

# Some anisopodoids (Insecta: Diptera: Anisopodoidea) from late Mesozoic deposits of northeast China

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## Abstract

Three new species of anisopodoids from the Daohugou (Inner Mongolia) and Haifanggou (Liaoning) formations, are described from six almost complete specimens, namely: *Protorhyphus neimonggolensis* sp. nov., *P. liaoningicus* sp. nov. and *Megarhyphus rarus* sp. nov. *Protorhyphus neimonggolensis* and *P. liaoningicus* are assigned to the Protorhyphidae, and *Megarhyphus rarus* to the Anisopodidae (Anisopodoidea, Diptera). The family designations of all Chinese specimens described previously within the Anisopodoidea are questionable; those of *Brachyopteryx weichangensis* Hong, *Eoanisopoditis fushunensis* Hong, *Hongocaloneura plectilis* (Hong), *Limnorhyphus haifanggouensis* Hong, *Mesobrachyopteryx shandongensis* Hong and Wang and *Sinorhyphus arcuatus* Hong are reassessed here.

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## 1. Introduction

The Protorhyphidae (Nematocera: Anisopodoidea) is a small, extinct family composed of a dozen species referable to three genera that range from the Triassic to the Upper Jurassic–Lower Cretaceous. These are: *Archirhyphus asiaticus* Rohdendorf, 1964, *A. geinitzi* Handlirsch 1939, *Protorhyphus arcuatus* (Hong, 1983) comb. nov., *P. major* Kovalev, 1990, *P. ovisimilis* Bode, 1953, *P. sibiricus* Kovalev, 1985, *P. simplex* (Geinitz, 1888), *P. stigmaticus* Handlirsch, 1920 (see Handlirsch, 1939), *P. turanicus* Rohdendorf, 1964, *Vymrhyphus tuomikoskii* Blagoderov, 1995, *V. triassicus* Blagoderov, 1995 and *V. blagoderovi* Krzeminski, 2003. *Acritorhyphus ramosus* Bode, 1953, *Heterorhyphus analivarius* Bode, 1953 and *H. latus* Bode, 1953 were originally placed in the Protorhyphidae but later transferred to other families by Blagoderov (see Shcherbakov et al., 1995). The family position of the Chinese species *Brachyopteryx weichangensis* Hong, 1984, previously associated with the Protorhyphidae, is revised here.

The Anisopodidae (Nematocera: Anisopodoidea) is a primitive, cosmopolitan, extant group consisting of small to moderate-sized flies (2–18 mm). Its fossil record includes more than 30 species referable to five extinct and four extant genera (Evenhuis, 1994; Ansoerge and Krzeminski, 1995; Grimaldi and Amorim, 1995; Shcherbakov et al., 1995; Ansoerge, 1996). The status of the following Chinese taxa assigned to the family is reassessed below: *Hongocaloneura plectilis* (Hong, 1981) (originally *Caloneura plectilis* Hong, 1981); *Mesobrachyopteryx shandongensis* Hong and Wang, 1990; *Sinorhyphus arcuatus* Hong, 1983; and *Eoanisopoditis fushunensis* Hong, 2002.

The Limnorhyphidae contains only a single genus and species, *Limnorhyphus haifanggouensis* Hong, 1983, placed in the Rhyphoidea (=Anisopodoidea). However, the description might be inaccurate, and its subordinal placement is uncertain (see discussion below).

Wing venational terminology here follows Wootton and Ennos (1989), and Shcherbakov et al. (1995). The vein traditionally named 1A is, in fact, CuP, as noted by these authors.

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## 2. Systematic paleontology

Order: Diptera Linnaeus, 1758

Suborder: Nematocera Latreille, 1825

Superfamily Anisopodoidea Knab, 1912

Family: Protorhyphidae Handlirsch, 1906

Genus *Protorhyphus* Handlirsch, 1906

*Type species. Phryganidium simplex* Geinitz, 1888

*Species included. Protorhyphus simplex*, Lower Jurassic, Germany (Handlirsch, 1906–08); *P. major*, Upper Jurassic or Upper Jurassic–Lower Cretaceous, Siberia, Russia (Kovalev, 1990); *P. sibiricus*, Middle Jurassic, Siberia (Kovalev, 1985); *P. stigmaticus*, Lower Jurassic, Germany (Handlirsch, 1939); *P. turanicus*, Lower Jurassic, Kyrgyzstan (Rohdendorf, 1964); *P. arcuatus*, Middle Jurassic–lowermost Upper Jurassic, Liaoning, China (Hong, 1983; see discussion below); and *P. neimonggolensis* sp. nov. and *P. liaoningicus* sp. nov., uppermost Middle Jurassic–lowermost Cretaceous of Inner Mongolia and Liaoning, China, respectively.

*Protorhyphus neimonggolensis* sp. nov.

Figs. 1A, B, 2A–E

*Derivation of name.* After Inner Mongolia (=Nei Monggol Autonomous Region), where the fossil was collected.

