New winter crane flies (Insecta: Diptera: Trichoceridae) from the Jurassic Daohugou Formation (Inner Mongolia, China) and their associated biota

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Abstract: Four extinct new species referable, respectively, to three extinct new genera within Trichoceridae have been recovered from the Jurassic Daohugou Formation in Ningcheng, Chifeng, Inner Mongolia, China: ***Archaeotrichocera ephemera*** gen. et sp. nov., ***Tanyochoreta integera*** gen. et sp. nov., ***Tanyochoreta chifengica*** sp. nov., and ***Sinotrichocera parva*** gen. et sp. nov. The specimen described earlier as trichocerids from China, *Mesotrichocera laiyangensis* Hong and Wang 1990, does not belong to this family. The Daohugou biota comprises a wide range of vertebrate and invertebrate organisms that inhabited, a small lake, luxurious everglade, streams, and forest with volcanoes nearby. The Daohugou Formation can be compared to the Karabastau and Haifanggou formations based on biostratigraphic correlation. The geological age for trichocerid-bearing nonmarine volcano-sedimentary rocks may be latest Middle Jurassic (Callovian) or earliest Late Jurassic (Oxfordian) rather than early–middle Middle Jurassic or Early Cretaceous.

Résumé : Quatre nouvelles espèces disparues attribuables, respectivement, à trois nouveaux genres disparus des Trichoceridae ont été obtenues de la Formation jurassique de Doahugou, à Chifeng, dans le comté de Ningcheng, en Mongolie intérieure (Chine), soient ***Archaeotrichocera ephemera*** gen. et sp. nov., ***Tanyochoreta integera*** gen. et sp. nov., ***T. chifengica*** sp. nov. et ***Sinotrichocera parva*** gen. et sp. nov. Le spécimen de *Mesotrichocera laiyangensis* Hong et Wang, 1990, décrit antérieurement comme étant un trichocéride de Chine, n'appartient pas à cette famille. Le biote de Doahugou comprend une grande diversité d'organismes vertébrés et invertébrés qui habitaient, respectivement, un petit lac, une région marécageuse luxuriante, des ruisseaux et une forêt à proximité de volcans. Une corrélation stratigraphique permet de comparer la Formation de Daohugou aux Formations de Karabastau et de Haifanggou. Les roches volcano-sédimentaires non-marines qui renferment les trichocérides pourraient être du Jurassique moyen (Callovien) ou du tout début du Jurassique tardif (Oxfordien) plutôt que du début–milieu du Jurassique moyen ou du Crétacé précoce.

[Traduit par la Rédaction]

Introduction

The family Trichoceridae, commonly called winter crane flies, constitutes some 110 species (Dahl and Alexander 1976) and is subdivided into four recent genera within two subfamilies: *Trichocera* Meigen, 1800; *Diazosma* Bergroth, 1913; *Nothotrichocera* Alexander, 1926 referable to the subfamily Trichocerinae; and *Paracladura* Brunetti, 1911 referable to the subfamily Paracladurinae (Krzeminska 1992*b*). The family is confined to temperate and cool climates. Adults are on the wing in spring and (or) autumn and, especially in temperate and warm-temperate regions, during winter or, in colder regions, in summer. Adults often occur in caverns, mine shafts, cellars, hollow trees, and other dark places, but they attract more attention by their habit of swarming. Larvae are scavengers in moist or wet terrestrial biotopes such as decaying leaves and vegetables, manure, fungi, stored roots and tubers, and burrows of rodents. From the southern islands of New Zealand, larvae have been reported from penguin droppings and bird nests (Oosterbroek 2004).

Additionally, 19 species of compression fossil and amber trichocerids have been recorded (Evenhuis 1994; Krzemiński and Evenhuis 2000; Podenas 2001). Among them, six species referable to six genera were recovered from the Mesozoic of Russia, Mongolia, and China: *Eotrichocera christinae* Kalugina, 1985; *Mailotrichocera jurassica* Kalugina, 1985; ?*Trichocera itatica* Kalugina, 1985; *Paleotrichocera mongolica* Kalugina, 1986; "*Trichonomites*" *aquaticus* Kalugina, 1986; and *Mesotrichocera laiyangensis* Hong and Wang 1990. Among them, "*Trichonomites*" *aquaticus* is based on a larva. *Mesotrichocera laiyangensis* bears a particular wing venation and does not belong to this family (see detailed discussion later in the paper). The oldest representative of trichocerids from Germany has been mentioned but undescribed (Krzemiński and Evenhuis 2000). Based on the report by Krzeminska (1992*a*), abundant material of fossil Trichoceridae has been

Received 20 December 2004. Accepted 14 September 2005. Published on the NRC Research Press Web site at http://cjes.nrc.ca on 10 March 2006.

Paper handled by Associate Editor J. Jin.

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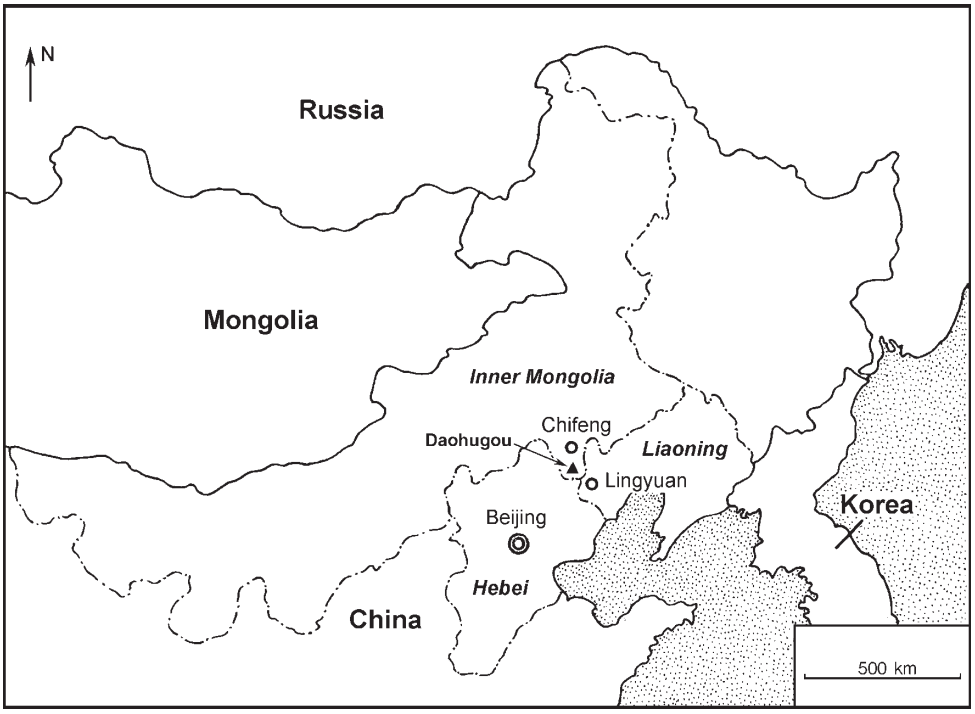
 doi:10.1139/E05-092

Fig. 1. Map showing the geographic location of trichocerid-bearing sedimentary rocks. The solid triangle represents the fossil site at the village of Daohugou.



collected. Their age varies from the Early Jurassic to Miocene. These fossil trichocerids will soon be published as a monograph (E. Krzeminska, personal communication, 2005).

Four extinct new species within three extinct new genera of winter crane flies from the Jurassic Daohugou Formation in Ningcheng, Chifeng, Inner Mongolia, China, are described herein and named *Archaeotrichocera ephemera* gen. et sp. nov., *Tanyochoreta integera* gen. et sp. nov., *Tanyochoreta chifengica* sp. nov., and *Sinotrichocera parva* gen. et sp. nov.

The biota from the trichocerid fossil locality contains a wide range of vertebrate and invertebrate organisms. Among these, the insects are very rich, and more than 100 species within 14 orders have been recovered. The geological age and stratigraphical correlation of fly-bearing, nonmarine, volcano-sedimentary rocks have been a matter of debate. Biostratigraphic correlation and new radiometric data suggest a latest Middle Jurassic (Callovian) or earliest Late Jurassic (Oxfordian) age. This differs from the early–middle Middle Jurassic or Early Cretaceous age proposed in previous works (see detailed discussion later in the paper).

Vein nomenclature used herein follows that of Wootton and Ennos (1989) and has also been adopted by Shcherbakov et al. (1995) and Blagoderov et al. (2002). The vein traditionally named 1A is, in fact, CuP.

Material and methods

Specimens NIGP (Nanjing Institute of Geology and Palaeontology, Nanjing, China) DHG200396, DHG200397, DHG200398, and DHG200399, four nearly complete male or female adults in shale, are well preserved. The trichocerid-bearing sedimentary rocks of the Daohugou Formation are located at the village of Daohugou in Ningcheng County, Chifeng City, Inner Mongolia (= Nei Monggol Autonomous Region), China (see Fig. 1). The fossil site is at latitude 41°18.979′N, longitude 119°14.318′E and has an altitude of 607 m according to Ren et al. (2002).

Specimen descriptions, photographs, and drawings were obtained with the application of glycerol to the surface of the specimens (with the exception of Figs. 1*a*, 1*b*, 3*a*, 5*a*, 5*c*, and 5*d*). The line drawings were executed with a camera lucida, and the digital photographs were taken using a stereomicroscope.

Anatomical abbreviations

t_1, first tarsomere; t_2, second tarsomere; t_1/t_2, joint between first and second tarsomeres. See Figs. 3*b* and 5*c* for explanation of other abbreviations: 1A, CuA, CuP, d (d cell), h, m-cu, m-m, M_1 to M_4, M, bM_{1+2}, dM_{1+2}, mM_{1+2}, bM_3, M_{3+4}, R_1 to R_5, R_{2+3}, R_{2+3+4}, bR_5, r-m, Rs, Sc_1, Sc_2.

