Contributions to the Study of Fossil Snipe-Flies (Diptera: Rhagionidae). The Genus *Palaeobolbomyia*

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Abstract—Five new species assigned to the genus *Palaeobolbomyia* are described from the Upper Mesozoic of Asia. The age of the deposits and the phylogeny of the genus *Palaeobolbomyia* are discussed. A key is provided to all known species of the genus *Palaeobolbomyia*.

INTRODUCTION

The genus *Palaeobolbomyia* was described by Kovalev (1982) for the single species *P. sibirica* included, based on two excellently preserved specimens from the Jurassic of northern Buryatiya. In the course of studying collections of Brachycera it was revealed that the genus *Palaeobolbomyia* was widely distributed in Asia and included at least six species. The type species is now recorded in both the Uda Formation of Transbaikalia and the Karabastau Formation of Kazakhstan. To date, this is the third instance when a rhagionid species has been found in deposits of different strata (Kovalev and Mostovski, 1997; Mostovski *et al.*, 2000). Additionally, new species of *Palaeobolbomyia* are found in the Ortsag Sequence, Bahar Group, in Mongolia and in the Upper Mesozoic of Yakutiya.

The genus *Palaeobolbomyia* is most diverse in the Karabastau Formation (Karatau-Mikhailovka locality) dated as Callovian–Kimmeridgian (Polyansky and Doludenko, 1978; Kirichkova and Doludenko, 1996). The snipe-flies appear to have flourished during the Middle and Late Jurassic. In the fauna of the Karatau-Mikhailovka locality rhagionids are represented by approximately a dozen genera comprising at least 20 species and forming 53 per cent of determinable brachycerans. Besides the Rhagionidae, the brachycer-ans assigned to 16 more families have been found here, making this the most complete fauna and maybe of all Jurassic faunas. The genus *Palaeobolbomyia* is represented in this locality by three species, one of them was found in Transbaikalian deposits.

The Ortsag Sequence of the Bahar Group in the Central Mongolia may be considered as contemporary to the Karabastau Formation or nearly so (Sinitza, 1993, 1996). The brachyceran fauna is notably more poor here. Besides the only specimen of *P. mongolica* sp. nov., a representative of the family Empididae (Protempidinae) (Mostovski, 1999b) and two specimens of asilomorph flies have been found. Ten individuals of Brachycera have been found in total in the underlying Togo-Huduk Sequence of the Bahar Group. Three of

them are more distinct and can most probably be assigned to the typical Jurassic family Archisargidae (Mostovski, 1997). Additionally, two rhagionids and two asilomorph flies are found in the Togo-Huduk Sequence.

The Upper Mesozoic deposits of Yakutiya exposed in the upper part of the Vilyui River Basin on the right bank of the Kempendyai River in the slope of the Ulakhan-Magan-Khaya Mountain are of particular interest. More than a thousand insect remains have been found here in the siltstone lenses that occurred among the poorly cemented obliquely laminated fine- and middle-grained sandstones. The deposits of the Ulakhan-Magan-Khaya Mountain were briefly described by Martinsson (1961), and Mesozoic deposits of the Kempendyai Depression were reviewed by Korchagin (1972). The insect remains are fragmentary due to the alluvial genesis of the sediments. Rare brachycerans are represented by the families Rhagionidae (four specimens) and Xylophagidae s.l. (a single specimen). The age of the Kempendyai insect assemblage is debatable (Sinitshenkova, 1992; Sukacheva, 1994). Its similarity to Jurassic (Rasnitsyn, 1969; Ponomarenko, pers. comm.) or Early Cretaceous (Rasnitsyn, 1980) faunas has been observed. The genus *Crenoptychoptera* Kalugina, 1985 (Eoptychopteridae) previously found in the Jurassic of Siberia (Kalugina and Kovalev, 1985) and the Kempendyai locality (Kalugina, 1989) is now recorded in Early Neocomian locality of Zhigansk (Lukashevich, 1996). The presence of the genus Palaeobolbomyia and the absence of true empidids in the Kempendyai suggest that the beds in question are of Jurassic age. It should be emphasized that Empididae in a broad sense (excluding, however, Protempidinae) are the most characteristic element of Cretaceous faunas and are recorded in the earliest Cretaceous of Mongolia (Ulaan-Tolgoi, Hotont, Har-Hutul (Hutel-Hara auct.), and Tsagaan-Tsav localities) and England. Of great interest is distribution of true empidids in the Purbeck Beds in southern England. The only wing assigned to the subfamily Atelestinae, which is extremely rare in the fossil record, is from the Lower Purbeck. Representatives of other subfamilies are diverse and not rare in the Middle Purbeck and Wealden (Mostovski, 1999a). This pattern of stratigraphical distribution may be explained by hot and dry conditions in early Purbeck times. Thus, the absence of Empididae in Kempendyai may reflect either sampling bias or climatic peculiarities of this area if Early Cretaceous age is proved. On the other hand, representatives of the genus *Palaeobolbomyia* are recorded neither in the geographically near localities in Transbaikalia and Mongolia where hundreds of brachycerans are found, nor in the Lower Cretaceous of Europe and China.

