

A new Middle Jurassic “grylloblattodean” family from China (Insecta: Juraperlidae fam. n.)

DI-YING HUANG¹ and ANDRÉ NEL²

¹Nanjing Institute of Geology and Palaeontology, State Key Laboratory of Palaeobiology and Stratigraphy, Chinese Academia of Sciences Nanjing, 210008, P.R. China; e-mail: huangdiying@sina.com

²CNRS UMR 5202, CP 50, Entomologie, Muséum National d'Histoire Naturelle, 45 Rue Buffon, F-75005 Paris, France; e-mail: anel@mnhn.fr

Key words. “Grylloblattodea”, Juraperlidae fam. n., Middle Jurassic, Daohugou, China

Abstract. The new family Juraperlidae is erected for the new genus and species *Juraperla daohugouensis* from the Chinese Middle Jurassic. Its wing venation has strong similarities with that of Mesozoic taxa currently included in the group “Grylloblattodea”, but its character “three (or four?)-segmented tarsi” questions its potential inclusion into the same order with the modern Grylloblattodea. This suggests that the systematic assignments of several fossil “grylloblattid” species, mainly based on wing venation, could be very different.

INTRODUCTION

“Grylloblattodea” is a small order of cryptic insects that is supposed to have been much more diverse during the Paleozoic and Early Mesozoic. About 50 extinct families have been described, mainly on the basis of wing structures, even if extant grylloblattids are apterous. The body structures of the great majority of these fossils are unknown. Storozhenko (2002) indicated that the group has no synapomorphy “because of paraphyletic state of the order in respect to other perlideans”. Fossil “Grylloblattids” are today as a kind of rag-bag for numerous fossil taxa with relatively similar wing venation. Thus the discovery of new potential representatives with preserved body structures is of great interest for a better understanding of the definition for the whole group.

The volcanic deposits near the Daohugou Village (Wuhua Township, Ningcheng County, Inner Mongolia, and North-east China) of the Middle Jurassic Jiulongshan Formation yielded a very rich fossil fauna since the end of the twentieth century, which represent a typical terrestrial ecosystem. Recent isotopic studies indicate that the geological age of superjacent volcanic rock of the Daohugou Bed is ca. 164–165 Ma (Chen et al., 2004; Liu et al., 2004). This fauna became famous because of the exquisite preservation of fossils and findings of soft tissues (Wang et al., 2002; Gao & Shubin, 2003; Wang, 2004; Ji et al., 2006). The invertebrates are mainly represented by several arthropod groups such as insects, conchostracans, anostracans and spiders (Huang et al., 2006). At least 20 different insect orders were recognized from this fauna. We report herein the discovery of a new insect with a grylloblattodean wing venation. This grylloblattodean fauna is very diverse and original as we already described a new family very similar to the Jurassic Blatto-gryllidae (Huang et al., in press). The new fossil has three (or four?) -segmented tarsi, which is very unusual for a

“Grylloblattodea”, as all the modern representatives and the few fossil taxa with preserved legs have five-segmented tarsi, and the Mantophasmatodea, potential modern sister group of recent Grylloblattodea (Cameron et al., 2006), also have five-segmented tarsi. Our fossil also has a supplementary longitudinal vein in the subcostal area, a rare character among the Neoptera, except for some orthopteroids.

MATERIAL AND METHODS

We follow the wing venation nomenclature of Storozhenko (1998), especially in the structure of the cubital veins, except for the still enigmatic nature of the strong arculus (crossvein) between median and cubital veins that Storozhenko (1998) considered as a convex posterior branch of median vein called “M5”. The drawing of the wing venation was made under a binocular Olympus SZX9 using a camera lucida.

SYSTEMATICS

Order Grylloblattodea Walker, 1914

Family Juraperlidae fam. n.

Type genus. *Juraperla* gen. n.