Systematic paleontology

Class Insecta Linnaeus, 1758
Order Diptera Linnaeus, 1758
Suborder Nematocera Latreille, 1825
Family Trichoceridae Kertész, 1902
Genus ***Archaeotrichocera*** gen. nov.

TYPE SPECIES: *Archaeotrichocera ephemera* sp. nov.

ETYMOLOGY: Greek, *Archaeo*, Archaian, *trichocera* (the feminine gender), the Recent genus *Trichocera*.

SPECIES INCLUDED: The type species only.

DIAGNOSIS: Medium-sized winter crane flies, wing length

7.1 mm. Venationally, Sc_1 more than three-quarters length of wing; d cell correspondingly long and wide (some one-sixth length of wing, and one-quarter width of wing), with its proximal angle high (some 60°), both bM_{1+2} and mM_{1+2} strongly flexed at r-m; 1A long, about one-quarter length of wing, curved evenly to wing margin; anal lobe prominent. Legs with tibial spurs present; basitarsomere longer than second tarsomere, joint between them articulated obliquely, basitarsomere with strongly terminal bristle and a pair of long setae. Male with lateromesal projection of gonocoxite, which from a bridge leaves gonocoxite at a higher acute angle; bridge incomplete, obtuse–conical.

REMARKS: This new genus bears close similarities in the structure of leg and wing venation to that of *Trichocera*, but it can be separated from the Recent genus by the larger d cell (in *Trichocera*, d cell about one-seventh length and one-fifth width of wing), the obliquely articulated joint between basitarsomere and second tarsomere, and the specialized shape and structure of gonocoxite and bridge in the male. On the other hand, in having the unusual shape of the d cell, *Archaeotrichocera* gen. nov. can be easily distinguished from all known genera from the Mesozoic of Russia and Mongolia (viz. *Eotrichocera* Kalugina, 1985; *Mailotrichocera* Kalugina, 1985; and *Paleotrichocera* Kalugina, 1986).

Recently, E. Krzeminska (personal communication, 2005) examined the monotype of *Eotrichocera christinae* Kalugina, 1985 and measured its basitarsomere, which is 1.25 times longer than the second tarsomere. This character of the leg is similar to that of the present new genus. However, the known genus from the Lower–Middle Jurassic of Transbaikalia, Russia, has a incompletely preserved d cell with its proximal angle distinctly lower (some 30°) and both bM_{1+2} and mM_{1+2} almost in line at r-m (Kalugina 1985, p. 49, figs. 14*a*, 14*b*). Therefore, a further comparison between them cannot be completed at this time and, until a redescription of *Eotrichocera* becomes available, *Archaeotrichocera* gen. nov. remains a self-existent genus of Trichoceridae.

Archaeotrichocera ephemera sp. nov.
(Figs. 2, 3)

ETYMOLOGY: Greek, *ephemera* (the feminine gender), short-lived, alluding to the short range of the species in the Jurassic.

HOLOTYPE: NIGP DHG200398, a nearly complete impression of a male, lateral aspect; from the uppermost Middle Jurassic (Callovian) or lowermost Upper Jurassic (Oxfordian) Daohugou Formation in the vicinity of Daohugou, Ningcheng, Chifeng, Inner Mongolia, China; deposited at the Nanjing Institute of Geology and Palaeontology, the Chinese Academy of Sciences.

DESCRIPTION: Head very small; eyes moderately large, suboval. Antennae filiform, tapering apically, some four times longer than head, with short and wide scape and pedicel, each nearly as long as wide, flagellomeres poorly preserved. Thorax correspondingly massive, nearly circular, with strongly convex scutum dorsally. Wing long and narrow (about 2.8 times longer than wide); venationally, Sc_1 ending basad to level of R_2; Sc_2 situated distal to level of midway of Rs stem; Rs arising from more than basal third of wing, with Rs stem less than one-third length of wing; R_{2+3+4} some three-fourths length of R_{2+3}; R_2 about one-fifth length of dR_1 (section of R_1 from R_2 to C), and nearly one-tenth length of R_{2+3}; R_3 about 1.3 times longer than R_{2+3}; bR_5 rather short, some one-eighth length of crossvein r-m; bM_{1+2} 1.4 times longer than r-m and three-fifths length of mM_{1+2}, dM_{1+2} somewhat shorter than mM_{1+2}, M_1 1.6 times longer than dM_{1+2}; crossvein m-m shorter than bM_3; dM_3 shorter than length of d cell, pentagonal, with its distal angle as an obtuse angle (near to 120°), M stem and M_{3+4} at an angle; m-cu meeting M_{3+4} a little before its fork; 1A weakly developed (only a middle section of 1A visible), about 0.28 times length of wing. Legs thin and long, covered with dense hairs; tibiae of forelegs and midlegs shorter than tarsi, but those of hind leg longer than tarsi; tibial spurs of foreleg inosculated with terminal parts of tibiae, basitarsomeres about 1.4 times longer than second tarsomeres, remainder of tarsomeres gradually shortened terminally; midleg with tibial spur not visible (probably poorly preserved); hind leg obviously long, with a pair of visible tibial spurs, basitarsomere 1.35 times longer than second tarsomere. Abdomen relatively thin and long, subcylindrical, with last abdominal segment distinctly short. Male with gonostylus large, falculate, strongly curved downward.

Length of head 0.3 mm, antenna, as preserved, 1.8 mm, thorax 1.5 mm, wing 7.1 mm; width of wing 2.5 mm; length of femur of foreleg 2.4 mm, tibia 3.2 mm, tarsus 3.83 mm (1.70:1.20:0.50:0.25:0.18), femur of midleg 2.85 mm, tibia 3.4 mm, tarsus 3.7 mm, femur of hind leg 2.8 mm, tibia 4.1 mm, tarsus 3.25 mm (1.35:1.00:0.45:0.25:0.20), abdomen 4.4 mm.

Tanyochoreta gen. nov.

TYPE SPECIES: *Tanyochoreta integera* sp. nov.

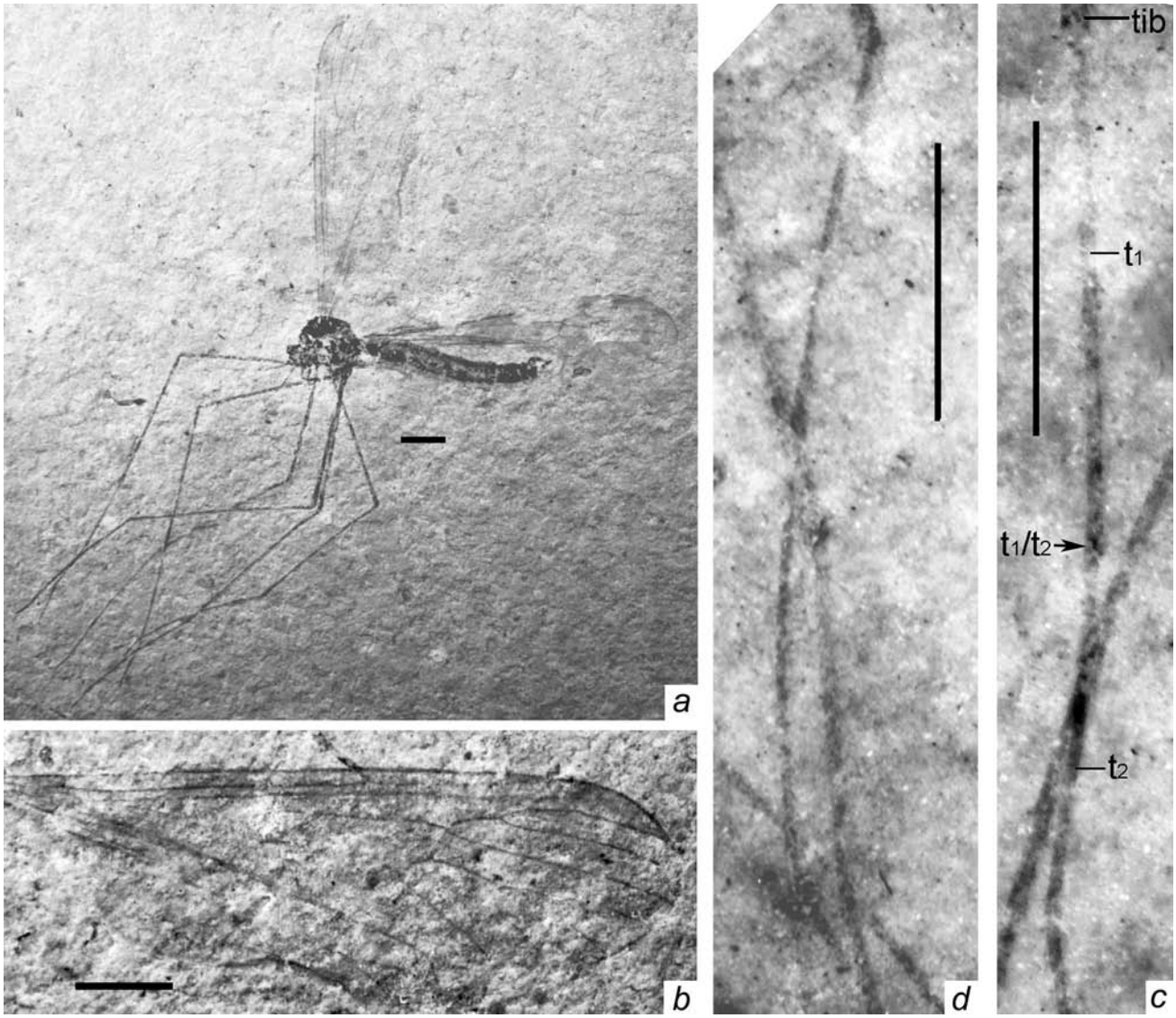
ETYMOLOGY: Greek, *tanyo*, elongate, *choreta* (the feminine gender), area, alluding to the discal cell.

SPECIES INCLUDED: *Tanyochoreta chifengica* sp. nov., besides the type species *Tanyochoreta integera* sp. nov.