*Material.* Holotype DHG200386, paratype DHG200387, two impressions of female protorhyphids, from the Middle Jurassic–Early Cretaceous Daohugou Formation in the vicinity of Daohugou, Ningcheng, Inner Mongolia (for detailed discussion of its age, see Zhang, 2006); deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPCAS).

*Diagnosis.* Venation similar to that of *P. simplex*, *P. stigmaticus* and *P. sibiricus*, r-m closer to  $R_4$  than  $R_{2+3}$ , but Pt present;  $R_{2+3}$  straight or nearly so, subparallel to  $R_1$  terminally;  $R_5$  smoothly curved downward; m-m meeting fork of  $M_{1+2}$ ; m-cu some four times as long as  $bM_4$ .

*Description.* Medium-sized protorhyphids, body covered with long hairs. Head suboval in lateral aspect. Eyes large, suboval. Antennae 16-segmented, more than three times longer than head length, with scape slightly shorter; thinner than first flagellomere, pedicel short, basal ten flagellomeres as long as, or slightly shorter than, wide, terminal four clearly longer than wide. Thorax massive, suboval. Wing nearly 2.3 times longer than wide; Pt elongate-oval, not reaching  $R_{2+3}$ ; Sc one-third and  $R_1$  two-thirds of wing length; Rs furcated just a little distad of Sc end and M fork;  $R_{2+3}$  straight or nearly so, subparallel to  $R_1$  terminally, slightly shorter than  $R_4$ ; r-m closer to  $R_4$  than  $R_{2+3}$ ;  $bR_{4+5}$  nearly twice as long as  $dR_{4+5}$ ;  $R_{4+5}$  furcated basad of both midwing, fork of  $M_{1+2}$ ; m-m just meeting fork of  $M_{1+2}$ ; CuP straight, long, convergent to CuA terminally, ending at hind margin of wing; cell

d pentagonal, nearly 3.2 times longer than wide, with  $bM_{1+2}$ ,  $M_{3+4}$  respectively longer than  $dM_{1+2}$  and  $bM_3$ , latter two convergent terminally; m-cu some four times as long as  $bM_4$ . Legs with clavate femora, thicker, shorter than tibiae; latter covered with at least three or four rows of short setae, tibial spurs well developed; basitarsi slightly shorter than remaining tarsomeres combined. Abdomen massive.

Measurements in mm: length of head, 0.5, antenna, 1.6, thorax, 1.9–2.2, abdomen, 4.1–5.0; length of wing, 5.6–5.8, width, 2.4–2.7; length of midleg tibia, 1.7, tarsus, 1.9 (0.9:0.4:0.3:0.2:0.1), tibiae of hindleg, 2.5, tarsus, 2.1 (1.0:0.5:0.3:0.2:0.1).

*Remarks.* This new species differs from *P. simplex*, *P. stigmaticus* and *P. sibiricus* by the crossvein m-m just meeting the fork of  $M_{1+2}$ ; and the long m-cu, about four times longer than  $bM_4$ .

*Protorhyphus liaoningicus* sp. nov.

Figs. 1C, D, 2F, G

*Derivation of name.* After Liaoning, where the fossil was collected.

*Material.* Holotype DHG200388 and 200389, part and counterpart, of a male from the Haifanggou Formation in the vicinity of Yushudonggou, Beipiao, Liaoning; deposited in the collections of NIGPCAS.

*Diagnosis.* Distinguished by wings with r-m closer to  $R_4$  than  $R_{2+3}$ ; Pt present;  $R_{2+3}$  distinctly sigmoid, convergent to  $R_1$  terminally;  $R_{4+5}$  furcated distad of both midwing, fork of  $M_{1+2}$ ;  $R_4$  nearly straight;  $R_5$  clearly curved downward at midway; m-m meeting  $M_2$  beyond fork of  $M_{1+2}$ ;  $dM_{1+2}$ ,  $bM_3$  subparallel; m-cu about twice length of  $bM_4$ .

*Description.* Small protorhyphids, body covered with a few long hairs (possibly poorly preserved). Head suboval in lateral aspect. Eyes apparently large, but poorly preserved. Antennae 16-segmented, about 3.7 times longer than head length, with scape slightly shorter, thinner than first flagellomere, pedicel slightly short, basal eight flagellomeres shorter than wide, terminal six nearly twice (or more) longer than wide. Thorax suboval. Wing nearly 2.2 times longer than wide; Pt large, elongate-oval, reaching  $R_{2+3}$ ; Sc one-third and  $R_1$  little more than two-thirds of wing length; Rs furcated just a little distad of Sc end, but just at level of M fork;  $R_{2+3}$  distinctly sigmoid, convergent to  $R_1$  terminally, clearly shorter than  $R_4$ ;  $bR_{4+5}$  1.2 times longer than  $dR_{4+5}$ ;  $R_{4+5}$  furcated distad of both midwing, fork of  $M_{1+2}$ ;  $bM_{1+2}$  1.3 times longer than  $dM_{1+2}$ ; m-m meeting  $M_2$  beyond fork of  $M_{1+2}$ ,  $bM_2$  about one-half length of m-m; CuP curved, parallel to CuA terminally, not reaching hind margin of wing; cell d hexagonal, nearly 3.8 times longer than wide, with  $M_{3+4}$  distinctly shorter than  $bM_3$ ;  $dM_{1+2}$ ,  $bM_3$  subparallel; m-cu about twice length of  $bM_4$ . Legs with coxae large, nearly two-thirds length of femora, latter thicker, shorter than tibiae; tibiae covered with one or two rows of short setae, tibial spurs not visible (probably

