

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

Ewa KRZEMIŃSKA, Vladimir BLAGODEROV, Wiesław KRZEMIŃSKI

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Abstract. A new fossil family, *Ellidae*, 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 *Ellidae* fam. n. is discussed; the family shows wing venation characters linking the *Axymyiomorpha* and the oldest, Triassic *Anisopodomorpha*.

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

Ewa KRZEMIŃSKA, Wiesław KRZEMIŃSKI, Institute of Systematics & Evolution of Animals, Polish Academy of Sciences, ul. Sławkowska 17, 31-016 Kraków, Poland.

Vladimir BLAGODEROV, Paleontological Institute, Russian Academy of Sciences, ul. Profsoyusnaya 123, 117647 Moscow, Russia.

### 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-*

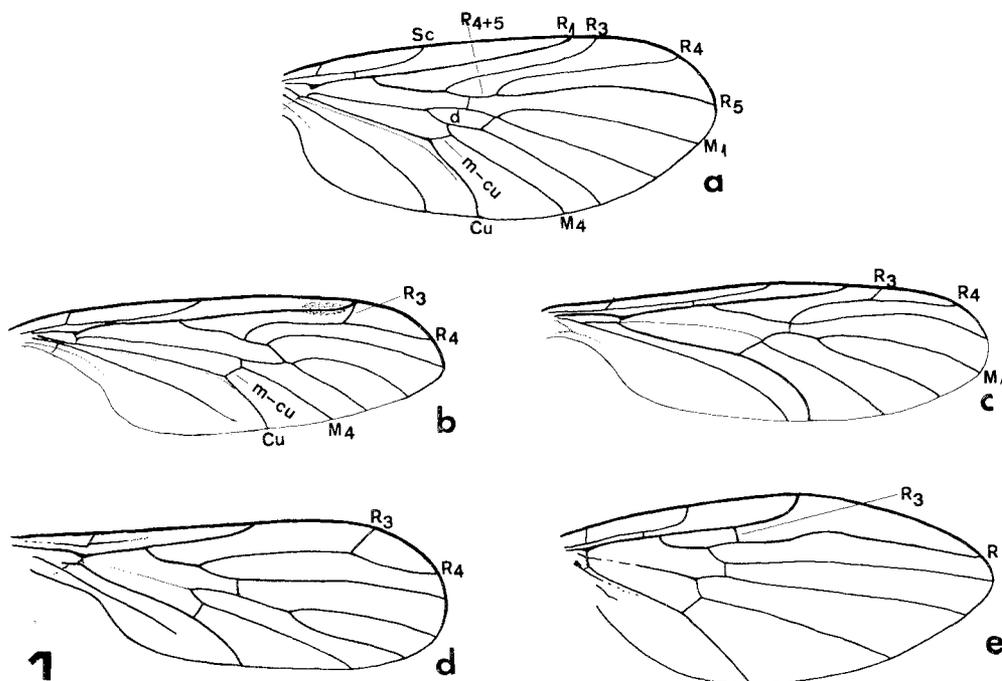


Fig. 1. Wing venation of *Anisopodomorpha* (a) and *Axymyiomorpha* (b-d); a, *Archyrhyphus* sp. (*Protorhyphidae*); b, *Axymyia furcata* MC ATEE (*Axymyiidae*); c, *Pachyneura fasciata* ZETTERSTEDT (*Pachyneuridae*); d, *Palaeoperissomma collessi* KOVALEV (*Perissomatidae*); e, *Mesothaumalea fossilis*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

SYSTEMATIC PART

*Ellidae* fam. n.

**Diagnosis.** 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  $R_5$ , proximally to cross-vein  $r-m$  (Fig. 4b) . . . . . *Polyanka* gen. n.

*Ellia* gen. n.

**Diagnosis.**  $R_{3+4}$  originates distally to cross-vein  $r-m$ . Type species: *Ellia colorissima* 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  $m-cu$  subsinuuous, 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.

**Diagnosis.** Wing with dark pattern;  $R_5$  1.5 times as long as  $R_3$ ; 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.

