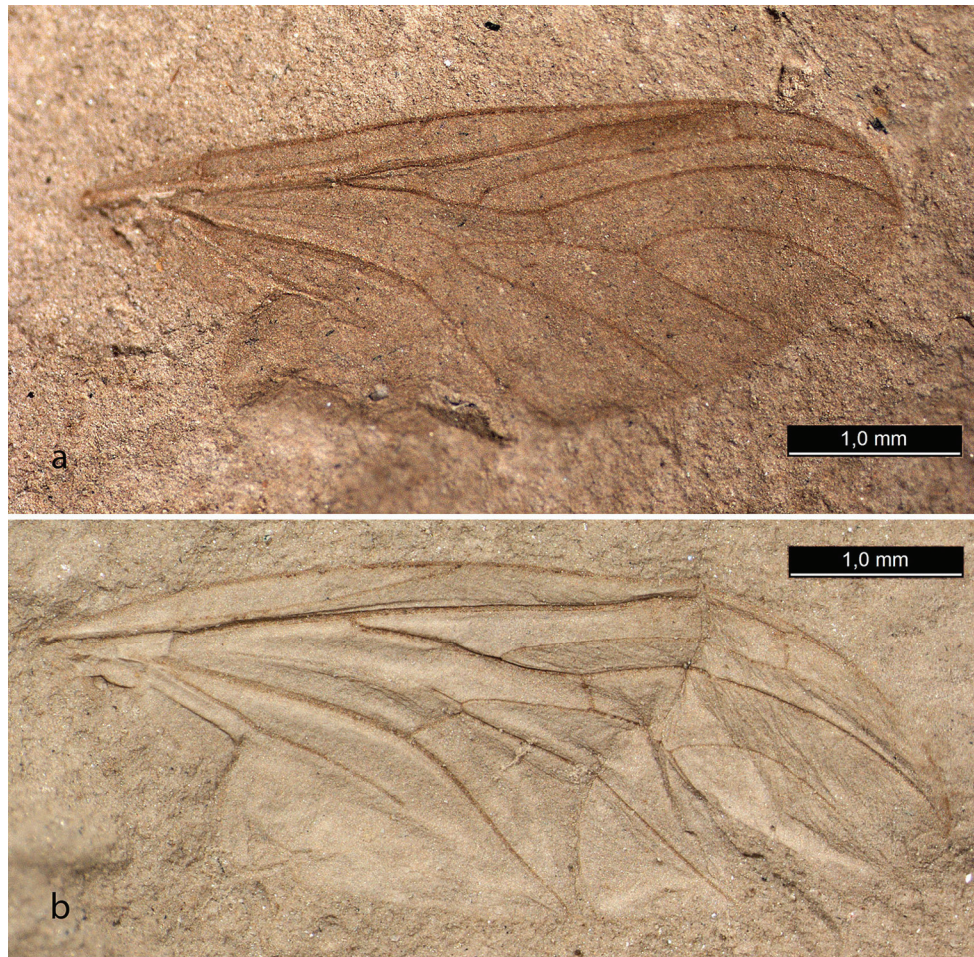


Fig. 3. *Juraxymia evae* sp. n.: a – holotype PIN 923/1075, wing, b – paratype PIN 923/1076.

### Genus *Sinaxymia* ZHANG, 2010

#### Type species

*Sinaxymia rara* ZHANG, 2010: 462.

The monotypic genus was described from a single male specimen from the uppermost Middle Jurassic–lowermost Upper Jurassic beds of China (Daohugou locality). The specimens described are assigned to this genus owing to the characteristic features of the wing venation: short Sc, ending just beyond level of Rs bifurcation, R<sub>3</sub> ending in C distad of R<sub>1</sub> apex, r-m situated at centre of wing, almost perpendicular to M<sub>1+2</sub> and much

shorter than  $dM_{1+2}$ ,  $R_s$  fork distad of level of  $M$  fork,  $bM_{1+2}$  shorter than  $dM_{1+2}$ ,  $CuP$  short, subequal to length of  $bm$  cell, ending far from hind wing margin. Moreover, haltere short and massive (stem less than twice as long as knob). Original diagnosis can be emended with the following characters: compound eyes broadly separated in female; each eye divided longitudinally into upper and lower hemispheres; leg short, without spurs or long setae; male gonocoxites fused to sternite forming massive hypandrium with paired elongate lateral lobes extended ventrally; female cerci two-segmented, apical segment shorter than basal.

