

辽宁早白垩世一新的反鸟化石

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摘要 本文记述了在辽宁朝阳地区, 早白垩世地层中发现的一种新的小型鸟类。依据它所具有的以下几点特征: (1) 胫跗骨远端踝间沟窄, 远视内踝前缘较为平缓; (2) 第四趾骨相对较为细弱; (3) 坐骨近端向背方伸出一个显著突起; (4) 胸骨侧突细长, 并在远端扩大。本文将之归入反鸟亚纲 (*Enantiornithes*)。此外, 依据新材料所特有的, 头骨及跗跖骨远端的结构, 不同于其它反鸟亚纲鸟类的特点, 本文建立了一鸟类的新属新种: 郑氏波罗赤鸟 *Boluochia zhengi*。最后, 本文通过对新材料和现生鸟类在爪的形态, 头骨结构等方面的比较后认为, *Boluochia* 可能为一类以树栖生活为主, 并较为凶猛的鸟类。

关键词 辽宁朝阳, 早白垩世, 反鸟亚纲, 生活习性

1990年9月, 本文作者在辽宁朝阳地区野外工作期间, 共发现了三件属于早白垩世的鸟类标本。其中保存最好的一件 (V9769) 已经初步研究, 并命名为燕都华夏鸟 (*Cathayornis yandica*) (周忠和等, 1992); 另有一件 (V9941) 只保存了一块胸骨的印痕, 其归类暂时尚未确定; 除此之外, 第三件标本 (V9770) 虽然多半只保存了骨骼的印痕, 但具有的骨骼特征较为特殊, 不仅与华夏鸟存在显著的差异, 而且也不同于后来在同一地点 (波罗赤乡) 发现的北山朝阳鸟 (*Chaoyangia beishanensis*, 侯连海等, 1993), 以及朝阳地区另外一个早白垩世化石地点 (胜利乡), 所发现的三塔中国鸟 (*Sinornis santensis*, Sereno and Rao, 1992)。这一标本保存的一些特征表明, 它应被归入反鸟亚纲。由于在我国已研究发表的早白垩世的鸟类中, 华夏鸟已被归入反鸟亚纲 (Zhou, in press), 因此, 这也是这一亚纲在我国出现的又一不同类型的代表。对这一新类型的记述, 不仅有助于进一步了解辽宁早白垩世鸟类动物群的完整面貌, 而且也探讨了反鸟亚纲的起源和早期演化提供了新的资料。

值得一提的是, 最近董枝明 (Dong, 1993) 还对我国内蒙鄂尔多斯盆地发现的一块早白垩世的鸟类化石, 作了初步报导, 并把它归入反鸟亚纲, 但未作详细描述和进一步的系统讨论。

一、标本记述

鸟纲 Aves Linnaeus, 1758

反鸟亚纲 Enantiornithes Walker, 1981

目·科未定 Order and Family indet.

波罗赤鸟(新属) *Boluochia* gen. nov.

郑氏波罗赤鸟(新属、新种) *Boluochia zhengi* gen. et sp. nov.