DIAGNOSIS: Medium-sized winter crane flies, wing length 5.4 mm. Mouthparts with labella large, surrounding tip of labrum and hyphopharynx. Venationally, Sc_1 about 0.7 times length of wing; d cell large (more than one-fifth length and width of wing), with its proximal angle moderately acute (some 55°); both bM_{1+2} and mM_{1+2} almost in line at r-m; 1A about one-fifth length of wing, curved evenly to wing margin; anal lobe prominent. Legs with tibial spurs present; basitarsomere clearly shorter than second tarsomere (0.3–0.4 times length of second tarsomeres), joint between them simple, straight. Female with three small spermathecae. Ovipositor (cercus) conical, fleshy, tapering clearly to tip, not curved downward.

REMARKS: By the shortened basitarsomeres, which are markedly shorter than the second tarsomeres, this new genus differs from the Mesozoic and Recent genera *Eotrichocera*, *Archaeotrichocera* gen. nov., *Trichocera*, and *Diazosma*. On the other hand, *Tanyochoreta* gen. nov. shares close similarity in the length proportions of t_1/t_2 (basitarsomere to second tarsomere) to those of Recent *Nothotrichocera* and *Paracladura*,

Fig. 2. Photographs of *Archaeotrichocera ephemera* sp. nov.: (*a*) holotype, NIGP DHG200398; (*b*) wing; (*c*) basal parts of tarsus of foreleg; (*d*) basal parts of tarsi of mid-leg and hind leg. tib, tibia; t_1, first tarsomere; t_2, second tarsomere; t_1/t_2, joint between first and second tarsomeres. All scale bars = 1 mm.



but it is distinct from the known genera in having the larger d cell, which is more than one-fifth the length and width of the wing. In *Nothotrichocera* and *Paracladura*, however, the d cell is smaller in area and usually one-seventh or one-eighth the length and width of the wing.

Kalugina (1985, 1986) described another two genera, *Mailotrichocera* Kalugina, 1985 and *Paleotrichocera* Kalugina, 1986, from the Middle–Upper Jurassic of Transbakailia, Russia, and the Lower Cretaceous of western Mongolia, respectively. It is difficult to compare both genera with the present new genus because the important diagnosis of the length proportions of t_1/t_2 is unknown. As far as the character of wing venation is concerned, *Mailotrichocera* bears shorter Sc, which is about 0.57 times the length of the wing, whereas *Paleotrichocera* apparently lacks R_2 (a short crossvein-like vein between R_1 and anterior branch of Rs). Nevertheless, Kalugina (1986) expressed an opinion that the absence of the vein on the *Paleotrichocera* may be due to incomplete preservation. Therefore, until such time as the type species from Russia and Mongolia can be reinvestigated or new material recovered, a detailed comparison between these Mesozoic genera could not be done.

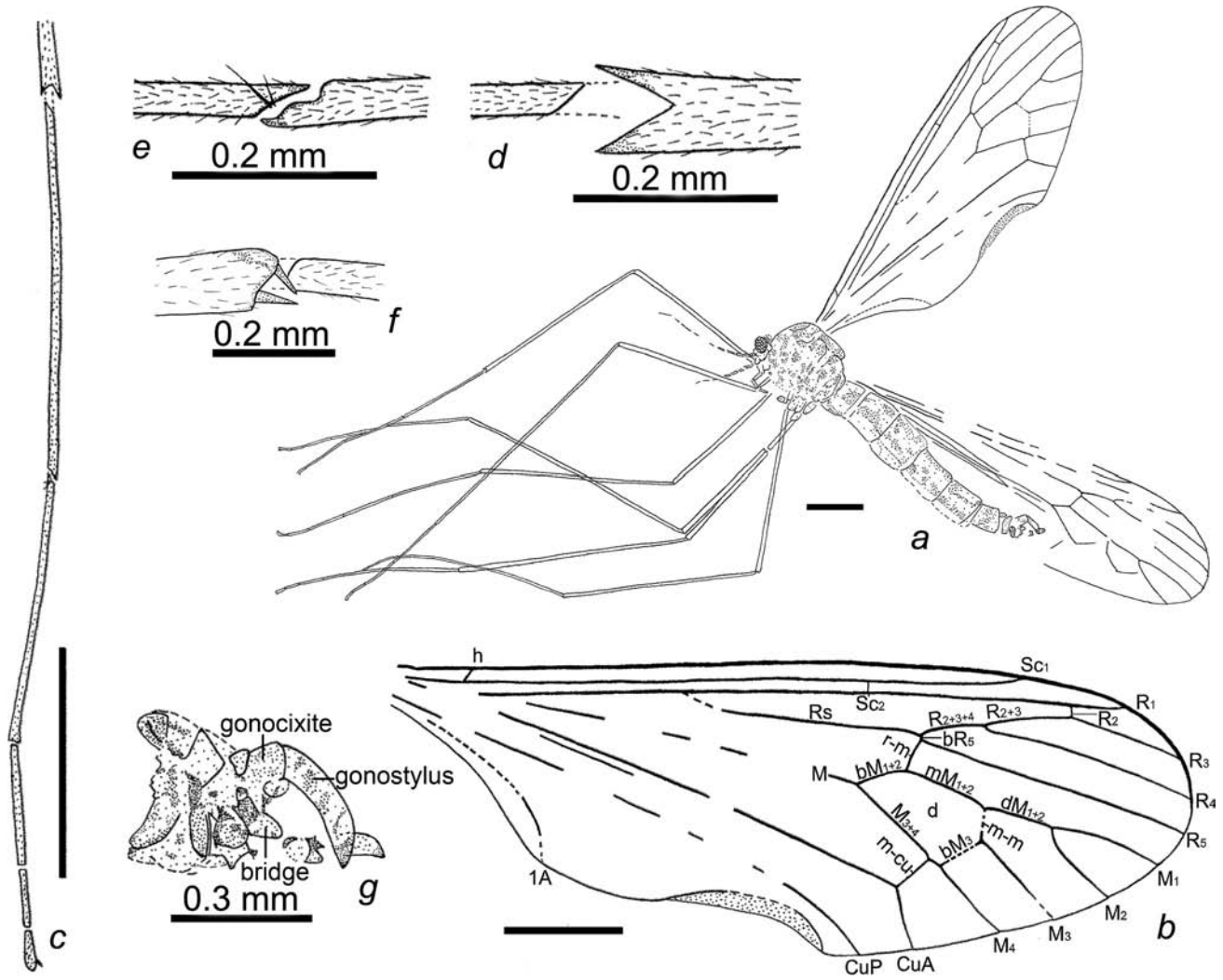
Tanyochoreta integera sp. nov.
(Figs. 4, 5)

ETYMOLOGY: Greek, *integera* (the feminine gender), integrate, alluding to the status of specimens preserved.

HOLOTYPE: NIGP DHG200396, a nearly complete impression of female, lateral aspect. For locality and repository, see under *Archaeotrichocera ephemera* sp. nov.

DESCRIPTION: Head relatively small; eyes large, oval. Antennae filiform, tapering apically; scape and pedicel short, wide, nearly as long as wide, and darker in color than that of flagellomere, with first flagellomere shorter than second one, remaining flagellomeres gradually shortened and thinned apically. Palps with terminal three segments visible, last one

Fig. 3. Camera lucida line drawings of *Archaeotrichocera ephemera* sp. nov., specimen NIGP DHG200398: (*a*) trichocerid fly; (*b*) wing; (*c*) tarsus of foreleg; (*d*) joint between tibia and tarsus of foreleg; (*e*) joint between first and second tarsomeres of foreleg; (*f*) joint between tibia and tarsus of hind leg; (*g*) male genitalia. Except as noted, scale bars = 1 mm.



long, about two times longer than penultimates, and slightly longer than second one. Thorax correspondingly small, with strongly convex scutum dorsally. Wing correspondingly long and narrow (some 2.6 times longer than wide); venationally, Sc_1 ending nearly at level of R_2; Sc_2 situated basad to level of midway of Rs stem; Rs arising from basal one third of wing, with Rs stem less than one-quarter length of wing; R_{2+3+4} nearly as long as R_{2+3}; R_2 some one-third length of R_{2+3}; R_3 nearly three times longer than R_{2+3}; bR_5 slightly shorter than crossvein r-m; d cell 2.6 times longer than wide, asymmetrically rhombic, its distal angle nearly orthogonal (some 85°), bM_{1+2} longer than r-m, and clearly shorter than mM_{1+2}, dM_{1+2} somewhat shorter than mM_{1+2}, M_1 twice as long as dM_{1+2}; crossvein m-m as long as bM_3; dM_3 apparently shorter than length of d cell; M stem and M_{3+4} slightly at an angle; both crossvein m-cu and bM_3 just in line; 1A about 0.23 times length of wing. Legs relatively thin and long, covered with dense hairs; a single tibial spur of foreleg present but rather small, tarsus clearly longer than tibia, basitarsomere about 0.4 times length of second tarsomere; midleg with tibial spur not visible (probably poorly preserved), tarsus slightly longer than tibia, basitarsomere about 0.3 times length of second tarsomere; hind leg obviously long, with tibial spur not visible, tarsus incomplete (terminal parts missing). Abdomen relatively stout and long, subcylindrical, with last abdominal segment tapering terminally. Spermathecae circular. Ovipositor small (distinctly shorter than eighth abdominal segment).

Length of head 0.5 mm, antenna, as preserved, 1.8 mm, thorax 1.4 mm, wing 5.4 mm; width of wing 2.1 mm; length of femur of foreleg 1.7 mm, tibia 2.3 mm, tarsus 2.65 mm (0.50:1.20:0.50:0.30:0.15), femur of midleg 2.0 mm, tibia 2.3 mm, tarsus 2.27 mm (0.40:1.20:0.30:0.20:0.17), femur of hind leg 2.6 mm, tibia 3.5 mm, tarsus, as preserved, 2.9 mm, abdomen 5.8 mm.