ZHANG believed that the short basal portion of  $R_5$  before  $r-m$  (his  $bR_{4+5}$ ) formed part of the generic diagnosis as well as the obtuse angle of the  $R_{3+4}$  furcation, but we suggest that the characters are diagnostic for a species or variable and thus include the new species with relatively long  $bR_5$  and various angle of  $R_{3+4}$  furcation in the same genus.

***Sinaxymia szadziewskii* sp. n.**

(Figs 4, 5)

**Material**

Holotype: PIN 5026/205±, female. Paratypes: PIN 5026/198±, adult; 199±, male; 200±, adult, 204±, isolated wing.

**Type locality**

Khasurty; Western Transbaikalia, Buryatia, Zakamensk District, in the middle reaches of the River Khasurty 10 km south of the village of Tsakir (50° 21'N 103° 37'E); Gusinoe Ozero Group, Lower Cretaceous.

**Etymology**

Named after the eminent dipterologist Dr Ryszard Szadziewski to commemorate his contribution to study of fossil insects.

**Diagnosis**

Vein  $bR_5$  twice as long as  $r-m$ ,  $R_{3+4}$  furcated from obtuse to acute angle,  $M_2$  no more than twice as long as  $dM_{1+2}$ .

**Description**

Medium-sized, body (including head) length about 4.2-6.4 mm, wing length 3.7-6.2 mm. Facets uniform in size in both hemispheres in female. Antenna moniliform, longer than head in female, each flagellomere wider than long; maxillary palpus robust. Wings large, broad, about equal in length to the entire body, with distinct pterostigma. Costa greatly reduced just at  $R_5$  apex, anterior margin of costal area straight;  $Sc$  relatively short, ending before midwing, proximad of  $R_s$  kink,  $sc-r$  rather basal, pterostigma dark.  $R_3$  reaching  $C$  well separated from  $R_1$ ,  $R_{3+4}$  furcated from obtuse to acute angle,  $bR_5$  twice as long as  $r-m$ .  $M$  stem weak and desclerotised except for distal portion,  $dM_{1+2}$  1.1-1.4 times



longer than  $bM_{1+2}$ ,  $M_2$  1.2-2.0 times longer than  $dM_{1+2}$ . Stem of haltere bare. Leg fairly short, lacking spurs and long setae; hind tibia with posteroventral apical comb; pretarsus with prominent claws; pulvillus shorter than claw. Female cerci large, pad-like, apical segment round. Male terminalia with hypandrial lobe narrow, relatively short, extended ventrally, other parts of male genitalia unclear.

#### Comments

In males of the type species from China the antennae are nearly as long as the head; in the female of the new species the antennae are longer and more robust. However, this is not a difference of specific value, but rather a sexual dimorphism, which is also observed in recent species (e.g. *Axymyia furcata* MCATEE, 1921, WIHLM et al. 2012).

