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A new fossil snipe fly with long proboscis from the Middle Jurassic of Inner Mongolia, China (Diptera: Rhagionidae)

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Abstract

A new genus and species of rhagionids with a long proboscis, *Elliprhagio macrosiphonius* **gen. et sp. nov.**, is described from the Middle Jurassic Jiulongshan Formation in Daohugou, Inner Mongolia, China, which is considered to be the earliest hematophagous rhagionid described hitherto according to the typically piercing and sucking mouthparts. All previously documented rhagionids from northeastern China are reviewed a key to genera of Rhagionidae from Daohugou is provided for the first time. The genus *Daohugorhagio* Zhang, 2013 is considered as a new synonym of *Trichorhagio* Zhang, 2013.

Key words: fossil**,** new species, new genus, Daohugou, hematophagous feeding

Introduction

Rhagionidae, as a relic family of lower Brachycera, have been in existence for more than 240 million years. The earliest rhagionid fossil hitherto, *Gallia alsatica* Krzemiński & Krzemińska, 2003*,* was described from the Arzviller, France (Lower/Middle Triassic) (Krzeminski & Krzeminska 2003). The rhagionids, commonly known as snipe flies, began a rapid radiation since the Triassic. Five species belonged to four genera were described from the Early Jurassic (Ansorge 1996; Mostovski & Jarzembowski; 2000; Krzemiński & Ansorge 2005). In the Middle Jurassic, Rhagionidae started to show species richness and morphological diversity (Kovalev 1981; Evenhuis 1994) with 21 species in 14 genera described so far. They comprise nine species within five genera from Transbaikalia, and 12 species within nine genera from Daohugou (Kovalev 1981, 1982; Kalugina & Kovalev 1985; Zhang K. *et al.* 2006, 2008; Zhang J. 2010, 2011, 2013; Zhang J. *et al.* 2012). In the Late Jurassic, the generic diversity of Rhagionidae decreased gradually. Up to date, 13 species in five genera have been reported, most of which are from the Karabastau Formation, except for *Palaeoarthroteles* Kovalev & Mostovski, 1997 from the Glushkovo and Godymboy Formations (Rohdendorf 1938, 1964; Kovalev 1982; Kovalev & Mostovski 1997; Mostovski 2000, 2008).

Comparing to the relatively restricted localities in the Jurassic, the Cretaceous rhagionids had much broader distribution with 20 species referred to 14 genera described from Asia, Europe, North America and Australia (Handlirsch 1906; Jell & Duncan 1986; Kovalev 1986; Zaitzev 1986; Hong *et al.* 1992; Zhang J. *et al.* 1993; Ren 1998; Grimaldi & Cumming 1999; Mostovski *et al.* 2000; Kraemer & Nel 2009; Angelini *et al.* 2016). In the Cenozoic, although exhibiting a low generic diversity with only three described genera so far, rhagionids had a noticeable diversification across species with 22 species found from Baltic, America, Germany and France (Meunier 1899, 1902, 1910, 1916; Cockerell 1908, 1911, 1921; Théobald 1937; Statz 1940; Melander 1949; Evenhuis 1994; Kerr 2010; Nel *et al.* 2016). Up to date, 35 fossil genera including 80 species have been attributed to Rhagionidae. Although significant progress on the taxonomy of fossil rhagionids have been made, a comprehensive review of the fossil rhagionids is still essential and crucial.

The Middle Jurassic Daohugou locality is well-known for its diversity and quantity of insect fossils (Gao *et al.* 2012; Gu *et al.* 2012; Wang *et al.* 2012; Yao *et al.* 2014), and so far, 12 species in nine genera of Rhagionidae have been described from this locality. Many rhagionids from this locality, having well-preserved complete body and other appendages, provide detailed morphological features for us. In this paper, we describe a new genus and species

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with a long proboscis, *Elliprhagio macrosiphonius* **gen. et sp. nov.** The well-preserved mouthpart structure infers that the new species was adapted to piercing and feeding on blood, which is proposed to be the earliest hematophagous rhagionid hitherto. In addition, a key to genera of fossil rhagionids from Daohugou is given.

