辽宁中生代鸟类综述

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摘要 本文对发现于辽宁中生代地层中的鸟类化石，进行了简单的总结。化石的系统分析表明，从晚侏罗世到早白垩世在这一地区存在两个亚纲的鸟类分子：蜥鸟亚纲（Sauriurae）和今鸟亚纲（Ornithurae）。其中，蜥鸟亚纲的成员不仅数量居多，而且存在较大的分异。今鸟亚纲的分子则种类和数量都相对较少。辽西中生代鸟类的大量出现，除了鸟类自身的发育原因外，晚侏罗世到早白垩世这一地区适宜的生态环境也为鸟类的繁荣提供了必要的条件。辽西地区陆相中生代地层义县组和九佛堂组的时代分别为晚侏罗世和早白垩世。

关键词 辽宁，中生代，鸟类，埋藏及演化，地层时代

1. 引言

我国中生代鸟类化石的研究开始于八十年代。甘肃鸟（Gansus）的发现和研究标志着这一研究领域的开端。自八十年代末以来，辽宁朝阳地区陆续发现了大量早白垩世的鸟类化石。此后不久，在内蒙古、河北的时代相近地层中便相继发现了更多的鸟类骨骼化石。并且，在山东、宁夏等地区还发现了鸟类的羽毛化石。特别是，1994 年，辽宁北票又发现了晚侏罗世的鸟类化石。这些新的发现不仅丰富了我国中生代鸟类的种类和数量，而且将鸟类在我国的历史向前推进了重要的一步。

迄今为止，我国发现的中生代鸟类化石，可以分别归入蜥鸟亚纲和今鸟亚纲（Martin, 1983）。其中，辽宁中生代鸟类化石不仅包括了这两个亚纲在我国的最早分子，而且，具有这两个亚纲分异产生的若干不同类型的代表。因此，辽西中生代鸟类动物群在早期鸟类的演化历史上占有无可争议的重要位置。近年来，蒙古、俄罗斯以及朝鲜等地发现的中生代鸟类化石在许多方面都可以与中国的材料进行对比。此外，由于义县组发现的鸟类化石，与德国海相晚侏罗世地层中发现的始祖鸟化石可以进行很好的对比，而且，
在辽宁又发现了不同层次的鸟类化石，因此，对这些鸟类的研究还将对这一地区生物地层学的研究产生重要的影响。

2. 系统简介

下面，将对辽西中生代发现的主要鸟类进行简单的总结和分析：

孔子鸟（*Confuciusornis*）产于辽宁北票上园地区的义县组底部，被归入蜥形鸟纲（侯连海等，1995），主要依据两点特征：一是坐骨中部具一个向上的突起，二是跗腓骨的愈合从近端开始。同时，孔子鸟具备一些特有的特征，包括：牙齿退化，代之以角质喙的出现；肱骨近端具有一特殊的气孔，不同于其它所有已知鸟类；第一指爪特别发育，其长超过第一指指骨等，可与已知古鸟次亚纲和反鸟次亚纲相区别，而且又因为不具备次次亚纲的近裔特征，故被视作代表一独立的目（侯等，1995），暂不作次

图 1 孔子鸟的前肢（V10918）

Fig. 1 The forelimb of *Confuciusornis sanctus*

ac: acetabulum; f: femur; iI: ilium; is: ischium; mII: metatarsal II; mIII: metatarsal III; mIV: metatarsal IV; mV: metatarsal V; pa: patella; pu: pubis; ti: tibiotarsus; II: digit II; III: digit III; IV: digit IV.

图 2 孔子鸟的腰带和后肢（V10895）

Fig. 2 The pelvis and hindlimb of *Confuciusornis sanctus*
亚纲级的归类。

与始祖鸟相比，孔子鸟具有一些较进步的特征，与反鸟类相比，则具有较多原始的性状。由于已知反鸟类的早期成员（如中国鸟、华夏鸟等）都还保留了牙齿这一原始的祖先特征，因此，很难认为孔子鸟就是反鸟类的直接祖先；同样，始祖鸟也具有一些特化的结构，如坐骨远端的分叉等，因而也不可能为孔子鸟的直接或最近的祖先。总之，早期鸟类的演化过程远比我们过去所认为的要复杂。

