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

VLADIMIR A. BLAGODEROV1 & ELENA D. LUKASHEVICH2

1Department of Science Facilities, Natural History Museum, London, United Kingdom, e-mail: vlab@nhm.ac.uk;
2Borissiak Palaeontological Institute RAS, Moscow, Russia, e-mail: elukashevich@hotmail.com

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.

INTRODUCTION

Axymyiidae is a small relict enigmatic family of nematocerous 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, STEGERBAKOV et al. 1995, WIEGMANN et al. 2011) or Axymiomorpha (WOOD & BORKENT 1989, KOVALEV 1989, KRZEMIŃSKA et al. 1993, KRZEMIŃSKI & KRZEMIŃSKA 2003). Recently, axymiids became a focus of attention as the subject of studies on morphology, life history and fossils (ZHANG 2004, 2010, WILDM & COURTNEY 2011, BORKENT & SINCLAIR 2012, WILDM 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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photos of the specimens from Kempendyay. The research of EL was partly supported by
grants from the Russian Foundation for Basic Research (No. 13–04–01839).

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 WOTTEN & 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 PALAEONTOLOGY

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

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, R3+4 furcates at an obtuse angle, R3 ending at R1, bR3 long (much longer than r-m), r-m drifted distally, oblique and much shorter than dM1+2, Rs fork distad of level of M fork, bM1+2 longer than dM1+2, CuP free, ending far from hind wing margin. Moreover, haltere relatively short (stem twice as long as knob).

ZHANG believed that bM1+2 less than 1.5 times longer than dM1+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 bM1+2 in the same genus (for the genus we presume that bM1+2 no more than twice as long as dM1+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. Juraxymia 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 (50º 21’N 103º 37’E); Gusinoe Ozero Group, Lower Cretaceous.

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

Diagnosis
Large fly, wing with anterior margin of costal area straight, basal portion of R₃ longer than dM₁₂, 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 R₃ apex, anterior margin of costal area straight, Sc relatively long, ending before midwing, distad of Rs kink, sc-r rather basal; pterostigma dark, R₃ reaching R₁ just at apex, basal portion of R₃ longer than dM₁₂, M stem weak and desclerotised except for distal portion, bM₁₂ 1.8 times longer than dM₁₂, 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

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

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

Diagnosis
Anterior margin of costal area convex, basal portion of R₃ shorter than dM₁₂, CuP relatively long, ending clearly distad of m-cu level, anal lobe prominent.
Fig. 2. Holotypes of *Juraxymyia 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 R₅ apex, anterior margin of costal area convex, Sc relatively long, ending before midwing, distad of Rs kink, sc-r rather basal; pterostigma pale, R₃ reaching R₁ clearly before apex, basal portion of R₅ shorter than dM₁+₂, M stem weak and desclerotised except for distal portion, bM₁+₂ 1.1-1.4 times longer than dM₁+₂; CuP relatively long, ending clearly distad of m-cu level, longer than cell bm, anal lobe prominent.
Genus *Sinaxymyia* ZHANG, 2010

**Type species**

*Sinaxymyia 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, R₃ ending in C distad of R₁ apex, r-m situated at centre of wing, almost perpendicular to M₁₂ and much...
shorter than dM_{1+2}, Rs 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 gonoxites 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_{5-3}) 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.

**Sinaxyymia 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 Szadzewski 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 Rs 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 bM₁+₂, M₂ 1.2-2.0 times longer than dM₁+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 R₃+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 R₃+₄ furcated at an obtuse angle, and vice versa in *Sinaxymyia szadziewskii* sp. n. (Figs 4a, d), which possesses R₃+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.
Comparison of illustrations of male genitalia of *Juraxyminia fossilis* (ZHANG 2010: figs 2G, 4D), *Protaxyminia 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 *Juraxyminia krzemiński* 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 Axyymiidae: 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, Shiratoriyma, 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* (WILHM 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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