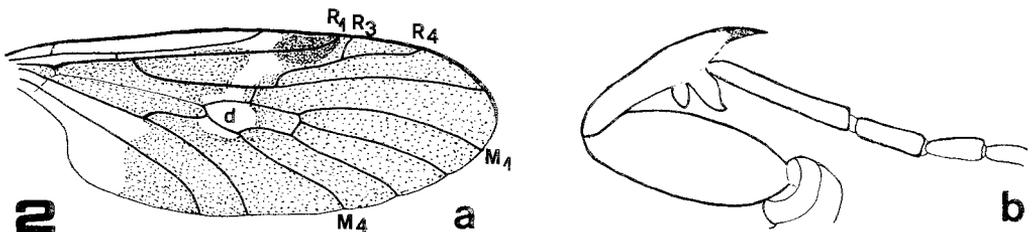


Fig. 2. *Ellia colorissima* sp. n., holotype; a, wing; b, fore leg.

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  $R_s:R_{3+4+5}:R_5$  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, subsinuuous, 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.

**Diagnosis.** Wing without pattern, but overall pigmented;  $R_5$  more than twice as long as  $R_s$ ; cross-vein *sc-r* positioned distally to fork of *Rb*; 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*;  $R_3$  very short, its length equals 1/3 of  $R_4$ ; length of  $R_5$  twice exceeding  $R_s$ ; length ratio  $R_s:R_{3+4+5}:R_5$  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 subsinuuous, 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.

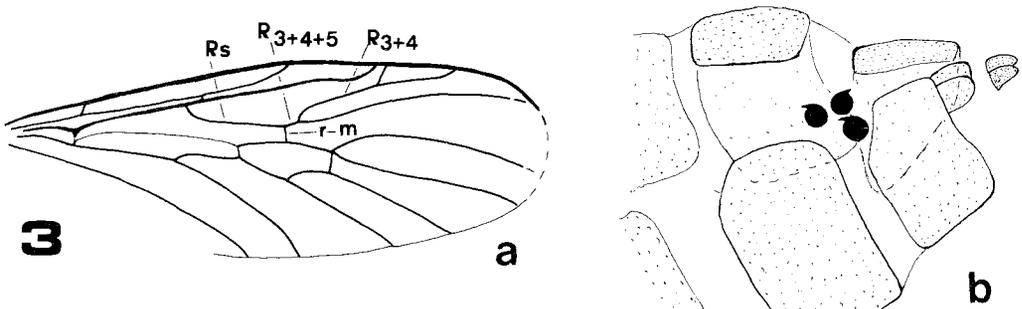


Fig. 3. *Ellia khara* sp. n., holotype: a, wing, b, female terminalia.

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.**

**Diagnosis.**  $R_{3+4}$  before cross-vein *r-m* (originates directly from  $R_5$ ).

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.**

Diagnosis 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  $R_5$ ; cross-vein *sc-r* at its 2-3 lengths before fork of  $R_b$ ;  $R_3$  2-3 times shorter than  $R_4$ ;  $R_5$  three times as long as  $R_3$ ; length ratio  $R_3:R_{3+4+5}:R_5$  is 5.5:1:17 in the holotype (while in all specimens examined variability

