

The oldest known net-winged midges (Insecta: Diptera: Blephariceridae) from the late Mesozoic of northeast China

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Abstract

Two fossil specimens of female net-winged midges from the Daohugou biota, Inner Mongolia, China are described. One new genus and two new species are established: *Brianina longitibialis* gen. et sp. nov. and *Megathon brodskyi* sp. nov. They are the oldest known representatives of the family Blephariceridae.

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1. Introduction

Net-winged midges constitute a very peculiar and isolated group of Nematocera, usually separated into a superfamily of their own. Almost 300 species in nearly 30 genera are known from all continents and many islands (Zwick, 1992). Pre-imaginal stages are attached to submerged stones in swift-flowing water, usually in mountain streams; adults occur in the immediate vicinity of these streams. Relationships of this group have been variously interpreted and are far from being resolved.

Cenozoic fossils previously assigned to Blephariceridae by Cockerell (*Paltostomopsis ciliata* Cockerell, 1915 and *Philorites pallescens* Cockerell, 1920) were regarded by Edwards (1929) and Alexander (1958) as belonging elsewhere, but they did not comment on *Philorites johannseni* Cockerell, 1908. Evenhuis (1994) listed all three species as questionably included in Blephariceridae. Moreover, he and Grimaldi et al. (2002) mentioned that Jarzembowski (1978) had reported a blepharicerid from the Eocene–Oligocene of the Isle of Wight without formally describing it; however, according to

Jarzembowski (pers. comm. 2004) he merely referred to the Cockerell's type of *Paltostomopsis*. After restudying the holotype of *Paltostomopsis ciliata* Cockerell, 1915, we have concluded that it definitely belongs to the Tipulomorpha, and perhaps the Limoniidae.

Edwards (1929, p. 35) considered that “no help can be expected from palaeontology in the elucidation of the phylogeny of the family, as the habitat of these insects would seem to make it very improbable that they would ever be preserved as fossils”. Certainly, probability of their preservation is low, but now we have several examples of such improbable occasions, the late Mesozoic finds of undoubted net-winged midges. They are known only from the Cretaceous of Asia: *Megathon zwicki* Lukashevich and Shcherbakov, 1997 from the locality of Obeshchayushchy (northern Russian Far East, Cenomanian or Turonian; Lukashevich and Shcherbakov, 1997) and a well-preserved male specimen reported, but not formally described (Grimaldi et al., 2002, fig. 35b), from Burmese amber (Upper Albian, Cruickshank and Ko, 2003). According to the photograph, the venation is quite advanced (?Blepharicerini), similar to *Philorus* Kellogg, 1903 (distal section of vein M₂ preserved, Rs with two branches, vein R₃ absent, cell R₄ long-petiolate), but this identification is preliminary.

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Recently, numerous animal and plant fossils have been collected from the Daohugou locality (Ningcheng, Inner Mongolia, China), in which the age is estimated by various authors to range from late Bajocian to Aptian (Wang et al., 2000; Ji and Yuan, 2002; Ren et al., 2002; Zhang, 2002a, b, 2003, 2004a, b, c; Gao and Shubin, 2003; Shen et al., 2003; Chen and Zhang, 2004; Chen et al., 2004a, b; He et al., 2004; Liu et al., 2004; Rasnitsyn and Zhang, 2004a, b; Wang, 2004). We consider that the age is debatable and needs to be investigated further based on additional biostratigraphic and more exact isotope dating.

In Zhang's collection of fossil insects from the Daohugou locality two specimens of Blephariceridae have been found. One of these is a new species of *Megathon* (Blepharicerinae), and the other represents a new genus and species. These are described below. The vein nomenclature is after Wootton and Ennos (1989: the vein traditionally named 1A in fact is CuP), followed by Shcherbakov et al. (1995) and Blagoderov et al. (2002).

2. Systematic palaeontology

Order: Diptera Linnaeus, 1758

Family: Blephariceridae Loew, 1862

Subfamily: incertae sedis

Genus *Brianina* gen. nov.

Type species. Brianina longitibialis sp. nov.