辽宁省的鸟类化石，可以分别归入蜥蜴亚纲中的反鸟类亚纲和今鸟亚纲。前者不仅包括较多的种类，而且数量也较多。在已发表的鸟类中，中国鸟（Sinornis）、华夏鸟（Cathayornis）以及波罗赤鸟（Boluochia）皆可归入这一类，而后者仅包括朝阳鸟（Chaoyangia）一种。

周忠等（1992）建立的华夏鸟目具有较多反鸟类亚纲的近似特征，如膝骨侧视向内侧倾斜，远侧可分为两部分。第三掌骨明显较第二掌骨长。乌喙骨与肩胛骨的关节与现代鸟类凹面结构相反，叉骨突长，胸骨具有两对胸骨凹，股骨端远端内侧较大，侧肋骨远端先愈合等等。中国鸟与华夏鸟的基本结构非常接近（Sereno 和 Rao，1992），但因仍保留腹膜肋这一原始的结构，而与华夏鸟不同。本文暂将中国鸟归入华夏鸟目的华夏鸟科。

波罗赤鸟（周忠和，1995）显然也可以归入反鸟类亚纲。它所具有的该次亚纲的共近似特征包括：（1）近趾骨远端缝间退化，内侧较发育；（2）第四趾骨较细；（3）胸骨的侧突细长并在端部扩大等。关于坐骨远端骨块的特征，周忠和（1995a，b）曾提出这是反鸟类的特征，但本文研究呈海等（1995）的看法，即这一特征也同时见于始祖鸟和孔子鸟中，因而应作为蜥蜴亚纲的特征。波罗赤鸟的骨和目一级的分类位置暂时没有确定，但显然不能归入华夏鸟目。它们的主要区别有：前者前肢骨的前端钩曲，腹缘不具牙齿；第 II－IV 趾骨长度比较接近；第四趾骨较细等等。与华夏鸟相比，波罗赤鸟的前肢以及后肢的一些特征显示出它为一较为特化的类型。在同时代鸟类中，波罗赤鸟的数量也相对较少。

朝阳鸟是辽宁省发现的唯一可以归入今鸟亚纲的中生代的鸟类。它所具有的这一亚纲的特征包括：助骨上具有钩状突起，耻骨与坐骨在远端形成一个小的闭孔，股骨骨发育等。迄今为止，今鸟亚纲的最早成员也只发现于早白垩世的地层中。中国的甘肃鸟和蒙古的Ambiortus 皆属于这一亚纲。尽管这些鸟类为这一亚纲已知的最早成员，但可以推测，它们还未出现该亚纲最早出现的分子。与这些鸟类的生同一层位的华夏鸟，中国鸟以及波罗赤鸟等更不是已知蜥蜴亚纲的最早分子，因此鸟类两个亚纲的分化至少在晚侏罗世已经明显发生。

通过对辽西早期鸟类的简单系统分析，我们可以得出以下几点认识：（1）早期鸟类的分异在晚侏罗世已经开始。孔子鸟的研究和朝鲜北时代鸟类化石的发现为这一结论提供了更进一步的依据；（2）孔子鸟喙的出现，使得我们对这一与觅食有直接关系的构造的发生和历史有了进一步的了解；（3）辽西鸟类的形态研究，使得我们对早期鸟类的演化，特别是与飞行有关的肩带、前肢和脊椎的演化有了比较系统的认识。如越原始的鸟类，肩带与前肢的联系越不密切；而越进步的鸟类则前肢与脊椎的愈合程度越高等。
3. 鸟类的发展分化与化石的形成条件

辽西中生代鸟类化石的大量发现，是众多因素影响的结果。从鸟类自身演变的角度来看，种类的繁多和种群数量的丰富，是导致化石大量出现的主要因素。如果从生物演化的外部条件来分析，那么，辽西地区晚侏罗世至早白垩世特殊的生存环境，无疑又是鸟类在该地区得以繁荣的基础。

