

Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia

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Abstract Recent fieldwork has extended the distribution of the Daohugou Bed deposits from the Daohugou Village to its several neighboring areas. The fossil-bearing Daohugou deposits unconformably overlie complex bedrocks, and comprise three major parts. The red shales in the lower part were misidentified as belonging to the Tuchengzi Formation. Field excavation has indicated that the shales of upper part of the bed are the major fossil-bearing horizon. Due to strong tectonic activities, sediments were often folded with the sequences inverted in the region. Some newly recognized contacts between the Daohugou Bed and the volcanic rocks showed that the ignimbrite of the Tiaojishan Formation (159–164 Ma) underlies the Daohugou deposits, rather than overlying the latter as previously proposed. Thus, the age of the Daohugou deposits should be younger than the age of the ignimbrite, and thus it was incorrect to correlate the Daohugou Bed with the Middle Jurassic Jiulongshan Formation. Although biostratigraphic studies based on conchostracans and insects support a Middle Jurassic-early Late Jurassic age for the Daohugou deposits, vertebrate fossils such as *Liaoxitriton*, *Jeholopterus* and feathered maniraptorans show much resemblance to those of the Yixian Formation. In other words, despite the absence of *Lycoptera*, a typical fish of the Jehol Biota, the Daohugou vertebrate assemblage is closer to that of the Early Cretaceous Jehol Biota than to any other biota. We propose that the Daohugou fossil assemblage probably represents the earliest evolutionary stage of the Jehol Biota based on both vertebrate biostratigraphy and the sedimentological and volcanic features which suggest the Daohugou deposit belongs to the same cycle of volcanism and sedimentation as the Yixian Formation of the Jehol Group.

Keywords: Inner Mongolia, Daohugou Bed, Yixian Formation, stratigraphic sequence, Early Cretaceous, Jehol Biota

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With the discovery of the salamander *Jeholotriton*^[1] in 2000, the Daohugou Bed^[2] has drawn much attention from

Chinese paleontologists. Many additional well-preserved vertebrates^[3–8], insects^[9–14], conchostracans^[15] and plants have since been recovered from this deposit. Yet the debate on its age remains unsolved^[2,16–23].

The Daohugou Bed comprises fresh water shales interbedded with tuffs. It was first reported from a small area near the Daohugou Village in Ningcheng, southeast Inner Mongolia, neighboring Lingyuan, western Liaoning. Deposits of the typical Yixian Formation are also widely distributed in this area. The Daohugou Bed had long been regarded as part of the Yixian Formation due to similar lithological features. In the past, the same deposit had been called the “Jingangshan Formation”, and the “overlying” ignimbrite named the “Tuhulu Formation” (both of them are now referred to the Yixian Formation), and both referred to the Late Jurassic^[1]. The Daohugou Bed was also compared to the “Second Member of the Huajiyi Formation”, with the “overlying” ignimbrite as the “Third Member of the Huajiyi Formation”, and both referred to the Early Cretaceous^[2]. Recently, several different opinions have been proposed regarding the Daohugou deposits, including the Middle Jurassic “Jiulongshan Formation” with the “overlying” ignimbrite as “Tiaojishan Formation”^[16], the Upper Jurassic Zhangjiakou Formation^[3], and the Early Cretaceous lower Yixian Formation^[2,19].

Our excavations made by the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences in the summer of 2003 had resulted in the discoveries of dozens of salamanders and hundreds of insects and plants as well as a few reptiles from two localities in the Daohugou Village (41°19′ 13.0″ N, 119°13′ 55.1″ E and 41°18′ 32.2″ N, 119°13′ 05.1″ E, respectively).

Further field investigation also indicates that the Daohugou deposits are also distributed in some other areas such as Zhujiagou of Shantou, Jiangzhangzi of Wuhua, Ningcheng and Wubaiding of Reshuitang, Lingyuan. Based on recent fossil discoveries and the stratigraphic correlation of the deposits as well as their relationship with ignimbrite, here we provide a new and modified summary of our understanding of the stratigraphic sequence of the Daohugou Bed^[2] and its age assignment.

1 Stratigraphic sequence of the Daohugou Bed

The fossil-bearing Daohugou deposits are well exposed near the Daohugou Village, Shantou, Ningcheng, Inner Mongolia. They are distributed along a northeast by east direction, and extend eastward to west Pijiagou in Lingyuan, Liaoning. Two sections are recognized. One starts from a bentonite quarry at Pijiagou (41°19′ 04.5″ N, 119°14′ 25.2″ E), with the deposits unconformably overlying the Archean gneiss, and extends to north Xiao-

1. Liaoning Geological Survey, Regional Geological Report of Lingyuan (1:200000), 1965; Regional Geological Report of Jianping (1:200000), 1968.