Material and methods

The specimens in this study were examined dry or under alcohol using a Leica M165C dissecting microscope with an attached digital camera system and illustrated with the aid of a drawing tube attachment. Line drawings are made in Adobe Photoshop CC 2014 (64 bit). The type specimens are deposited in the fossil insect collection of the Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China. Vein nomenclature used here follows Wootton & Ennos (1989).

Systematic Paleontology

Key to genera of rhagionids from the Daohugou locality (some questionable genera are omitted)

1	R_4 diverging from R_5, forming a short and wide cell r4	2
-	R_4 nearly parallel to R_5, forming a long and narrow cell r4	3
2	M_1 and M_2 converging to a point	***Archrysopilus*** Zhang, Yang & Ren, 2008
-	M_1 and M_2 nearly parallel	***Ussatchovia*** Rohdendorf, 1964
3	R_{2+3} curved at the middle	4
-	R_{2+3} nearly straight	6
4	M_3 absent	***Palaeobolbomyia*** Kovalev, 1982
-	M_3 present	5
5	CuP and A_1 converging to a point and with a short petiole	***Elliprhagio*** **gen. nov.**
-	CuP and A_1 converging	***Protorhagio*** Rohdendorf, 1938
6	M_3 parallel to M_4	7
-	M_3 slightly diverging from M_4	9
7	d cell rather narrow and long	***Sinorhagio*** Zhang, Yang & Ren, 2006
-	d cell wide and long	8
8	bM_3 much shorter than dM_3	***Parachrysopilus*** Zhang, 2013
-	bM_3 nearly as long as dM_3	***Palaeoarthroteles*** Kovalev & Mostovski, 1997
9	M_3 and M_4 converging to a point	***Lithorhagio*** Zhang, 2012
-	M_3 and M_4 converging	***Trichorhagio*** Zhang, 2013

Order Diptera Linneaus, 1758

Suborder Brachycera Zetterstedt, 1842

Family Rhagionidae Latreille, 1802

Genus *Elliprhagio* gen. nov.

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Type species. *Elliprhagio macrosiphonius* **sp. nov.**

Diagnosis. Flagellum with 10 flagellemeres; proboscis long, labium fleshy, labella small. Wings elliptic and wide; R_{2+3} sinuate at the middle, and sharply up-curved distally; crossvein r-m intersecting the upper margin of d cell at basal one third (1/3); four medial veins present, bM_3 and dM_3 straight; anal cell closed before wing margin. Midtibiae with 1 spur.

Etymology. From "*ellip-* ", which means elliptic and genus *Ragio*, referring to the elliptic wings. Gender: masculine.

Remarks. Among the snipe flies from the Daohugou locality, the new genus is most similar to *Trichorhagio*

Zhang, 2013 in appearance, especially in venation and body configuration. But they can be distinguished by elliptic wing (vs. triangular wing in *Trichorhagio*), and the equal length of bM_3 and dM_3 (vs. the bM_3 longer than dM_3). The similar long mouthparts and elliptic wing also present in two other genera *Protorhagio* Rohdendorf, 1938 and *Palaeoarthroteles* Kovalev & Mostovski, 1997, which have also been found from the Daohugou. In *Protorhagio*, costal section between Sc-R_1 is obviously longer than that between R_1-R_{2+3}, while not distinct in *Elliprhagio*. *Elliprhagio* is distinguished from *Palaeoarthroteles* (Kovalev & Mostovski 1997; Zhang J. 2011) by the configuration of anal cell being closed (vs. open in *Palaeoarthroteles*); up-curved R_{2+3} at the middle (vs. almost straight R_{2+3}); straight bM_3 and dM_3 (vs. curved bM_3 and S-shaped dM_3 in *Palaeoarthroteles*); costal section of R_1-R_{2+3} slightly shorter than Sc-R_1 (vs. costal section of R_1-R_{2+3} no shorter than Sc-R_1 in *Palaeoarthroteles*) and mesotibiae with 1 apical spur (vs. 2 spurs in *Palaeoarthroteles*). Moreover, the genus *Sinorhagio* Zhang, Yang & Ren, 2006, and some species of *Palaeobolbomyia* (Kovalev 1982; Zhang 2010) in the same locality also possess elliptical wings resembling *Elliprhagio*. But *Sinorhagio* can be separated by their straight R_{2+3}, long R_4 and R_5 branches, and long and narrow d cell. Although *Palaeobolbomyia* resembles the new genus with similar R_{2+3}, they can be separated by the absence of M_3 in the former.