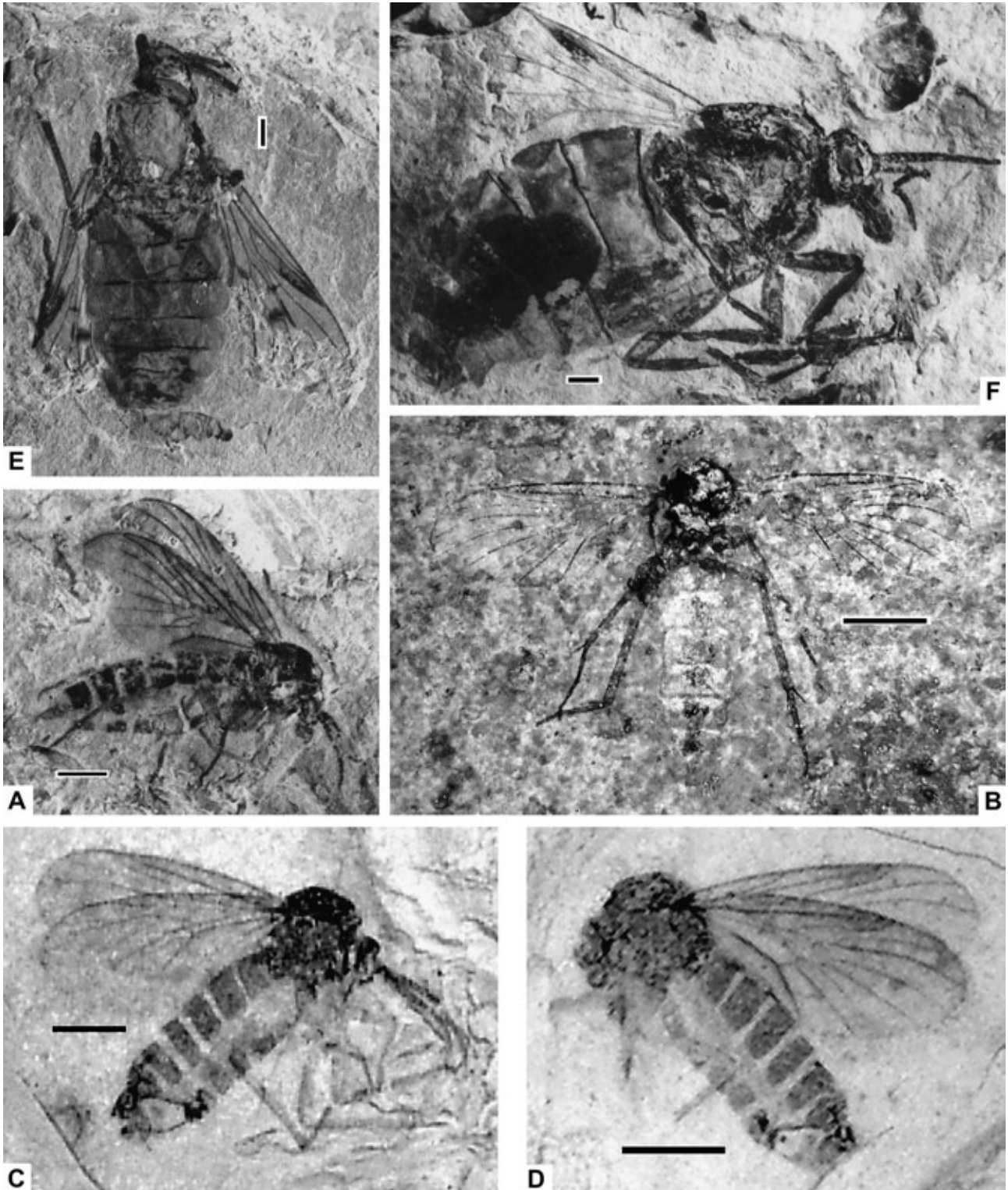


Fig. 1. A, B, *Protorhyphus neimonggolensis* sp. nov. A, holotype, DHG200386. B, paratype, DHG200387. C, D, *Protorhyphus liaoningicus* sp. nov., holotype. C, part, DHG200388. D, counterpart, DHG200389. E, F, *Megarhyphus rarus* sp. nov. E, holotype, DHG200390. F, paratype, DHG200391. Scale bars represent 1 mm.

poorly preserved); Abdomen massive, cylindrical; outer gonostylus large, strongly curved ventrally.

