Elliidae, a new fossil family of the infraorder *Axymyiomorpha* (*Diptera*)

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Abstract. A new fossil family, *Elliidae*, of the infraorder *Axymyiomorpha* is described from Upper Jurassic and Lower Cretaceous of Central Asia. It comprises two new genera: *Ellia* gen. n. and *Polyanka* gen. n.; the first with two species, *E. colorissima* sp. n. and *E. khara*, sp. n., the second with *P. minuta* sp. n. Age and phylogenetical relations of *Elliidae* fam. n. is discussed; the family shows wing venation characters linking the *Axymyiomorpha* and the oldest, Triassic *Anisopodomorpha*.

Key words: Axymyiomorpha, fossil, new family, Elliidae, Perissommatidae, Thaumaleidae, Axymyiidae, Pachyneuridae, Jurassic, Cretaceous.

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INTRODUCTION

The Axymyiomorpha were distinguished by MC ALPINE et al. (1981) and WOOD and BORKENT (1989) as a separate infraorder comprising a single family, Axymyiidae, known only from the Recent species. The distinction was made on the basis of larval and pupal characters, with only one that of adults, the surface of scutum. However, also the wing venation of Axymyiidae (Fig. 1b) shows the characters unique for the group: radial field with a long R_{3+4} , a very short R_3 vein and four radial veins terminating in wing margin, while in the medial field only three medial veins reach the wing margin and d cell is open. This type of venation resembles that observed in the families Pachyneuridae, Perissommatidae and Thauma-



Fig. 1. Wing venation of Anisopodomorpha (a) and Axymyiomorpha (b-d); a, Archyrhyphus sp. (Protorhyphidae); b, Axymyia furcata MC ATEE (Axymyiidae); c, Pachyneura fasciata ZETTERSTEDT (Pachyneuridae); d, Palaeoperissomma collessi KOVALEV (Perissommatidae); e, Mesothaumalea fossilis KOVALEV (Thaumaleidae).

leidae (Fig. 1 c,d,e, respectively) and flies of all four groups in question are closely related, according to KOVALEV (1989, 1990). The latter author (KOVALEV, 1990) also includes to this suborder the family *Limnorhyphidae* with one species, *Limnorhyphus haifanggouensis* described by HONG (1983) in the infraorder *Bibionomorpha*. We refrain herein from including this taxon into the *Axymyiomorpha*, before the specimen in question is accessible for the revision.

Among the fossil materials from the central Asiatic localities (Upper Jurassic and Lower Cretaceous) numerous specimens were found and are included herein into the infraorder *Axymyiomorpha* on the basis of their venation of radial field as defined above, while the medial field is plesiomorphic, resembling the *Anisopodomorpha*, with *d* cell closed and all four medial veins terminating in the wing margin (Fig. 2a; compare *Anisopodomorpha*, 1a). This unique combination of primitive and derived characters, linking both infraorders, forced us to create a new family, *Elliidae*.

SYSTEMATIC PART

Elliidae fam. n.

D i a g n o s i s. Mesonotum only slightly concave. Venation: four long radial veins terminate in wing margin, R_3 very short, with very long R_{3+4} ; all four medial veins present; d cell closed, large. Three small spermathecae present.

Type genus: *Ellia* gen. n. with two species from the Upper Jurassic and Lower Cretaceous of Asia.

Key to the genera

1. Vein R_{3+4} originating from R_{3+4+5} , distally to cross-vein *r-m* (Fig. 2a) *Ellia* gen. n. - R_{3+4} originating directly from *Rs*, proximally to cross-vein *r-m* (Fig. 4b) . . . *Polyanka* gen. n.

Ellia gen. n.

D i a g n o s i s R_{3+4} originates distally to cross-vein *r-m*. Type species: *Ellia colorissi*ma sp. n. from the Lower Cretaceous locality Baysa (Asia, Transbaikalia). Two species of this genus were distinguished, described below.

Description. Flies sized 8-12 mm, wing 4.5-7 mm long, distinctly patterned or overally pigmented, with conspicuous stigma. Head with palpi and antennae unknown (not preserved). Venation: Sc slightly exceeding midlength of wing; cross-vein sc-r close to Rb fork; R_{3+4+5} present, very short; cross-vein r-m positioned centrally at the upper edge of d cell; M_1 exceeding double length of d cell upper edge; cross-vein m-m connecting M_2 and M_3 or fork of M_{1+2} and M_3 ; cross-vein m-cu subsinuous, parallel to costal wing margin; terminating section of A_1 more or less curved to wing margin. Female cerci shorter than width of 8. abdominal segment.

Ellia colorissima sp. n.

D i a g n o s i s. Wing with dark pattern; R_5 1.5 times as long as R_s ; cross-vein sc-r before fork of Rb; cross-vein m-m between M_2 and M_3 .