2) Shijiazhuang Institute of Economy, Regional Geological Report of Songzhangzi (1:50000), 1998.

3) Liaoning Geological Institution, Regional Geological Report of Lingyuan (1:250000), revised version, 2003.

baishan and contacts the ignimbrite (41°19' 23.4 N, 119°14' 08.3 E). The second section starts at southeast of the excavation site (41°18' 26.6 N, 119°13' 18.6 E), with the deposits unconformably overlying the Meso- and Neo-Proterozoic Dahongyu Formation. It is notable that the sequence of the middle and upper parts of the deposits are often inverted, resulting in the repeating occurrence of deposits in the first section. It is also important to point out that the bottom part of the Daohugou Bed at the Daohugou Village comprises reddish shale, mudstones and lentoid conglomerates. These reddish deposits had been misidentified as belonging to the Tuchengzi Formation^[2] while some other workers had either ignored the presence of such reddish deposits in the Daohugou Bed^[16,17], or regarded them as belonging to the “Jiulongshan” Formation^[23]. The reddish deposits being recognized as the bottom part of the Daohugou Bed have now been confirmed in several other neighboring localities, such as Zhujiagou and Jiangzhangzi, where the shales that conformably overlie the reddish deposits contain the same fossil assemblages (i.e. conchostracans, insects and salamanders) as those of the Daohugou Village.

At the Wubaiding locality in Reshuitang, Lingyuan, the Daohugou Bed comprises a similar stratigraphic sequence as that of the Daohugou Village, yielding fossils such as salamanders^[6,7], insects and conchostracans that are generally comparable to those of the Daohugou Village.

Through comparing the Daohugou Bed exposed in several different localities, we are now able to provide a better description of its stratigraphic sequence and its relationship relative to volcanic rocks. Although the bottom of the Daohugou Bed has been well revealed, little is known about its contact with its overlying deposits. Due to strong tectonic activities and the subsequent folding of sediments, the exact thickness of the bed is difficult to determine, however, we estimate it to be between 100m and 150m. From the bottom up, it comprises three parts: 1) the lower part comprises gray, grayish tuffs with reddish interbedded shales or mudstones (Fig. 1(a) (c)), with an estimated thickness of 5–20 m. Conchostracans are found in the shales; 2) the middle part comprises thick grayish tuffs (often weathered into bentonite) with interbedded thin gray or greenish tuffaceous shales, with an estimated thickness of 60–80 m. The tuffs also contain lentoid conglomerates, which had their origin from the underlying ignimbrite of the Tiaojishan Formation. The fossil assemblage includes the salamander *Chunerpeton tianyiensis*, insects, conchostracans and plants; and 3) the upper part comprises interbanded gray or grayish tuffs and shales, with an estimated thickness of 40–60m. This part contains relatively more shales and less tuffs compared to the middle part (Fig. 1(f)). The shales yield a diverse and rich vertebrate assemblage, including the salamanders *Chunerpeton tianyiensis*, *Jeholotriton paradoxus*, and

Liaoxitriton daohugouensis, pterosaurs *Jeholopterus ningchengensis* and *Pterorhynchus wellnhoferi*, dinosaurs *Epidendrosaurus ningchengensis* and *Pedopenna daohugouensis* as well as some undescribed reptiles. In addition, insects, conchostracans and plants are also abundant.

2 Relationship between the Daohugou Bed and the underlying stratum

The fossil-bearing Daohugou deposits sit on complex bedrocks, which include the Archean gneiss, Meso- and Neo-Proterozoic marine deposits and ignimbrite of the Middle-Late Jurassic Tiaojishan Formation. Little controversy exists about the contact between the Daohugou deposits and the Precambrian rocks. For instance, the lower part of the Daohugou Bed contains conglomerates that had their exclusive origin from the gneiss near the eastern end of the Daohugou Village. The controversy about the Daohugou Bed is mainly about its relationship to the Tuchengzi and Tiaojishan formations.