Diagnosis. Legs: three (or four?) segmented-tarsi. Fore wing: a long slightly curved vein between Sc and C (unique apomorphy in Grylloblattodea); M divided into simple MA and simple MP at arculus level; RS simple; CuA2 simple; CuA1 pectinate; a long and broad cell in anal area; A1 simple, A2 pectinate with three posterior branches.

Genus *Juraperla* gen. n.

Type species. *Juraperla daohugouensis* gen. n., sp. n.

Diagnosis. As for the family.

Etymology. Named after the Jurassic and *Perla*.

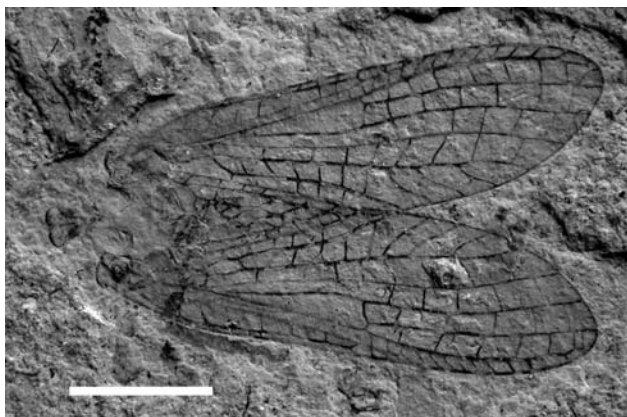


Fig. 1. *Juraperla daohugouensis* gen. et sp. n., holotype NIGP 142190, photograph (scale bar = 5 mm).

Juraperla daohugouensis sp. n.

(Figs 1–2)

Diagnosis. As for the family.

Description. Two fore wings and hind leg attached to thorax. Fore wing 16.3 mm long, 4.9 mm wide; costal area broad (0.8 mm), with long vein between Sc and anterior wing margin slightly curved at base, and distally straight, with eight cells and reaching anterior wing margin 7.8 mm distal of wing base, miming a subcosta anterior but flat, neither concave nor convex; distal crossveins between Sc and C simple; Sc ending in C; series of crossveins regularly disposed between Radius and Sc; RS emerging from R 8.2 mm from wing base, apical part of R and RS simple with one row of cells between them; basal stem of M separated from radial stem, but strongly approximate; M divided into MA and MP 3.3 mm from wing base, at arculus level, MA and MP simple; strong crossvein between MA and RP near the base of the latter; MP desclerotised; strong arculus between M and CuA (“M5” sensu Storozhenko, 1998); series of slightly sigmoidal crossveins between MP and CuA; CuA divided into CuA1 and CuA2 3.1 mm from wing base, just basal of arculus; CuA basally straight, CuA1 pectinated with four posterior branches; CuA2 simple, with six crossveins between it and CuA; CuP concave, simple; A1 simple; A2 with three branches; elongate hexagonal cell between A1 and A2; A3 simple and sigmoidal.

Hind leg with tibia armed with some short and broad spines and slightly contracted at apex; tip of first tarsal segment oblique, second segment very short triangle-shape, with apical margin strongly oblique, third segment longest with an apical row of setae; small joint with setae at base of claws (arolia or fourth segment?); pair of claws simple and sharp with broad base.

Material. Holotype NIGP 142190, print with two complete fore wings, one hind leg and fragments of thorax, deposited in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Etymology. Named for the type locality Daohugou.

Stratigraphic horizon. Middle Jurassic Jiulongshan Formation (ca. 165 Ma); Inner Mongolia, NE China.

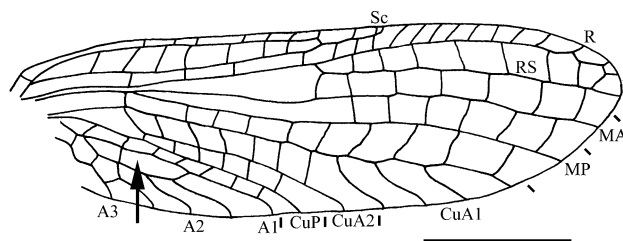


Fig. 2. *Juraperla daohugouensis* gen. et sp. n., holotype NIGP 142190, drawing of right fore wing, arrow indicates the large anal cell between A1 and A2 (scale bar = 4 mm).