The material studied including types are housed in the collection of Paleontological Institute, Russian Academy of Sciences (PIN).

SYSTEMATIC PALEONTOLOGY

Family Rhagionidae Latreille, 1802

Genus Palaeobolbomyia Kovalev, 1982

Palaeobolbomyia: Kovalev, 1982, p. 94; Kalugina and Kovalev, 1985, p. 184; Nagatomi and Yang, 1998, p. 131.

Paleobolbomyia: Grimaldi and Cumming, 1999, p. 17. (Incorrect subsequent spelling.)

Type species. *P. sibirica* Kovalev, 1982; Upper Jurassic; Transbaikalia.

D i a g n o s i s. Palps not enlarged, 2-segmented. Antennal flagellum five- to six-segmented, first flagellomere enlarged, ovoid, slightly asymmetrical, wider than scape or pedicel. Scutellum bears bristles at hind margin. Costal vein encircles wing. Costal section R_1-R_{2+3} longer than Sc- R_1 . Vein R_{2+3} S-shaped, strongly curved under point of R_1 insertion. Fork R_{4+5} rather long. R_5 ends at wing tip. M_3 absent. Basal section of M_4 usually absent. Anal cell closed. Pterostigma present. Alula developed. Hind coxa bears blunt tubercle anteriorly. Hind tibia bears two short ventral spurs. Three (?) spherical spermathecae. Ovipositor short, weakly extended. Cerci 2-segmented, basal segment lacking large ventral lobe, distal segment short oval.

Composition. Besides the type species, *P. kazakhstanica* sp. nov., *P. devia* sp. nov., *P. yakuten*sis sp. nov., *P. angustalata* sp. nov., and *P. mongolica* sp. nov. from the Middle–Upper Jurassic of Asia (Fig. 1).

C o m p a r i s o n. The genus differs from *Jurabrachyceron* Kovalev, 1981 in less number of flagellomeres, more strongly curved R_{2+3} and the costal section R_1-R_{2+3} being longer. It differs from *Ussatchovia* Kovalev, 1982 in S-shaped R_{2+3} and R_{4+5} fork being longer, from *Probolbomyia* Ussatchov, 1968, *Austroleptis* Hardy, 1915, and *Bolbomyia* Loew, 1850 in proximal position of M_4 , additionally from the latter in greater number of the flagellomeres and in S-shaped R_{2+3} .

R e m a r k s. The opinion expressed by Kovalev (1982) regarding the close position of *Palaeobol*-



Fig. 1. Map of localities where *Palaeobolbomyia* species are found: (1) Karatau-Mikhailovka, (2) Bahar, (3) Uda, (4) Kempendyai.

bomyia to ancestral forms of Austroleptis and Bol*bomyia* is now being confirmed. Firstly, re-examination of the *P. sibirica* type resulted in the discovery of two spurs on the hind tibiae of this species as well as in P. kazakhstanica sp. nov. Secondly, the hind margin of the discoidal cell is angled at the point of the M_3 origin in *P. kazakhstanica* sp. nov. and the discoidal cell is narrowing distally in P. devia sp. nov. similarly to that of representatives of Bolbomyia (Hennig, 1967; Webb, 1987). Both facts argue in favor of shifting M_4 towards the wing tip after M_3 reduction. This is expressed in the contemporary Probolbomyia modesta Ussatchov, 1968 (Karabastau Formation). The anal cell is clearly petiolate in Austroleptis, and the beginning of this process is fixed in P. yakutensis sp. nov. having the anal cell with short petiole.