Description (Plate I). Female with thorax and abdomen in good condition, head not preserved. Body length 10 mm (without head), wing length 7 mm.



Fig. 2. Ellia colorissima sp. n., holotype; a, wing; b, fore leg.

Wing (Fig. 2a): dark pattern over a greater part of wing; Sc ending between cross-vein r-m and fork of R_{3+4+5} ; cross-vein sc-r at its two lengths before fork of Rb; length ratio $Rs:R_{3+4+5}:R_5$ is like 7:1:12; d cell closed; M_1 slightly longer than twice the length of d cell upper edge; cross-vein m-m between M_2 and M_3 , (i.e., positioned beyond M_{1+2} fork); cross-vein m-cu long, subsinuous, parallel to costal wing margin; terminating section of A_1 curved to wing margin.

Legs short and stout, only one fore leg is well preserved (Fig. 2b), with a very thick femur, three times as long as thick; tibia thick, short, ca. 1/3 shorter than femur, with large, single spur and two or three lobes at inner side (probably the sensible organs); first tarsomere more than twice as long as the second one.

Female genital organs: poorly visible, cerci short, round, covered with dense, delicate trichiae; three small spermathecae present (diameter 0.12 mm).

Material examined: holotype No. 3064/9730, female, from Baysa (Central Asia), Lower Cretaceous (ca. 130 Ma). Housed in the Paleontological Institute, Russian Academy of Sciences, Moscow.

Ellia khara sp. n.

D i a g n o s i s. Wing without pattern, but overally pigmented; R_5 more than twice as long as R_5 ; cross-vein *sc-r* positioned distally to fork of R_b ; cross-vein *m-m* between M_{1+2} and M_3 (at the M_{1+2} fork).

Description (Plate II). Female with only abdomen and one wing preserved, 5.5 mm and 4.5 mm long, respectively. Head, thorax and legs lacking.

Wing (Fig. 3a): uniformly pigmented, well preserved, only a small, most distal portion lacking. Sc ending opposite fork of R_{3+4+5} ; cross-vein sc-r at its two lengths beyond the fork of Rb; R₃ very short, its length equals 1/3 of R₄; length of R₅ twice exceeding Rs; length ratio $Rs:R_{3+4+5}:R_5$ is 6:1:14; M_1 more than twice as long as the upper edge of d cell; cross-vein m-m at the fork of M_{1+2} ; cross-vein m-cu long, conspicuously subsinuous, parallel to costal wing margin; A_1 almost straight, curved to wing margin at a lower angle when comparing with the previous species. Anal lobe folded; distal margin of wing invisible.



Fig. 3. Ellia khara sp. n., holotype: a, wing, b, female terminalia.

Genitalia: ovipositor (Fig. 3b) with cerci distinctly twofold, densely covered with delicate trichiae; three small spermathecae poorly visible but recognizable, diameter equals 0.1 mm.

Material examined: holotype No. 3965/2977, female, from Khutel-khara (Mongolia), turn of Jurassic to Cretaceous. Housed in Paleontological Institute, Russian Academy of Sciences, Moscow.

Polyanka gen. n.

D i a g n o s i s. R_{3+4} before cross-vein r-m (originates directly from Rs).

Description of the genus is covered by that of the type species.

Type species: *Polyanka minuta* sp. n. from Karatau (Kazakhstan, Asia), Upper Jurassic. Only one species of this genus is distinguished.

Polyanka minuta sp. n.

D i a g n o s i s of the species is identical with the generic one.

Description (based on all specimens included; holotype, Plate III). Body length 4.5-6.7 mm, wing length 3.0-4.7 mm.

Head rounded, rostrum somewhat shorter than the rest of the head; antennae (Fig. 4c) slightly longer than head, 15-16 segmented, flagellomeres short and thick, tapering towards the end; palpi (Fig. 4a) 5-segmented, not longer than the head, last palpomere shorter than the preceding one.

Wing clear (Fig. 4b,d,e): Sc ending opposite fork of Rs; cross-vein sc-r at its 2-3 lengths before fork of Rb; R3 2-3 times shorter that R4; R5 three times as long as Rs; length ratio $Rs:R_{3+4+5}:R_5$ is 5.5:1:17 in the holotype (while in all specimens examined variability



Fig. 4. Polyanka minuta sp. n., holotype: a, palpus, b, wing; paratype No. 2904/1406: c, antenna, d, wing; specimen No. 2904/1499: e, wing.

ranges 4-6.5:1:13-17, respectively); cross-vein *m-m* positioned between M_2 and M_3 ; M_1 3.5-4 times as long as M_{1+2} (which makes upper edge of *d* cell); cross-vein *m-cu* long, slightly subsinuous to almost straight; A1 curved to wing margin at the end.

Legs with tibial spurs, one in fore legs, two in middle and hind ones.

Genitalia: poorly identifiable in all specimens; cerci sharpened at the end, covered with delicate trichiae; three small spermathecae of a diameter 0.075-0.1 mm.