REMARKS: For comparison, see under *Tanyochoreta chifengica* sp. nov.

Fig. 4. Photographs of *Tanyochoreta integera* sp. nov.: (*a*) holotype, NIGP DHG200396; (*b*) head; (*c*) tarsus of foreleg; (*d*) tarsus of midleg; (*e*) female genitalia. All scale bars = 1 mm.

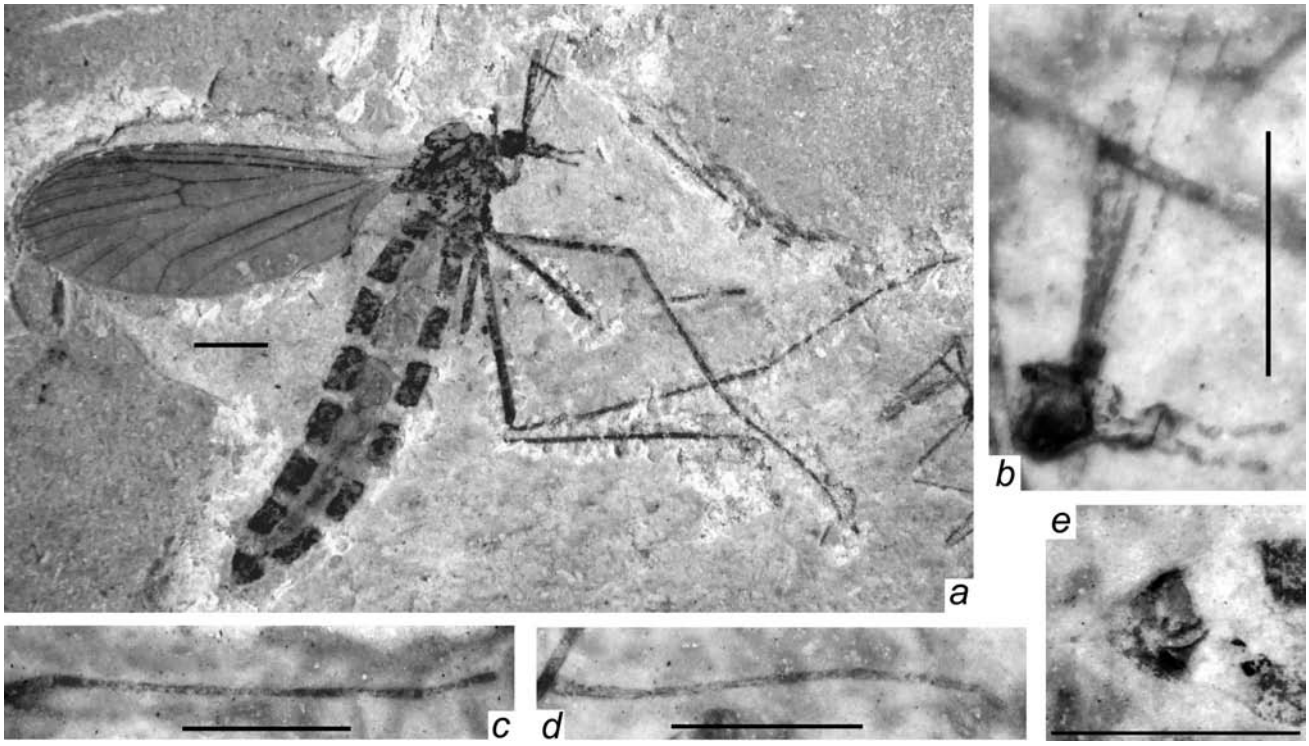
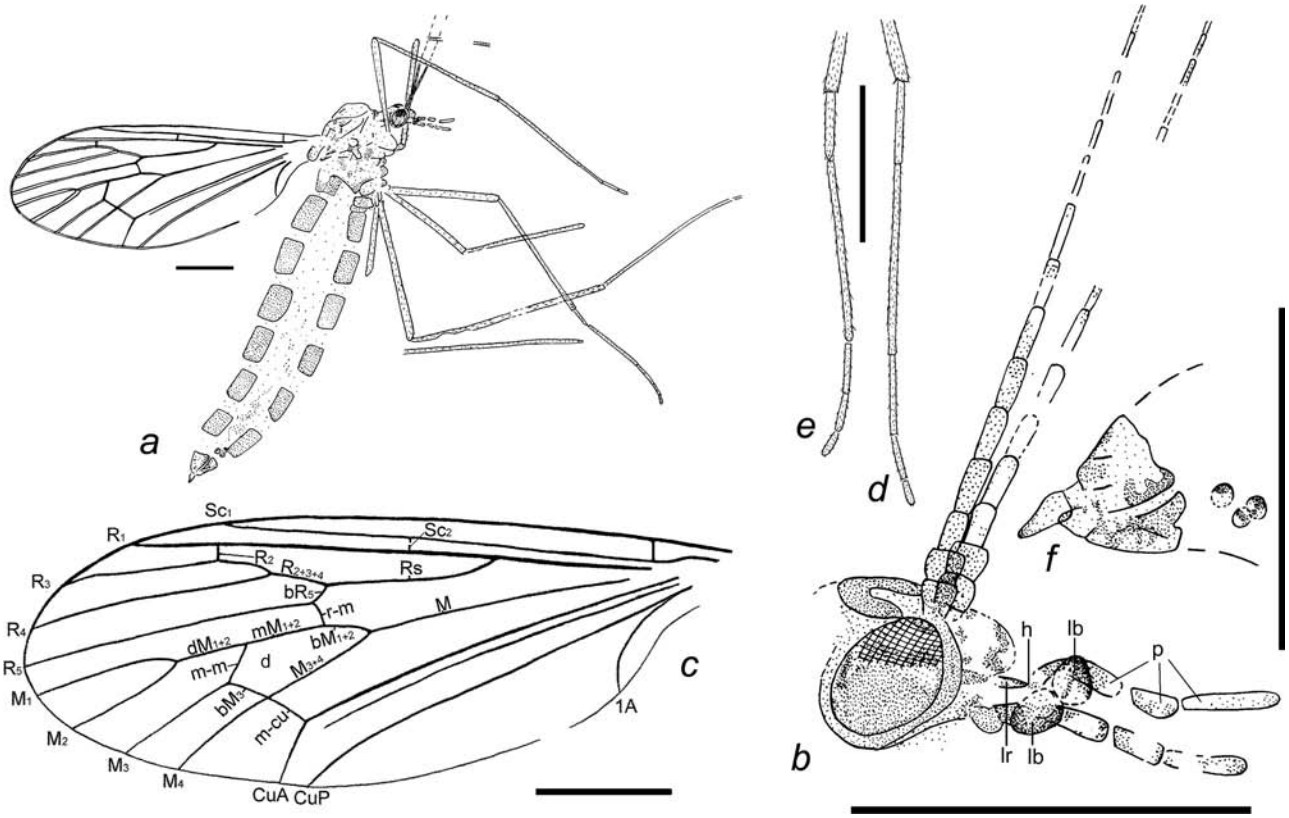


Fig. 5. Camera lucida line drawings of *Tanyochoreta integera* sp. nov., specimen NIGP DHG200396: (*a*) trichocerid fly; (*b*) head; (*c*) wing; (*d*) tarsus of foreleg; (*e*) tarsus of midleg; (*f*) female genitalia. h, hyphopharynx; lb, labella; lr, labrum; p, palp. All scale bars = 1 mm.



Tanyochoreta chifengica sp. nov.
(Figs. 6, 7)

ETYMOLOGY: After Chifeng City (Inner Mongolia, China) where the fossil was collected.

HOLOTYPE: NIGP DHG200397, a nearly complete impression of female, head and thorax nearly lateral aspect, wings and abdomen nearly dorsoventrical aspect. For locality and repository, see under *Archaeotrichocera ephemera* sp. nov.

DESCRIPTION: Head small, almost completely covered by scutum, with moderately large, suboval eyes. Antennae filiform, tapering apically; scape and pedicel wider than long; first flagellomere longest, about two times longer than second one, third through seventh somewhat shortened apically, and slightly longer than second. Thorax correspondingly small, with clearly convex scutum dorsally. Wing correspondingly short and wide (some 2.2 times longer than wide); venationally, Sc_1 ending nearly at level of R_2; Sc_2 situated distad to level of midway of Rs stem; Rs arising from basal one-quarter of wing, with Rs stem nearly one-third length of wing; R_{2+3+4} nearly as long as R_{2+3}, which is three times longer than R_2; R_3 nearly 3.5 times longer than R_{2+3}; bR_5 about one-half length of crossvein r-m; bM_{1+2} 1.7 times longer than r-m and 0.6 times longer than mM_{1+2}, dM_{1+2} nearly two-thirds length of mM_{1+2}, M_1 2.5 times longer than dM_{1+2}; crossvein m-m slightly shorter than bM_3; dM_3 apparently shorter than length of d cell; d cell widened (some one-quarter width of wing; and two times longer than wide), asymmetrically rhombic, with its proximal angle moderately acute (some 50°), distal one forming an obtuse angle (some 105°), both bM_{1+2} and mM_{1+2} as well as M stem and M_{3+4} slightly at an angle; m-cu meeting M_{3+4} before its fork; 1A weak and thin, about one-quarter length of wing. Halter spoon-shaped, with its handle markedly thin and long. Legs thin, long, and covered with dense hairs; midleg with tibiae slightly shorter than tarsi, tibial spur not visible (probably poorly preserved); first tarsomere about 0.47 times length of second one, joint between them straight; hind leg strongly elongated, with a single tibial spur visible, basitarsomere nearly 0.41 times length of second tarsomere, joint between them almost straight. Abdomen subcylindrical, with last abdominal segment tapering terminally. Spermathecae small. Ovipositor as long as eighth abdominal segment, elongate–triangular, and tapering clearly to tip.