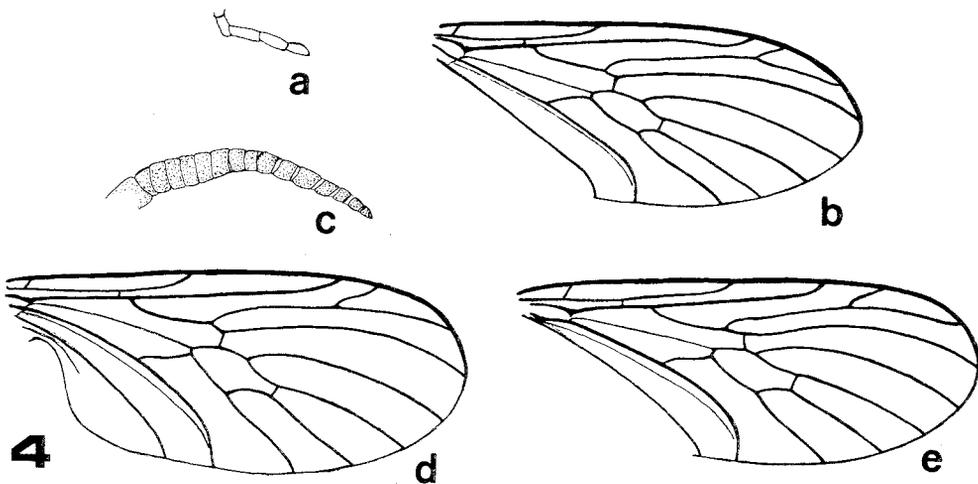


Fig. 4. *Polyanka minuta* sp. n., holotype: a, palpus, b, wing; paratype No. 2904/1406: c, antenna, d, wing; specimen No. 2904/1499: e, wing.

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 subsinuuous 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.

**Material 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.

**Remarks.** 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 *Ellidae* fam. n. resembles the fossil *Anisopodomorpha* of the families: *Procramptonomyiidae* and *Protorhynchidae* 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 *Ellidae* 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