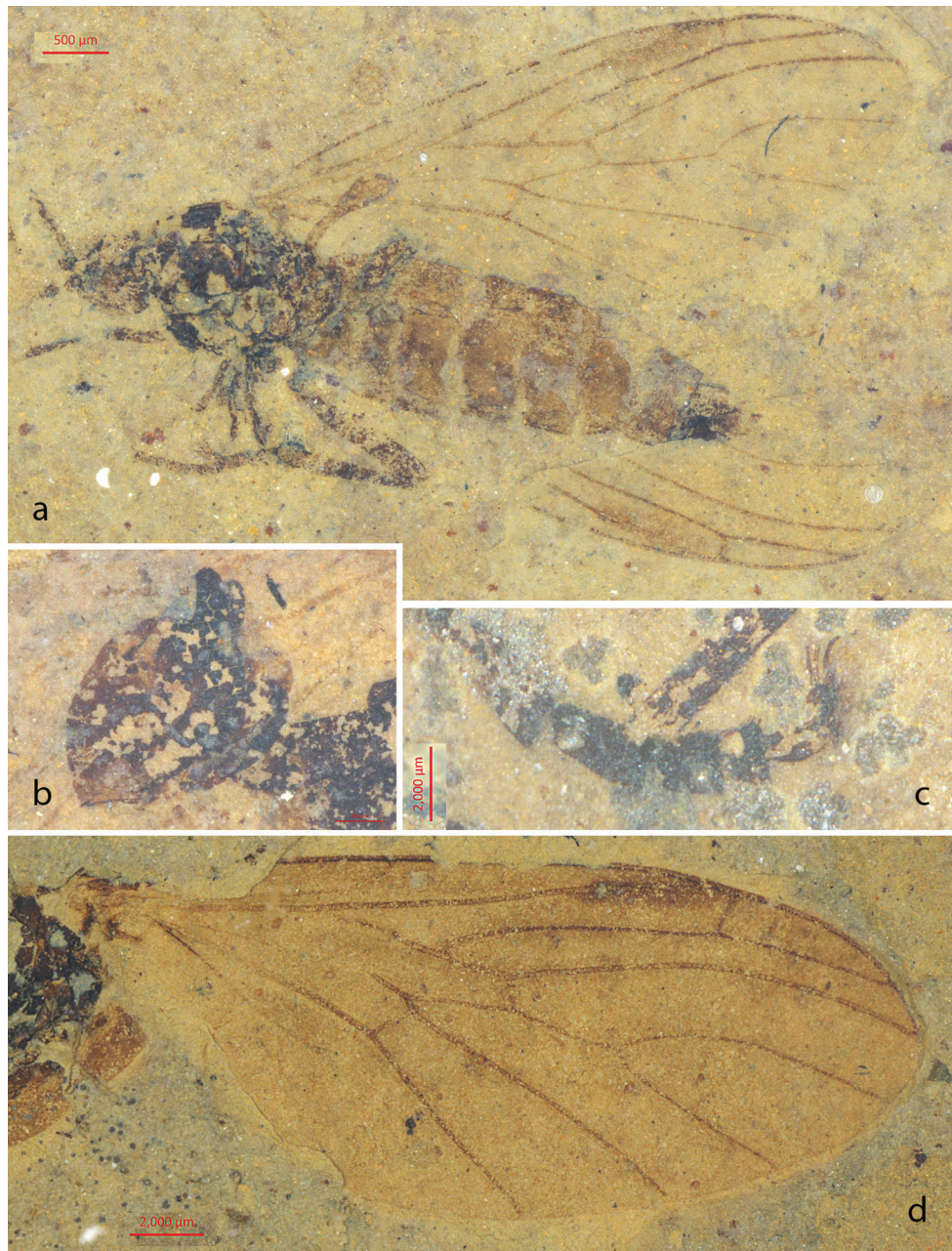
Both axymyiid species from Khasurty are described in the genera known from the famous Daohugou locality (Ningcheng, Chifeng, Inner Mongolia, China; uppermost Middle Jurassic–lowermost Upper Jurassic). Common genera for these two localities were reported also in other insects e.g. within Plecoptera; genus *Jurataenionema* LIU ET REN (Taeniopterygidae) (SINITSHENKOVA 2011).