Comparing with genera from other localities, the genus *Orsobrachyceron* Ren, 1998 from Liaoning (China) also has similar long proboscis and venation as those of the *Elliprhagio* **gen. nov.**, but differs from *Elliprhagio* in the M_3 and M_4 strongly converged to a point at the margin of wing and cell cu closed without a short petiole apically. The other two genera *Palaeobrachyceron* Kovalev, 1981 and *Jurabrachyceron* Kovalev, 1981 from the Transbaikalia (Upper Jurassic to Lower Cretaceous) show some similarities in the elliptic wings and configurations of venation with *Elliprhagio*. However, they can be separated by their configuration of M_3 and M_4: bM_3 much shorter than dM_3, and M_3 parallel to M_4. In addition, *Palaeobrachyceron* has an extremely long and straight R_5 that is distinctly different from the new genus.

***Elliprhagio macrosiphonius* sp. nov.**

(Figs 1, 2, 3)

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Holotype. CNU-DIP-NN2015101, well preserved, female. **Paratypes.** CNU-DIP-NN2015103, antennae and genitalia absent, sex unknown. CNU-DIP-NN2015105, antennae and genitalia absent, sex unknown. CNU-DIP-NN2015106, genitalia absent, sex unknown. All the type fossils are housed in the Capital Normal University, Beijing, China.

Type locality and horizon. Jiulongshan Formation, in the village of Daohugou, Ningcheng, Inner Mongolia, China (Middle Jurassic).

Diagnosis. As for the genus.

Description. Moderate-sized flies. Body and legs dark, abdomen covered with short hairs, and legs covered with short bristle. **Head:** Moderately large, spherical, occiput weakly convex and with short hairs in the lower part. Eyes bare, dichoptic in female (Figs 1A, 2D). The antenna almost as long as the head, scape short, triangular, pedicel longer than scape, bearing short hairs. Flagellum with 10 subsegments, the first segment enlarged obviously, almost two times wider than long. The following three segments slightly narrower than the previous segment in sequence, 5^{th} to 10^{th} segments getting narrower and shorter gradually, the terminal one conical, rather small and short (Figs 1A, B, 2A). Proboscis apparently long, exceeding the length of the head. Labrum long and strongly sclerized, the details of piercing structures indiscernible. Maxillary palpi two-segmented, much shorter than the proboscis. Labium fleshy, labella inflated and enwrapping the distal of the labrum and piercing structures (Figs 1B, 2D).

Legs: Coxae of legs bear moderately long setae. All trochanters bearing very short setae. Femora completely covered with short dense setae. Tibiae of legs slightly longer than corresponding femora, covered with short dense setae. Tibial spurs formula 0:1:1 (Fig. 2B, C).

Wings: Broad and elliptic, pterostigma blurry, and jugal region undeveloped. Sc ended at the middle of costal vein, crossvein h close to the basal of wing. R_1 straight, covered with setae; R_{2+3} sinuate at the middle, and sharply up-curved distally. Costal section between Sc-R_1 nearly as long as that between R_1-R_{2+3}. Fork of R_4-R_5 generally long, and nearly as long as the fork of M_1-M_2. Crossvein r-m intersecting the upper margin of discal cell at the basal one third (1/3). Four medial veins present. M_1 slightly arched. Discal cell narrow, presenting at the middle of the wing. M_3 and M_4 converged distally. dM_3 with equal length to bM_3. Cell cu closed and with a very short petiole apically (Fig. 2G).

Abdomen: Slender, nearly twice as thorax, covered with short setae. Cerci two-segmented, with short setae, 1th segment nearly lobe-like and 2th segment sub-oblong (Figs 1C, 2F).