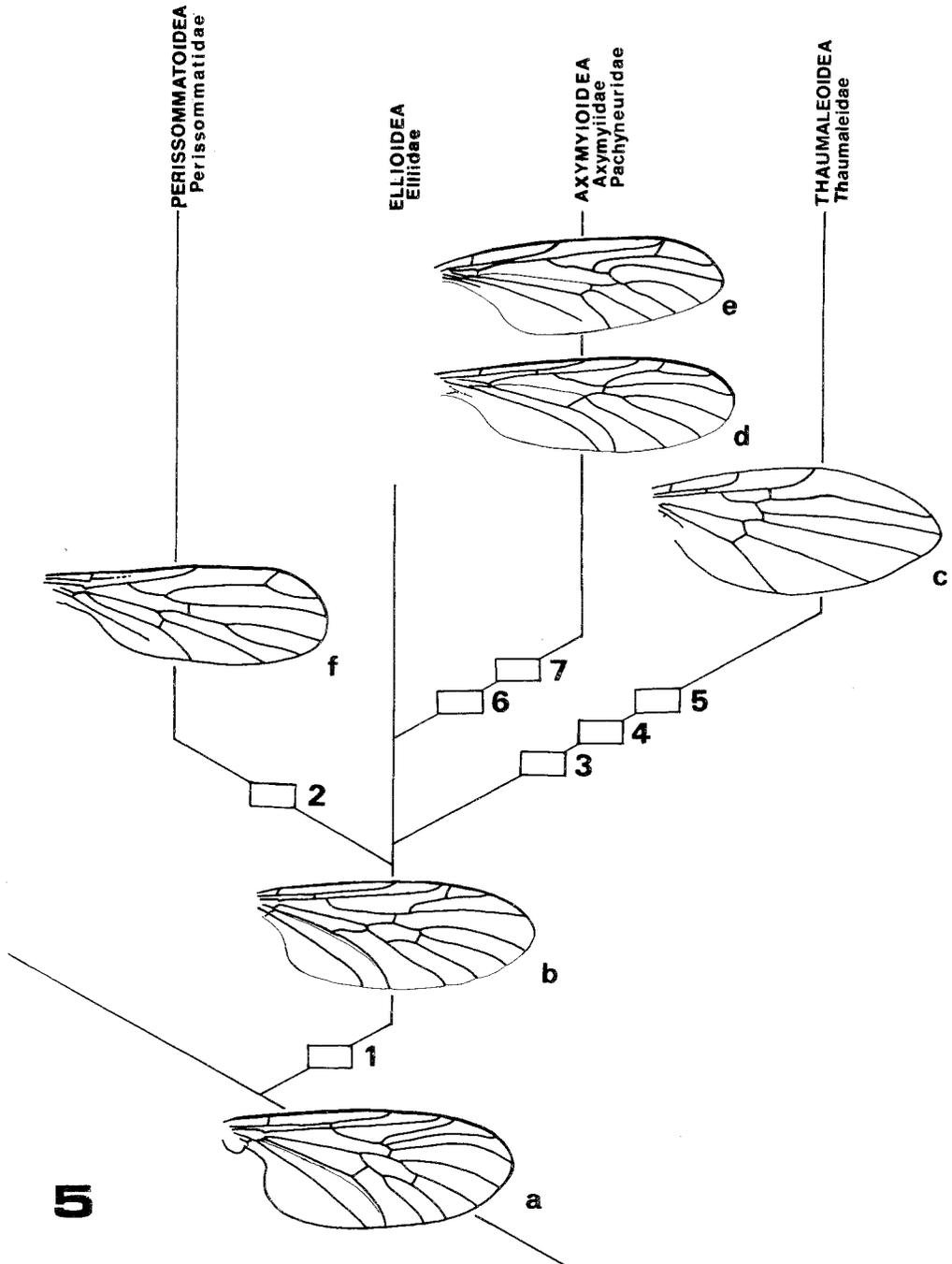


Fig. 5. Phylogenetic tree of *Axymyomorpha*. Apomorphies: 1,  $R_{3+4}$  present; 2,  $Sc$  strongly reduced, not reaching costa; 3,  $R_3$  positioned as cross-vein; 4,  $R_4$  bent medially; 5, only two medial veins present; 6,  $R_s$  wavy; 7,  $M_{1+2}$  very short. Superfamilies' system is applied after KOVALEV (1990).

