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The oldest occurrence of Chaoboridae (Insecta: Diptera)

Древнейшая находка Chaoboridae (Insecta: Diptera)

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КЛЮЧЕВЫЕ СЛОВА: Culicomorpha, ископаемые насекомые, новые таксоны, триас, жилкование крыла.

ABSTRACT. The fossil record of Triassic Culicomorpha is extremely poor, with the oldest member of the infraorder having been described, as Chironomoidea *incertae familiae*, from the the 'Grès à Voltzia' Formation (Upper Buntsandstein, early Anisian, France). In this paper, the oldest member of another superfamily, Culicoidea, is described from the Madygen Formation (Ladinian–Carnian, Kyrgyzstan) based on an isolated wing. The new genus, *Triassomyi*a, **gen.n.**, is assigned to the family Chaoboridae.

РЕЗЮМЕ. Триасовые находки Culicomorpha исключительно редки, а древнейший представитель инфраотряда описан как Chironomoidea *incertae familiae* из формации Гре-а-Вольция (верхи пестрого песчаника, ранний анизий, Франция). В данной работе древнейший представитель другого надсемейства, Culicoidea, описывается из формации Мадыген (ладин–карний, Киргизия) по изолированному крылу. Новый род, *Triassomyi*a, **gen.n.**, отнесен к семейству Chaoboridae.

Introduction

The extremely poor fossil record of Triassic Culicomorpha includes only three reports, all of them assigned, with variable degree of certainty, to Chironomoidea. The oldest member of the infraorder, *Anisinodus crinitus* Lukashevich et al., 2010, has been described, as Chironomoidea *incertae familiae*, based on a larva from the 'Grès à Voltzia' Formation (Upper Buntsandstein, early Anisian, France). The oldest Chironomidae, *Aenne triassica* Krzemiński et Jarzembowski, 1999, has been described based on an isolated wing from the Cotham Member of the Lilstock Formation (Rhaetian, United Kindom). Six adults are known from the Cow Branch Formation (Carnian–Norian, USA), but they cannot be described and named formally due to poor preservation, so they have been variably listed as Culicomorpha *indet* or ?Chironomoidea [Krzemiński, Jarzembowski, 1999; Blagoderov et al., 2007; Lukashevich et al., 2010]. No certain representatives of Culicoidea have yet been found in Triassic deposits.

Chaoboridae, commonly known as "phantom midges," is a small relict family of Culicoidea. At present, the family is represented by only six genera, together including about fifty species [Borkent, 2014]. In the past it was more diverse: 17 Mesozoic genera can be considered valid, although this number can be overestimated. For example, *Jordanobotomus* Kaddumi, 2005 and *Libanoborus* Azar et al., 2009, from Jordanic and Lebanese ambers, close in geography and age, are candidates for synonymization once the type material is revised [Lukashevich, 2011]. Chaoboridae flourished in Jurassic and Early Cretaceous fresh waters of Asia; their immatures and/or adults often quantitatively dominate in taphocenoses [Kalugina, 1980; Kalugina, Kovalev, 1985; Lukashevich, 1996b, 2008]. However, such abundance and diversity are recorded only since the Middle Jurassic [Kalugina, Kovalev, 1985], whereas from the Lower Jurassic deposits no immatures and only two chaoborid wings have been described. Both of the latter are representatives of *Rhaetomyi*a Rohdendorf, 1962, known from Asia (Dzhil Formation, Sinemurian; Sogyuty locality, Kyrgyzstan) and Europe (Toarcian "Grünen Serie"; Grimmen locality, Germany) [Rohdendorf, 1964; Ansorge, 1996; Lukashevich, 1996a]. The systematic position of *Rhaetomyia* has been subject of debate: Ansorge [1996] separated it as a monotypic family, ancestral to all other Culicoidea, whereas Amorim [1993] included the genus in Axymyiomorpha, a monophyletic group additionally including Axymyiidae, Perissommatidae, and Pacheneuridae. Arguments in favor of the chaoborid affinity of the genus have been presented previously [Lukashevich, 1996a], while a photograph of a *Rhaetomyia* wing is being published here for the first time.

The new genus, described herein from the Triassic Dzhailoucho locality (Madygen Formation, Ladinian–Carnian, Kyrgyzstan), is the oldest member of the family.