辽西晚侏罗世至早白垩世鸟类的迅速分异和发展，首先证明了早期鸟类演化的复杂性。已知最早的鸟类始祖鸟以及我国发现的孔子鸟都不是现代鸟类的直接祖先。它们都只不过是鸟类早期发展中的一个旁支。而真正的现代鸟类的更为接近的祖先目前仅见于早白垩世的层中。朝阳鸟以及蒙古的 Ambiortus 可以作为这一类的代表分子。但可以推测，鸟类最早的祖先应当在晚侏罗世以前已经出现。而到了晚侏罗世及早白垩世，鸟类的演化已经进入了首次较大发展的时期。无论是种类和数量都已十分丰富。事实上，在相同的时期里，我国而言，目前已经在内蒙古、甘肃、河北、山东及宁夏等地都已发现了鸟类化石的证据，就世界范围而言，朝鲜、蒙古、俄罗斯、西班牙以及澳大利亚等国近几十年来都有鸟类发现的报道。总之，晚侏罗世至早白垩世，鸟类已成全球分布之势。

辽西中生代鸟类的大量出现，还不单纯是生物自身的原因。包括鸟类在内的热河生物群的其它主要成员，在相同的时期内，也同样得到了较大的发展。我们同意王思恩（1990）提出的观点，即：热河生物群的发生演化外因包括古气候、古地理、地壳运动、火山活动和古地磁磁场极性的转换等可能的重要因素。我们认为，除这些因素外，鸟类以外的其它门类的生物的发展保证了整个生态系统的良性循环和发展。辽西中生代鸟类，从已有的发现来看，还具有一个共同的特点，即都具有十分精细的脚爪。从趾和爪的结构以及鸟类骨骼的其它特征来看，它们都属于树栖鸟类（Feduccia，1993）。相同层位中发现的大量植物树干、树叶和种子化石表明它们不仅为鸟类提供了丰富的食物，而且，显然也为鸟类提供了理想的栖息环境。

总之，早白垩世鸟类的大量出现并不是像有人所提出的在极短的时间里爆发的结果（Kurochkin，1985）。换句话说，鸟类在晚侏罗世－早白垩世的较大发展和分化不过是更早时期内鸟类累积发展的结果。其次，晚侏罗世至早白垩世东亚地区（以辽西为代表的）复杂多变的地理环境无疑为鸟类在这些地区的发展创造了条件。

化石的形成离不开必要的埋藏条件。晚侏罗世的鸟类化石地点，目前仅有一处即辽宁北票上园地区（黄半截子沟），该地点同时还发现了大量的鸟类羽毛的印痕化石。它们或附着于长骨的两侧，或呈零散状态保存。骨骼都保存较为完整，主要骨骼还以关节相连。同层鱼类化石也保存十分完整。与此形成对比的是早白垩世的化石地点。迄今为止，尚未发现羽毛的痕迹。以波罗赤化石地点为例，就骨骼化石而言，保存状态也有较大变化，或较为完整，或非常分散，代表了一种不太稳定的沉积环境。伴生的鱼化石的保存状态也有多种变化。羽毛化石没有保存，可能和水体的动荡有关。另外一种可能的解释是鸟类在死亡后，有短暂的可能漂浮于水面。从鱼类化石保存的位置分析，可以发现，鸟类死后多数腹面朝上。这一现象可能与鸟类在被覆盖前，有短暂的漂浮于水面
有关。
辽西中生代鸟类化石，无论是发现于晚侏罗世的义县组，还是早白垩世的九佛堂组，除以上埋藏状况的不同，它们还具有一些共同的埋藏特点，地层的岩性多为灰色的泥岩或页岩。同层发现的化石都具有大量的鱼类（北票鱼及真骨鱼类等），介形虫、昆虫和植物化石。通常情况下，丰富的介形虫的出现标志着浅水埋藏的环境。大量的植物碎片的存在也指示近岸浅水的环境。