Type locality. Near the Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, NE China.

Discussion. A median vein completely separated from the radial vein excludes an attribution to the Blattoneoptera, Hemineoptera, and Endoneoptera (= Holometabola) (sensu Kukalová-Peck & Lawrence, 2004). The remaining groups are the orthopteroid orders and the Pleconeoptera (Plecoptera, “Grylloblattodea” and related groups). An attribution to the archaeorthopteran orders is unlikely because this fossil lacks the characteristic pattern of the median and cubital veins in these groups (Béthoux & Nel, 2002), despite of the presence of a supplementary longitudinal vein in the area between Sc and the anterior wing margin, similar to the subcosta anterior of several Orthoptera. However, this vein is neither convex nor concave; this suggests that it is simply a secondary vein.

The current classification of the Grylloblattodea and Plecoptera, including the fossil groups “Protoperlaria” or “Protoperlina” is very confusing, viz. compare the phylogenetic hypotheses of Grimaldi & Engel (2005) to those of Storozhenko (2002) and Sinitshenkova (2002). Nevertheless, all the families currently included in the Plecoptera have a long median stem with a fork into MA and MP in distal half of wing, unlike *Juraperla* gen. nov. (Sinitshenkova, 1987, 2002). An attribution to the Plecoptera is also unlikely because in modern Plecoptera CuP separates from CuA well distal of a basal stem, and not at the very base of the wing, as in *Juraperla* (Béthoux, 2005).

Juraperla has several characters present in some Grylloblattodea, viz. a strong arculus between M and CuA, a simple concave CuP, CuA forked into a simple posterior branch CuA2 and a pectinate anterior branch CuA1, a pectinate series of posterior branches of CuA1, a strong first crossvein between MA and RS, and a simple RS.

An attribution to the Protoperlina is excluded because the most basal division of CuA is situated in the anterior half of the wing, and the branches of CuA1 are not forming a series of marginal veinlets along the posterior wing margin. Also, every family currently included in the “Protoperlina” has a simple costal area between C and Sc, except for some Permian Aliculidae Storozhenko, 1997 in which there is a rudimentary and strongly zigzagged vein between C and Sc, clearly less developed than in *Juraperla* (Aristov, 2004).

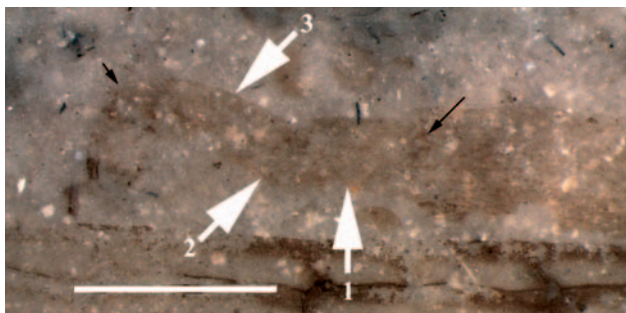


Fig. 3. *Juraperla daohugouensis* gen. et sp. n., holotype NIGP 142190, photograph of hind leg apex. Medium black arrow – apex of tibia with short and broad spines; short black arrow – small joint with setae at base of claws; white arrow 1 – first tarsal segment; white arrow 2 – second tarsal segment; white arrow 3 – third tarsal segment (scale bar = 1 mm).