Key to species of the genus Palaeobolbomyia

1. Discoidal cell narrow, lanceolate, basal section of M ₂ absent (Fig. 3b) <i>devia</i> sp. nov.
—Discoidal cell broader, basal section of M ₂ present2
2. Wing narrow, 2.8 times as long as wide; posterior margin of discoidal cell weakly S-shaped curved, smooth (Fig. 3d)
angustalata sp. nov.
—Wing broader, at most 2.4 times as long as wide
3. R_{4+5} stem at least twice longer RS1, transverse <i>rm</i> shifted towards <i>d</i> midlength4
$-R_{4+5}$ stem at most 1.3 times longer RS1, transverse <i>rm</i> shifted towards <i>d</i> base
4. Posterior margin of discoidal cell markedly angled, R_5 longer, M_1 and M_2 less arched forwards and backwards respectively (Fig. 3a)
kazakhstanica sp. nov.
—Posterior margin of discoidal cell evenly curved, R_5 shorter, M_1 and M_2 stronger arched forwards and backwards respectively (Fig. 2)sibirica Kovalev
5. Anal cell with short petiole, <i>d</i> narrowed distally (Fig. 3c)
yakutensis sp. nov.
—Anal cell closed at point, anterior and posterior margins of <i>d</i> more or less parallel (Fig. 3e) <i>mongolica</i> sp. nov.

Palaeobolbomyia sibirica Kovalev, 1982

Holotype. PIN, no. 3053/1081, female impression; Buryatiya, upper reaches of the Uda River Material. Besides the holotype and paratype PIN, no. 2022/8(61), specimen no. 2239/2214, moderately preserved fly from the Karatau-Mikhailovka locality. This specimen differs from the holotype in rm shifted somewhat distally and shorter costal section M_1-M_2 .

Palaeobolbomyia kazakhstanica Mostovski, sp. nov.

Plate 11, fig. 1

Holotype. PIN, no. 2239/2178(2204), part and counterpart of fairly well preserved female; Southern Kazakhstan, Chimkent Region, Chayan District, Karatau-Mikhailovka locality; Middle–Upper Jurassic, Karabastau Formation.

Description (Fig. 3a). The body and legs are dark. The forehead is as wide as the third antennal segment or slightly wider, parallel sided from above, somewhat broadened downwards, sparsely covered with short hairs. The eyes are transverse oval, ca. 1.3 times as high as long. The antennae are equal to the head in length, the flagellum is 6-segmented, the first flagellomere is slightly wider than the pedicel, the second flagellomere is as long as wide, the third flagellomere is slightly longer than wide, the fourth and fifth flagellomeres are elongate and the sixth flagellomere is the longest. The ocellar triangle is wide, occupying almost the whole forehead at the top, slightly raised, the ocellar bristles are very short. The mesonotum has sparse short bristles probably arranged in rows. The scutellum is rounded trapeziform, twice as wide as long, with short bristles in its apical half. The wing is twice as long as broad, obtusely rounded apically. The wing membrane is evenly microtrichose. The hair fringe is present at the hind edge of the wing. The pterostigma is developed as pale brown spot mainly under R_1 . The vein R_1 has no setae. The R_{4+5} stem is twice as long as RS1, R_5 is 1.9– 2 times as long as R_{4+5} . The transverse *rm* divides the anterior margin of the discoidal cell as 1:1.8. The basal section of M_2 is equal to *rm*. The posterior margin of the discoidal cell between M_2 and M_4 is angled. M_1 is nearly straight or very weakly arched anteriorly, M_2 is weakly arched backwards. The costal section M1-M2 is slightly shorter than the section M₂-M₄. The apical portion of CuA is gently arched. CuP is straight. The anal cell has short or point petiole. The haltere is dark, its stem paler. The legs are evenly covered with short adjacent hairs. The hind tibia is slightly more than twice as long as the first tarsomere. The claws are small, weakly curved. The 8th abdominal segment is slightly shorter when compared with the 7th one, and somewhat more heavy sclerotized than the previous segments.

M e a s u r e m e n t s (mm): holotype: body length, 4.8, wing length, 2.8, wing width, 1.1; paratype: body length, 3.8, wing length, 2.7, wing width, 1.3.

R e m a r k. The holotype body length should be less since the abdomen is obviously elongated postmortem.