Length of head 0.3 mm, antenna 2.0 mm, thorax 1.7 mm, wing 6.0 mm; width of wing 2.7 mm; length of femur of midleg 1.9 mm, tibia 2.0 mm, tarsus 2.08 mm (0.42:0.90:0.40:0.20:0.16), femur of hind leg 2.6 mm, tibia 3.0 mm, tarsus 2.57 mm (0.53: 1.30:0.40:0.20:0.14), abdomen 6.1 mm.

REMARKS: *Tanyochoreta chifengica* sp. nov. can be distinguished from *T. ephemera* sp. nov. by the longer first flagellomere, which is two times longer than second flagellomere, the shorter and wider wing, which is 2.2 times longer than wide, the wider d cell, which is about one-quarter width of wing, and the crossvein m-cu, which links up with M_{3+4} before its fork.

Genus ***Sinotrichocera*** gen. nov.

TYPE SPECIES: *Sinotrichocera parva* sp. nov.

ETYMOLOGY: Greek, *Sino*, China, *trichocera* (the feminine gender), the Recent genus *Trichocera*.

SPECIES INCLUDED: The type species only.

DIAGNOSIS: Small-sized winter crane flies, wing length 3.4 mm. Venationally, Sc_1 about 0.7 times length of wing; d cell large (about one-fifth length of wing), with its proximal angle moderately acute (some 55°); both bM_{1+2} and mM_{1+2} clearly flexed at r-m; 1A short, about 0.12 times length of wing, curved evenly to wing margin but nearly vertical to longitudinal axis of wing; anal lobe markedly wide. Legs with tibial spurs present; basitarsomere clearly shorter than second tarsomere (some 0.5 times length of second tarsomeres), joint between them articulated obliquely. Female with three spermathecae. Ovipositor conical, fleshy, not curved downward.

REMARKS: *Sinotrichocera* gen. nov. shows the closest resemblance in structure of leg and wing venation to that of *Tanyochoreta* gen. nov., but differs from the latter genus by the following aspects: both bM_{1+2} and mM_{1+2} are clearly flexed at r-m; 1A becomes very short (about 0.12 times length of wing) and runs nearly vertical to longitudinal axis of wing; joint between basitarsomere and second tarsomere is articulated obliquely; body is quite small (wing length 3.4 mm).

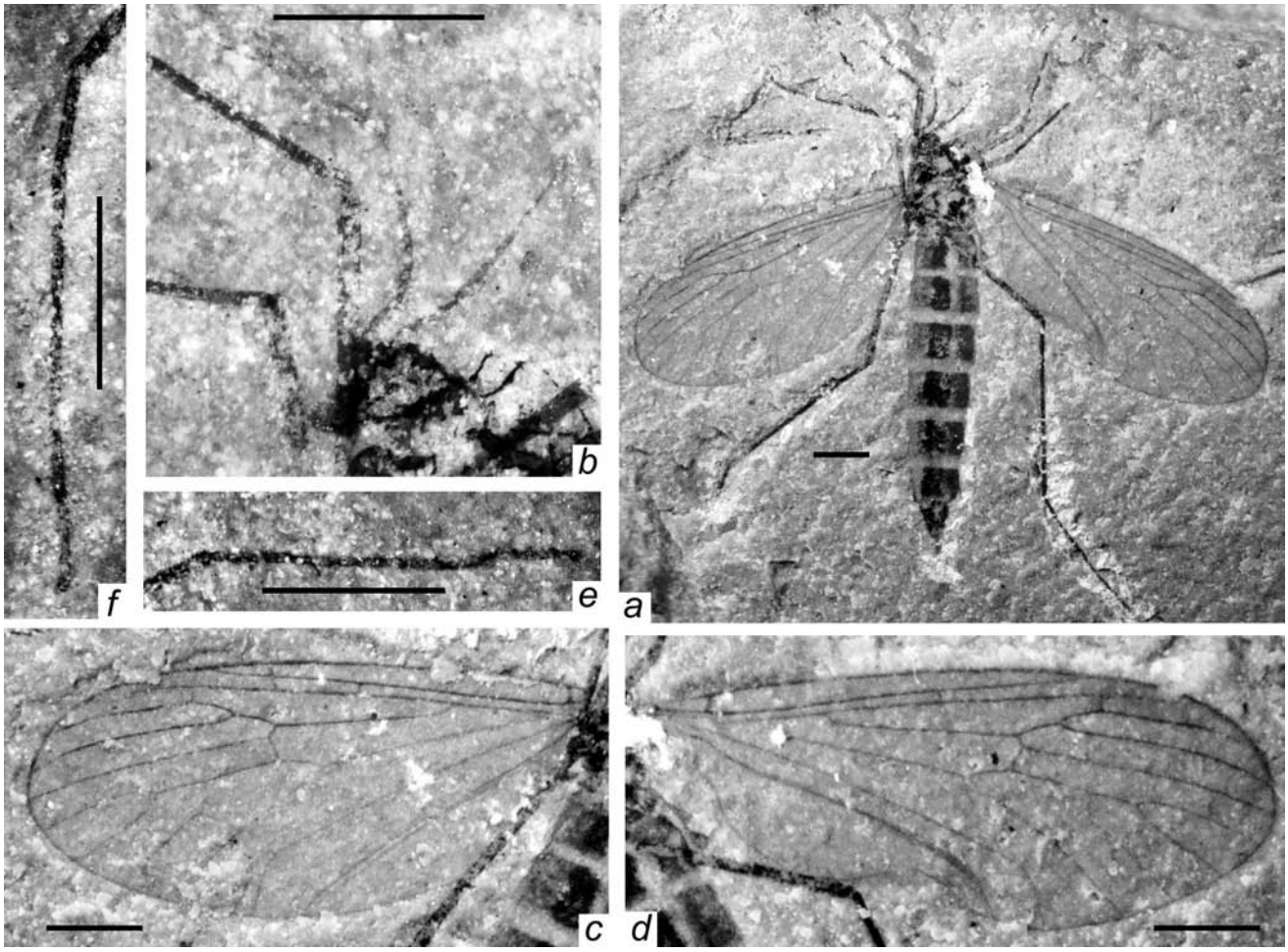
Sinotrichocera parva sp. nov.
(Figs. 8, 9)

ETYMOLOGY: Latin, *parva* (the feminine gender), small, alluding to the size of this species.

HOLOTYPE: NIGP DHG200399, a nearly complete impression of female, lateral aspect. For locality and repository, see under *Archaeotrichocera ephemera* sp. nov.

DESCRIPTION: Head correspondingly large, with moderately large, oval eyes. Antennae filiform, tapering apically; scape and pedicel short and wide, nearly as long as wide; basal three flagellomeres nearly identical in length, remaining flagellomeres gradually shortened and thinned apically. Thorax relatively massive, with strongly convex scutum dorsally. Wing long and narrow (2.8 times longer than wide); venationally, Sc_1 ending basad to level of R_2; Sc_2 situated distad of midway of Rs stem; Rs arising from basal one third of wing, with Rs stem more than one-quarter length of wing, R_{2+3+4} less than one-half length of R_{2+3}; R_{2+3} five times longer than R_2; R_3 two times longer than R_{2+3}; bR_5 as long as r-m; bM_{1+2} meeting mM_{1+2} at an angle, two times longer than r-m, and one-half length of mM_{1+2}, m-m nearly vertical to mM_{1+2} and dM_{1+2}; M stem and M_{3+4} slightly at an angle. Halter spoon-shaped, with correspondingly short handle. Legs relatively short and stout, covered with dense hairs; a single tibial spur of foreleg present but rather small, tarsus with terminal parts missing, basitarsomere some one-half length of second tarsomere; hind leg with femora and tibiae probably identical in length, and distinctly longer than tarsi, a single tibial spur visible, basitarsomere slightly shorter than one-half length of second one. Abdomen correspondingly stout and long, subcylindrical, with last abdominal segment tapering terminally.

Fig. 6. Photographs of *Tanyochoreta chifengica* sp. nov.: (*a*) holotype, NIGP DHG200397; (*b*) head; (*c*) left wing; (*d*) right wing; (*e*) tarsus of foreleg; (*f*) tarsus of hind leg. All scale bars = 1 mm.



Spermathecae moderately large. Ovipositor small (clearly shorter than eighth abdominal segment).

Length of head 0.24 mm, antenna, as preserved, 1.2 mm, thorax 1.1 mm, wing 3.4 mm; width of wing 1.2 mm; length of femur of foreleg 1.3 mm, tibia 1.6 mm, tarsus, as preserved, 1.3 mm, femur of midleg 1.3 mm, tibia 1.3 mm, femur of hind leg 1.7 mm, tibia 2.0 mm, tarsus, 1.47 mm (0.30:0.60:0.30:0.16:0.11), abdomen 3.6 mm.