Measurements in mm: length of head, 0.5, antenna, 1.7, thorax, 1.4, abdomen, 2.7; length of wing, 3.2, width, 1.5; length of hind coxa, 0.7, femur, 1.0, basitarsus (?), 0.6.

*Remarks.* The diagnosis easily separates *Protorhyphus liaoningicus* from *P. neimonggolensis* sp. nov., but the wing venation is similar to that of *P. sibiricus*. It differs in that Rs arises closer to the wing base (viz. Sc ends far from Rs base), cell d is longer,  $bM_{1+2}$  is only slightly longer than  $dM_{1+2}$ , and

both  $M_2$  and  $M_3$  are distinctly divergent terminally. The new species is distinct from *P. simplex* and *P. stigmaticus* by its characteristic  $R_5$ , which runs clearly downward at its midpoint.

Family: Anisopodidae Knab, 1912

Genus *Megarhyphus* Kovalev, 1990

*Type species. Megarhyphus sophiae* Kovalev, 1990

*Species included.* *M. sophiae*, Glushkovo Formation, Daya, and *M. rectinervis*, Godymboi Formation, Onohoi, both eastern Transbaikalia, Russia (Kavalev, 1990); and *M. rarus* sp. nov., described below.

*Megarhyphus rarus* sp. nov.

Figs. 1E–G, 2H–M

*Derivation of name.* Latin, *rarus*, rare, alluding to the scarcity of specimens (gender masculine).

*Material.* Holotype DHG200390, paratype DHG200391 and 200392, part and counterpart. Locality and repository as for *Protorhyphus neimongolensis*.

*Diagnosis.* Venationally, stem of  $R_s$  twice length of  $bR_{4+5}$ ;  $R_s$  furcated distad of fork of  $M$ ;  $M_1$ , strongly flexed before mid-length; crossvein m-m just meeting fork of  $M_{1+2}$ ; cell d higher (crossvein m-m long, about one-quarter of length of cell d).

*Description.* Stout, moderate anisopodids. Head suboval in lateral aspect, occiput covered with dense setae. Eyes large, oval. Antennae 16(?) segmented, more than 2.5 times longer than head length, with scape slightly shorter, thinner than first flagellomere, pedicel quite short, less than one-half length of scape, first to sixth flagellomeres somewhat thicker than long, remaining flagellomeres as long as, or slightly longer than, thick, with sixteenth missing apically. Proboscis conical, sclerotized, nearly as long as head. Mesonotum oval, flat, covered with dense setae medially. Wing nearly 2.5 times longer than wide, wing venation closely similar to that of *M. sophiae* and *M. rectinervis*, but with stem of  $R_s$  twice as long as  $bR_{4+5}$ ;  $R_s$  furcated distad of fork of  $M$ ;  $M_1$  strongly flexed before mid-length; crossvein m-m just meeting fork of  $M_{1+2}$ ; cell d wider (crossvein m-m elongate, about one-quarter length of cell d); all crossveins (r-m, m-m and m-cu) covered with elongate-oval, dark brown markings. Legs relatively thin, long, with femora thicker than, and nearly as long as, tibiae; latter covered by at least three rows of short setae, tibial spurs well developed; basitarsi covered with at least one row of short setae, midleg setae slightly shorter, and hindleg setae clearly longer, than remaining tarsomeres combined. Abdomen massive, suboval, widest between third and fourth segments; apex of abdomen rounded.

Measurements in mm: length of head, 1.6–1.8, antenna, ca. 4.4, thorax, 4.3–5.0, abdomen, 8.7–9.0; length of wing, 10.4, width ca. 4.3; length of femur of midleg, ca. 5.7, tibia, 5.6, tarsus, 5.0 (2.5:0.9:0.7:0.4:0.5), femur of hindleg, as preserved, 5.5, tibia, 6.3, tarsus, 6.2 (3.2:1.3:0.7:0.5:0.5).

*Remarks.* *Megarhyphus rarus* closely resembles both *M. sophiae* and *M. rectinervis* in wing venation but can be readily distinguished from them by the wing characters noted in the diagnosis.

### 3. Discussion

*Sinorhyphus arcuatus* from the Haifanggou Formation in Liaoning was originally described as a new genus and species of the extant family Rhyphidae within the Rhyphoidea (Hong, 1983). Based on the original description of wings it is a representative of *Protorhyphus* and shares many venational character states with *P. liaoningicus*, which is from the same locality and horizon. Their relationship must remain uncertain, however, until the specimen of *S. arcuatus* can be re-examined because the original description, line drawing and photograph (Hong, 1983, pp. 130–131, fig. 124a, b, pl. 24, fig. 3; Fig. 3C, D herein) are unsatisfactory and need to be improved; the photograph provided is blurred, with significant characters not discernible. This species is, therefore, considered provisionally to belong to *Protorhyphus*, viz. *Protorhyphus arcuatus* (Hong, 1983) comb. nov.