Fig. 2. *Palaeobolbomyia sibirica* Kovalev, 1982, female, holotype, PIN, no. 3053/1081: (a) general appearance, (b) tip of abdomen. Scale bars 1 mm in (a) and 0.2 mm in (b). (After Kovalev, 1982, with changes.)

between camps Ulai-Mailo and Ashei, the Uda locality; Middle–Upper Jurassic, Uda Formation.

D i a g n o s i s (Fig. 2). Flagellum at least 5-segmented, first flagellomere somewhat wider than pedicel and slightly asymmetrical. Wing twice as long as broad. R_1 bears fine setae. R_{4+5} stem 2.3 times as long as RS1. Vein R_5 1.5 times as long as R_{4+5} stem. Transverse *rm* divides anterior margin of discoidal cell as 1 : 2. M_1 arched anteriorly immediately after the fork, M_2 arched backwards. Costal sections M_1 – M_2 and M_2 – M_4 subequal. Posterior margin of discoidal cell between M_2 and M_4 evenly curved. Pterostigma very pale. Hind tibia slightly more than 2.5 times as long as first tarsomere.

Measurements (mm): body length, 4–4.5, wing length, 2.8, wing width, 1.3.

Occurrence. Transbaikalia, Uda Formation; Kazakhstan, Karabastau Formation.



Explanation of Plate 11 Fig. 1. Palaeobolbomyia kazakhstanica sp. nov., holotype PIN, no. 2239/2178. Fig. 2. Palaeobolbomyia devia sp. nov., holotype PIN, no. 2239/2196. Fig. 3. Palaeobolbomyia mongolica sp. nov., holotype PIN, no. 3791/2858.

Material. Besides the holotype, paratype PIN, no. 2904/1576, fairly well preserved female from the same locality.

Palaeobolbomyia devia Mostovski, sp. nov. Plate 11, fig. 2

E t y m o l o g y. From Latin *devia* (deviated). H o l o t y p e. PIN, no. 2239/2196, fairly well preserved male; Southern Kazakhstan, Chimkent Region,

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Chayan District, Karatau-Mikhailovka locality; Middle–Upper Jurassic, Karabastau Formation.

Description (Fig. 3a). The head and thorax are dark, the abdomen and legs slightly paler. The head is hemispherical in profile, the occiput is convex. The ocellar triangle is raised. The scutellum has short bristles apically. The wing membrane is evenly microtrichose. There is a hair fringe at the hind edge of the wing. The pterostigma is very pale, more visible under





Fig. 3. New species of the genus *Palaeobolbomyia*: (a) *P. kaza-khstanica* sp. nov., holotype PIN, no. 2239/2178, (b) *P. devia* sp. nov., holotype PIN, no. 2239/2196, (c) *P. yakutensis* sp. nov., holotype PIN, no. 923/1083, (d) *P. angustalata* sp. nov., holotype PIN, no. 923/1125, (e) *P. mongolica* sp. nov., holotype PIN, no. 3791/2858. Scale bar 1 mm.

 R_{2+3} . The vein R_1 bears sparce and short setae at least in its distal part. R_{4+5} stem is 2.3 times as long as RS, R_5 is 1.9 times as long as R_{4+5} . The transverse *rm* divides the anterior margin of the discoidal cell as 1 : 2. The transverse *rm* is connected with M_{1+2} immediately before M_1 and M_2 bifurcation. The discoidal cell is narrow, lanceolate. M_1 and M_2 are symmetrically diverged, M_2 and M_4 are parallel. The costal section M_1 - M_2 is half as long as the section M_2-M_4 . The apical portion of CuA is weakly arched. CuA and CuP meet at the wing margin. The legs are evenly covered with short adjacent hairs. The hind tibia is 1.8 times as long as the first tarsomere. Abdominal tergites are covered with sparce hairs that are somewhat longer at the hind edge of each tergite. The gonocoxae are weakly swollen, covered with very short hairs.

Measurements (mm): body length, 3, wing length, 1.9, wing width, 0.8.

Material. Holotype.

Palaeobolbomyia yakutensis Mostovski, sp. nov.

Holotype. PIN, no. 923/1083, well preserved wing impression; Yakutiya, Suntar District, right bank of the Kempendyai River, 2.5 km downstream of Ulakhan-Magan-Khaya Mountain, Kempendyai locality, outcrop 1, bed 16; Upper Jurassic.