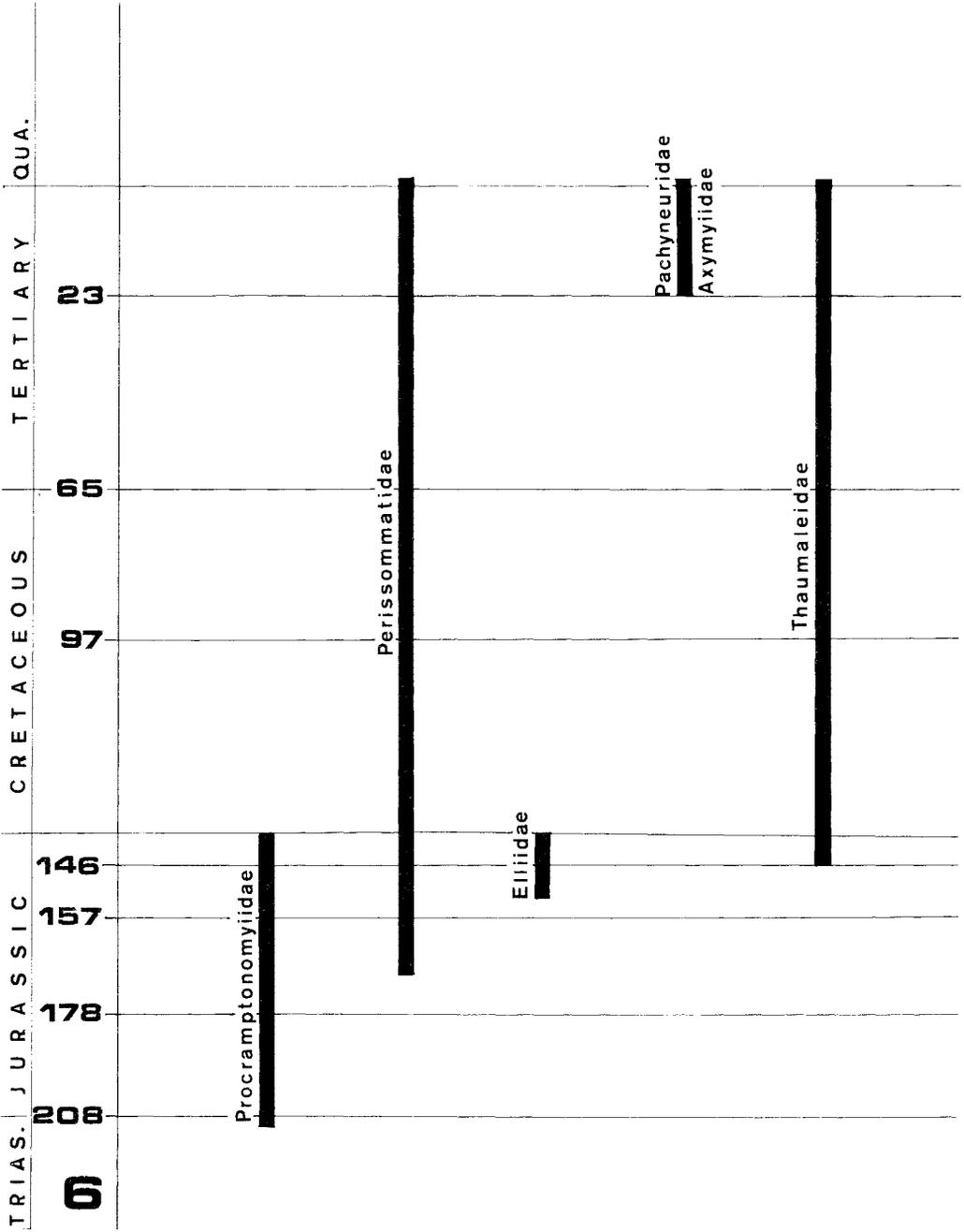


Fig. 6. Age of families included in *Axymiomorpha*.