Hong (1984) established another new species (and genus), *Brachyopteryx weichangensis*, from the Dabeigou Formation in Weichang, Hebei, which he assigned to the Protorhyphidae. However, the distinctive character states of its wings all suggest that it does not belong to this family (Fig. 3F, G), namely:  $M$  with five branches; crossvein r-m meeting fork of  $R_{4+5}$  or meeting  $R_5$  clearly beyond fork of  $R_{4+5}$  (Hong, 1984, figs. 53a and 53c, respectively); and the enlarged cell d situated near to margin of wing instead of midwing. Nevertheless, an alternative placement cannot be suggested until further investigation of the specimen is possible.

Hong and Wang (1990, pp. 148–149, fig. 6-5-148) described and illustrated *Mesobrachyopteryx shandongensis* (Rhyphoidea: Rhyphidae) on the basis of a single specimen from the Laiyang Formation in the vicinity of Tuanwang, Laiyang, Shandong. They stated that the antenna consists of “about five segments” and appears “stout and short”. I have collected two further specimens from the same formation and horizon that bear marked similarities in the characteristics of body structure to those of *M. shandongensis*, and appear to belong to this species. The antenna, however, have only three segments, with an elongate arista at the top, and the wing venation as described (Hong and Wang, 1990, p. 149, figs. 6-5-148, 6-5-149) might be incorrect (see Figs. 3H, I, 4, 5 herein); hence *M. shandongensis* is considered here to belong to the Brachycera.

A species known from amber, *Hongocaloneura plectilis* (originally *Caloneura plectilis* Hong, 1981) from the Eocene Guchengzi Formation in Fushuen, Liaoning, was originally placed in Rhyphidae (Rhyphoidea) (Hong, 1981). Later, Evenhuis (1994, p. 282) stated that the fossil *Caloneura* Hong has a peculiar wing venation and that the depictions in the two illustrations in Hong (1981) differ from each other and from that in the photograph (Hong, 1981, pl. 49) and is unlike Anisopodidae. As a result he noted that until “such time as the type