Discussion

It is difficult to classify the fossil Trichoceridae based only on the wing venation because it is not treated as a main feature in the taxonomy of recent winter crane flies. Fortunately, the fossil material recovered from the Jurassic of China contains almost complete impressions of sexual trichocerids that show many well-preserved characteristics of body structures. Recently, Krzeminska (1992*a*, 1992*b*, 1997, 2001) and Pratt (1992, 2003) proposed the diagnoses of some Recent trichocerid taxa, which are followed partially in the present study to separate these new genera from the extant and fossil forms:

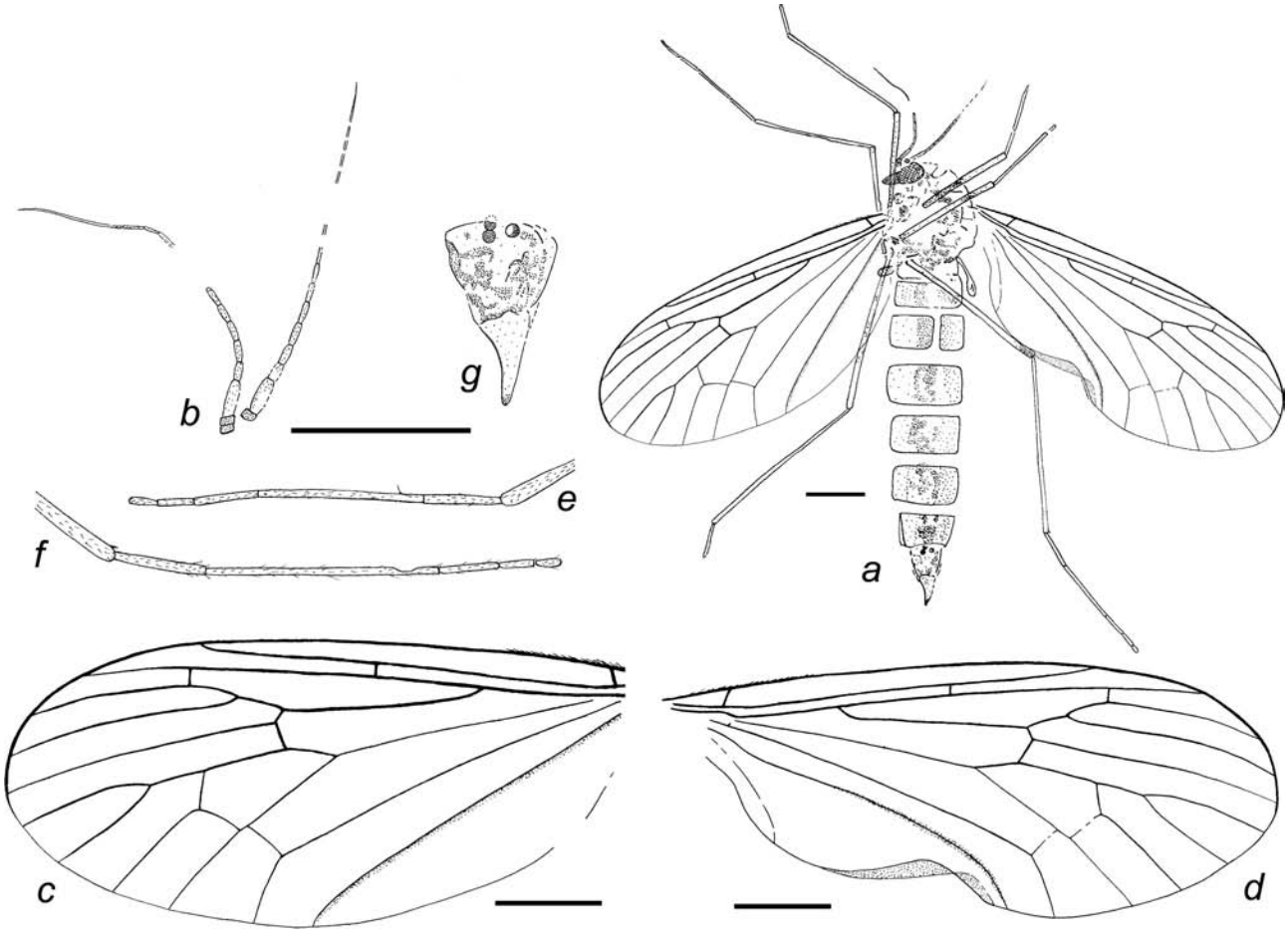
(1) Mouthparts — The relationship between labrum, hyphopharynx, and labella.
(2) Wing venation — The characters of proximal angle of d cell; flexing of bM_{1+2} and mM_{1+2} at r-m; length and aspect of 1A; and anal lobe.
(3) Legs — The length ratio of basitarsomere and second tarsomere; the structure character of joint between them; and the tibial spurs.
(4) Structure characters of male and female terminalia.

On the basis of these diagnostic characters, the genera *Archaeotrichocera* gen. nov., *Tanyochoreta* gen. nov., and *Sinotrichocera* gen. nov. may be well founded and easily distinguished from other known extant and extinct genera. However, some supplementary characters have been found to be treated for defining fossil genera:

(5) Size of d cell — All taxa described herein share markedly enlarged d cells. This state also occurs in other Mesozoic genera from Russia and Mongolia (viz. *Mailotrichocera* and *Paleotrichocera*). Thus, this feature of enlarged d cells is most likely symplesiomorphic in the evolutionary lineage of Trichoceridae.
(6) Other wing vein – Sc_1 (in relation to wing length).
(7) Size of fly (wing length).

Mesotrichocera laiyangensis from the uppermost Jurassic – lowest Cretaceous Laiyang Formation in Shandong, China, was previously recognized as a member of winter crane flies. The species has a peculiar wing venation, however: very narrow costal area; much weaker and thinner Sc; absence of

Fig. 7. Camera lucida drawings of *Tanyochoreta chifengica* sp. nov., specimen NIGP DHG200397: (*a*) trichocerid fly; (*b*) antennae; (*c*) left wing; (*d*) right wing; (*e*) tarsus of foreleg; (*f*) tarsus of hind leg; (*g*) female genitalia. All scale bars = 1 mm.



R_2; evidently elongated R_{2+3+4}, which is clearly longer than R_3 and R_4; and much shortened and widened d cell and flexuously curved M_{3+4} (Hong and Wang 1990, p. 122, fig. 6-5-87). These characters suggest that the species does not belong to Trichoceridae.

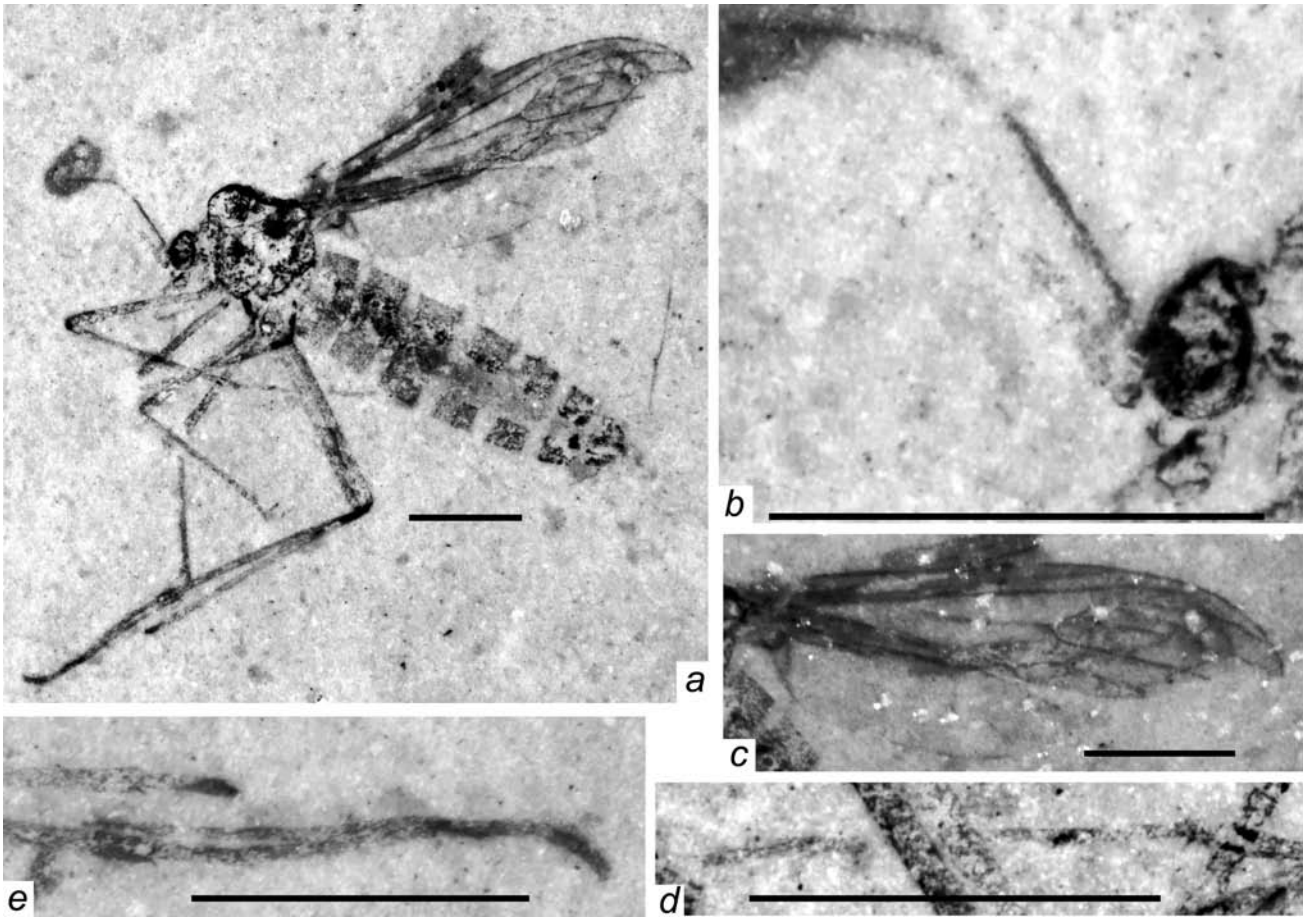
Daohugou biota

Lately (from 2000 to 2004), thousands of animal and plant specimens have been discovered from the Daohugou Formation in the vicinity of Daohugou, Ningcheng, Chifeng, Inner Mongolia, China. The Daohugou biota comprises seven new vertebrate species. Among them, unlike other freshwater sedimentary rocks, fish are entirely absent. In the invertebrate fauna, four known conchostracan species within a single known genus are identified. Numerous insects are recovered, namely mayflies (Ephemeroptera), dragonflies, damselflies (Odonata), cockroaches (Blattaria), grasshoppers (Orthoptera), earwigs (Dermaptera), stoneflies (Plecoptera), cicadas, hoppers, bugs (Hemiptera), thrips (Thysanoptera), beetles (Coleoptera), snakeflies (Raphidioptera), lacewings (Neuroptera), scorpionflies (Mecoptera), flies (Diptera), sawflies, and parasitic wasps (Hymenoptera); nevertheless, most have not yet been treated taxonomically, with the exception of long-horned flies (Nematocera) of Diptera, in which nine species referable to four genera within four families have been normally described, besides two species referable to two genera within one family of short-horned flies (Brachycera) recorded. Meanwhile, the following taxa have been recovered: a single adult dragonfly species referable to a single genus, which was mistakenly discovered in the Jehol biota (younger in age than that of Daohugou biota) (Fleck and Nel 2002); two new earwig species in two new genera; one new species of one new genus referable to one new hymenopteran family; and 14 neuropteran species referable to 11 genera of five families. A few spiders and some bivalves are also collected but not further authenticated. In the botanic assemblage, the representatives referable to six genera have been determined (see the following list).

