

Discussions on the age of the Daohugou fauna—evidence from invertebrates*

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Abstract Volcanic tuff deposits near Daohugou village, Ningcheng County of Inner Mongolia have yielded many well-preserved fossils. Here we briefly introduce our recent findings of invertebrates from the Daohugou fauna: mainly insects, conchostracans, anostracans, and spiders. The age of the Daohugou fauna is considered to be Middle Jurassic on the basis of an analysis of various invertebrates especially insects and conchostracans, showing strong similarities to the Yanliao fauna of north China and the Karatau fauna of Kazakhstan.

Keywords: Daohugou fauna, Middle Jurassic, Inner Mongolia, insects, conchostracans, spiders.

Our knowledge of animal evolution comes particularly from exceptional fossil preservation. Some Jurassic exceptional terrestrial and marine faunas are quite well known from Europe such as the Early Jurassic Osteno Lagerstätte of Italy, the Early Jurassic Posidonia Shales of Luxembourg, England and Germany, the Middle Jurassic La Voulte-sur-Rhône of France, the Middle—Late Jurassic Oxford Clay of the UK, and the well-known Late Jurassic Solnhofen Plattenkalk from Germany^[1 2]. However, purely freshwater and terrestrial ecosystems are much less known than marine ones. Volcanic deposits near Daohugou village (Wuhua Town¹), Ningcheng County, Inner Mongolia, northeast China) have, since the end of the 20th century, yielded very rich collections of fossils that represent a typical non-marine ecosystem.

Daohugou village is close to the boundaries of Inner Mongolia, Hebei, and Liaoning provinces. The official name of the village (Daohugou) was changed recently due to its fusion with Dongsanjia village. However, we normally still use the former name here. Daohugou village consists of three parts named Xiayingzi (first team), Donggou (second team), and Beigou (third team), which are separated from each

other by several hundreds metres. The fossil bed that concerns us in the present discussion is represented by a greyish to brownish volcanic tuff. It is found at Xiayingzi, Beigou, east of Donggou, and particularly from east of Beigou. Wang et al.^[3] reported more outcrops of the Daohugou Bed in adjacent areas. The Daohugou Bed is surrounded by outcrops of the Early Cretaceous Yixian Formation, which have yielded the famous Jehol fauna.

The Daohugou fauna has come to the forefront more and more due to its yielding many soft-bodied invertebrates and vertebrates. The vertebrates of the Daohugou fauna include pterosaurs, dinosaurs, and salamanders. Proto-feathered pterosaurs are represented by two forms of Rhamphorhynchoidea: *Jeholopterus ningchengensis* Wang et al., 2002, of the Anurognathidae^[4] and *Pterorhynchus wellnhofers* Czerkas et Ji, 2002^[5]. The salamanders, with three described species (*Jeholotriton paradoxus* Wang, 2000^[6], *Chunerpeton tianyiensis* Gao et Shubin, 2003^[7] and *Liaoxitriton zhongjiani* Wang, 2004^[8]), are very common in the Daohugou fauna; they always bear soft tissues. The dinosaurs *Epidendrosaurus ningchengensis* Zhang et al., 2002 and *Pedopenna daohugouensis* Xu et Zhang, 2005 (Mani-

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1) The former Shantou Town in reference has been incorporated by Wuhua Town recently

raptora) have been described from the Daohugou fauna^[9, 10]. Particularly a swimming mammaliaform has recently been discovered^[11]. Moreover, a fossil tadpole has also been described from Daohugou^[12].

However, a uniform opinion on the geological age of Daohugou fauna has never hitherto been consolidated. The Daohugou Bed was considered to correspond to an Early Cretaceous fauna in the first published papers^[6, 13]. Ji and Yuan named this assemblage the "Daohugou biota" and argued for an age of Late Jurassic base on an analysis of vertebrate fossils^[14]. Zhang^[15] accepted this opinion and suggested that the Daohugou insect fauna resembles that of the Karatau fauna of Kazakhstan. However, most palaeontologists and geologists insisted that the Daohugou fauna corresponds to the Middle Jurassic Jiulongshan Formation^[7, 11, 16–20] or Middle Jurassic to early Late Jurassic^[21]. Zhang and Wang considered the Daohugou Bed to belong to the Middle Jurassic Haifanggou Formation^[22].