Derivation of name. In honour of the distinguished entomologist Prof. Brian R. Stuckenberg, Pietermaritzburg, South Africa.

Species included. Type species only.

Diagnosis. Rs without backward spur at origin; Rs forking into R_{2+3} and short R_{4+5} stalk; “cord” absent; M_2 connected to M_1 without connection with M_{3+4} ; desclerotized CuP not reaching margin; no macrotrichia in wing cells; eyes undivided, ommatidia of uniform size; hind tibiae curved; tibiae longer than femora and not longer than tarsi; hind and fore tibiae subequal.

Remarks. “Cord” is a term in common use for Ptychopteridae and several other families and means vertical alignment of basal sections of Rs and R_5 , r-m and basal section of M_{3+4} . It also seems to be useful for Blephariceridae because of the presence of “cord” in recent *Edwardsina* Alexander, 1920 and its absence from Blepharicerinae.

Brianina longitibialis sp. nov.

Figs. 1–4

Derivation of name. Latin, *longa*, long, *tibialis*, tibia, with reference to the character of the tibiae.

Holotype. DHG 200406, a single complete impression of female, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Type locality. The late Bajocian–Aptian Daohugou Formation in the vicinity of Daohugou, Ningcheng, Inner Mongolia, China (for detailed discussion of its age, see Zhang, 2006).

Description. Female (male unknown). Antenna short. Sc poorly visible, appears to be short. Rs stem longer than R_{4+5} , basal section of Rs desclerotized. R_{2+3} distally nearer to R_1 than to R_4 . Straight R_5 entering margin at wing tip. Macrotrichia on radial veins not visible. Distal section of CuA straight. Anal lobe rounded, incision at base of anal lobe without dark callus. Net-like folds of wing membrane untraceable. Legs densely covered with short hairs. Fore femora straight, hind femora stouter than others. Spur formula 1-2-2; spurs of hind tibia of equal length, about as long as tibial diameter. First hind tarsomere subequal to remaining four; fifth longer than fourth, with pollex (or calcipala: Zwick, 1977), a group of bristles on basi-ventral swelling; claws toothed. Setae on terminalia not visible.

Measurements in mm: length of head 0.8, thorax 1.4, abdomen 3.5, wing 7.6; width of wing ca. 2.6; length of fore leg: femur 2.0, tibia 2.9, basitarsus 1.5; length of middle leg: femur 1.9, tibia 2.3, tarsus 2.8 (1.4:0.6:0.4:0.1:0.3); length of hind leg: femur 2.1, tibia 2.9, tarsus 2.9 (1.5:0.6:0.3:0.2:0.3).

Subfamily: Blepharicerinae Loew, 1862

Genus *Megathon* Lukashevich and Shcherbakov, 1997

Type species. Megathon zwicki Lukashevich and Shcherbakov, 1997.

Species included. *Megathon zwicki* from Obeshchayushchy (northern Russian Far East, Cenomanian or Turonian) and the new species described below.

Megathon brodskyi sp. nov.

Figs. 5–8

Derivation of name. In honour of distinguished Russian entomologist K. A. Brodsky.

Holotype. DHG 200407, a single complete impression of female with crumpled wings, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Type locality. See under *Brianina longitibialis* sp. nov.

Diagnosis. Long Sc terminates before wing midlength, distal to Rs bifurcation. Rs stem as long as R_{4+5} . Tip of R_4 not close to tip of R_1 ; R_{2+3} subequal to R_{1+2+3} . Macrotrichia on radial veins absent. CuP reaching only two-thirds distance across “anal cell”.

Description. Female (male unknown). Antennae with basal ten subquadrate segments, last three segments more or less elongated and sparsely covered with short setae. Upper eye division at least as large as lower one, and with ommatidia twice diameter of those of the latter. Interocular distance about 1–2 diameters of upper ommatidia. Long Sc terminates before



Fig. 1. *Brianina longitibialis* gen. et sp. nov., holotype, female, lateral aspect. Scale bar represents 1 mm here and those in Figs. 2–4, which all refer to specimen DHG200406.

wing midlength, distal to R_s bifurcation. Base of R_s weak. Macrotrichia on radial veins not visible. CuP reaching only two-thirds distance across anal cell. Incision at the base of well-developed subacute anal lobe with callus. Anal loop distinct. Net-like folds of wing membrane untraceable. Legs densely covered with short hairs. Last tarsomere rather straight, of uniform width, not bristly at base; claws simple.