Juraperla has the synapomorphy of the subgroup {Skaliciidae, Idelinellidae, Pinideliidae, Stegopteridae, Bajanzhargalanidae, Liomopteridae, Havlatiidae, Madygenophlebiidae, Gorochoviidae, Tomiidae, Tunguskapteridae, Euremiscidae, Sylvaphlebiidae} of the “Grylloblattina” sensu Storozhenko (2002: 282–283), viz. “fore wing CuA divided into CuA1 and CuA2”. Storozhenko (2002) considered this character as convergently developed in the Lemmatophoridae Sellards, 1909 (Lemmatophorina). An attribution to this family is excluded because *Juraperla* has retained a strong crossvein between MA and RP near the base of the latter (“M5”) (absent in Lemmatophoridae), and its MP is simple, instead of being two- or three-branched as in Lemmatophoridae.

Attribution to the Skaliciidae, Idelinellidae, or Pinideliidae is excluded because the CuA2 of *Juraperla* is simple. Affinities with Stegopteridae and Bajanzhargalanidae are excluded because the costal area of *Juraperla* is rather broad, RS is simple, and the fore wing is not tegminised. Madygenophlebiidae and Havlatiidae have the fore wing Sc S-shaped, unlike *Juraperla*. Gorochoviidae have the fore wing RS pectinate, unlike *Juraperla*. Sylvaphlebiidae have their fore wing CuA branches compressed, without pectinations. Tomiidae have a CuA1 simple, not pectinate, and an anal area without a large cell. Euremiscidae have a fore wing anal vein simple, and a very particular shape of MP and CuA1.

The fore wing of *Juraperla* looks very similar to those of the Permian Tunguskapteridae Storozhenko & Vršanský, 1995, in the simple RS, MA, MP, CuA2, and CuP, and the presence of a group of cells delimited by anal veins. The two genera *Tunguskaptera* Storozhenko & Vršanský, 1995 and *Ferganamadygenia* Storozhenko & Vršanský, 1995 have a vein A1 pectinate with four to ten posterior branches, and their group of cells delimited by main anal veins is in a very basal position and distinctly shorter than in *Juraperla*.

Lastly, *Juraperla* differs from all the known Grylloblattodea in the presence of a secondary longitudinal vein between Sc and the costal margin.

PHYLOGENETIC IMPLICATIONS

The modern Grylloblattodea have five-segmented tarsi, as in their putative sister group Mantophasmatodea (Cameron et al., 2006), which is a plesiomorphic condition (Grimaldi & Engel, 2005). The number of tarsomeres is unknown in the great majority of the fossil taxa currently attributed to the Grylloblattodea, and those with such structures preserved have five-segmented tarsi (Blattogrillidae and a new Chinese family, Huang & Nel, in prep.). The character “three (or four?)-segmented tarsi” of *Juraperla* is very specialized and surprising for a Grylloblattodea. It would suggest that at least some fossil taxa attributable to this group on the basis of their wing venation had some body structures very different from those of the modern clade Grylloblattodea + Mantophasmatodea. This would justify the possible separation of an undetermined subset of the fossil taxa currently attributed to the “Grylloblattodea” into a separate order, maybe for the subgroup {Skaliciidae, Idelinellidae, Pinideliidae, Stegopteridae, Bajanzhargalanidae, Liomopteridae, Havlatiidae, Madygenophlebiidae, Gorochoviidae, Tomiidae, Tunguskapteridae, Euremiscidae, and Sylvaphlebiidae} in which the Juraperlidae fall on the basis of one (but homoplastic) wing venation character. But such an important change in the grylloblattodean systematics has to wait for the discovery of the homologous body structures in these taxa. The real position of numerous fossil taxa based on wing structures only and currently included in the probably paraphyletic (or even polyphyletic) Grylloblattodea will remain uncertain until their body structures are known.

ACKNOWLEDGEMENTS. HDY is pleased to acknowledge this project supported by the National Foundation of Natural Sciences of China (grants no. 40672013 and no. 40632010), the Major Basic Research Projects of MST of China (2006CB806400), the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS, no. 053106), and the MNHN, Paris for a grant as invited Maître de Conférence. We sincerely thank two anonymous referees for their very useful comments and discussions.