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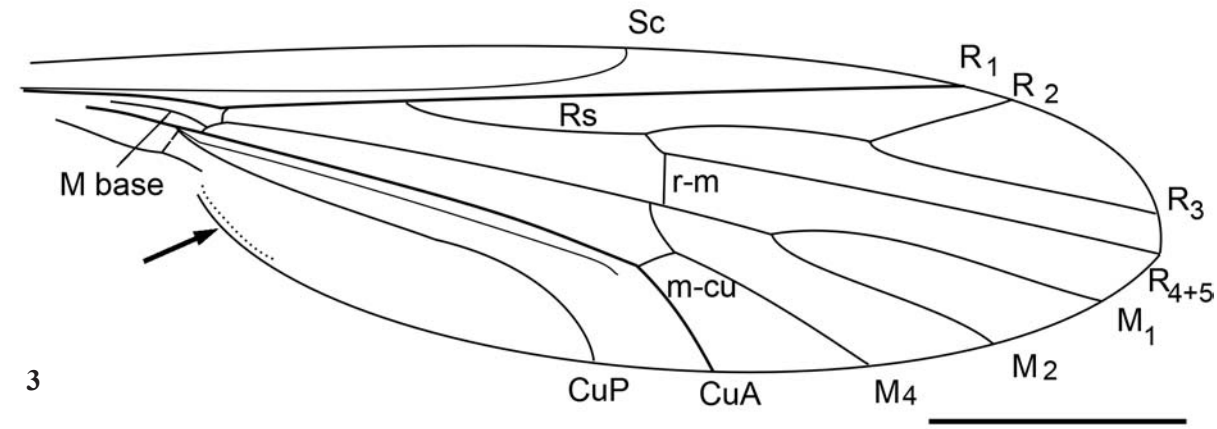
Material and methods

The famous fossil site near the village Madygen is situated about 50 km west of Batken in southwestern Kyrgyzstan, Central Asia. The Madygen Formation, dated to the Ladinian–Carnian based on its flora, crops out in five adjacent areas covering about 10 km [Dobruskina, 1982; 1995], among which the northern one, Urochishche Dzhailoucho, is the richest in fossil insects [Shcherbakov, 2008; 2021]. Nearly all Madygen Diptera (except for *Dilemmala*) have been found in Dzhailoucho. The dipterans collected at Madygen by expeditions of the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN) in 1957–1971 have been described earlier [Shcherbakov et al., 1995]. The specimen of Chaoboridae described herein was collected during the first of three more recent



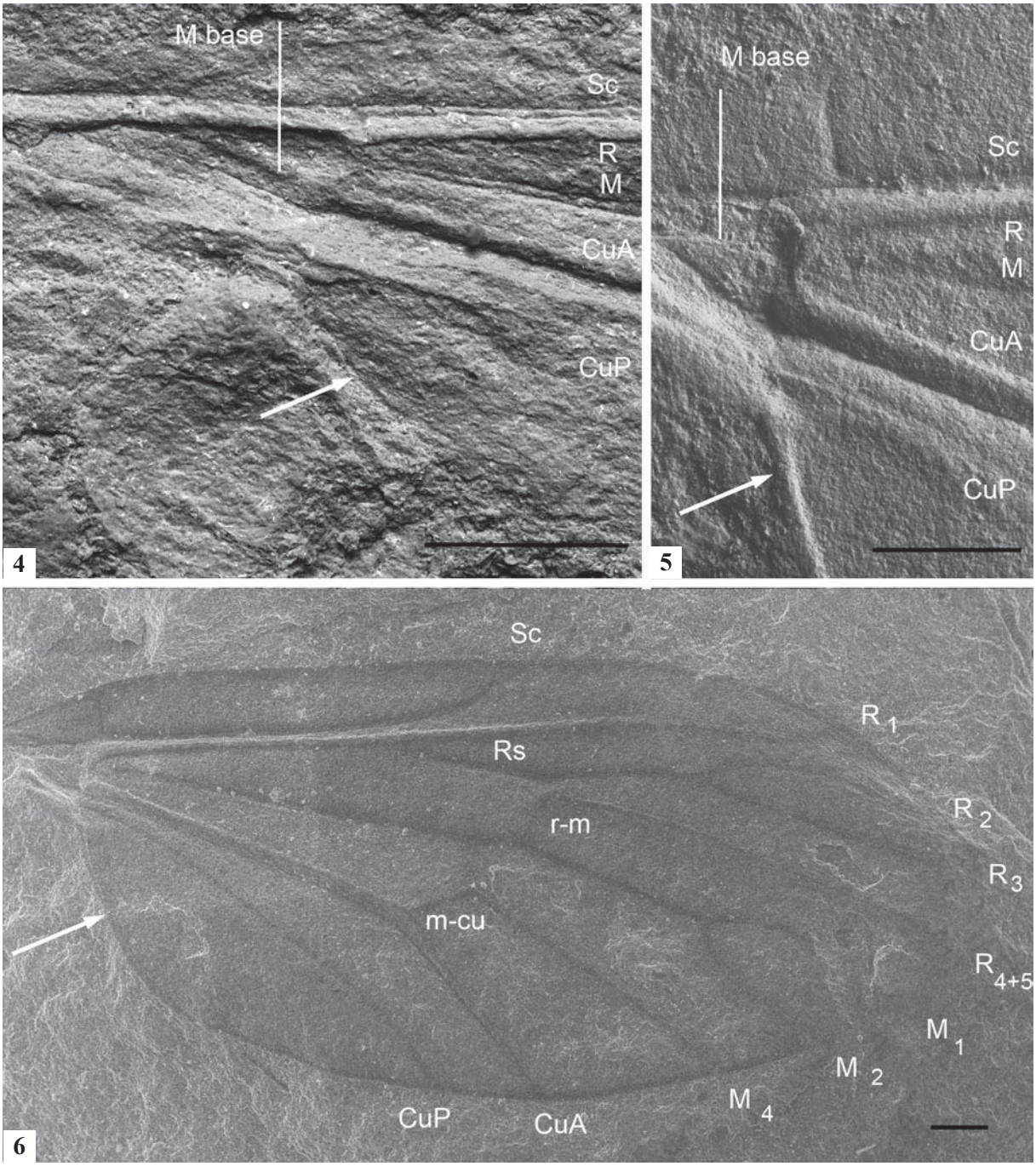
Figs 1–3. *Triassomyia shcherbakovi* **gen.** et **sp.n**., Madygen, Triassic; holotype: 1 — photograph; 2 — SEM, uncoated, BSE; 3 — drawing. Arrows mark the anal fold. Scale bars, 500 μm.