Measurements in mm: length of head 0.9; width of head 1.3; length of antenna 1.0, thorax 1.8, abdomen 4.3, wing 6.5; width of wing ca. 2.1; length of fore femur 2.6, midleg: femur 2.3, tibia 2.7, tarsus 2.6 (1.2:0.5:0.3:0.3:0.3), hindleg: femur, as preserved, 3.7.

Remarks. Because of the crumpled wings of the holotype of the new species, the course of distal R_5 is uncertain (either straight or curved backwards as in *M. zwicki*), but it seems to be straight. Most of the other characters originally included in the generic diagnosis are confirmed in the new species (antenna not longer than head width; eyes bisected, glabrous, dichoptic in female; wing widest about midlength; ninth abdominal tergum of female normal; very long hairs absent from both eyes and female terminalia; fore femora straight).

Relative lengths of R_s stem and R_{2+3} vein, as well as position of R_4 tip, are characters of specific level in *Agathon* von Röder, 1890 and *Biocephala* Osten Sacken, 1874. The presence of macrotrichia on radial veins and the degree of R_5 curvature are constant in these genera, but variable, e.g., within *Blepharicera* Macquart, 1843 and *Edwardsina* (Edwards, 1929). The markedly incomplete CuP of *Megathon brodskyi* is unique among Blepharicerini and is not an effect of wing crumpling. *Agathon* and *Biocephala* always possess complete CuP; however, in derived Blepharicerini some variations occur. In species of *Philorus*, for example, CuP is normally

complete, but in *P. yosemite* (Osten Sacken, 1877) it sometimes does not reach the wing margin (Hogue, 1966). In the holotype of *Megathon zwicki* CuP is at most slightly incomplete (it is not preserved apically) and clearly longer than that in *M. brodskyi*; we assume this difference to be of specific value, as in *Paltostoma* Schiner, 1866 (Paltostomatini) where it constitutes an important species character (Edwards, 1929).

3. Discussion

An adequate subfamilial placement of *Brianina* gen. nov. is not possible at present because the most diagnostic characters

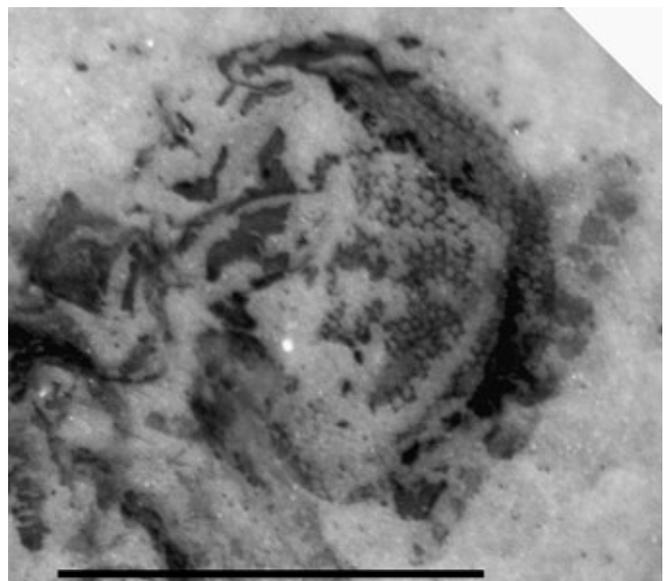


Fig. 2. *Brianina longitibialis* gen. et sp. nov., head.