In recent years we have found various invertebrate fossils of insects, conchostracans, anostracans, spiders, harvestman, flatworms, and bivalves from the Daohugou beds. The present paper discusses the geological age of this fauna on the basis of its comparison with potentially related faunas.

1 Insects

The most representative animals from this Middle Jurassic terrestrial ecosystem are the conchostracans and the very diverse insect fauna. Hitherto, at least 18 insect orders have been distinguished from our collections housed in Nanjing Institute of Geology and Palaeontology (ca. 30000 specimens). These are: Ephemeroptera, Odonata, Blattaria, Orthoptera, Dermaptera, Grylloblattodea, Plecoptera, Psocoptera, Hemiptera (incl. Heteroptera), Megaloptera, Raphidioptera, Neuroptera, Mecoptera, Coleoptera, Trichoptera, Diptera, Hymenoptera, and Lepidoptera. In quantity and diversity, this entomofauna is dominated by three orders, the Neuroptera, Orthoptera and Diptera. Aquatic insects are represented by many *Mesoneta* (Ephemeroptera) and *Yanliaocorixa* (Heteroptera), etc. Representative insect species of the Jehol biota such as *Ephemeropsis trisetalis* and *Coptoclava longipoda*, have never been recorded in the Daohugou Bed.

The Daohugou insect fauna shows remarkably

strong similarities to the Yanliao entomofauna^[23], especially to that in the Haifanggou Formation on the basis of several shared species such as *Mesobaetis sibirica*, *Rhipidoblattina* (*Canaliblatia*) *hebeiensis*, *Sinotaeniopteryx chengdeensis*, *Yanliaocorixa chinensis* (Fig. 1(b)), etc.^[15, 24].

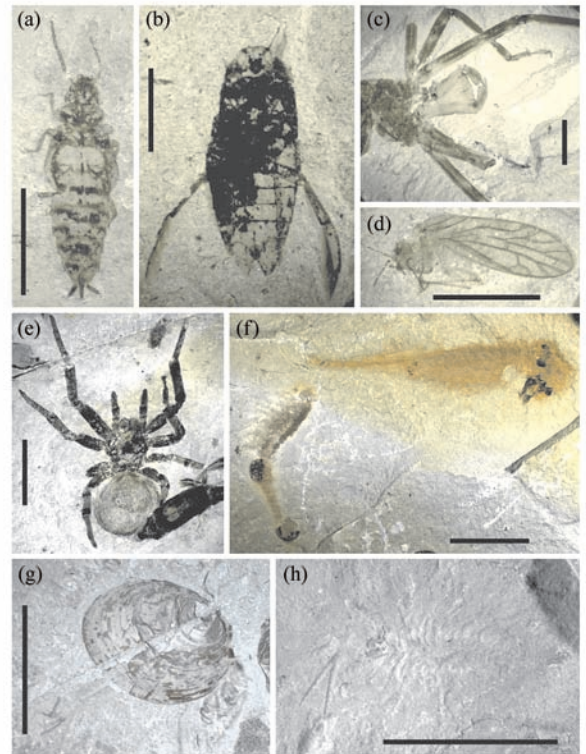


Fig. 1 The general representatives of the Middle Jurassic Daohugou fauna. (a) *Leicarabus parvus* Hong, 1983 (= *Jurassimedella orientalis* Zhang, 2002), (NIGPAS 140528); (b) *Yanliaocorixa chinensis*, (NIGPAS 140529); (c) a isophlebioid larva, (NIGPAS 140530); (d) *Archipsylla* sp., (NIGPAS 140531); (e) *Uloboridae* sp. (NIGPAS 140532); (f) male and female anostracans (NIGPAS 140533); (g) a male *Euestheria luanpingensis* with soft parts, (NIGPAS 140534); (h) a shell-less *E. luanpingensis* (NIGPAS 140535). Scale bars: 5 mm.