First, it had been proposed that the Daohugou Bed has been found overlying the Tuchengzi Formation^[2], which was criticized by some other workers^[16,17]. Recent field investigations have confirmed that the reddish shales, which yield the same conchostracan fossil assemblage as that of other Daohugou deposits, should be regarded as the lower part of the Daohugou Bed, rather than the Tuchengzi Formation. At the localities in Zhujiagou and Tongjianggou the Yixian Formation is found unconformably overlying the Tuchengzi Formation, however, up to now, no direct contact between the Daohugou Bed and the Tuchengzi Formation has ever been recognized in the field.

Second, the widely-distributed ignimbrite in Daohugou area has been dated as 159–165 Ma^[21–23]. It has been controversial as to whether it underlies or overlies the Daohugou Bed. The ignimbrite was previously mistaken as belonging to the Early Cretaceous Tuhulu Formation or Huajiyang Formation (Third Member), however, it is now generally accepted that it is probably equivalent to the “Lanqi Formation” as described in the Liaoning Geological Map (1:200000). Wang et al.^[2] had also compared the ignimbrite to the volcanic rocks overlying the Yixian Formation, which now proves to be wrong. Although most workers have now referred the ignimbrite to the Tiaojishan Formation, they regarded it as overlying the Daohugou Bed^[16,22,23], and consequently further referred the Daohugou Bed to the Middle Jurassic “Jiulongshan Formation”. Our field investigations, however, have confirmed that the ignimbrite referable to the Tiaojishan Formation actually underlies the Daohugou Bed, contrary to previous opinions.

Direct contact between the Daohugou Bed and the Tiaojishan ignimbrite was first recognized at a site called Xigou in Daohugou Village (Fig. 2(a), (b)). The Daohugou Bed was found unconformably overlying a weathered



Fig. 1. Lithostratigraphic features of the fossil-bearing Daohugou Bed. (a) (c) Lower part of the Daohugou Bed: (a) Reddish deposits in Daohugou Village ($41^{\circ}18' 41.3$ N; $119^{\circ}13' 11.3$ E); (b) outcrops at another site of Daohugou Village ($41^{\circ}19' 07.0$ N; $119^{\circ}13' 43.6$ E), showing strong folding; (c) Zhujiagou locality ($41^{\circ}22' 52.8$ N; $119^{\circ}08' 58.2$ E), showing folding of deposits. (d) (e) Middle part of the Daohugou Bed: (d) Outcrop in Daohugou Village ($41^{\circ}18' 26.5$ N; $119^{\circ}13' 14.3$ E), showing lentoid conglomerate originally from the underlying Tiaojishan Formation; (e) Conglomerates at another site of Daohugou Village ($41^{\circ}19' 01.1$ N; $119^{\circ}13' 26.8$ E), showing its exclusive origin from the ignimbrite of the underlying Tiaojishan Formation. (f) Upper part of the Daohugou Bed at an excavation site in Daohugou Village.

layer of the ignimbrite. Due to strong tectonic activities, the weathered layer is nearly upright, and the Daohugou deposit also has a big direction of tilt. The reddish sediments of the lower part of the Daohugou Bed are about

20–40 cm thick, with no sign of volcanic baking. At the locality of Jiangzhangzi, the Daohugou Bed also unconformably overlies the ignimbrite (Fig. 2(c)). To confirm the relationship between the Daohugou deposits and the



Fig. 2. Contact between the Daohugou Bed and the underlying strata and the inverted fold of the Daohugou deposits. (a), (b) Direct contact between the Daohugou Bed and the underlying Tiaojiangshan ignimbrite in Daohugou Village ($41^{\circ}19'05.6''\text{N}$; $119^{\circ}12'56.3''\text{E}$), (b) is a close-up view of part (a), which clearly shows that the Daohugou Bed unconformably overlies the Tiaojiangshan Formation; (c) Direct contact between the Daohugou Bed and the underlying Tiaojiangshan ignimbrite at the Jiangzhangzi locality ($41^{\circ}24'26.8''\text{N}$; $119^{\circ}15'31.6''\text{E}$), showing the former unconformably overlying the latter; (d)–(f) Inverted fold of the Daohugou Bed: (d) the middle part of the Daohugou Bed is inverted, thus the “upper part” is actually older, and the ignimbrite forming the top of the hill actually is underlying the Daohugou deposits; (e) is a close-up view of the fold as in (d), showing the strong deformation of the strata as a result of the inverted fold ($41^{\circ}19'08.3''\text{N}$; $119^{\circ}14'28.6''\text{E}$); (f) Inverted fold of the Daohugou Bed in another locality of Daohugou Village ($41^{\circ}18'37.4''\text{N}$; $119^{\circ}13'20.2''\text{E}$).

ignimbrite is important because: 1) it clarifies that the widely distributed ignimbrite in this region that has long

been held as the “overlying Tuhulu Formation” in fact represents the Tiaojiangshan Formation underlying the Dao-

hugou deposits; 2) it further indicates that the Daohugou deposits cannot be referred to the Middle Jurassic “Jiulongshan Formation”, a conclusion mainly inferred from the hypothesis that the Tiaoishan Formation overlies the Daohugou deposits.