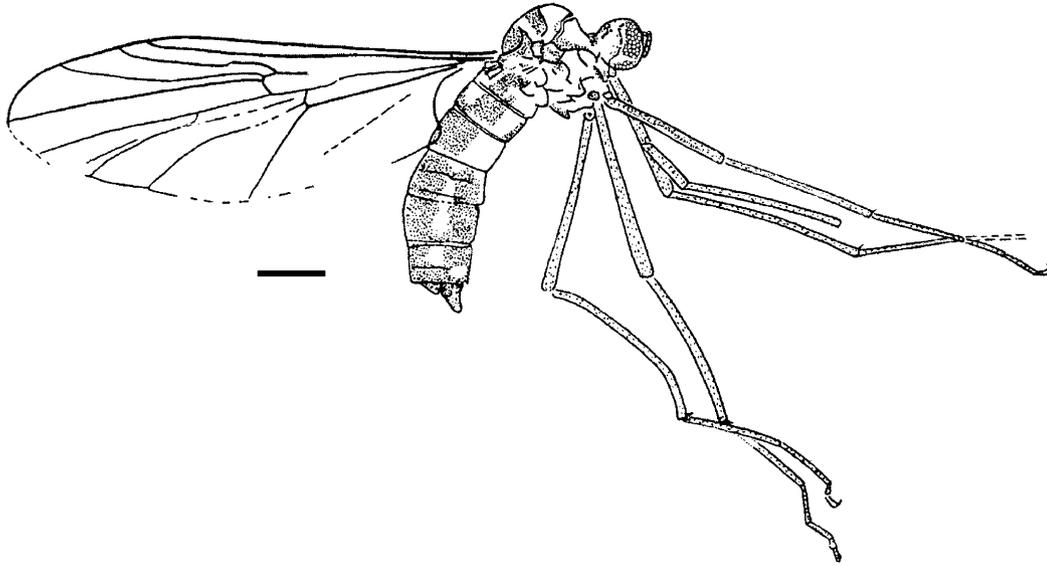


Fig. 3. *Brianina longitibialis* gen. et sp. nov., camera lucida drawing.

of blepharicerid subfamilies are details of genitalia and preimaginal structure, which are not visible in the single impression. Assignment of the genus to the subfamily Edwardsiniinae could be based mainly on the primitive features, namely four

radial veins reaching the wing margin and the spur formula 1-2-2 (simple eyes are not diagnostic because of their presence in several genera of Blepharicerinae), and possibly also on one derived character, the Sc (poorly visible), which seems to be