1.1 Dragonflies

The Daohugou Odonata are mainly different small and large isophlebioid species (Fig. 1(c)), suggesting a more ancient group than the younger Jehol fauna represented by the anisopteran *Sinaeschnidia heishankowense*. A few specimens of *Aktassia* (Anisoptera: Petalurida) are also recorded, which are nearly identical to the type species from Karatau^[25]. In addition, our new material comprises specimens showing for the first time the non-venational structures of the Aktassidae.

1.2 Earwigs

The Mesozoic record of the Dermaptera is very

scarce. Thus, the presence of various earwigs in the Daohugou beds is of great importance for the history of this order and reconstruction of this ecosystem. They can be assigned to the suborder Aechi-dermaptera^[26]. Our collection (HDY) contains more than 1000 specimens dominated by *Leicarabus parvus* Hong, 1983 (= *Jurassimeleola orientalis* Zhang, 2002) (Fig. 1(a)). *L. parvus* was first described as a beetle from the Middle Jurassic Haifanggou Formation of the Liaoning Province, on the basis of a single specimen with head, pronotum, and fore-wings^[23]. The Jurassic earwigs are well known from the Karatau biota, Kazakhstan^[27], with a tarsal formula 4-4-5, contra 3-3-3 in recent forms. Most earwigs from Daohugou have a tarsal formula 5-5-5^[26], a more primitive state than in the taxa from Karatau. Furthermore, we also found a few Daohugou earwigs from Daohugou with a 4-4-5 tarsal formula that might therefore be related to the earwigs from Karatau.

1.3 Other forms

In Daohugou, we have found more than 100 specimens of Psocoptera. There is a large form that can be well compared with *Archipsylla* from Karatau^[28]. This form displays rather primitive features in its wing venation and tarsal formula (Fig. 1(d)). Zhang reported the occurrence in Daohugou of the genus *Globoides* (Coleoptera: Staphylinidae, first described from Karatau)^[15]. More forms of this group are present in our material.

In addition, Wang and Zhang suggested a possible Early - Middle Jurassic age for Daohugou fauna after the study of the Palaeontinidae (Hemiptera)^[1].

2 Conchostracans

Conchostracans are the most common fossils in the Daohugou fauna. They always occur densely on single bedding planes. Conchostracans from the Daohugou fauna are represented by *Euestheria*, with four species (*E. luanpingensis*, *E. haifanggouensis*, *E. ziliujingensis* and *E. jingyuanensis*). Some specimens of *E. luanpingensis* and *E. haifanggouensis* display very well preserved soft parts (Fig. 1(g)). The conchostracan fauna (*Euestheria ziliujin-*

gensis fauna) indicates that the age of the Daohugou fauna might be Bajocian-middle Bathonian^[17]. The taphonomy of some shell-less *E. luanpingensis* is of special interest (Fig. 1(h)) because similar preservation can be found in both Daohugou and Zhouyingzi (Luanping County, Hebei Province) of the Jiulongshan Formation^[29]. It is distinctly different from the Upper Jurassic *Nestoria* fauna of the Dabeigou Formation and the famous *Eosestheria* fauna from the Lower Cretaceous Yixian Formation. For Branchiopoda, another exciting finding is thousands of anostracans (males and females; see Fig. 1(f)), which represent the earliest fossil record of this group. The formerly unique Mesozoic anostracan was reported from the Early Cretaceous of Transbaikalia, Russia^[30]. However, these rare arthropods have no special stratigraphic significance.

3 Spiders

Hitherto, only two specimens of spiders have been described from Jurassic strata^[31, 32], thus the recovery of some 200 new specimens from the Daohugou fauna marks a dramatic increase in information on fossil spiders of this period^[2]. The new specimens mainly belong to the superfamilies Deinopoidea (probably Uloboridae; see Fig. 1(e)), Araneoidea, and also Palpimanoidea, including true archaoids. All are represented by adult males, females, and juveniles in excellent preservation. *Jurarchaea zherikhini* was described from the Karabastau Formation of Karatau, Kazakhstan^[32]. It was placed in the extant family Archaoidae. A few specimens of this small group are present in our collection, suggesting it was more common in the Jurassic than today, when it is restricted to some parts of the former Gondwanaland.