A list of taxa described from the Daohugou biota is as follows:

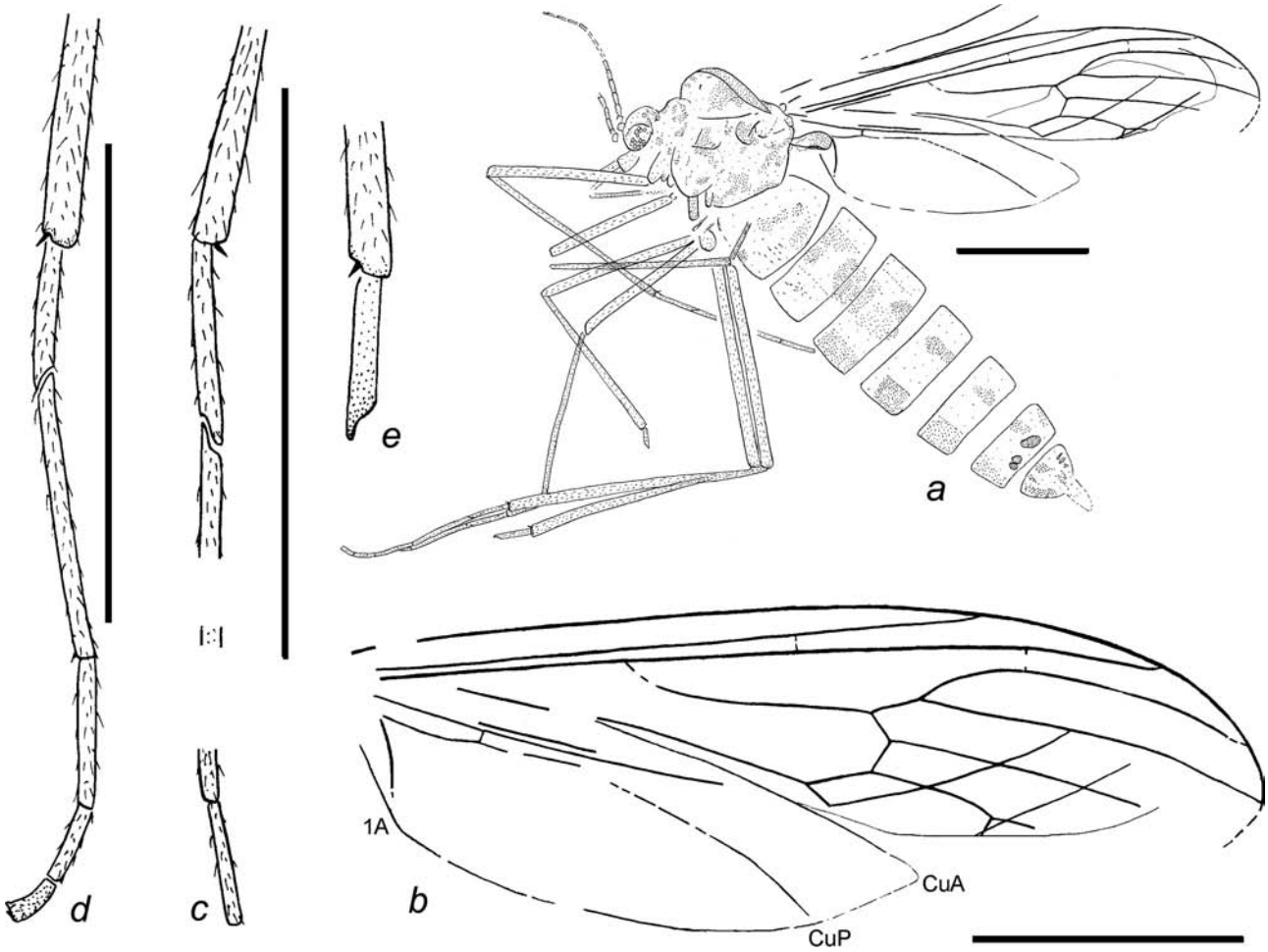
- Vertebrata
  - Class Amphibia
    - Order Orodela
      - Family Cryptobranchidae
        - *Chunerpeton tianyiensis* Gao et Shubin, 2003
      - Family incertae sedis
        - *Jelolotriton tianyiensis* Gao et Shubin, 2003
        - *Liaoxitriton daohugouensis* Wang, 2004
  - Class Reptilia
    - Order Pterosauria
      - Family Rhamphorhynchidae
        - *Pterorhychus wellnhoferi* Czerkas et Ji, 2002

Fig. 8. Photographs of *Sinotrichocera parva* gen. et sp. nov.: (*a*) holotype, NIGP DHG200399; (*b*) head; (*c*) wing; (*d*) incomplete tarsus of foreleg; (*e*) tarsi of mid-leg and hind leg. All scale bars = 1 mm.



Family Anurognathidae
Jeholopterus ningchengensis Wang, Zhou, Zhang et Xu, 2002
Order Saurischia
Family incertae sedis
Epidendrosaurus ningchengensis Zhang, Zhou, Xu et Wang, 2002
Pedopenna daohugouensis Xu et Zhang, 2005
Invertebrata
Class Branchiopoda
Order Conchostraca
Family Estheriellidae
Euestheria ziliujingensis Chen, 1976
Euestheria haifanggouensis Chen, 1976
Euestheria jingyuanensis Chen, 1976
Euestheria luanpingensis Shen et Niu, 1987
Class Insecta
Order Odonata
Family Campterophlebiidae
Bellabrunetia catherinae Fleck et Nel, 2002
Order Dermaptera
Family Sinopapaeodermatidae
Sinopapaeodermata neimonggolensis Zhang, 2002
Jurassimedeola orientalis Zhang, 2002
Order Neuroptera
Family Kalligrammatidae
Kallihemerobius pleioneurus Ren et Oswald, 2002
Sinokalligramma jurassicum Zhang, 2003
Family Polystoechotidae
Meilingius giganteus Ren, Engel et Lu, 2002
Jurapolystoechotes melanolomus Ren, Engel et Lu, 2002
Family Grammoplingiidae
Grammolingia boi Ren, 2002
Litholingia rhora Ren, 2002
Litholingia eumorpha Ren, 2002
Litholingia polychotoma Ren, 2002
Leptolingia jurassica Ren, 2002
Leptolingia tianyiensis Ren, 2002
Family Epiosmylidae
Epiosmylus panfilovi Ren et Yi, 2002
Family Osmylidae
Saucrosmylus sambneurus Ren et Yin, 2003
Rudiosmylus ningchengensis Ren et Yin, 2003
Laccosmylus calophlebius Ren et Yin, 2003
Order Diptera
Family Eoptychopteridae
Eoptychoptera ansorgei Ren et Krzemiński, 2002
Eoptychoptera jurassica Ren et Krzemiński, 2002
Eoptychopterina elenae Ren et Krzemiński, 2002
Eoptychopterina gigantea Zhang, 2004
Family Tanyderidae

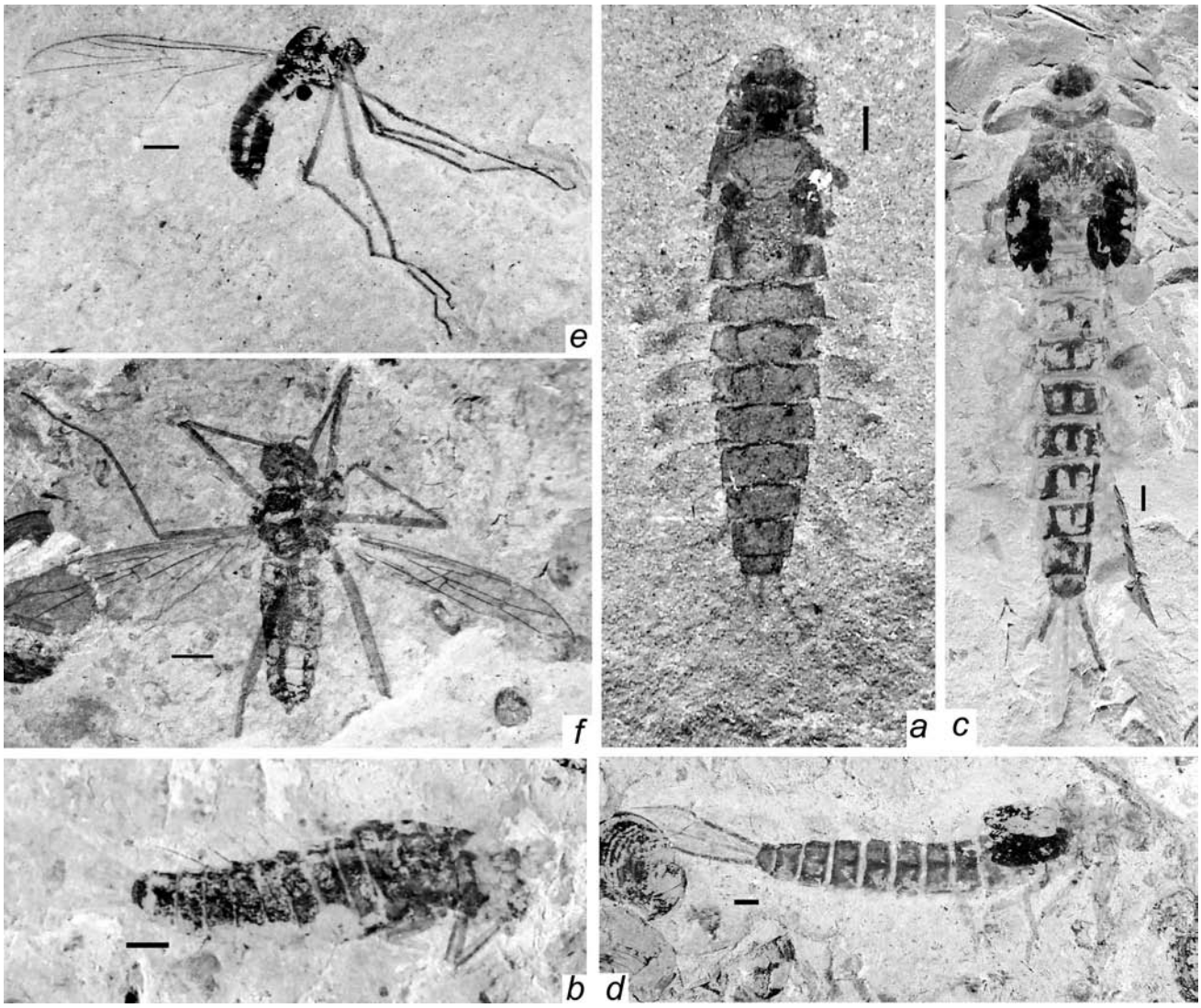
Fig. 9. Camera lucida line drawings of *Sinotrichocera parva* gen. et sp. nov., specimen NIGP DHG200399: (*a*) trichocerid fly; (*b*) wing; (*c*) incomplete tarsus of foreleg; (*d*) tarsus of hind leg; (*e*) joint between tibia and tarsus (second through fifth tarsomeres missing). All scale bars = 1 mm.