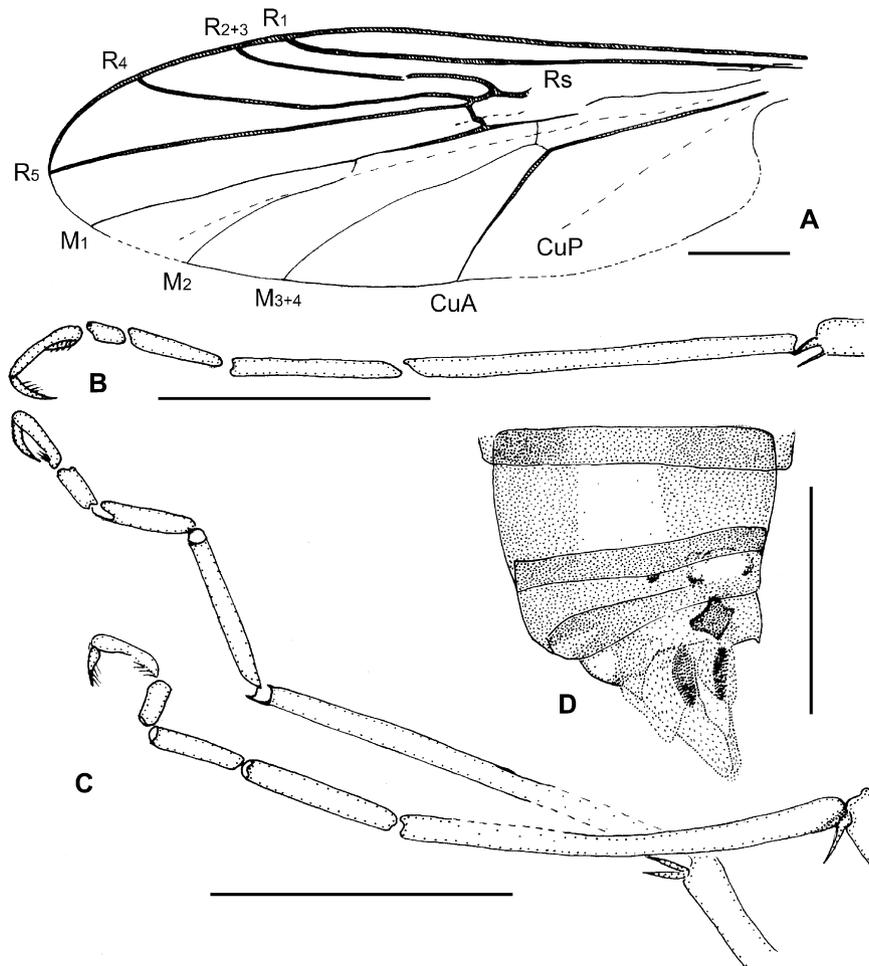


Fig. 4. *Brianina longitibialis* gen. et sp. nov., camera lucida drawings. A, wing. B, tarsus of midleg. C, tarsi of hindleg. D, apex of abdomen.

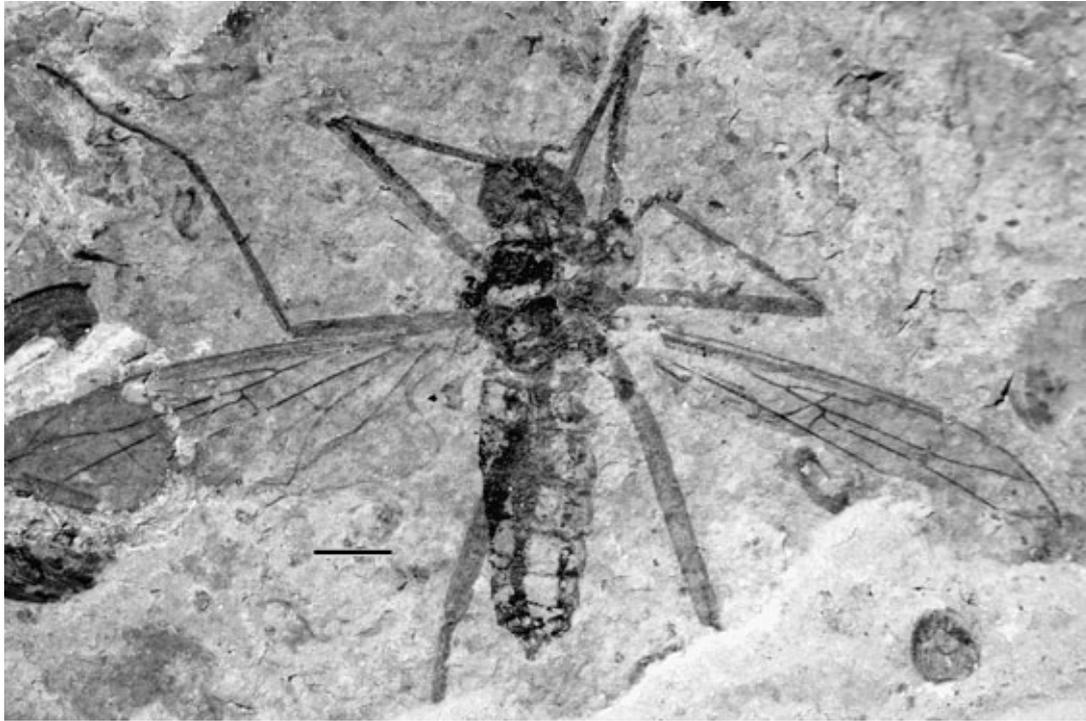


Fig. 5. *Megathon brodskyi* sp. nov., holotype, female, dorsoventral aspect. Scale bar represents 1 mm here and those in Figs. 6–8, which all refer to specimen DHG200407.

short. However, some other characters contradict such an attribution: (1) Rs without backward spur at origin (the presence of an Rs spur is considered an important peculiarity of this subfamily and mentioned in all keys, though in *Eupaulianina*, a subgenus of *Paulianina* Alexander, 1952, the spur is sometimes almost absent: Stuckenberg, 1958); (2) Rs forking into R_{2+3} and short R_{4+5} stalk, instead of forking into R_{2+3+4} and R_5 (such variations appear to be of significance at generic level and are known in *Agathon* and *Bibliocephala* in another subfamily, Blepharicerinae); (3) absence of the “cord” formed by the basal sections of Rs and R_5 , r-m and basal section of M_{3+4} almost in vertical alignment; present in Recent *Edwardsina* and to a lesser degree (in some species only as a trend) in *Paulianina*; not developed in Blepharicerinae.