Comparison of the Daohugou araneofauna with that of the Karabastau Formation of Karatau, the Ichetyu Formation of Transbaikalia, and younger formations such as Yixian and Montsec, Spain may be considered premature because there are so few specimens described. However, some palaeoecological similarities are already apparent. These faunas are dominated by orb-web weavers, both cribellate (Uloboridae) and ecribellate (Araneoidea). Orb-weavers abound along lake margins, where they feed on the plentiful insects that inhabit these conditions, and

1) Wang B. and Zhang H. C. Palaeontinidae (Insecta, Homoptera) from Daohugou, China and its stratigraphic implications. International Symposium on the Jurassic Boundary Events, 2005, 89—90.

2) The spiders of Daohugou were briefly reported by Selden and Ren in 2002. See: Selden P. and Ren D. Ancient weavers on the silk road: Jurassic spiders from China. The 46th Palaeontological Association Annual Meeting, 2002, 35.

such was the clearly case in the Mesozoic as today. Palaeontological evidence is amassing that the araneofauna throughout the Mesozoic might have differed little from that which we still see today.

4 Bivalves

We collected a few tens of specimens of the small bivalves *Ferganoconcha sibilica* identified by Jiang^[1]. *F. sibilica* is a typical Early—Middle Jurassic taxon distributed in north Asia. Thus, Jiang suggested the Daohugou deposits might correspond to the Haifanghou or Jiulongshan formations, indicative of an Early—Middle Jurassic age.

5 Discussion and conclusions

Recent isotopic studies indicate that the age of superjacent volcanic rock of the Daohugou Bed is ca. 164—165 Ma, which may correspond to the Tiaojishan Formations (Middle Jurassic of Hebei Province)^[34]. The intermediate—basic rocks are characterized by the age of 152 Ma^[20] and 164—165 Ma^[20,33] by SHRIMP zircon U-P dating. These rocks have been dated as 159 Ma^[34] and 164 Ma^[33] by ⁴⁰Ar/³⁹Ar dating. Thus, most of the above authors considered that the age of the fossil-bearing beds of Daohugou is Middle Jurassic^[20,33]. However, Wang et al. suggested that the strata are reversed in the Daohugou area. Thus, the fossil-bearing beds should be younger than the Tiaojishan Formation^[3]. We consider that the reversed strata are only a local phenomenon and not of wide extent.

The insects and conchostracans of the Daohugou Bed show strong affinities with the Middle Jurassic Yanliao fauna (mainly represented by the Jiulongshan Formation of north Hebei and the Haifanggou Formation of west Liaoning)^[16,17,23]. Therefore, the Daohugou fauna may be regarded as corresponding to the Yanliao biota. Nevertheless, the Yanliao biota is a name used in broad sense for a Middle Jurassic fauna of North China. Thus, we still use the name Daohugou fauna for our specific Middle Jurassic biota.

The insect fossils from Daohugou display distinct differences to the Early Cretaceous Jehol entomofauna, with more ancient groups and the presence of pleiomorphic characters in some taxa. Representatives of the Jehol entomofauna have not yet been discovered in Daohugou, although some authors have mentioned

similarities between these entomofaunas by informal report^[3]. However, no evidence for these opinions is present in our material.

Some insects of Daohugou are very similar, if not identical, to those from Karatau at least at generic level, viz. *Aktassia* (Ononata), *Archipsylla* (Psocoptera), *Globoides* (Coleoptera), and *Epiosmylus* (Neuroptera) described by Ren and Yir^[35]. The rare spiders from Karatau and the present data indicate also a comparable evolutionary level for the two faunas. Previously, most authors considered the Karabastau Formation of Karatau, Kazakhstan to be Late Jurassic. However, a Middle Jurassic age for Karatau has been suggested in recent years^[36]. Nevertheless, we are inclined to consider that the Daohugou fauna is slightly older than the Karatau fauna, as evidenced by the evolutionary series of tarsal segmentations of the Dermaptera.

To summarize, the Middle Jurassic Daohugou fauna may be compared with the Yanliao fauna of North China and the Karatau fauna of Kazakhstan. The suggested palaeoenvironment is that of a seasonal shallow lake on the basis of the very rich fossil records of conchostracans and anostracans, and the absence of fishes.

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