特征 小型鸟类。嘴具利钩。胸骨侧突细长,远端略见扩大。龙骨突很不发育,呈低矮的脊状。髌骨自髌臼向后显著缩减。坐骨近端伸出一个背向的突起。耻骨明显后伸,并

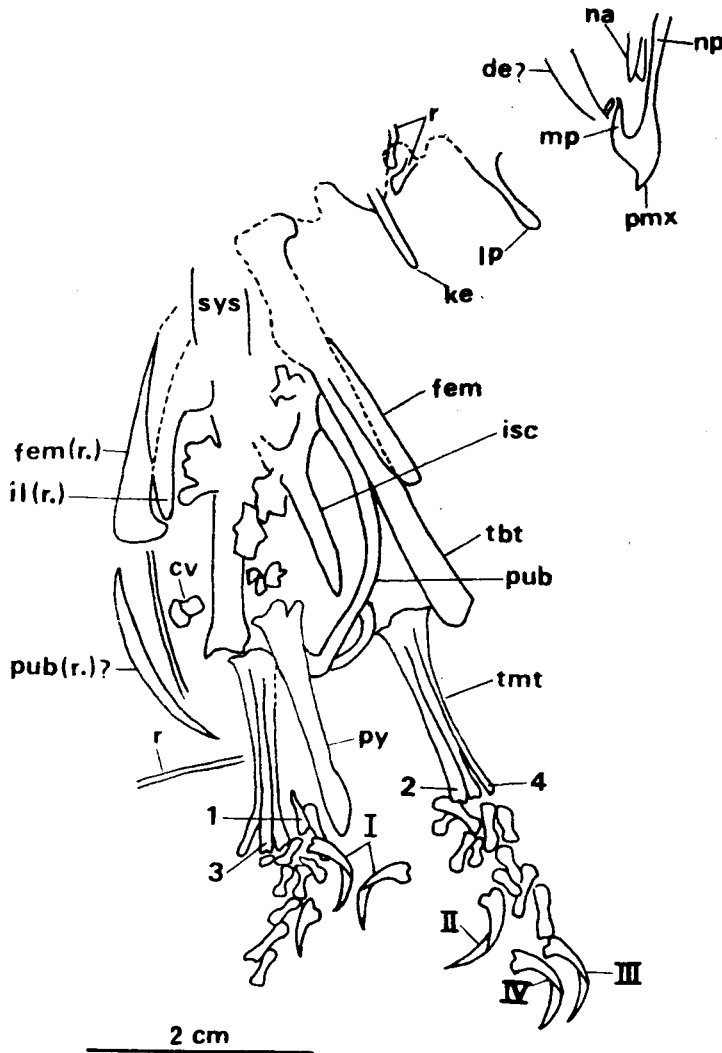


图1 (Fig. 1) 郑氏波罗赤鸟 (*Boluochia zhengi*). V9770
虚线表示复原部分 (dashed line indicates restored part)。见简字说明

强烈弯曲,远端具有脚状突起。胫跗骨远端髁间沟窄,远视内髁前缘较为平缓。跗蹠骨只在近端愈合,跗蹠骨中段显著缩窄,第四跗骨相对较为细弱。跗蹠骨三个趾骨滑车高度比较接近。趾爪强烈钩曲,末端尖锐,爪长超过其它趾节长。尾综骨长。

正型标本 一件不完整的个体。主要保存较完全的后肢、腰带及尾综骨,以及头骨前端、部分胸骨和脊椎。古脊椎动物与古人类研究所标本编号 V9770。

产地与层位 辽宁省,朝阳县,波罗赤乡;九佛堂组蓝灰色泥岩(早白垩世)。

词源 属名取自化石产地乡名;种名谨献给我国现代鸟类研究的开拓者郑作新教授。

描述 个体基本呈自然状态保存。由于主要保存骨骼印痕,因此以下描述主要参考以 V9770 标本为原型的塑料印模。

头骨 前颌骨 (pmx) 保存近于完整,鼻突 (np) 较直,呈扁平棒状,鼻突前端较薄。前颌骨前部主体部分背缘凸出,最前端形成一尖锐的突起,并呈钩状。前颌骨前端与鼻突之间形成一个向上的凹面。前颌骨的上颌突 (mp) 向后延伸,并逐渐变细。前颌骨上未发现牙齿。下颌骨(?)保存不完全,后端缺失。下颌骨似较粗壮,在靠前的位置上保存一枚牙齿。牙齿形态略呈锥形,齿冠基部明显收缩。鼻骨 (na) 保存不很清楚,保存部分的左右两骨似乎仍在中间相接。

脊柱 标本只保存了自愈合荐椎向后部分的脊椎,保存状态总体较差。尾椎结构趋于简单。尾综骨 (py) 保存完全,全长超过跗蹠骨(表 1),尾综骨背面是一条纵向分布的、窄长的脊板,脊板总体较为低平。

胸骨 (ste) 保存尽管不完整,但主要结构和特征都能观察到。胸骨主体的形态可以从保存的后部推知略圆。龙骨突 (ke) 尚很不发育,呈十分低矮的脊状,分布仅局限于胸骨后部。两对胸骨凹依稀可见。后突较短,侧突 (lp) 细长,远端稍见扩大,侧突向后伸展超过龙骨突,侧突与龙骨突略呈平行但略向外侧偏移。