Brianina demonstrates primitive states of these three characters, but is derived in at least the desclerotized CuP not reaching the margin, a feature unknown in living Edwardsiniinae, although atrophy of this vein at the apex is considered to be one of the “obvious convergences which have taken place in the family” (Stuckenberg, 1958, p. 188). Moreover, the middle branch of M in the new genus is connected with M_1 , not with M_{3+4} ; therefore, “ M_3 ” of authors in fact represents M_2 . In *Edwardsina* M_2 is connected with M_{3+4} (not with M_1), which can be explained only by a reduction of the basal section of M_2 and retention of the im crossvein (in *Paulianina* im is reduced apart from in *P. umbra* Stuckenberg, 1958, which retains its vestiges: Stuckenberg, 1958, fig. 2). Hence, *Brianina* cannot be ancestral to any other genus of Blephariceridae, only a branch from the common stem.

It is worth mentioning that an analogous transformation (reduction of vertical section of longitudinal vein instead of

reduction of cross-vein as a whole) can be seen in this family: in all higher Blepharicerinae the basal section of M_{3+4} is reduced and the vein that simulates a forked cubitus is in fact a composite vein, its anterior branch being the combined m-cu and distal portion of M_{3+4} , the posterior branch CuA alone (Alexander, 1958).

One more character, differentiating Edwardsiniinae from Blepharicerinae, is “unmodified front trochanters and large coxae, which are all inserted relatively close to one another” (Zwick, 1977, p. 6). Unfortunately, it is impossible to understand the structure of coxae and trochanters in *Brianina*, but

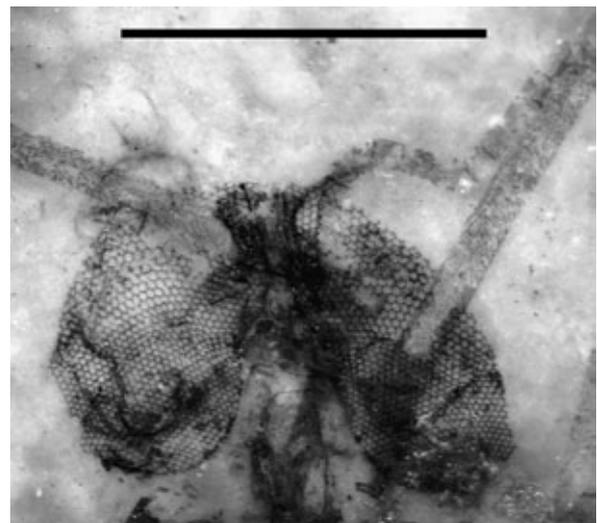


Fig. 6. *Megathon brodskyi* sp. nov., holotype, head.