4. 地层时代

辽西地区含狼鳍鱼化石地层（义县组和九佛堂组）的时代问题，长期以来一直没有得到很好的解决。不同的研究者往往各持已见，如王思恩（1990）通过对热河动物群的研究，认为义县组和九佛堂组的时代应为晚侏罗世，而李佩贤等（1994）则综合了生物地层学和同位素的有关资料，提出这两个组的时代皆为早白垩世。除以上两种意见外，地学界还存在其它不同的看法。导致这一混乱局面的重要原因之一就是缺少可靠的能与海相化石进行对比的化石证据。义县组孔子鸟的发现无疑为解决该地层的时代提供了一些新的依据。如果说九佛堂组的鸟类化石还是早白垩世鸟类的面貌（周忠和等，1992），那么，孔子鸟则更多具有了晚侏罗世鸟类的特点。目前，朝鲜的“始祖鸟”化石尚未正式发表，因而可靠的晚侏罗世的鸟类只有始祖鸟一属两种（Wellnhofer，1993）。始祖鸟产于海相地层中，其时代被确认为晚侏罗世提堂阶（Tithonian）下部。与之相比，孔子鸟与其非常相似，如头部骨骼还未愈合，肱骨近端内结节及顶沟皆不发育，尺骨和桡骨长度还不如肱骨，腕骨和掌骨尚未愈合，第一掌骨较长，第二和第三掌骨长度接近，指骨及指爪长，第五指骨尚未退化，坐骨仍较粗壮。所有这些特征都比早白垩世鸟类的相应特征原始。

九佛堂组的鸟类化石，除包括华夏鸟、中国鸟以及波罗赤鸟等属于反鸟亚纲的鸟类外，还包括今鸟亚纲的朝阳鸟。因而不仅种类较多，而且数量也十分丰富。此外，产自同一层位的还有一件未描述的标本，显然可归入今鸟亚纲。它具有与同现代鸟类十分接近的胸骨、叉骨和鸟喙骨的特征。这些特征与蒙古早白垩世的鸟类 Ambiortus 非常相似。与之相比，义县组的鸟类化石不仅数量较少，种类单调，而且鸟类的飞行能力也非常有限，或者说还不具备持续飞行的能力。这些特征都均与晚侏罗世的始祖鸟化石最为相似。基于以上理由，我们认为含孔子鸟的义县组的地层时代更可能为晚侏罗世的晚期。

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INTRODUCTION TO MESozoIC BIRDS FROM LIAONING, CHINA

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Summary

This paper summarizes the recent discoveries of Mesozoic birds from Late Jurassic to Early Cretaceous in Liaoning, China. Most of these fossils can be referred to the avian subclass: Sauriurae, only Chaoyangia to Ornithurae. The earliest diversification and big development of birds from Late Jurassic to Early Cretaceous as well as the peculiar geological background and depositional environment in Western Liaoning constitute the main reasons for the appearance of abundant Mesozoic bird fossils in this area. In this region, the continental Jurassic-Cretaceous boundary being put between the Confuciusornis bearing Yixian Formation and the Cathayornis and Chaoyangia bearing Jiufotang Formation is proposed.

1. Introduction

The study of Mesozoic birds in China dated back to the early eighties of this century, when Gansus was discovered and described (Hou et Liu, 1984). Since the late eighties, a number of Early Cretaceous birds have been found, firstly in Western Liaoning (Zhou, 1995), and shortly later in Inner Mongolia (Dong, 1993; Hou, 1994) and Hebei Province. At the same time, feather impressions were also recovered in Shandong Province (Zhang, 1992) and Ningxia Autonomous Region. Particularly important is that since 1994 some Late Jurassic birds have been found from the Yixian Formation also in Western Liaoning Province.

So far, the Mesozoic birds from China can be referred to Sauriurae and Ornithurae respectively. Among them, those from Liaoning Province are most important not only in having the oldest birds in China but also in possessing the oldest representative of Ornithurae.

2. Systematics and analysis

Recent studies show that Archaeopteryx is not the direct ancestry of modern birds. On the basis of this understanding, the classification of birds has also been greatly modified. Martin (1983) put Archaeopteryx and its allies in the avian subclass of Sauriurae, and set all the other birds into another subclass: Ornithurae. This proposal has become gradually accepted (Feduccia, 1994; Hou et al., 1995). In this paper we are going to give a general analysis of the systematics of the Mesozoic birds from Liaoning, China.

Confuciusornis (Hou et al. 1995) from Late Jurassic, Yixian Formation, Beipiao Liaoning, can be referred to Sauriurae according to the following two synapomorphies: (1) presence of a dorsal process on the anterior ischium; (2) tarsometatarsus begins ossified proximally. This bird is obviously distinguished from the two infraclasses of Sauriurae, mainly by (1) absence of teeth on the jaws; (2) presence of horny beak;
wing claw on first digit robust and slightly longer than the first phalange on the same digit; (4) presence of a peculiar foramen on the proximal humerus. *Confuciusornis* appears to be slightly more advanced than *Archaeopteryx*, but much more primitive than Enantiornithes. Both *Archaeopteryx* and *Confuciusornis* are very specialized birds. Although they might be very close to the ancestry of Enantiornithes, they are not the direct ancestor of enantiornithine birds. And *Archaeopteryx* is not the direct ancestor of *Confuciusornis* either. This fact may indicate that the early evolution of birds is much more complicated than we have ever imagined, and the fossil evidences we have already known are only a very small portion of the early bird types that had actually existed.