REFERENCES

- ARISTOV D.S. 2004: The fauna of the grylloblattid insects (Grylloblattida) of the upper half of Upper Permian and lower half of Triassic. *Paleontol. J. (Suppl. 2)* **38**: S80–S145.
- BÉTHOUX O. 2005: Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia* **1**(9): 52–81.
- BÉTHOUX O. & NEL A. 2002: Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa* **96**: 1–88.
- CAMERON S.L., BARKER S.C. & WHITING M.F. 2006: Mitochondrial genomics and the new insect order Mantophasmatodea. *Mol. Phylog. Evol.* **38**: 274–279.
- CHEN WEN, JI QIANG, LIU DUN-YI, ZHANG YAN, SONG BIAO & LIU XIN-YU 2004: Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geol. Bull. China* **23**: 1165–1169 [in Chinese with English abstr.].
- GAO KE-QIN & SHUBIN N.H. 2003: Earliest known crown-group salamanders. *Nature* **422**: 424–428.

- GRIMALDI D.A. & ENGEL M.S. 2005: *Evolution of the Insects*. Cambridge University Press, Cambridge, xv + 755 pp.
- HUANG DI-YING, NEL A., SHEN YAN-BIN, SELDEN P.A. & LIN QI-BIN 2006: Discussions on the age of the Daohugou fauna – evidence from invertebrates. *Progr. Nat. Sci. (Suppl.)* **16**: 308–312.
- Ji QIANG, LUO ZHE-XI, YUAN CHONG-XI & TABRUM A.R. 2006: A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science* **311**: 1123–1127.
- KUKALOVÁ-PECK J. & LAWRENCE J.F. 2004: Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *Eur. J. Entomol.* **101**: 95–144.
- LIU YONG-QING, LIU YAN-XUE, LI PEI-XIAN, ZHANG HONG, ZHANG LI-JUN, LI YIN & XIA HAO-DONG 2004: Daohugou biota-bearing lithostratigraphic succession on the southeastern margin of the Ningcheng basin, Inner Mongolia, and its geochronology. *Geol. Bull. China* **23**: 1180–1185 [in Chinese with English abstr.].
- SINITSHENKOVA N.D. 1987: [Historical development of the stoneflies (Plecoptera = Perlida).] *Trudy Paleontol. Inst. Akad. Nauk SSSR* **221**: 1–142 [in Russian].
- SINITSHENKOVA N.D. 2002: Chapter 2.2.2.2.2. Order Perlida Latreille, 1810. The stoneflies (Plecoptera Burmeister, 1839). In Rasnitsyn A.P. & Quicke D.L.J. (eds): *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston, London, pp. 281–287.
- STOROZHENKO S.Y. 1998: [Systematics, Phylogeny and Evolution of the Grylloblattids (Insecta: Grylloblattida).] Dal'nauka, Vladivostok, 207 pp. [in Russian].
- STOROZHENKO S.Y. 2002: Chapter 2.2.2.2.1. Order Grylloblattida Walker, 1914 (= Notoptera Crampton, 1915, = Grylloblattodea Brues et Melander, 1932, + Protorthoptera Handlirsch, 1906, = Paraplecoptera Martynov, 1925, + Protoperlaria Tillyard, 1928). In Rasnitsyn A.P. & Quicke D.L.J. (eds): *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston, London, pp. 278–284.
- WANG XIAO-LIN, ZHOU ZHONG-HE, ZHANG FU-CHENG & XU XING 2002: A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and “hairs” from Inner Mongolia, northeast China. *Chin. Sci. Bull.* **47**: 226–230.
- WANG YUAN 2004: A new Mesozoic caudate (Liaoxitriton daohugouensis sp. nov.) from Inner Mongolia, China. *Chin. Sci. Bull.* **48**: 858–859.

Received April 26, 2007; revised and accepted July 4, 2007