腰带 髌骨 (il) 主要保存了自髌臼向后的一段,这一部分已显著缩减,背缘较为平直。左侧趾骨与坐骨 (isc) 在近端相连,但可能并未愈合。坐骨近端还向髌骨方向伸出一个背向的突起,坐骨向后逐渐变细。耻骨 (pub) 细长,向上强烈弯曲。耻骨前段伸展方向与坐骨近似平行,皆显著向后伸展。耻骨末端保留脚状突起,从已暴露的部分加以推测,其形态略呈三角形,尖

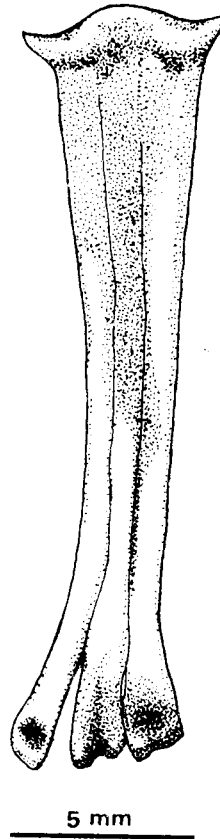


图 2 (Fig. 2) 郑氏波罗赤鸟的跗蹠骨(左侧),后视 Tarsometatarsus of *Boluochia zhengi*, left side, in posterior view (V9770)

表 1 标本测量(毫米)

(Table 1) (measurements in mm)

*, 近似值 (approximate measurements)

+, 估量值 (estimated measurements)

胸骨侧突远端最大宽度 (maximum width of the distal end of the lateral process of the sternum)	1.7
尾综骨 (pygostyle)	
全长 (total length)	21.5
近端最大宽度 (maximum proximal width)	4.7
远端最大宽度 (maximum distal width)	4.0*
最小宽度 (minimum width)	1.8
股骨骨体宽度 (shaft width of the femur)	3.0
胫跗骨 (tibiotarsus)	
全长 (total length)	37.0 ⁺
骨体宽度 (shaft width)	2.5
远端最大宽度 (maximum distal width)	3.5
跗蹠骨 (tarsometatarsus)	
全长 (total length)	17.5
近端宽度 (proximal width)	4.0
最小宽度 (minimum width)	1.8
第 I 趾骨 (metatarsal I)	
全长 (total length)	4.1
远端宽度 (distal width)	1.6
趾骨滑车宽度 (trochlea width for digit)	
II	1.3*
III	1.2*
IV	1.0*
最长趾节长 (length of the longest pedal phalange)	4.8
最短趾节长 (length of the shortest pedal phalange)	2.4
第 I 脚爪长 (length of the first digital claw)	6.5
第 III 脚爪爪弧弧度 (claw curvature of the third digital claw)	130°*

端朝上。

股骨 左侧股骨 (fem) 主要保存远端部分,远端宽约和骨体宽相当,内外二髁都不明显向两侧突出,前视远端具有一条较深的纵沟。右侧股骨 (fem_(r)) 上下保存方向与自然状态时正好相反,在标本上表现为近端朝下,骨体稍弯曲。近端保存较好,股骨头大,转子较发育,其外侧边缘略向外凸出。

胫跗骨 (tbt) 左侧胫跗骨保存较全,但前后位置与自然状态时相反。近端,胫脊不发育;远端未见骨质腱桥,髁间沟窄,内髁宽度尚不明显超过外髁宽度,内髁前缘远视较平缓。内外两髁都不明显向前突出。右侧胫跗骨主要保存远端后面的结构,韧带内隆已较发育。

跗蹠骨 (tmt) 保存完全。第 V 趾骨已完全退失。II—IV 这三个主要趾骨至少在近端已愈合较好。远列跗骨愈合形成跗帽,在其背面形成二个杯状凹,跗帽似由 2—3 个跗骨愈合而成。由于跗帽已和三个主要趾骨基本愈合,因而真正的跗蹠骨已经形成。第

二趾骨相对较直,第IV趾骨较弯曲,并相对比较细弱。跗趾骨中段两侧明显向内收缩变窄。趾骨因侧向压扁,而前后稍稍加高。跗趾骨的三个趾骨滑车高差较小,第III、IV趾骨滑车高度接近,二者都略低于第II趾骨滑车(图2)。第II趾骨滑车的宽度稍大于第III趾骨滑车的宽度,并明显大于第IV趾骨滑车的宽度。趾骨滑车的结构都很简单,一般不向后翻转,因而三个趾骨滑车大致位于同一平面上。第IV趾骨滑车稍许向外侧偏移。第I趾骨呈倒“丁”形,它与第II趾骨关节的位置可能较低。