#### DISCUSSION

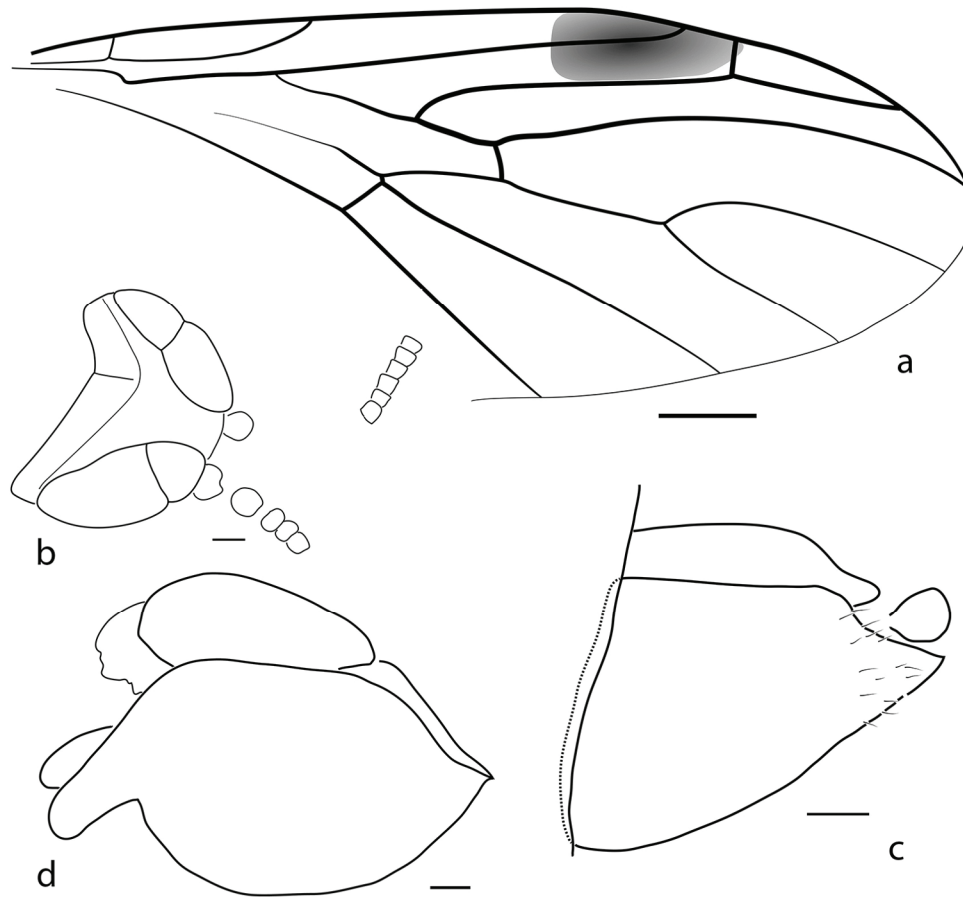
Now, after the description of recent *Plesioaxymyia* and new species of fossil *Juraxymyia* and *Sinaxymyia*, it has become obvious that extant and extinct axymyiid genera cannot be distinguished by wing venation, as suggested by ZHANG (2010) in a key. It was thought that extinct genera possess short CuP (shorter than half of CuA length) whereas in extant genera CuP is longer, ending at or close to, hind margin of wing. However, *P. vespertina* SINCLAIR, 2013 possess extremely short CuP, whereas in both new species of *Juraxymyia* CuP is relatively long and comparable with that of e.g. extant *Axymyia furcata*.

Another suggested character for diagnosis was  $R_{3+4}$ , putatively furcated at an obtuse angle in Mesozoic genera and at an acute or nearly right angle in recent ones. However, recent *Protaxymyia japonica* (ISHIDA, 1953) (Fig. 6b) possess  $R_{3+4}$  furcated at an obtuse angle, and vice versa in *Sinaxymyia szadziewskii* sp. n. (Figs 4a, d), which possesses  $R_{3+4}$  furcated at an acute or almost right angle. Therefore, this character also can only indicate a trend.