M a terial examined: holotype – female No. 2904/1339 (+,-); paratypes: 2384/988; 2784/87 (+,-); 2784/414 female, 2904/1406 female, all from Karatau (central Asia; turn of Jurassic to the Cretaceous). Other materials: 1701 = 1789/121; 2066/1313; 2384/87 (+,-); 2384/988; 2554/1121; 2554/1207; 2784/388; 2784/407; 2784/414; 2904/1286; 2904/1339; 2904/1499; 2997/1041; 2997/3467; 2997/3775; 2997/3487; 2997/4769; 2997/4785, same locality.

R e m a r k s. Specimens Nos. 2904/1499 and 2997/1041 slightly differ from the remaining ones in the d cell shape (compare Fig. 4b,d,e). Although the materials listed comprise males and females, their separation is not possible.

DISCUSSION

Proposed phylogeny of the group

The phylogenetic tree of the Axymyiomorpha is shown in Fig. 5. It comprises also the relations of this infraorder with the Anisopodomorpha, through the oldest representative of the latter, Yala argentata KRZEM. from the family Procramptonomyiidae (KRZEMIŃSKI 1992). The main difference in wing venation between the two infraorders considers the details of the radial field: while in the Axymyiomorpha R_4 is fused with R_3 (Fig. 1b,c,d,e) over a section called R_{3+4} (apomorphy 1 in Fig.5), in the Anisopodomorpha the vein R_4 is fused with R_5 , thus forming the vein R_{4+5} (Fig. 1a). This latter vein is very short in the fossil family Procramptonomyiidae, and especially in its Upper Triassic representative, Yala argentata from USA (Fig. 5a). Hence it can be conceived that the similar species could make an ancestor line for the Axymyiomorpha. Within the latter group, the Elliidae fam. n. resembles the fossil Anisopodomorpha of the families: Procramptonomyiidae and Protorhypidae in having a complete of four radial and four medial veins terminating in wing margin, and d cell closed; these characters are plesiomorphic when compared with the further reduction in both respective infraorders. Thus the Elliidae show the characters of a stem group within the Axymyiomorpha.

It seems plausible that the remaining families of this infraorder represent three main evolutionary lines. Within each of them the medial field had undergone reduction of veins, but independently, resulting in somewhat different final pattern.

The first lineage, family *Perissommatidae* is characterized by a strongly reduced *Sc* and R_1 veins, the former ending freely, not reaching the costa (apomorphy 2). In the medial field, the vein M_{1+2} is extremely long. The second lineage, family *Thaumaleidae*, is distinctly separated by the following three autapomorphies: R_3 taking the position of a cross-vein (apomorphy 3), R_4 bent in the middle (apomorphy 4) and reduction of two

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Fig. 5. Phylogenetic tree of Axymyiomorpha. Apomorphies: 1, R₃₊₄ present; 2, Sc strongly reduced, not reaching costa; 3, R₃ positioned as cross-vein; 4, R₄ bent medially; 5, only two medial veins present; 6, Rs wavy; 7, M₁₊₂ very short. Superfamilies' system is applied after KOVALEV (1990).



Fig. 6. Age of families included in Axymyiomorpha.





medial veins and a cross-vein *m-m* (*d* cell open) (apomorphy 5). The position of R_3 may indicate that this vein is not homologous with R_3 vein in the other families; maybe it is an additional cross-vein. If this is true, then possibly the bending in R_4 is a trace left after the origin of completely reduced R_3 . This family is so distinct that was included into the *Culicomorpha* by HENNIG (1973) and WOOD and BORKENT (1989); KOVALEV however, basing on wing venation studies classified it to the Axymyiomorpha (KOVALEV 1989, 1990) and we share his opinion herein. The third lineage encloses two families, *Pachyneuridae* and Axymyiidae which share 2 synapomorphies, Rs wavy and M_{1+2} very short (apomorphies 6 and 7, resp.).

The age of all families mentioned, based on their oldest representants, is shown in Fig. 6. With the exception for the *Elliidae*, all are represented also by the Recent species. Surprisingly, the *Elliidae* which exhibit the most ancient characters in wing venation, were found not before the Upper Jurassic, as for now. Basing on the arguments given in this discussion we presume that its age is much older and anticipate the discoveries of the *Elliidae* in much older deposits, at least from the Lower Jurassic.

The distribution of the Recent and Mesozoic Axymyiomorpha is shown in Fig. 7. Noteworthy is the South American and Australian distribution of *Perissommatidae* suggesting their origin in Gondwana; however, their presence in fossil state in Asia denies it, as was already stated by ESKOV and GOLOVATCH (1986).

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Plate I. Ellia colorissima sp. n. (holotype).



Plate II. Ellia khara sp. n. (holotype).



Plate III. Polyanka minuta sp. n. (holotype).

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