趾和爪 趾节和爪几乎保存完全,但排列较散乱。趾节长短差别较大,多数比较长。爪节明显长于其它趾节。爪(含爪鞘)强烈钩曲,末端尖锐,屈肌结节不发育。

二、比较和讨论

1. 系统分析及比较

1981年, Walker 依据化石 *Enantiornis lealis* 建立了一个新的鸟类亚纲: 反鸟亚纲 (*Enantiornithes*)。当时,他在研究了阿根廷的 Salta 省 Elbret 地区发现的一批晚白垩世的鸟类材料后发现,它们的形态极其特殊,很难将它们归入当时已经存在的三个鸟类亚纲,即: 始祖鸟亚纲 (*Archaeornithes*)、齿鸟亚纲 (*Odontornithes*) 和今鸟亚纲 (*Neornithes*)。因而把它们全部归入他新建立的反鸟亚纲。“反鸟”之意得自这些鸟类所特有的,肩胛骨与鸟喙骨的关节同其它鸟类相比,凹凸情况正好相反的结构。

不久, Martin (1983) 在分析了 *Enantiornithes* 所具有的几点共近裔特征后,又将另外二种分别发现于蒙古和墨西哥晚白垩世的鸟类,即 *Gobipteryx* (Elzanowski, 1974) 和 *Alexornis* (Brodkorb, 1976) 加入到这一亚纲。

此外, Molnar (1986) 将在澳大利亚发现的一件早白垩世 (Albian) 的鸟类跗骨的材料,定名为 *Nanantius*, 并依据它所具有的“内踝明显比外踝宽; 踝间沟窄”的特征,把它归入到反鸟亚纲。这同时也是反鸟亚纲的化石在早白垩世地层中出现的首次报导。

近年来,对反鸟亚纲鸟类化石的研究和发现,都取得很大进展。Chiappe (1991) 报道了在阿根廷的 Patagonia 晚白垩世地层中新发现的反鸟亚纲的化石后,又对 *Avisaurus* (Brett-Surman and Paul, 1985) 进行了重新研究,确立了一些新的反鸟亚纲的特征 (Chiappe, 1992)。他在重新将 *Avisaurus* 归入反鸟亚纲的同时,也将这一亚纲的分布范围扩大到了北美。此外,美国、蒙古等地又新发现一批晚白垩世的反鸟化石,目前还在研究之中 (Chiappe, Ericson, Kurochkin pers. comm.)。更为重要的是: 近年来在西班牙,中国及蒙古等地早白垩世的地层中,发现的许多鸟类,如华夏鸟等,也已被确认为反鸟亚纲的早期分子 (Zhou, in press; Martin and Chiappe pers. comm.)。因此,迄今为止,反鸟亚纲的地理分布已遍及北美、南美、欧洲、亚洲及澳大利亚。其地质历史也从早白垩世早期 (Neocomian) 一直延续到晚白垩世晚期 (Maastrichtian)。

本文记述的材料至少具备以下几点反鸟亚纲的近裔特征: (1) 跗骨远端踝间沟窄 (Walker, 1981; Molnar, 1986); 远视内踝前缘较为平缓。(2) 第IV趾骨相对较为细弱 (Chiappe, 1992); (3) 坐骨近端具有一个显著的背向的突起 (Martin, 1983; Zhou, in press); (4) 胸骨侧突细长,并在远端扩大。根据以上特征,本文将波罗赤鸟归入反鸟亚

纲。

在以上列举的特征中,对于特征(1)需作一简单分析。在 *Nanantius* 及阿根廷发现的晚白垩世的反鸟中,胫跗骨远端,不仅髁间沟窄,而且内髁明显比外髁要宽。而在波罗赤鸟中,内髁并不明显比外髁更宽,这一点应当属于原始的状态。但另据笔者观察,在波罗

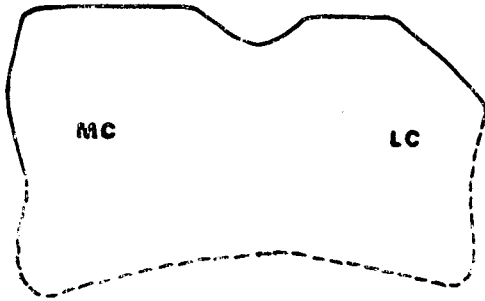


图3 (Fig. 3) 郑氏波罗赤鸟胫跗骨远端(左侧),远视。见简字说明 Distal end of tibio-tarsus of *Boluochia zhengi*, left side, in distal view (V9770)