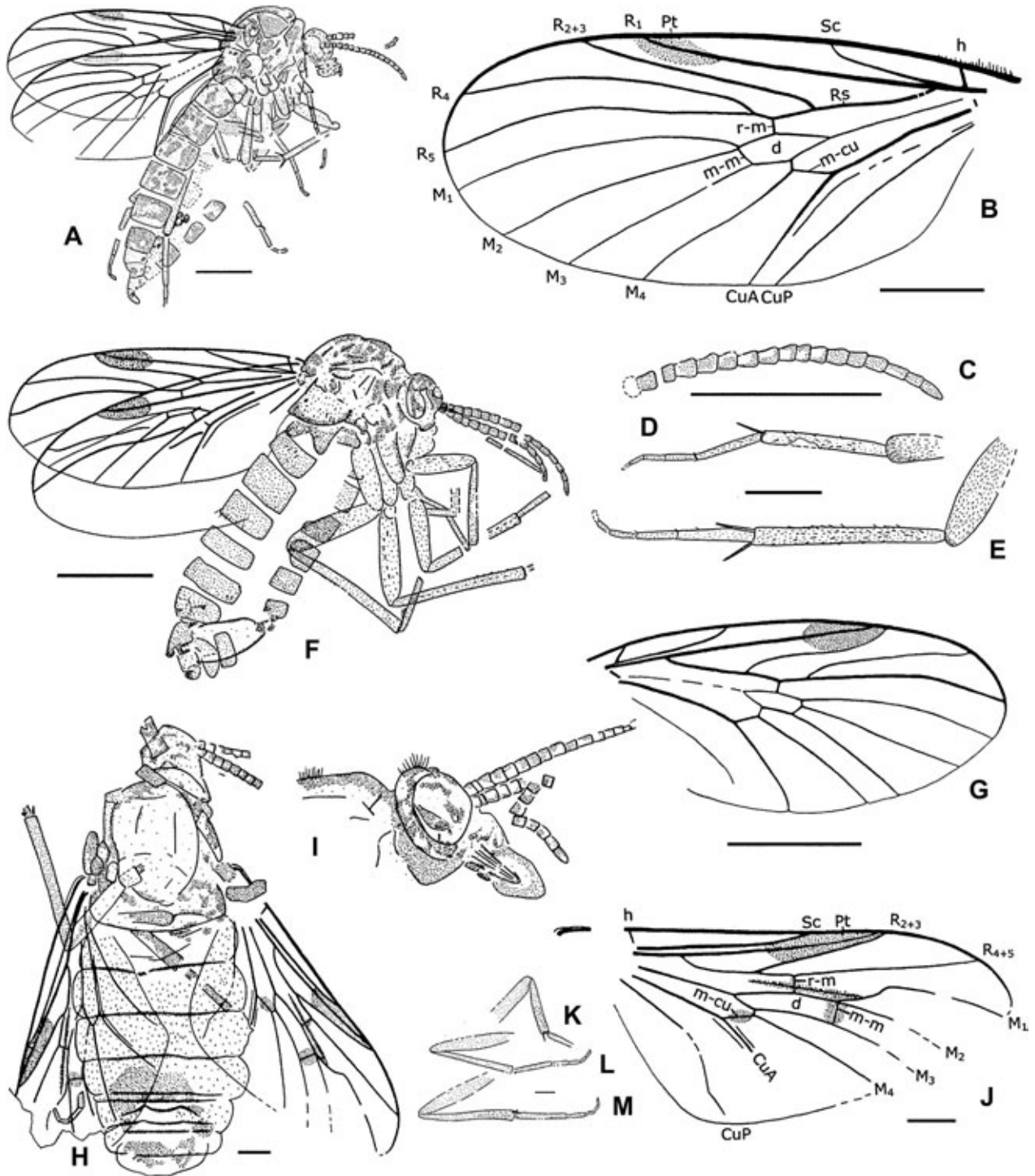


Fig. 2. Camera lucida drawings. A–E, *Protorhyphus neimongolensis* sp. nov. A, female, lateral aspect, specimen DHG200386. B, wing, specimen DHG200387. C, antenna, specimen DHG200386. D, E, midleg and hindleg, respectively of specimen DHG200387. F, G, *Protorhyphus liaoningicus* sp. nov.; F, female, lateral aspect, specimen DHG200388. G, wing, specimen DHG200389. H–M, *Megarhyphus rarus* sp. nov. H, I, female(?), dorsoventral aspect; and head, lateral aspect, respectively of specimen DHG200391. J, wing, specimen DHG200390. K–M, fore leg (incompletely preserved), midleg and hindleg, respectively of specimen DHG200391. Scale bars represent 1 mm.

specimen can be restudied, it is transferred in this catalog (under the new replacement name *Hongocaloneura*) to unplaced Nematocera”. Hong (2002) subsequently disagreed with Evenhuis’ comments, arguing that the wing venation had been correctly illustrated, and named the new family Hongocaloneuridae Hong,

2002 in the Anisopodoidea, based on his previous descriptions (Hong, 2002, pp. 331–333).

Clearly, the taxonomic position of this species remains unresolved. For example, most striking is the character of M, which possesses six terminal branches (Hong, 1981, p. 92, fig. 96;