The Early Cretaceous birds from Liaoning Province can be referred to Enantiornithes and Ornithuridae respectively. The former has more number and taxa than the later in this area.

Among the Enantiornithes members in this region, *Cathayornis* (Zhou et al. 1992) from Jiufotang Formation, Chaoyang, Liaoning, is mainly diagnosed by the following enantiornithine characters: head of humerus slanting internally in lateral profile and bivided distally, metacarpal III obviously longer than II, articulation of coracoid and scapula opposite to that of modern birds, hypercledium long and slender, sternum with two pairs of notches and a pair of long and distally expanded lateral processes. Medial condyle of tibiotarsus large, tarsometatarsus fused proximally. *Sinornis* (Sereno and Rao, 1992) from Chaoyang, Liaoning, is basically the same as *Cathayornis*, but probably slightly more primitive for retaining the gastralia. It is here suggested to be referred to the family of Cathayornithidae.

*Boluoichia* (Zhou, 1995) is another enantiornithine bird that is from the Lower Cretaceous of Liaoning Province. The main synapomorphies of Enantiornithes found in this bird include: (1) intercondylar fossa of tibiotarsus narrow, medial condyle large; (2) metatarsus IV relatively reduced; (3) lateral processes of sternum slender and expanded distally. The presence of a dorsal process on the proximal ischium was once suggested by Zhou (1995) as a character of Enantiornithes. This character was later found to be also present in *Archaeopteryx* and *Confuciusornis*, hence it is regarded as a saurian character (Hou et al. 1995). *Boluoichia* is markedly distinguished from *Cathayornis* and *Sinornis* by such characters as main metatarsals close in length, premaxilla hooked anteriorly and with no teeth on its margin. The population of this bird is probably not as big as that of *Cathayornis* if simply referred from the numbers of specimens belonging to each of them from the same site (Boluoichi).

*Chaoyangia* is the only Mesozoic bird from Liaoning Province that can be referred to Ornithuridae. The advance characters of this bird include: presence of uncinate process on rib; presence of small obturator foramen between ischium and pubis; cnemial crest of tibiotarsus developed. Up to present, the earliest record of the
ornithurine members is from the Early Cretaceous strata. *Ambiortus* and *Gansus* from Mongolia and China respectively. *Gansus* is a specialized wading bird. None of these birds could be regarded as the oldest representative of Ornithurae because they are all very much derived. It is reasonable to assume the oldest ancestry of birds had appeared previous to Late Jurassic.

3. Geology and the fossil appearance

The great diversification and big development of birds from Late Jurassic to Early Cretaceous in Liaoning Province could not be well understood without a clear general understanding of the early evolution of the class of birds. Both of the known oldest birds, *Archaeopteryx* and *Confuciusornis*, are belonged to the extinct avian subclass: Sauriurae. The oldest and well-known Ornithurine birds (*Ambiortus, Chaoyangia*) are now found from the Early Cretaceous strata. They are already very advanced in many important structures like the keeled sternum, coracoid, uncinate process on the ribs etc. The oldest ancestor of birds must have appeared earlier than Late Jurassic. In other word, Late Jurassic to Early Cretaceous time had already been the second evolutionary stage of birds. Both the taxa and population of birds had been greatly enriched by that time. In China, Early Cretaceous birds have been found in Inner Mongolia, Gansu, Hebei, Shandong, and Ningxia Autonomous Region. Outside China, from Late Jurassic to Early Cretaceous, bird fossils have been reported in North Korea, Mongolia, Russia, Australia etc. In a word, By Late Jurassic-Early Cretaceous, birds had nearly been worldwidely distributed.