赤鸟中,内髁远视前缘较为平缓的特点,与反鸟亚纲已知鸟类非常相似,而不同于所有其它鸟类。由于在始祖鸟及鸟类的祖先类群中,没有发现这一特征,因而可以认为这也是反鸟亚纲的特征之一。而“内髁明显比外髁宽”的特征可能是较特化的反鸟的种类才具有的。

顺便指出,中生代已发现的鸟类一般都保留牙齿, *Gobipteryx* 是一个例外。Elzanowski (in press) 据此认为,牙齿的缺失可能也是反鸟亚纲的共近裔特征之一。由于已知华夏鸟和波罗赤鸟都或多或

少保留牙齿,因此“牙齿缺失”显然不能被看作反鸟亚纲的共近裔特征,尽管牙齿的退化和消失可能是反鸟亚纲的鸟类演化的趋势之一。

Martin (1983) 曾依据一些特征,认为始祖鸟和反鸟亚纲是一对姐妹类群,并把它们合而归入 Sauriurae。但由于缺乏十分确凿的证据,他的这一观点迄今没有得到普遍接受。波罗赤鸟在许多方面都明显较始祖鸟进步。如出现了尾综骨和较进步的胸骨。最新发现的一块始祖鸟化石,虽然也保存了骨化的胸骨 (Wellnhofer, 1993),但与波罗赤鸟相比,显然更加原始,主要表现为缺少龙骨突,胸骨前后很短,后缘缺少结构的分化。囿于波罗赤鸟局限的材料,本文暂不讨论它和始祖鸟的系统关系。

蒙古早白垩世的 *Ambiortus* (kurochkin, 1985), 我国早白垩世的甘肃鸟 (*Gansus yumenensis*, 侯连海等, 1984) 以及朝阳鸟(侯连海等, 1993), 都明显较同期的其它许多鸟类进步,不少特征与现生鸟类更加接近。根据已有的材料,它们和反鸟亚纲之间没有较直接的关系。

华夏鸟,最初只是被笼统认为和反鸟比较相似(周忠和等, 1992), 不久便被建议归入反鸟亚纲 (Zhou, in press)。尽管在许多方面,波罗赤鸟和华夏鸟都很相似,但仍然存在显著的区别。前者至少具备以下几点不同于后者的特征:(1) 嘴具利钩;(2) 前颌骨的前端主体部分与鼻突之间具有一个向上的浅凹;(3) 胸骨的侧突在远端只稍许扩大;(4) 股骨近端转子较为发育;(5) 跗蹠骨的三个趾骨滑车高差较小。此外,波罗赤鸟的前颌骨上未见牙齿,如果确已退化,那么这也是区别于华夏鸟的特征之一。

中国鸟在腕掌骨、坐骨等结构上具有的一些特征表明,这一鸟类也应归入反鸟亚纲。在三个趾骨滑车的相对高度这一特征上,它和波罗赤鸟存在明显不同(图4)。另一可能的区别是:波罗赤鸟的尾综骨比跗蹠骨长,而中国鸟的情况相反。

值得提出的是,最近董枝明 (Dong, 1993) 报导了内蒙鄂尔多斯盆地发现的一块早

白垩世的鸟类化石。由于标本上只保存了肩带和前肢的骨骼, 因此无法与波罗赤鸟进行对比。笔者同意董枝明将这一尚未命名的鸟类归入反鸟亚纲的意见, 但同时又认为这一结论仍需通过进一步的特征分析才能得以证实。

西班牙发现的三种早白垩世的鸟类, 即: *Noguerornis* (Lacasa, 1989; 1991), *Concornis* (Sanz et al., 1992) 和 *Iberomesornis* (Sanz et al., 1992) 可能都可以归入反鸟亚纲。其中, *Noguerornis* 只保存了叉骨和前肢, 因而暂时与 *Boluochia* 无法比较; *Concornis* 保存的骨骼也十分有限, 在跗蹠骨远端结构等方面也容易和波罗赤鸟相区别; *Iberomesornis* 曾被认为是早白垩世最原始的鸟类 (Sanz et al., 1992; Chiappe pers. comm.)。