Dimensions. Length of body 6.93–9.38 mm; head 0.90–1.08 mm; thorax 1.98–2.62 mm; abdomen 4.05–5.68 mm; length of wing 5.89–6.22 mm; width of wing 2.22–2.61 mm.

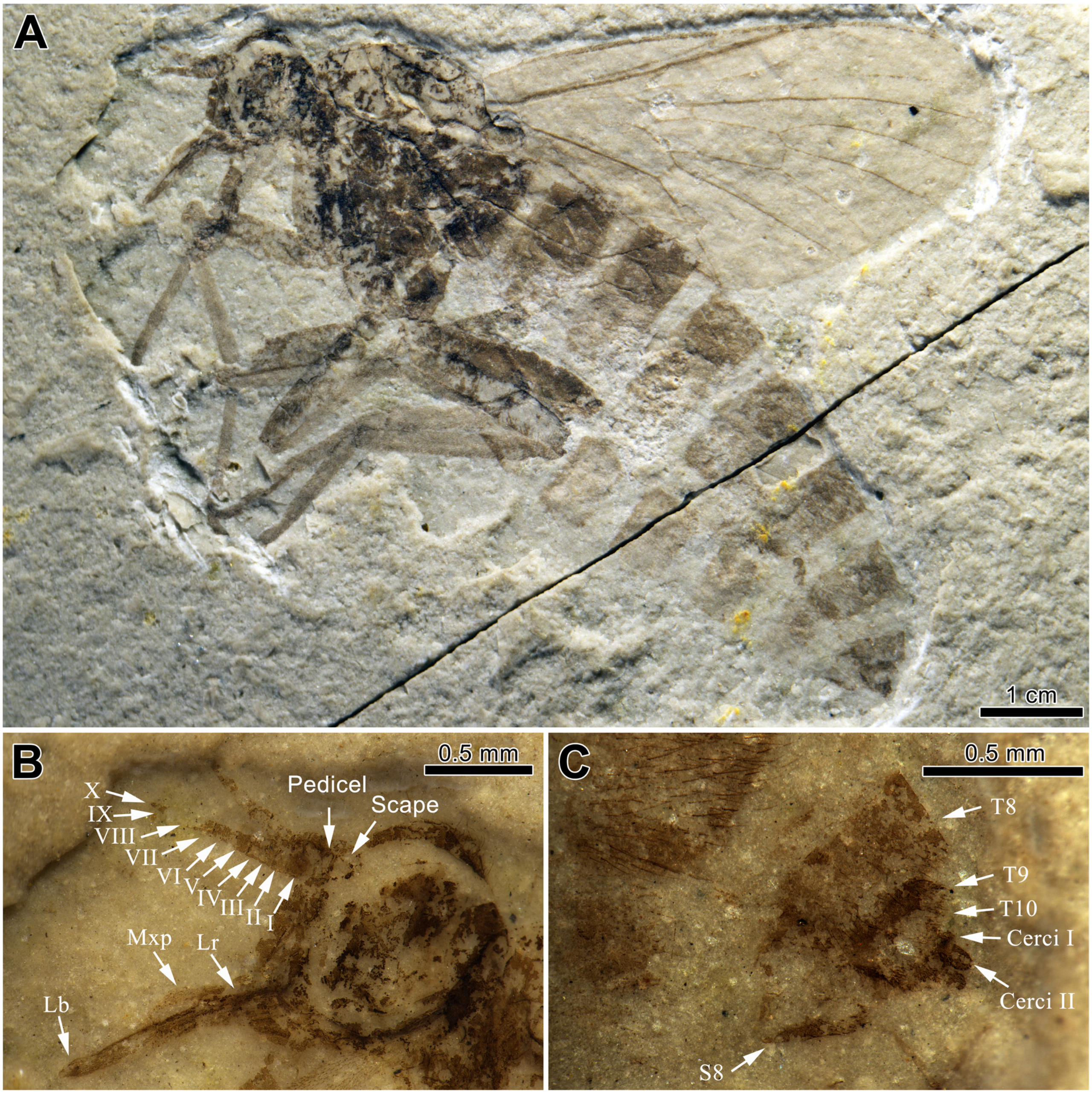

FIGURE 1. *Elliprhagio macrosiphonius* **gen. et sp. nov. Holotype** CNU-DIP-NN2015101. **A** body. **B** head. **C** female genitalia. Scale bars: 0.5mm. **B, C** are under alcohol.