Description (Fig. 3c). The apex of the wing is obtusely rounded. The pterostigma is pale, developed as an elongate spot mainly under R_1 . The vein R_1 is bare. The costal section $Sc-R_1$ is greater than the R_1 - R_{2+3} section. The stem R_{4+5} is 1.3 times as long as RS1, R_5 is twice as long as R_{4+5} . The transverse *rm* divides the anterior margin of the discoidal cell as 1:3. A convex fold is developed from the wing base, it crosses *rm* and disappears at the level of R_{4+5} fork. The basal section of M_2 is equal to *rm*. The discoidal cell is narrowed distally, its posterior margin between M_2 and M_4 is gently S-shaped. M_1 is nearly straight or just weakly arched anteriorly, M₂ is nearly straight, these veins seem to be parallel. The costal section M_1-M_2 is nearly half as long as the M_2-M_4 section. The apical portion of CuA is more or less straight and somewhat bent just before its fusion with straight CuP. The anal vein has short petiole.

Measurements (mm): wing length, 2.4, wing width, 1.1.

Material. Holotype.

Palaeobolbomyia angustalata Mostovski, sp. nov.

Etymology. From Latin *angustus* (narrow) and *ala* (wing).

Holotype. PIN, no. 923/1125, well preserved wing impression and body fragments; Yakutiya, Suntar District, right bank of the Kempendyai River, 2.5 km downstream of Ulakhan-Magan-Khaya Mountain, Kempendyai locality, outcrop 1, bed 16; Upper Jurassic.

Description (Fig. 3d). The body is brown, the legs are somewhat paler. The head is nearly hemispherical. The mesonotum bears sparce short hairs. The apex of the wing is obtusely rounded. The pterostigma is very pale, placed under R_1 . The vein R_1 is bare. The costal section Sc- R_1 is equal to the R_1 - R_{2+3} section. The stem R_{4+5} is 2.3 times as long as RS1, R_5 is 1.3 times as long as R_{4+5} . The transverse *rm* is placed in the basal third of the discoidal cell. The convex fold is developed from the wing base, it crosses *rm* and disappears at the level of R_{4+5} fork. The basal section of M_2 is equal to *rm*. The discoidal cell is narrow, its posterior margin between M_2 and M_4 is gently S-shaped. M_1 is slightly arched anteriorly, M_2 is nearly straight and subparallel to M_4 . The M_2 - M_4 section is 1.5 times as long as the costal section M_1 - M_2 . The transverse *mcu* divides M_4 into very short basal and long distal sections. The apical portion of CuA is very weakly arched. The wing membrane is densely microtrichose, and seems to be unfuscated.

M e a s u r e m e n t s (mm): body length, ca. 3, wing length, 2.5, wing width, 0.9.

Material. Holotype.

Palaeobolbomyia mongolica Mostovski, sp. nov.

Plate 11, fig. 3

H o l o t y p e. PIN, no. 3791/2858, moderately wellpreserved fly, preserved in profile; Central Mongolia, Bayanhongor Aymag, northeastern outlying areas of Gobi-Altai depression, Bahar locality, outcrop 208/4; Middle–Upper Jurassic, Bahar Group, Ortsag Sequence.

Description (Fig. 3e). The body and legs are dark. The head is nearly hemispherical. The apex of the wing is obtusely rounded. The pterostigma is pale, developed as an elongate spot mainly under R₁. The costal section $Sc-R_1$ is shorter than the R_1-R_{2+3} section. The stem R_{4+5} is subequal to RS1, R_5 is 1.7 times as long as R_{4+5} . The transverse *rm* divides the anterior margin of the discoidal cell as 1 : 3. The convex fold is developed from the wing base, it crosses rm and disappears just beyond rm. The discoidal cell is not narrow, nearly parallelsided. The basal section of M_2 is slightly longer than rm. The posterior margin of the discoidal cell is not angled. M_1 is faintly arched anteriorly, M_2 is straight, these veins seem to be slightly diverged, M_2 and M_4 are subparallel. The M_2 - M_4 section is 1.3 times as long as the costal section M_1-M_2 . The transverse mcu divides M₄ into very short basal and longer distal sections. The apical part of CuA is weakly arched. CuP is straight. The tips of CuA and CuP are very close but the point petiole is absent. The halteres are dark, however they are paler than the thorax.

Measurements (mm): body length, 2.5, wing length, 2.3, wing width, 1.

Material. Holotype.

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