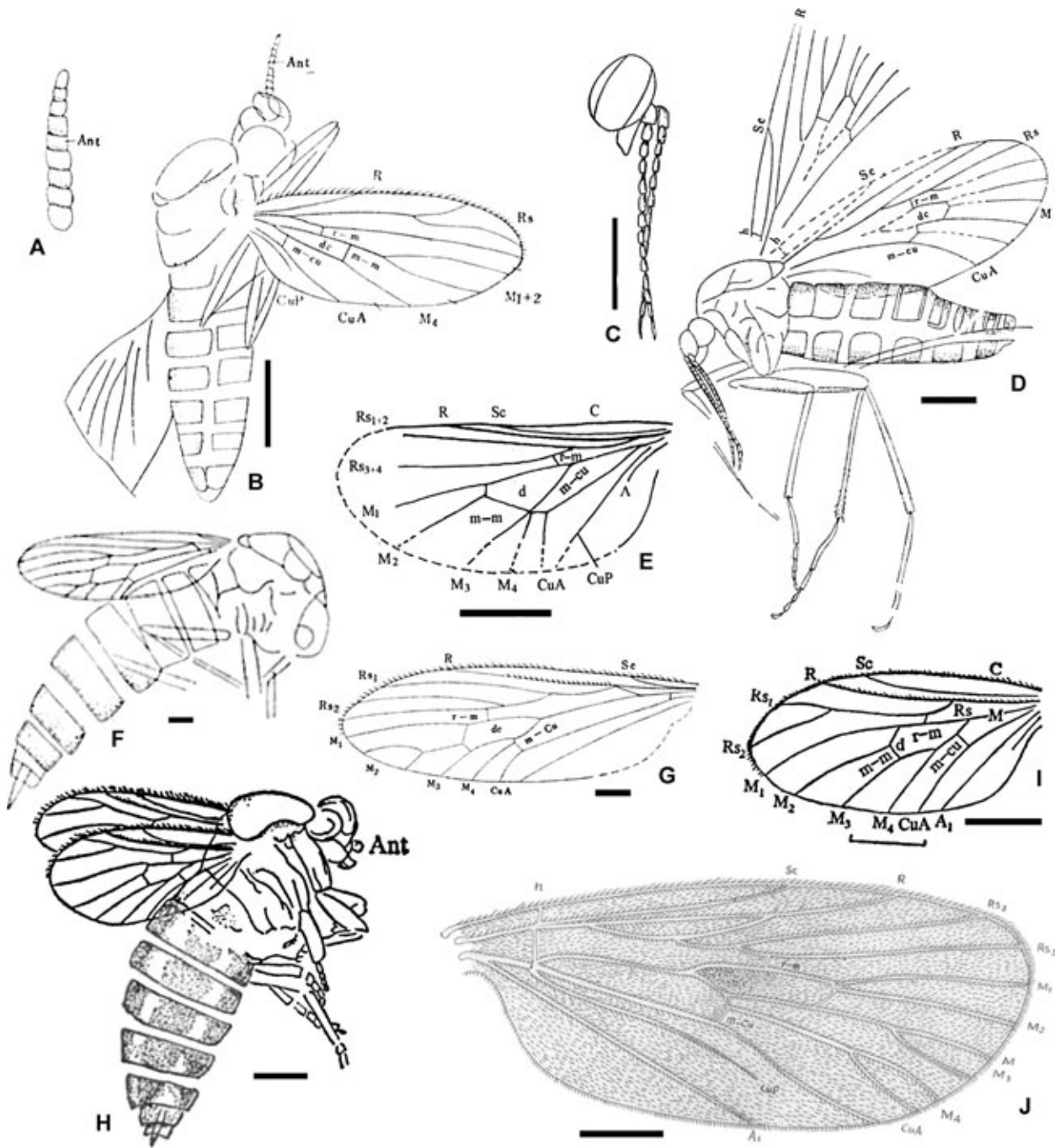


Fig. 3. A, B, *Limnorhyphus haifanggouensis* Hong, 1983. A, antenna; B, entire fly (after Hong, 1983). C, D, *Sinorhyphus arcuatus* Hong, 1983. C, head; D, entire fly (after Hong, 1983). E, *Eoanisopoditis fushunensis* Hong, 2002, wing (after Hong, 2002). F, G, *Brachyopteryx weichangensis* Hong, 1984. F, entire fly; G, wing (after Hong, 1984). H, I, *Mesobrachyopteryx shandongensis* Hong and Wang, 1990. H, entire fly; I, wing (after Hong and Wang, 1990). J, *Hongocaloneura plectilis* (Hong, 1981), wing (after Hong, 1981). Scale bars represent 1 mm.

p. 94, fig. 97-4; Fig. 3J herein). This character state might be an artifact, as all known Diptera, including the most primitive representatives from the Triassic (see Shcherbakov et al., 1995), have no more than four terminal branches of M. It is apparent that until reinvestigation of the specimen is possible, this species remains an enigmatic element of the Nematocera. Alternatively, it would not be a true fly if its wing venations have been correctly drawn.

Hong (2002) also described another new genus and species of Anisopodidae, *Eoanisopoditis fushunensis* Hong, 2002, from the same locality and horizon (locality and repository, as for *Hongocaloneura plectilis*). He did not, however, provide a photograph. On account of its ten-segmented antenna and the extremely enlarged cell d (Hong, 2002, pp. 330, 331, fig. 2-7-549; Fig. 3E herein) it is difficult to see how it might be referred to the Anisopodoidea, let alone the Anisopodidae.