The appearance of abundant Mesozoic bird fossils from Liaoning is also closely related to the peculiar geological background in this area. Except for birds, all the other members of the Jehol Fauna became well developed. In fact, the Jehol Fauna is distributed in most of the northern part of China, Mongolia, Russia, North Korea, Japan and some other Asian areas. Thus, the Mesozoic birds found in China, Mongolia and North Korea are not only possibly phylogenetically closely related, but also share a very similar geological background. Wang (1990) pointed out that the origin and evolution of the Jehol Fauna is affected by many important factors, such as paleoclimatological and paleogeographical environments, crustal movements, volcanic activities, and geomagnetic reversals etc. According to him, the duration of the Jehol Fauna is right the time while the geomagnetical field alternations happened most frequently. In the meanwhile, the humid and warm climate, the active volcanic activities and crustal movements are all very significant. It seems to us that, in addition to above individual factors, the development of all the other lives except birds ensure a stable and good ecological environment for the development of birds.

All the Mesozoic birds from Liaoning Province also share a very similar character: long and strongly curved pedal claws that show the perching habit of birds in this
area. The plant fossils (including seeds, leaves and trunks) associated with the birds clearly indicate an ideal place for perching and feeding.

So far there is only one Late Jurassic bird site in China. Together with the skeleton fossils are many feather impressions. They are either attached to the long bones like femur and tibia, or preserved separately. The skeleton is preserved well, with most of the bones articulated. The fish fossils associated with the birds are also completely preserved. The fortunes of the Early Cretaceous birds are not so good. So far there are two Early Cretaceous bird sites in Liaoning Province: Shengli and Boluochi. No feather has been recovered from these sites. We take the site of Boluochi as an example, the preservational condition varies. The skeleton is either nearly completely preserved or very fragmentary, indicating a changing depositional environment. These changes are also confirmed by the minor differences of the fossil-bearing rocks. Obviously there exist diverse depositional speeds with accordingly different aquatic dynamic conditions. The preservational conditions of the associated fish fossils also change like birds. We explain the absence of feather in this site as due to the instable aquatic environments. An alternative explanation is that the birds had been floated on the surface of the water and exposed to the air after death for certain time.

The Mesozoic bird fossils from Liaoning Province, both from the Late Jurassic Yixian Formation and from the Early Cretaceous Jiufotang Formation, are all recovered from the grey mudstone or shale deposits. They are usually found together with abundant fish, ostracods, insects and plants. The presence of abundant ostracods indicates the environment of fresh water. The conclusion is further confirmed by the association of plentiful plant fossils with the birds.

4. Jurassic-Cretaceous boundary

The continental Jurassic-Cretaceous boundary in Western Liaoning Province has been a long standing controversial problem. Various workers usually hold different viewpoints. One of the important reasons that has caused this confusion is that there has been no very convincing correlation with marine fossils. The discovery of Confuciusornis provides one important clue to solving this problem. If the birds from the Jiufotang Formation are basically characteristic of those of Early Cretaceous birds, then the birds from Yixian Formation is obviously closest to the Late Jurassic Archaeopteryx. The overwhelming resemblances of Confuciusornis to Archaeopteryx include: skull bones unfused, internal tuberosity and capital groove on humerus undeveloped, humerus longer than ulna or radius, carpus and metacarpals unfused, first metacarpal still developed, second and third metacarpals close in length, manual phalanges and claws long and unreduced, fifth metatarsal retained, ischium robust etc. All these characters are markedly more primitive than in Cretaceous enantiornithine birds.
The birds from Jiuhotang Formation include *Cathayornis*, *Sinornis*, *Boluochia* and *Chaoyangia*. *Chaoyangia* is absolutely an ornithurine bird. It should be noted here that in our collection from the same site, there is also another specimen that can be at least referred to Ornithurae. It has a keeled sternum that is longer than wide, a furcula and coracoid that are all very similar to modern birds. They show a lot resemblance to the Mongolia bird *Ambiortus* too.

In conclusion, the sauririne birds from Yixian Formation and Jiuhotang Formation represent two different evolutionary stages of the avian subclass: Sauriurae. The sauririne birds from Jiuhotang Formation has demonstrated not only more taxa but also more number of birds than those from Yixian Formation. In addition, the Jiuhotang Formation has also yielded the so far oldest ornithurine birds. Based on above reasons, we propose the continental Jurassic-Cretaceous boundary in Western Liaoning Province should be put between Yixian Formation and Jiuhotang Formation.