It is also notable that the strong tectonic activities had also resulted in the folding and inverted sequence of strata in the Daohugou Village (Fig. 2(d) (f)), which might explain why the underlying ignimbrite has often been mistaken as the overlying strata of the Daohugou deposits.

Another line of evidence in support of the abovementioned relationship between the Daohugou Bed and the ignimbrite comes from the analysis of the gravel content of the conglomerates and clastics from the coarse tuffaceous sediments of the lower part of the Daohugou Bed. First, the ignimbrite gravels of the Daohugou Bed has a low degree of roundness and grading, reflecting that they came from nearby resources, and had not been transported for a long distance. Second, majority of the gravels are from ignimbrites with only a few exceptions (such as gneiss) (See Fig. 1(d), (e)). The presence of the ignimbrite gravels in the Daohugou Bed clearly indicates that the Daohugou Bed had been deposited later than its source rock, ignimbrite.

3 Relationship between the Daohugou Bed and the Yixian Formation in the region

Compared to the limited and sporadic distribution of the Daohugou deposits in Shantou, and Wuhua of Ningcheng and Reshuitang of Lingyuan, the typical Jehol Biota-bearing Yixian Formation deposits are widely distributed in surrounding areas. For instance, it was found at the Tumen and Xitaizi localities about 2 km north to the Daohugou Village (41°21' 44.5" N, 119°09' 30.3" E) and at the Xishanjia locality (lower Yixian Formation) north-west to the Daohugou Village. The Daxinfangzi Bed, middle Yixian Formation deposits are also found to the east or southeast of the Daohugou Village^[24] (41°19' 37.2" N, 119°19' 38.9" E) or at Shanzui of Lingyuan and Niuyingzi (41°14' 37.9" N, 119°16' 41.6" E). The age of these deposits has been dated as 122 Ma^[25].

Fossils from the Daohugou Bed have been excavated by the farmers since 1998. At about the same time, farmers have also collected many Jehol Biota fossils from the Yixian Formation at such localities as Tumen, Xitaizi and Xishanjia, etc., which are very close to the Daohugou Village. Fossil assemblages from those localities include abundant *Eosetheria*, *Ephemeropsis trisetalis*, *Protopsephurus*, *Yanosteus*, a few of *Peipiaosteus*, *Lycoptera*, *Monjurosuchus*, *Psittacosaurus*, sauropods and *Confuciusornis*. Unfortunately, these fossil-bearing Daohugou deposits had been incorrectly compared to the Yixian deposits in neighboring areas^[2].

Recent excavation and studies have shown that the Daohugou fossil assemblage is different from that of the

Yixian Formation, particularly in the invertebrate and plant assemblages. Although no direct contact between the Daohugou Bed and Yixian Formation has been reported, the bottom of the Yixian Formation was found overlying the Tiaoishan ignimbrite at the Tumenyingzi locality near the Daohugou Village. The Daohugou Bed should be lower than the Yixian Formation. On the other hand, they probably belong to the same cycle of volcanism and sedimentation.

4 Datings of the Daohugou Bed and its underlying strata

In recent years, several datings have been done on the age of the ignimbrite^[21, 23]. Among them, the $^{40}\text{Ar}/^{39}\text{Ar}$ age on the K-feldspar is 159 Ma^[21] and 164 Ma^[22]; SHRIMP U-Pb age of the single zircon crystal is 164–165 Ma^[22, 23]. According to the latest international stratigraphic table^[26], the ignimbrite of the Tiaoishan Formation should be referred to the late Middle Jurassic-early Late Jurassic, hence the overlying Daohugou Bed cannot be older than the Late Jurassic^[21].

In addition, the tuffs interbedded in the shales of the Daohugou Bed in the Daohugou Village have been dated. Although an age of about 160 Ma has been obtained by both $^{40}\text{Ar}/^{39}\text{Ar}$ and SHRIMP U-Pb methods, it remains unsolved as to whether it represents the age of the deposit or the age of the older bedrock, which is around 160 Ma. The presence of a large amount of ignimbrite in the conglomerate of the middle part of the Daohugou Bed appears to cast further doubt on this.