Рис. 1–3. *Triassomyia shcherbakovi* **gen.** et **sp.n**., Мадыген, триас, голотип: 1 — фотография; 2 — СЭМ, без напыления, BSE; 3 — рисунок. Стрелки маркируют анальную складку. Длина масштабных линеек 500 μm.

expeditions by the Paleontological Institute (2006, 2007, 2009), which together yielded three dozen dipteran specimens. The specimen is housed in PIN, Moscow.

Light images were taken with a Leica MZ9.5 stereomicroscope equipped with a Leica DFC420 digital camera and edited in Adobe Photoshop. Scanning electron images of uncoated specimens were taken using a Tescan Vega III microscope, operated in a low-vacuum mode, using a backscattered electron (BSE) or a secondary electron (LVSTD) detectors.

Wing venation terminology follows the Manual of Afrotropical Diptera [Cumming, Wood, 2017].



Figs 4–6. Wings of Mesozoic Chaoboridae (SEM, uncoated): 4 —*Triassomyia shcherbakovi* **gen.** et **sp.n**. (BSE), Madygen, Triassic; holotype; 5–6 — *Rhaetomyia necopinata*, Sogyuty, Jurassic, holotype; 4–5 — basiala (BSE); 6 — wing (LVSTD). Arrows mark the anal fold. Scale bars, 200 μm.

Рис. 4–6. Крылья мезозойских Chaoboridae (СЭМ, без напыления): 4 — *Triassomyia shcherbakovi* **gen.** et **sp.n**. (BSE), Мадыген, триас, голотип; 5–6 — *Rhaetomyia necopinata*, Согюты, юра, голотип; 4–5 — базиала (BSE); 6 — крыло (LVSTD). Стрелки маркируют анальную складку. Длина масштабных линеек 200 μm.

Systematic Paleontology

Family Chaoboridae Edwards, 1920

*Triassomyi*a, **gen.n.**

TYPE SPECIES. *Triassomyia shcherbakovi*, **sp.n.**

DIAGNOSIS (only wing characters). Wing elongate, without spots. Sc short, ending near wing midlength, before r-m, Rs stem long, subequal to R_{2+3} stem; wide R_{2+3} fork longer than R_{2+3} stem, with R_2 apex closer to R_1 than to R_3; r-m in distal half of wing; M_{1+2} fork long, longer than R_{2+3} fork and M_{1+2} stem; m-cu far from Rs origin; CuP subparallel to CuA, CuP terminating distal to Rs base and proximal to m-cu.

COMPOSITION. Type species.

COMPARISON**.** The new genus differs from all other members of the family in the shape of the R_{2+3} fork, which is wide, with R_2 apex closer to R_1 than to R_3. A similar, wide fork R_{2+3} has been recorded in *Jordanobotomus* and *Libanoborus*, but in both of these genera R_2 is very short, touching R_1 at its apex. A similar short Sc, ending near wing midlength, has been described in *Rhaetomyia.* Besides the shape of the R_{2+3} fork, the latter genus is distinct in having a wider wing with short Rs stem and M_{1+2} fork.