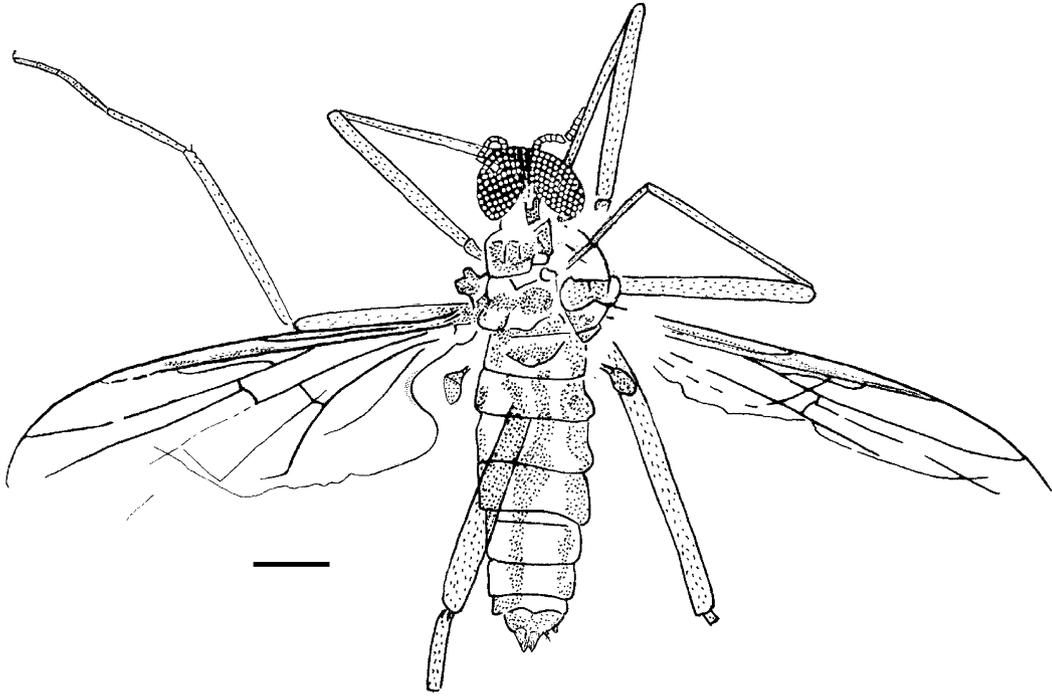


Fig. 7. *Megathon brodskyi* sp. nov., camera lucida drawing.

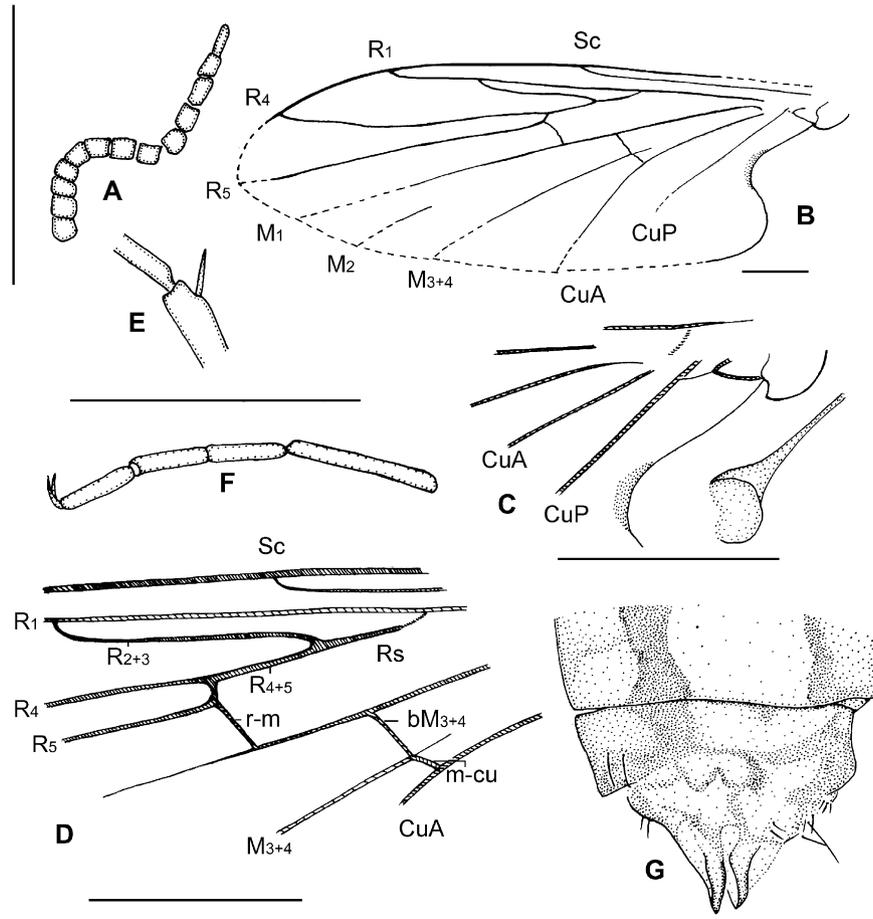


Fig. 8. *Megathon brodskyi* sp. nov., camera lucida drawings. A, antenna. B, wing (posterior margin folded under holotype shown in natural position by broken line). C, basal part of wing and halter. D, middle part of wing. E, tibial spur of midleg. F, second to fifth tarsomeres of midleg. G, apex of abdomen.