5 Vertebrate assemblage and biostratigraphy of the Daohugou Bed

The Daohugou Bed has preserved a plethora of fossils of exceptional completeness, including many vertebrates with soft tissues (Table 1). Invertebrates and plants are both diverse and abundant, including over 200 species of insects belonging to at least 50 families and 14 orders^[18], one genus and 4 species of conchostracans^[15]. Important vertebrates include 3 genera and species of salamanders^[1, 6, 7], 2 genera and species of pterosaurs^[3, 5], 2 genera and species of feathered maniraptoran dinosaurs^[4, 8] (Table 1). No fish has been reported from the Daohugou Bed, contrary to a previous report^[2] that was based on incorrect information on horizon.

The conchostracan from the Daohugou Bed was recently described as *Euestheria*, and based on this study a Middle Jurassic age was suggested for the fossil-bearing deposit, which was referred to the Jiulongshan Formation, comparable to the Haifanggou Formation in Liaoning^[15]. Studies on the Daohugou insects arrived at different conclusions on the biostratigraphy^[9, 14, 18, 20]. For instance, Ren et al.^[9, 10] compared the Daohugou Bed with the Jiulongshan Formation based on an assumed similarity of insect assemblage^[16]. Rasnitsyn et al.^[20] also held a Middle Ju-

Table 1 Vertebrate fossils known from the Daohugou Bed

Amphibia
Lissamphibia
Urodela
Cryptobranchidae
<i>Chunerpeton tianyiensis</i> Gao et Shubin, 2003
Family incertae sedis
<i>Jeholotriton paradoxus</i> Wang, 2000
<i>Liaoxitriton daohugouensis</i> Wang, 2004
Reptilia
Archosauromorpha
Pterosauria
Rhamphorhynchoidea
Rhamphorhynchidae
<i>Pterorhynchus wellnhoferi</i> Czerkas et Ji, 2002
Anurognathidae
<i>Jeholopterus ningchengensis</i> Wang, Zhou, Zhang et Xu, 2002
Saurischia
Theropoda
Maniraptora
Family incertae sedis
<i>Epidendrosaurus ningchengensis</i> Zhang, Zhou, Xu et Wang, 2002
<i>Pedopenna daohugouensis</i> Xu et Zhang, 2005

rassic age for the deposit based on the studies of the Hymenoptera assemblage. Zhang^[11–13], on the other hand, argued that the Daohugou insect assemblage is most similar to that of the Late Jurassic Karabastau Formation in Kazakhstan. Therefore, he proposed a new formation for the Daohugou deposits, the Daohugou Formation, and called the biota in this formation the “Pre-Jehol Biota”^[18]. It is noteworthy that Zhang also noticed that the Daohugou deposits share some insects with the Yixian Formation (Zhang, pers. comm., 2004).

The most abundant vertebrates from the Daohugou Bed are salamanders. Among them, *Jeholotriton paradoxus* is the most common species^[11]. Another salamander, *Chunerpeton tianyiensis*, is represented by relatively few individuals^[6]. The major horizon of the *Jeholotriton* is probably slightly higher than that of the *Chunerpeton*. At the Wubaiding locality in Reshuitang, Lingyuan, only *Chunerpeton* has currently been known, probably indicating that the deposits at this site are equivalent to the middle part of the Daohugou Bed. *Liaoxitriton* was first described from the Yixian Formation in Huludao, Liaoning Province^[27]. Recently a new species of *Liaoxitriton* (*L. daohugouensis*), has been reported from the Daohugou Bed^[7]. Studies on the salamanders from Inner Mongolia and western Liaoning indicate that they are approximately at the same evolutionary stage and show some more derived appearance than *Karaurus* from the Late Jurassic of Kazakhstan^[7,28]. Further comparisons between the Daohugou salamanders and *Karaurus* suggested that the Daohugou Bed is probably referable to the Late Jurassic to Early Cretaceous, rather than Middle Jurassic^[28].