REMARKS. The wing venation of the new genus shows the following characters typical of the family: Sc complete, R_1 long and straight, Rs with three branches, R_{2+3} forked, r-m connecting R_3 not far from base with M_{1+2} stem, M with three branches, M_{1+2} forked, discal cell absent, and CuP complete.

A distinct M base is found in the wing basiala of the new genus (Figs 1–4). In the Triassic Bibionomorpha (*sensu* Shcherbakov et al., 1995, i.e. including Pachyneuroidea) a distinct M base is absent, whereas in the Triassic representatives of other nematoceran infraorders a strong convex M base between R and Cu bases occurs [Shcherbakov et al., 1995]. Moreover, such an M base is also known in the extant Chaoboridae but is absent in the extant Axymyiidae and Perissommatidae [Shcherbakov et al., 1995: figs 7, 9–10]. Distinct M bases, found in the holotypes of the new genus and *Rhaetomyia necopinata* Rohdendorf, 1962 (Figs 4–5), rule out the bibionomorphan but do not contradict the chaoborid affinities of these genera.

The characteristic proximal fold along the margin of the anal lobe of the new genus (Figs 1–4) is also known in Mesozoic Chaoboridae (e.g., *Libanoborus* and *Mesocorethra* Kalugina, 1993) and Dixidae (*Eucorethrina* Kalugina, 1985 and *Syndixa* Lukashevich, 1996) [Lukashevich, 1996a: figs 1–2; Azar et al., 2009: fig. 6; Lukashevich, 2011: Plate 6, fig. 4]. A similar fold is found in *Rhaetomyia* (Figs 5–6), additionally suggesting a culicomorphan affinity of the genus.

ETYMOLOGY. From "Triassic" and the Greek "*myia"* (fly).

*Triassomyia shcherbakovi***, sp.n.**
Figs 1–4.

MATERIAL. Holotype PIN 5329/12, positive impression of an isolated wing, Dzhailoucho (Madygen, northern area); Leilek District, Batken Region, SW Kyrgyzstan; Madygen Formation, Ladinian–Carnian.

DESCRIPTION. Wing length 2.1 mm, width 0.6 mm. R_1 straight, Rs connecting R_1 evenly, Rs stem subequal to R_{2+3} stem, 1.3 times as long as R_2; Rsa absent, Rs forking symmetrically; fork R_{2+3} 1.3 times as long as its stem, forming acute angle, about 45°, R_{2+3} fork thrice as long as wide, R_3 1.8 times as long as R_2, distance between apices of R_2 and R_3 thrice as long as between apices of R_1 and R_2 and apices of R_3 and R_{4+5}; r-m longer than basal part of R_{4+5} and subequal to basal part of M_4, level to m-cu; M_{1+2} forking well before R_{2+3} forking; anal lobe somewhat reduced.

ETYMOLOGY. The species epithet honors Dmitry Shcherbakov, a collector of the holotype and a recognized expert on fossil insects.

Discussion

Such a wide fork R_{2+3} has previously been unrecorded in the family, but its existence could be predicted based on venation of Early Cretaceous *Jordanobotomus* and *Libanoborus,* with wide forks where an oblique R_2 is not free but fused with R_1 [Kaddumi, 2005; Azar et al., 2009]. Alexander referred to such fusion as cephalization of the vein R_2, which "has swung cephalad and forms a fusion with R_1 backwards from the margin" [Alexander, 1927: 44]. The trend is commonly observed among extant taxa, e.g. in Tipulomorpha. The next step, a complete atrophy of R_2 and cephalization of the next longitudinal vein, R_3, has also been described in the infraorder [Stary, 1992]. The ancestral stage, with a free oblique R_2, is unknown in extant representatives but was found recently in Jurassic Pediciidae as an exception [Lukashevich, Ribeiro, 2019]. Among Culicomorpha, such cephalization is well-known in Chironomoidea and is recorded already in the oldest representative of Chironomidae, *Aenne triassica* from the Late Triassic [Krzemiński, Jarzembowski, 1999]. In another superfamily, Culicoidea, it is, to my knowledge, unrecorded among extant representatives but was found in the Mesozoic Dixidae and Chaoboridae [Lukashevich, 1996a; Azar et al., 2009]. It is clear that the confluence of R_2 with R_1 in *Jordanobotomus* and *Libanoborus* is not an occasional aberration, but a manifestation of a trend not preserved among the extant Culicoidea.

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