Etymology. The specific epithet, "*macrosiphonius"* is an adjective, and refers to the long mouthparts of this species. Gender: masculine.

Remarks. The flagellum of Rhagionidae shows significant morphological diversity that is generally used in the taxonomic treatment. Most extant and Cenozoic rhagionids have little segmented flagellum that the distal part is shrunk to a thin appendage, called arista. However, multi-segmented flagellum is often present in Mesozoic rhagionids. The Middle Jurassic species of *Trichorhagio gregarius* from Daohugou possesses a nine-segmented flagellum, see figs 1F, 2B in Zhang (2013). It is notable that antennae with 10-segmented flagellum are reported for the first time in *E. macrosiphonius* **gen. et sp. nov.** from Daohugou. Therefore, it is deduced that the multi-segmented flagellum is likely a plesiomorphic character of Rhagionidae. Based on these antennal data, it seems that the antennae of rhagionids have a simplified trend leading to fewer and thinner flagellum segments from the Mesozoic to the present, even though phylogenetic relationships among fossil and extant rhagionids have not been clearly elucidated yet.

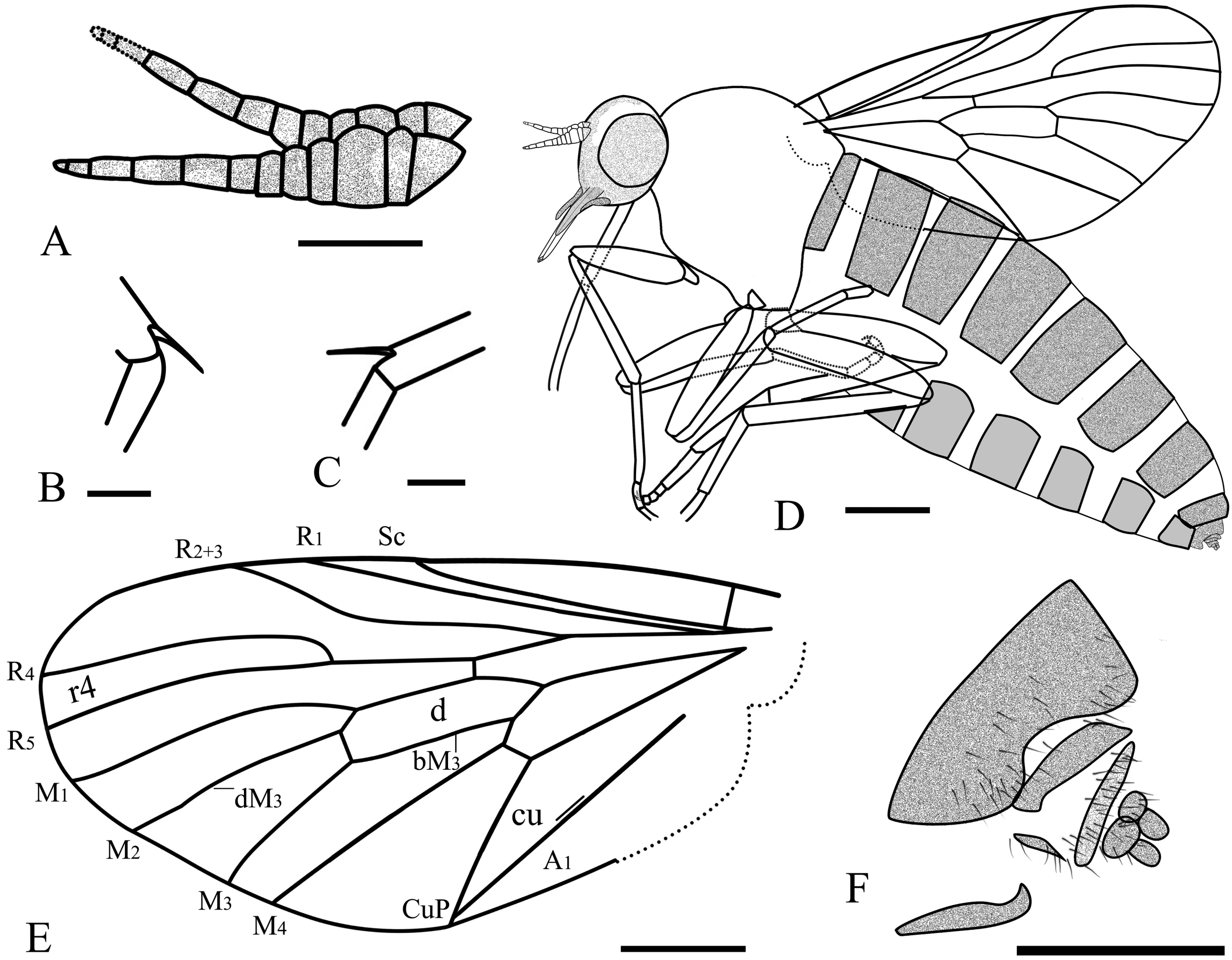

FIGURE 2. *Elliprhagio macrosiphonius* **gen. et sp. nov. Holotype** CNU-DIP-NN2015101. **A** antenna. **B** tibial spur of middle leg. **C** tibial spur of hind leg. **D** body. **E** left wing. **F** female cerci. Scale bars: 1 mm (**B–E**); 0.5mm (**A, F**).

Discussion

As we know, only a few extant Rhagionidae have evolved prolonged proboscis and the mouthpart structure is used for piercing and feeding on blood. Generally, extremely long proboscis within the family is related to the blood-feeding habit (Kovalev & Mostovski 1997; Lukashevich & Mostovski 2003). Burger (1995) outlined blood-sucking process of extant snipe flies and considered that paired sword-like mandibles for cutting and penetrating, and "retrorse teeth" on outer surface of maxilla should be decisive parts for blood-sucking. Nevertheless, the feeding habit of fossil Rhagionidae was seldom studied because the components of mouthparts in the fossil insects are rarely preserved completely. In 2003, Lukashevich and Mostovski described the species *Palaeoarthroteles mesozoicus* from the Early Cretaceous and deemed it the most ancient hematophagous brachycerous fly principally derived from the conspicuously long mouthparts and elongate, downcurved palps and unmodified legs (Lukashevich & Mostovski 2003). Interestingly, the new species shows the high similarities of the mouthpart with *P. mesozoicus*, and it is deduced that *E. macrosiphonius*, representing the oldest hematophagous rhagionid hitherto, possibly has the similar feeding habit like *P. mesozoicus*.