Praemacrochile chinensis Krzemiński et Ren, 2001
Praemacrochile vulcanium Zhang, 2004
Family Limoniidae
Architipula chinensis Zhang, 2004
Family Axymyiidae
Psocites pectinatus (Hong, 1983)
Psocites fossilis Zhang, 2004
Family Archisargidae
Mesosolva daohugouensis Zhang et Zhang, 2003
Archirhagio striatus Zhang et Zhang, 2003
Order Hymenoptera
Family Daohugoiidae
Daohugoia tobiasi Rasnitsyn et Zhang, 2004
Plantae
Class Filicopsida
Order Filicales
Family Osmundaceae
Cladophlebis (*Osmunda*?) sp.
Class Bennetitopsida
Order Bennettitales
Family incertae sedis
Anomozamites haifanggouensis (Kimura et al.) Zheng et Zhang, 2002
Anomozamites (*Trymia*?) sp.
Class Pinopsida
Order Pinales
Family Pinaceae
Cycadolepis sp.
Pityocladus sp.
Class Ginkgoopsida
Order Ginkoales
Family Ginkoaceae
Ginkgoites (cf. *Ginkgo coriacea* Florin)
Class Coniferopsida
Order Coniferales
Family incertae sedis
Elatocladus (*Yanliaoia*)? sp.

The larval mayflies and water boatmen (Corixidae, Heteroptera, Hemiptera) are the dominating groups in the Daohugou biota in terms of specimen abundance. Two undescribed new forms of mayflies that can be assigned to an extinct family Hexagenitidae and a new unknown family are present (Figs. 10*a*–10*d*), although these were mistakenly assigned to two known species from Russia, namely *Mesobaetis sibirica* Brauer, Redtenbacher et Ganglbauer, 1889 and *Mesoneta antiqua* Brauer, Redtenbacher et Ganglbauer, 1889 (Ren et al. 2002), respectively. Like other Mesozoic mayfly larvae,

Fig. 10. Photographs of (*a*, *b*) one new undescribed larval mayfly (Hexagenitidae); (*c*, *d*) one new undescribed larval mayfly (unnamed new family); (*e*) *Brianina longitibialis* Zhang and Lukashevich (2006), holotype, NIGP DHG200406; and (*f*) *Megathon brodskyi* Zhang and Lukashevich (2006), holotype, NIGP DHG200407. All scale bars = 1 mm.



both Daohugou forms may be lacustrine rather than rheophilous (J. Zhang and N.J. Kluge, in preparation)[1], although Ren et al. (1996) and Tan and Ren (2002) determined that they are lotic. Also, some rare extant groups of true flies, namely the net-winged midges (Blephariceridae) (Figs. 10*e*, 10*f*), coexisted with the winter crane flies (Trichoceridae). Biostratigraphic, taphonomic, and sedimentological data indicate that, during the Jurassic (Callovian–Oxfordian), the Daohugou biota lived in a small, shallow, low-energy freshwater lake, enveloped by luxurious everglades, streams, and forests with volcanoes nearby. The lake hosted a large number of larval mayflies, water boatmen, and conchostracans and some larvae of dragonflies, damselflies, and bivalves. Caudate amphibians, the largest aquatic animal, might be the dominator in the aquatic ecosystem. They could catch almost all the aquatic insects, and sometimes could catch terrestrial insects when on land. On the other hand, the aquatic insects are also mainly predaceous on minute or small insect larvae, but some smaller species might feed on algae and minute organisms. Various terrestrial groups of insects are mesic or sylvatic, such as the adult mayflies, dragonflies, damselflies, cockroaches, grasshoppers, earwigs, stoneflies, cicadas, hoppers, bugs, beetles, lacewings, scorpionflies, flies, sawflies, and parasitic wasps, where the climates were warm temperate. Their natural enemies might be the pterosaurs in the sky and the maniraptors on land that could climb trees. The net-winged midges, winter crane flies, and snakeflies were probably confined to temperate or correspondingly cool mountains. The former, like their living relative, presumably did not travel far from their breeding sites, i.e., rapidly flowing waters (Zhang and Lukashevich in press); the winter crane flies probably lived in caverns, hollow trees, and other dark places in forest or mountains; and snakeflies could have lived at high altitudes in the mountains. Of course, this

[1] Zhang, J. and Kluge, N.J. Jurassic larvae of mayflies (Insecta: Ephemeroptera from the Daohugou Formation in Inner Mongolia, China. In preparation.

deduction of paleoenvironment, paleoclimate, and palaeoecological characteristics reconstructed for Daohugou is only beginning to emerge, and further investigations are necessary, especially of the biostratigraphical data and insect classification.

Age of the Daohugou Formation

The geological age of the Daohugou Formation has been the focus of much debate. It has been dated variously as Early Cretaceous (Wang 2000; Wang et al. 2000, 2002), Late Jurassic – Early Cretaceous (Wang 2004), Late Jurassic (Ji and Yuan 2002; Zhang et al. 2002), late Aalenian – early Bajocian (Ren et al. 2002), Bajocian – middle Bathonian (Shen et al. 2003), Bathonian (Gao and Shubin 2003), and Middle Jurassic (Rasnitsyn and Zhang 2004*a*, 2004*b*; P. Chen et al. 2004). The entomofaunas of the Daohugou and Karabastau (Karatau, Kazakhstan) formations, however, are very similar in composition of taxa and age (Oxfordian or Kimmeridgian). It remains debatable whether the age extends to the Callovian (Zhang 2002*a*, 2002*b*, 2003, 2004*a*). Recently, radiometric dating gave an age of about 165–159 Ma for the ignimbrite overlying the Daohugou Formation (Gao and Shubin 2003; Chen and Zhang 2004; W. Chen et al. 2004; Liu et al. 2004; He et al. 2004). The age coincides approximately with Callovian–Oxfordian (164.7–155.7 Ma) (Gradstein et al. 2004). This suggests that the age of Daohugou Formation is Callovian or Oxfordian rather than late Aalenian – mid Bathonian (173.6–166.2 Ma) because the "golden spike" at the Aalenian–Bajocian boundary is dated at 171.6 Ma (Gradstein et al. 2004), which is much older than the Daohugou Formation. Previous interpretation of an Early Cretaceous age for the Daohugou Formation is probably incorrect because the isotope dating of Daohugou Formation is much older than 145.5 Ma, the boundary of the Jurassic and Cretaceous (Gradstein et al. 2004). The Daohugou, Haifanggou, and Karabastau formations are largely correlative because a terrestrial axymyiid fly, *Psocites pectinatus*, has recently been recovered from the first two formations (Zhang 2004*b*). Also, a single specimen of Axymyiidae has been recovered from the Karabastau Formation (Blagoderov et al. 2002). These axymyiid impressions are the exclusive records of this group worldwide. In addition, many other Daohugou species of insects described show a close relationship to those from the Karatau (Kazakhstan) and Shara-Teg (Mongolia) localities (both traditionally as Late Jurassic), according to the taxonomic comparison of different authors in various articles (Krzemiński and Ren 2001; Ren and Krzemiński 2002; Ren and Yi 2002; Zhang 2002*b*, 2004*a*, 2004*c*; Zhang and Zhang 2003; Rasnitsyn and Zhang 2004*b*). This conclusion can apply in many species of true flies: *Archirhagio stratus*, *Eoptychoptera ansorgei*, *Eoptychoptera jurassica*, *Eoptychopterina elenae*, *Eo. gigantea*, *Praemacrochile chinensis*, and *P. vulcanium*. In addition, *Epiosmylus panfilovi*, a lacewing-like insect, is closely related to *Ep. longicornis* Panfilov, 1980; both become the exclusive representatives within the extinct family Epiosmylidae in the world.

Acknowledgments

I would like to express my sincere gratitude to Dr. Elena D. Lukashevich (Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia), Dr. Vladimir A. Blagoderov (Department of Entomology, Iowa State University, Ames, Iowa, USA), and Drs. Wieslaw Krzemiński and Ewa Krzeminska (Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland) for critical remarks in a previous version of the manuscript. The research was supported by the Pilot Project of the Knowledge Innovation Program, Academia Sinica (grant KZCX2-SW-129), and the Major Basic Research Projects of the Ministry of Science and Technology, China (grant G2000077700).

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