All the known pterosaurs from the Daohugou Bed belong to the primitive rhamphorhynchoids. Among them, *Jeholopterus* was referred to the Anurognathidae^[31], and *Pterorhynchus* to the Rhamphorhynchidae^[5]. These two

families often coexisted in fossil record. They have previously been found from the early Late Jurassic Karabastau Formation of Kazakhstan (Oxfordian-Kimmeridgian), and the late Late Jurassic Solnhofen limestones (Tithonian)^[29]. In addition, *Dendrorhynchoides*^[30–32], also referred to the Anurognathidae, has been discovered from the lower Yixian Formation (Jianshangou Bed)^[33] in the Sihetun area in Beipiao, Liaoning Province, with a dated age of 125 Ma^[34–36]. The Jianshangou Bed is one of the most important pterosaur horizons in the Jehol Group. Many derived pterodactyloids have been discovered, including *Haopterus*^[37] and *Eosipterus*^[31,38] belonging to the Pterodactylidae, which is also well represented in the Solnhofen limestones. *Dendrorhynchoides* from the Jianshangou Bed shows much resemblance to *Jeholopterus* from the Daohugou Bed, and the Jianshangou pterosaur assemblage is obviously more derived than the Solnhofen pterosaur assemblage. Therefore, based on the pterosaur comparisons, we propose that the age of the Daohugou Bed is probably older than the Jianshangou Bed, but younger than the Solnhofen limestones.

Several feathered maniraptoran dinosaurs have also been reported from the Daohugou Bed, including the arboreal *Epidendrosaurus ningchengensis*^[41]. A synonym of this species, “*Scansoripteryx heilmanni*”^[39,40], probably came from the same horizon in Daohugou Village, contrary to the originally reported middle Yixian Formation at the Dawangzhangzi locality^[41], which was dated as 122 Ma^[25]. *Pedopenna daohugouensis* is the second maniraptoran reported from the Daohugou deposits, and also represents an arboreal dinosaur^[8]. Because all other known feathered dinosaurs have been discovered from the Jehol Biota^[42], the Daohugou dinosaur assemblage shows a close relationship to that of the Yixian Formation.

In sum, vertebrate assemblage from the Daohugou Bed

shows a closer relationship to that of the Yixian Formation than to those from other horizons. A comprehensive analysis of the lithostratigraphic, biostratigraphic and chronological evidence of the Daohugou Bed indicates that it cannot be referred to the Middle Jurassic “Jiulongshan Formation”, which is older than 165Ma. The Daohugou fossil assemblage probably represents the earliest evolutionary stage of the Jehol Biota.

6 Conclusions

(1) The Daohugou Bed is currently known to have been distributed in a small area across the border of Ningcheng, Inner Mongolia and Lingyuan, Liaoning. Major fossil localities include the Daohugou Village, Zhujiagou, Jianguzhangzi, Wubaiding etc. The Daohugou Bed comprises three parts in sequence: the lower part is mainly composed of grayish tuffs with interbedded thin and reddish shales, which had previously been misidentified as belonging to the Tuchengzi Formation; the middle part is composed of thick grayish tuffs with interbedded thin gray or greenish tuffaceous shales; and the upper part is composed of interbedded grayish tuffs and shales, representing the major fossil-bearing horizon of the Daohugou Bed.

(2) The Daohugou fossil-bearing deposits sit on complex bedrocks, including the Archean gneiss, Meso- and Neo-Proterozoic marine deposits and ignimbrite of the Middle-Late Jurassic Tiaojishan Formation. The Daohugou deposits were often folded or inverted due to strong tectonic activities. The Tiaojishan ignimbrite previously held as overlying the Daohugou Bed actually represents the underlying stratum.

(3) Several recent isotope datings, using both $^{40}\text{Ar}/^{39}\text{Ar}$ and SHRIMP U-Pb methods, have indicated that the age of the ignimbrite is between the late Middle Jurassic and early Late Jurassic, or 159–164 Ma. Therefore, the Daohugou Bed cannot be older than this age, and is not comparable to the Middle Jurassic Jiulongshan Formation.

(4) Studies on the conchostracan and insect assemblages of the Daohugou Bed suggested an age between the Middle Jurassic and Late Jurassic despite the fact that some Daohugou insects also occurred in the Yixian Formation. On the other hand, vertebrate evidence suggested a younger age for the deposit, showing that its assemblage is closer to that of the Yixian Formation than to any other horizons. Important vertebrates fossils from the Daohugou deposits include salamanders, rhamphorhynchoid pterosaurs and feathered maniraptoran theropods.

(5) Despite the lithological similarity between the Daohugou Bed and the Yixian Formation, they have yielded two distinctive fossil assemblages. They probably belong to the same cycle of volcanism and sedimentation although the Daohugou Bed is lower than the Yixian Formation. And it is possible that the Daohugou fossil assemblage represents the earliest stage of the evolution of the

Jehol Biota.

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