Almost all fossil snipe flies were established based on the morphological diagnostic characters, especially the wing venation, and this approach and methodology have been widely accepted for the studies of fossil insects (Grimaldi & Cumming 1999). However, the identification is often misguided under the conditions of the limited or incomplete specimens. Two monotypic genera *Trichorhagio* and *Daohugorhagio* were described from Daohugou based on minor differences in appearances, e.g. density of hairs on the body, length of antenna, and features of venation, see figs 1–4 in Zhang (2013). We have collected a large number of rhagionid fossils from Daohugou, which can be clearly attributed to both genera. After detailed examinations of these specimens, it seems that the diagnostic characters of these two genera emphasized by Zhang (2013) are too equivocal to distinguish them. In the original description, one of the important diagnostic characters is the length of antenna: as long as the head in *Trichorhagio* vs. half as long as head in *Daohugorhagio*. In fact, the orientations of head in the specimens of *Trichorhagio* and *Daohugorhagio* are distinctly different that could not reflect the actual dimension of the head. Therefore, the length ratio between head and antenna is not a preferred diagnostic character. In addition, the other key character to separate these two genera is configuration of R_1, i.e. R_1 up-curved near the terminus in *Daohugorhagio* vs. straight in *Trichorhagio*. Accordingly, when more specimens were examined, the character of R_1 states became continuous, suggesting that R_1 has conspicuous intraspecific individual variants. Furthermore, variation of the length and the opening of cell r4 between *Daohugorhagio* and *Trichorhagio* is minor and should not be treated as intergeneric variation. The similar variations are also observed in *E. macrosiphonius*: the opening of cell r4 varies slightly within a narrow range (marked by red arrows in Fig. 3A-D). Based on the afore-mentioned, differences between *Trichorhagio* and *Daohugorhagio* should probably just represent interspecific variations, therefore, it is justifiable to treat *Daohugorhagio* as a synonym to *Trichorhagio*. The diagnosis of *Trichorhagio* is emended as follows: body slender, antennae eight or nine-segmented, getting thinner gradually. First flagellomere swollen, thicker than long. R_1 straight, costal section of R_1-R_{2+3} much shorter than costal section of Sc-R_1. M_3 slightly converged to M_4.