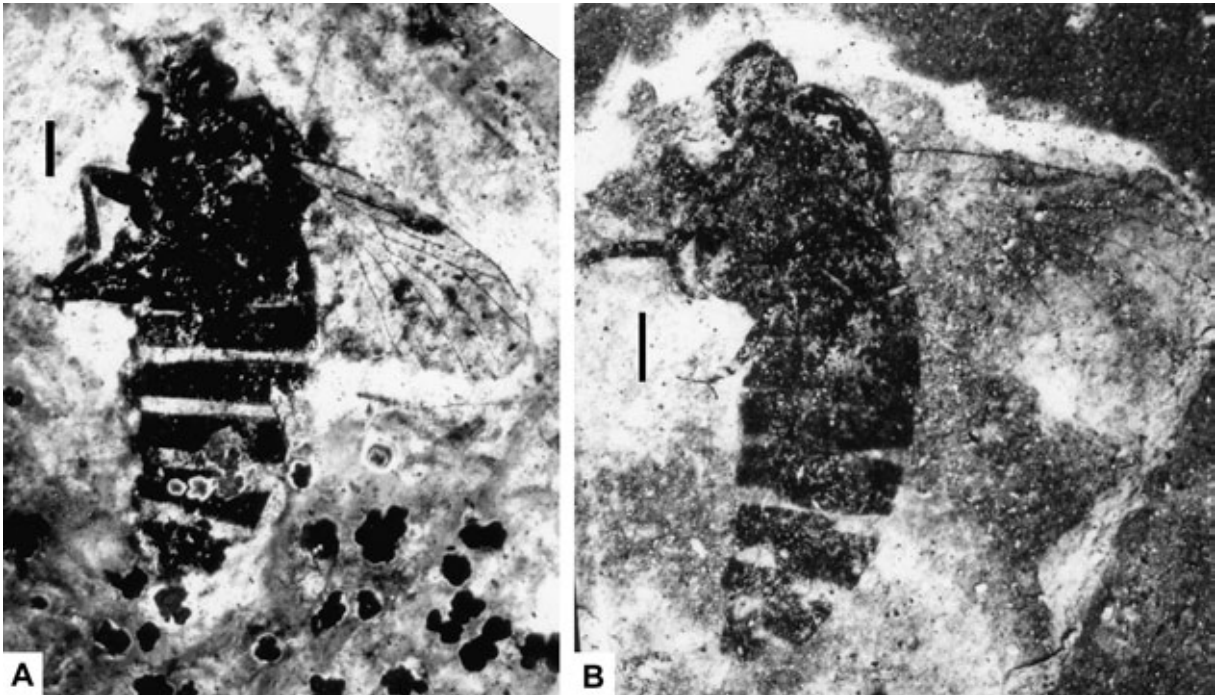


Fig. 4. *Mesobrachyopteryx shandongensis* Hong and Wang, 1990. A, B, topotypes L91816 and L91817, respectively. Scale bars represent 1 mm.

Hong (1983) described the family Limnorhyphidae from the Callovian–Oxfordian Haifanggou Formation. He regarded it to belong to the Rhyphoidea, closely related to the Oligophryneidae and Rhyphidae (Hong, 1983). It was erected to contain a single genus and species: *Limnorhyphus haifanggouensis* Hong, 1983. Later, Kovalev (1990) transferred it to the Bibionomorpha. Krzemińska et al. (1993) refrained from including it in the Axymyiomorpha, until the specimen is re-examined. I

think that although the wing venation drawn by Hong (1983, p. 132, fig. 125; Fig. 3A, B herein) more or less resembles that of species of the Perissommatidae (Perissommatoida, Axymyiomorpha) with the exception of the closed cell d, the line drawing seems to differ from the photograph (Hong, 1981, pl. 24, fig. 3) in which CuA appears to be coalesced with CuP for a considerable distance, a characteristic of the Brachycera. Thus, the phylogenetic position of the species is

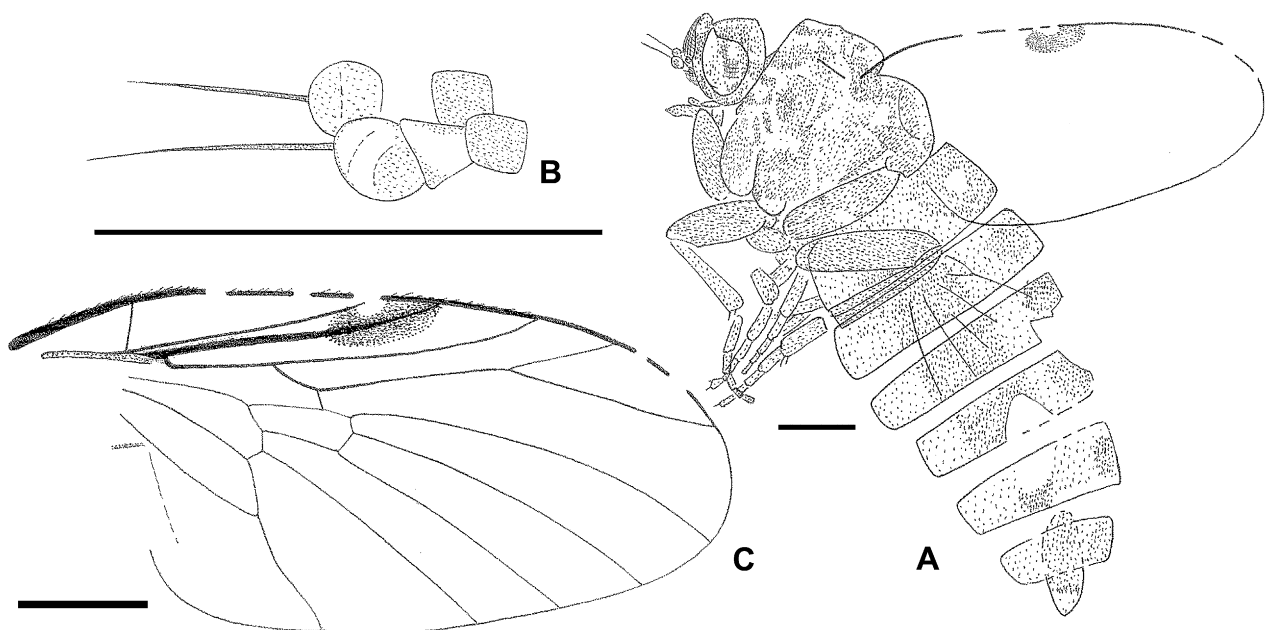


Fig. 5. *Mesobrachyopteryx shandongensis* Hong and Wang, 1990, camera lucida drawing of specimen L91816. A, female, lateral aspect, wing venation omitted. B, antennae. C, wing. Scale bars represent 1 mm.

uncertain even at suborder level, and is worthy of further investigation.

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