Many other very characteristic features of the recent genera, such as the patterns of the eyes and legs, are found in Mesozoic genera, too. The general structure of female genitalia in fossils is very similar to that in recent taxa, but rod-like sensilla cannot be seen in the fossils, very probably because of the state of preservation. The only character that could potentially distinguish fossil genera from recent ones is the structure of the male genitalia, where separate gonocoxites were reported for *Juraxymyia* and *Sinaxymyia* (ZHANG 2010).



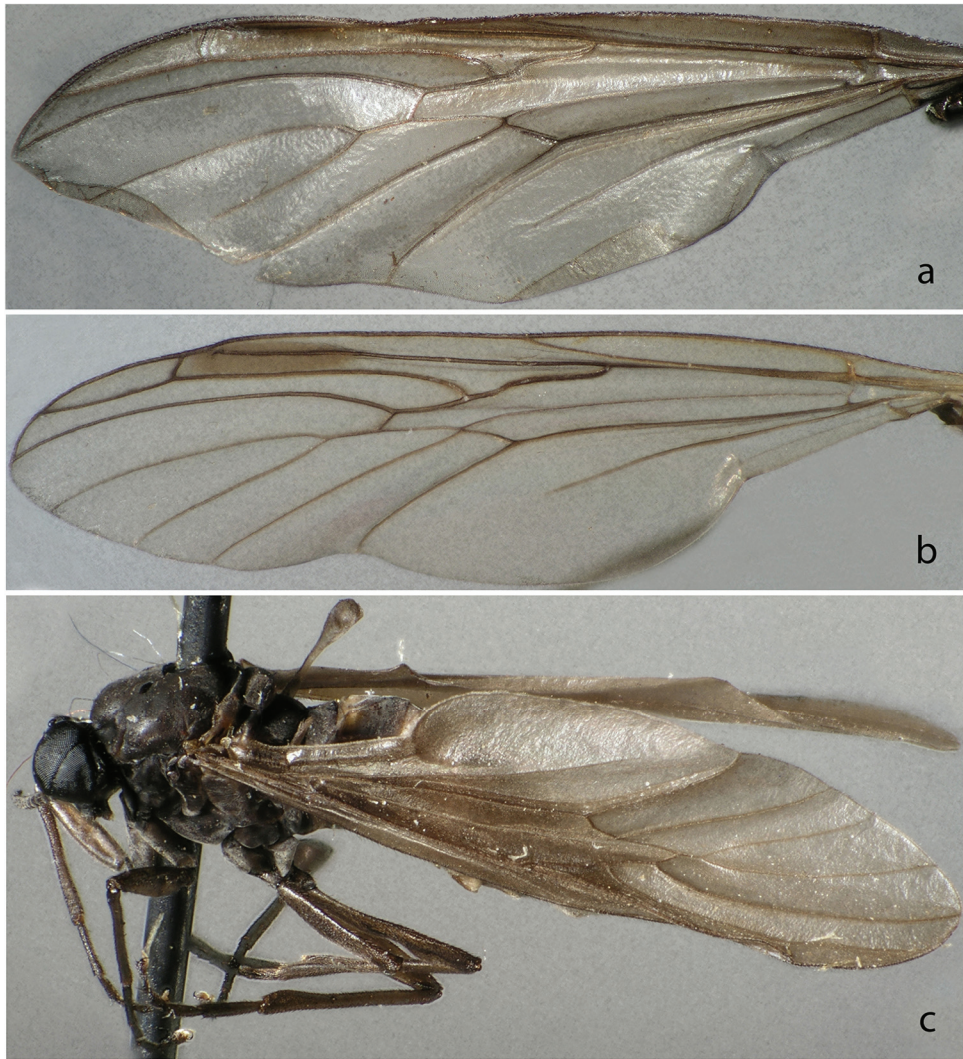
**Fig. 4.** *Sinaxymia szadziewskii* sp. n.: a – holotype PIN 5026/205, habitus; b, c – paratype PIN 5026/199; b – male terminalia; c – tarsus; d – paratype PIN 5026/200, wing.