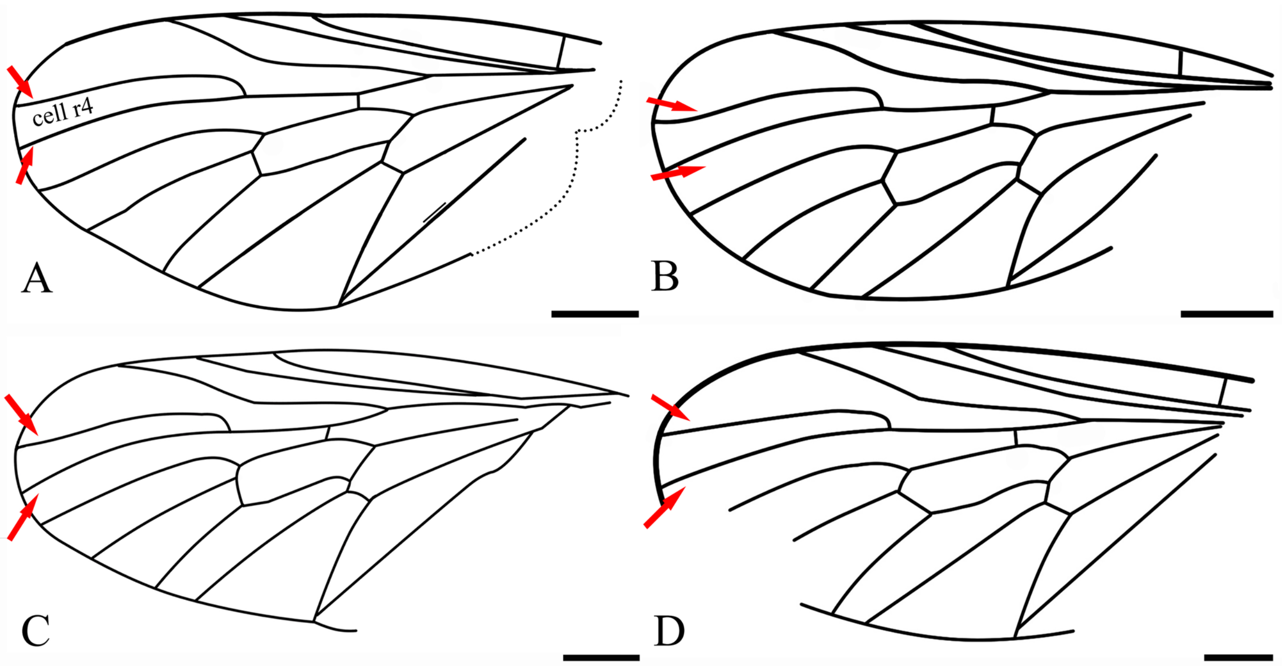

FIGURE 3. *Elliprhagio macrosiphonius* **gen. et sp. nov.**, line drawings of wings. **A Holotype** CNU-DIP-NN2015101. **B–D Paratypes**. **B** CNU-DIP-NN2015103. **C** CNU-DIP-NN2015105. **D** CNU-DIP-NN2015106. Red arrows mark the opening of cell r4. Scale bars: 1 mm.

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