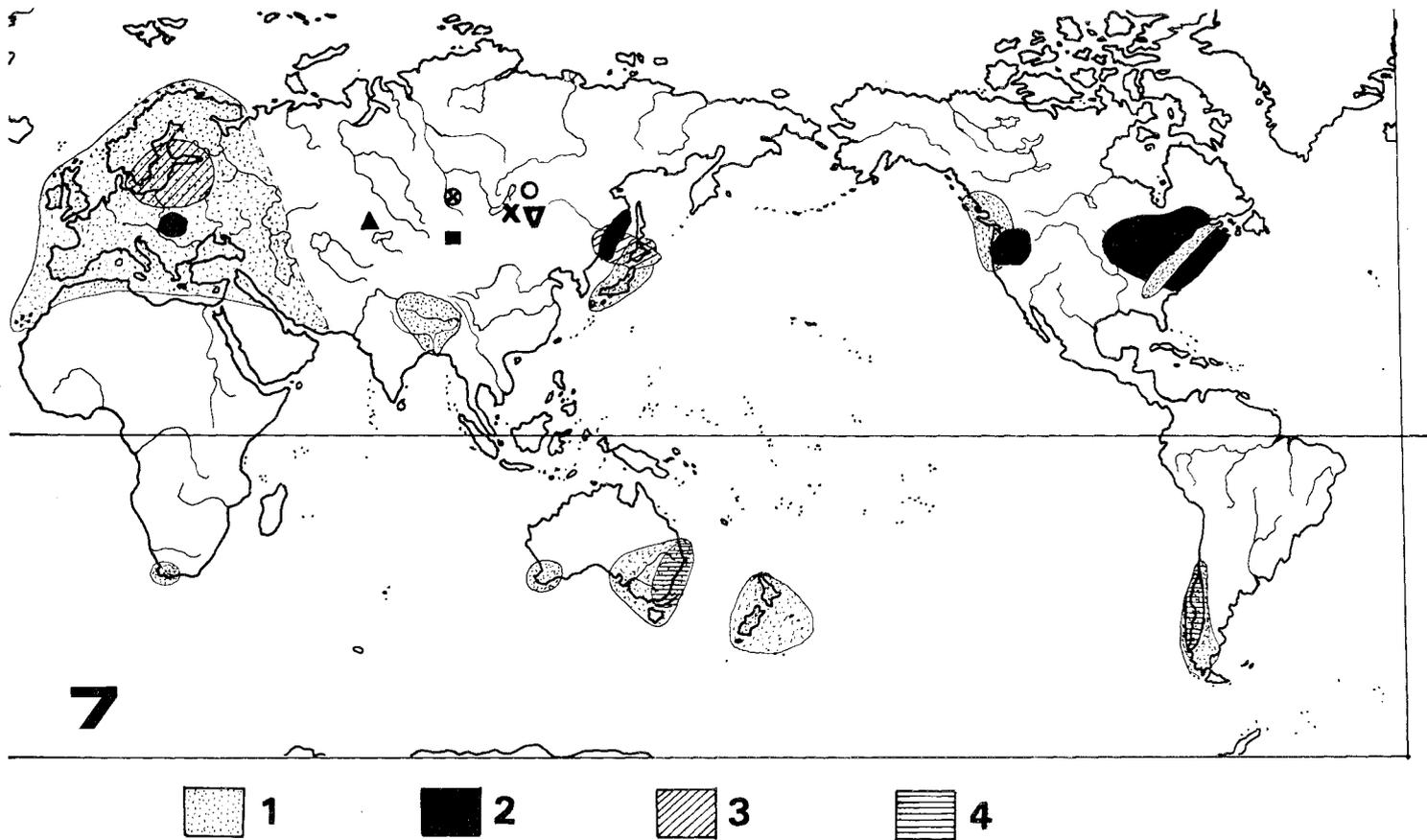


Fig. 7. Distribution of the Recent and Mesozoic Axymyiomorpha. Recent: 1 – *Thaumaleidae*, 2 – *Axymyiidae*, 3 – *Pachyneuridae*, 4 – *Perissomatidae*. Fossil: *Elliidae*: circle, *Ellia colorissima* sp. n. (Baisa, Transbaikalia, Lower Cretaceous); square, *E. khara* sp. n. (Khutel-khara, Mongolia, Jurassic/Cretaceous); triangle, *Polyanka minuta* sp. n. (Kratau, Kazakhstan, Upper Jurassic); *Perissomatidae*: cross in circle, *Palaeoperissomma collessi* KOVALEV (Kubekovo, East Siberia, Middle Jurassic); reversed open triangle, *P. demetrii* KOVALEV (Turga, Transbaikalia, Lower Cretaceous); *Thaumaleidae*: X, *Mesothaumalea fossilis* (KOVALEV – Daya, Transbaikalia, Jurassic/Cretaceous).

medial veins and a cross-vein *m-m* (*d* cell open) (apomorphy 5). The position of *R*<sub>3</sub> may indicate that this vein is not homologous with *R*<sub>3</sub> vein in the other families; maybe it is an additional cross-vein. If this is true, then possibly the bending in *R*<sub>4</sub> is a trace left after the origin of completely reduced *R*<sub>3</sub>. 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*<sub>1+2</sub> 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 *Ellidae*, all are represented also by the Recent species. Surprisingly, the *Ellidae* 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 *Ellidae* 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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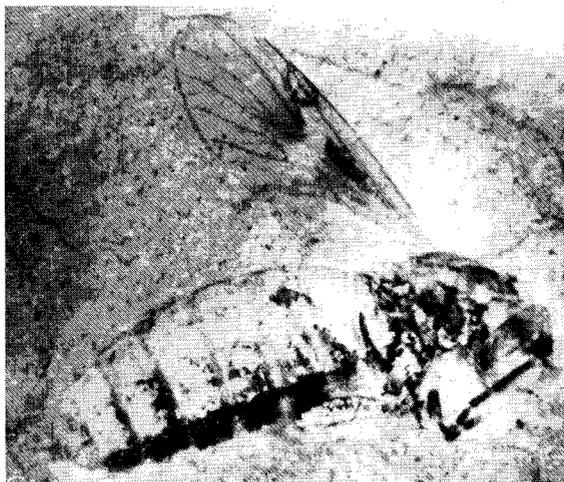


Plate I. *Ellia colorissima* sp. n. (holotype).



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



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