**Fig. 5.** *Sinaxymyia szadziewskii* sp. n.: a-c – holotype PIN 5026/205; a – wing; b – head; c – female terminalia; d – paratype PIN 5026/199, male terminalia. Scale: a = 0.5 mm, b-d = 0.1 mm.

Comparison of illustrations of male genitalia of *Juraxymyia fossilis* (ZHANG 2010: figs 2G, 4D), *Protaxymyia taiwanensis* PAPP, 2007 (PAPP 2007: figs 14, 15) and *Axymyia furcata* (WOOD 1991: fig. 9) reveals that large, narrowed basally and flattened apically, lobes of the fossil species (considered by ZHANG to be well-developed gonostyli), may in fact be spoon-shaped elongate lateral lobes of the massive hypandrium, resembling gonostyli in form and position. True gonostyli of *J. fossilis* looking like small elongate plates are situated internally to lateral lobes as in recent Axymyiidae (KRIVOSHEINA 2000). Male genitalia of *Juraxymyia krzeminskii* sp. n. from Transbaikalia (Fig. 1d) are preserved

in another (dorso-lateral compared to ventral in *J. fossilis*) position; but a similar interpretation (hypandrium with large lobes and small elongate gonostyli) is also possible in this case.



**Fig. 6.** Recent Axymyiidae: a – *Protaxymyia melanoptera* MAMAEV et KRIVOSHEINA, 1966 [Primorye Territory, Ussuriisk, 18.05.1969, larva in elm wood, reared, HMNH], wing; b – *Protaxymyia japonica* (ISHIDA, 1953) [Kyushyu, Shiratoriyama, Kimamoto, 26.05.1970, HMNH], wing; c – *Mesaxymyia stackelbergi* MAMAEV, 1968 [Primorye Territory, Ussuriisk, 18.04.1967, larva in lime wood, reared, HMNH], habitus.

Based on illustrations of male genitalia of *Psocites pectinatus* (HONG, 1983) and *Sinaxymyia rara* in ZHANG (we did not study the specimens from Daohugou) one also cannot be sure that the gonocoxites are separated from the abdominal sternite; on the contrary, the gonocoxites seem to be completely fused to the abdominal sternite. Drawings of the genitalia of *P. pectinatus* and *S. rara* (ZHANG 2010: fig 1G, 3F and 2E, 5F) are readily compared with those of *A. furcata* (WIHLM et al. 2012: figs 45, 62): it seems that the presumed separate gonocoxites of *S. rara* are in fact hypandrial lobes. Moreover, on the male of *Sinaxymyia szadziewskii* sp. n. (Fig. 4b; apex of abdomen partly disintegrated and terminalia curved upward; its position is not natural) one can see the fused capsule (=hypandrium) and two small narrow hypandrial lobes without any traces of articulation.

If our interpretation is correct, the pattern of male genitalia of extinct and extant genera is similar and gonocoxites were completely fused to the abdominal sternite in males of at least Jurassic *Psocites* and *Sinaxymyia*. It is worth mentioning that the wing venation of *Psocites* is very similar to that of *Axymyia* and *Mesaxymyia*. One cannot rule out the possibility that extant axymyiid genera were already present in the Mesozoic, as in the case of many other nematocerous families, e.g. Ceratopogonidae (SZADZIEWSKI 2008), but only additional material with well-preserved male genitalia can help to resolve this problem.

SINCLAIR (2013) discussed the preliminary phylogeny of Axymyiidae. Several character states could be clarified following the present descriptions. The cluster of setae on the haltere seems to be absent in both fossils and *Plesioaxymyia*. The M stem is weakened not only in *Plesioaxymyia* but also in some recent species (Fig. 6a) and in most fossil Axymyiidae (in the new species, and in those described previously; this is clearly visible in the original photographs, ZHANG 2010: fig. 1C, 2F). More material is needed before a reconstruction of the phylogeny of this enigmatic family can be attempted, but it is clear that fossils have much to contribute to such a study.

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