the front coxa and trochanter were probably not large, and the relative length of the leg segments, so far as we are aware, is also not typical of Edwardsiniinae. In *Edwardsina* hind tarsi are usually very short, about half as long as the tibia; in Blepharicerinae they are at least two-thirds as long (Edwards, 1929); and in *Bibiocephala grandis* Osten Sacken, 1874 the hind tarsi are longer than the tibiae and the fore tibiae longer than the femora (Hogue, 1987). However, in Recent genera fore tibiae, even if long, are much shorter than the hind ones; in *Brianina* they are subequal. The fore tarsi are incompletely preserved in *Brianina*, but according to the long first tarsomere the fore tarsus was probably longest (as in Edwardsiniinae: Zwick, 1977) and the fore femur undoubtedly longer than the middle, so fore legs, even if not the longest, were surely unusually long with all segments (not only tarsi) elongated, as in Ansorgiidae, presumably the most primitive Blepharicerioidea (Shcherbakov et al., 1995).

Up to now Ansorgiidae are known only from Karatau (Kazakhstan) where Blephariceridae have not yet been found, but this cannot be used to infer the age of the Daohugou Formation, by comparison with Karabastau Formation, because the finds of Blephariceridae are very occasional and more likely to be correlated with the palaeoecological peculiarities of the locality (due to the association of net-winged midges with streams) than with age.

The Diptera is one of the dominating groups in the Daohugou biota (in terms of both specimen abundance and species number), but their taxonomic description is at early stage: 13 species referable to nine genera of six families have been recorded hitherto (including Blephariceridae described above). The commonest group, Mycetophiloidea, has not yet been treated taxonomically; among very diverse and numerous Brachycera only two species in two genera have been described (Archisargidae: *Mesosolva daohugouensis* Zhang and Zhang, 2003 and *Archirhagio striatus* Zhang and Zhang, 2003). Several species of Eoptychopteridae (*Eoptychoptera ansorgei* Ren and Krzemiński, 2002, *E. jurassica* Ren and Krzemiński, 2002, *Eoptychoptera elenae* Ren and Krzemiński, 2002, *E. gigantea* Zhang, 2004), Tanyderidae (*Praemacrochile chinensis* Krzemiński and Ren, 2001, *P. vulcanium* Zhang, 2004), Limoniidae (*Architipula chinensis* Zhang, 2004) and Axymyiidae [*Psocites pectinatus* (Hong, 1983) and *P. fossilis* Zhang, 2004] have been described, but this does not mean that taxonomic treatment of these families in the Daohugou biota is complete. It is interesting that the Daohugou species are often closely related to those from the localities of Kubekovo, Karatau and Shara-Teg (Middle or Late Jurassic) according to various authors (Ren and Krzemiński, 2002; Zhang and Zhang, 2003; Zhang, 2004a, b, c).

Currently it seems premature to draw any conclusions about the Daohugou dipteran assemblage, but it is clear that conditions at this locality were far from usual. The find of two different adult blepharicerids, which like their living relatives presumably did not travel far from their breeding sites, rapidly flowing waters, implies an environment similar to that reconstructed for the Obeshchayushchy locality in north-east Russia, “a volcanic region with mountain streams”

(Lukashevich and Shcherbakov, 1997, p. 640). Limoniidae (commonly dominating or subdominating) are unexpectedly rare there (less than 10% of the Diptera specimens). On the other hand, Eoptychopteridae, Axymyiidae, Protopleciidae and Protorhaphidae are exceptionally diverse and numerous at Daohugou (each about 10% of the total dipteran assemblage), whereas they are extremely rare at the Karatau locality, i.e. a single specimen of Axymyiidae among thousands of dipteran fossils known from there (Blagoderov et al., 2002).

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