但本文作者有幸对此标本进行过观察, 结果发现这很可能是一个未成年的个体。无论是其脊椎疏松的结构, 还是许多长骨远端不完全的骨化, 都充分显示了其未成年的特点。Kurochkin (pers. comm.) 与本文作者在这一点上看法不谋而合, 他认为, 跗蹠骨近端没有愈合是这一鸟类未成年的证据之一。因此, *Iberomesornis* 具有的“愈合荐椎只包含五枚脊椎”, “尾综骨前几枚脊椎不完全愈合”等都可能是幼体特征, 因而不能被用作该鸟比其它同期鸟类更加原始的证据。尽管由于上述原因, *Iberomesornis* 的许多骨骼特征都不明显, 但同 *Concornis* 一样, 在跗蹠骨远端结构的特征上, 与 *Boluochia* 存在显著区别。

澳大利亚早白垩世的 *Nanantius*, 时代比波罗赤鸟稍晚。尽管只有一根胫跗骨的材料, *Nanantius* 显然已更加特化, 这表现在内踝宽已显著大于外踝宽。

总之, 根据以上比较和分析, 波罗赤鸟可与早白垩世已知所有鸟类相区别。但由于反鸟亚纲在早白垩世的分子多数保存不完整, 它们之间进一步的关系还有待将来更多的工作去探讨。

反鸟亚纲在晚白垩世的代表, 一般都更加特化, 飞行能力比早期类型有所提高。同时, 也产生了更大的分异, 并最终在中生代末期绝灭。

2. 有关波罗赤鸟生活习性的讨论

本文记述的材料虽然保存不全, 但已有的头骨及后肢等结构的一些特征, 多少能够指示这一小型鸟类生活的一些习性。

在鸟类后肢结构中, 除各骨骼的比例等特征外, 脚爪的形态对于识别鸟类栖息生活的习性也十分重要。波罗赤鸟的脚爪不仅明显长于其它趾节, 而且还十分钩曲。这是树栖鸟类的特征之一。为便于精确比较, 本文参照 Feduccia (1993) 对 500 种现生鸟类趾爪爪弧弧度的测量方法和分析的数据, 采用同一方法 (Feduccia, 1993, p. 790, Fig 1) 对波罗赤鸟的第 III 脚爪进行了测量, 测得其爪弧弧度约为 130° 左右。Feduccia 对三种现

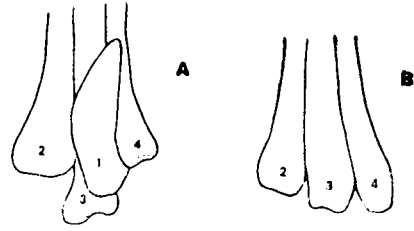


图 4 (Fig. 4) 右侧跗蹠骨远端的比较 (不按比例)。A: 三塔中国鸟 (自 Sereno et Rao, 1993, 并稍作修改), B: 郑氏波罗赤鸟。见简字说明 Comparison of the distal end of right tarsometatarsus (not to scale). A: *Sinornis santensis* (modified from Sereno et Rao, 1993); B: *Boluochia zhengi* (V9770)

生鸟类适应类型,即地栖鸟类(如鸡),树栖鸟类(如杜鹃)和攀援树干的鸟类(如啄木鸟)第 III 趾爪的爪弧弧度测量统计,得到的平均值分别是: 64.3° , 116.3° 和 148.7° 。很显然,波罗赤鸟同中国鸟($130-135^{\circ}$)一样,爪的钩曲与具有较强树栖能力的鸟类接近。

除脚爪的特征外,在后肢结构中,波罗赤鸟跗蹠骨的三个趾骨滑车的高度比较接近。本文作者曾对美国国家自然博物馆内收藏的 103 个科现生鸟类代表的类比标本进行过观察、比较,结果发现,三个趾骨滑车高度比较接近的鸟类通常为树栖类型。此外,在一些以地栖生活为主的鸟目中(如鸡形目,鹤形目),少数具有树上生活能力的类型,与其它种类相比,三个趾骨滑车高度的差异通常较小。由此可见这一特征与树栖生活适应的关系。

因此,如果认为始祖鸟脚爪的强烈钩曲是对其总体树栖能力不足的一种补偿 (Feduccia, 1993),那么,波罗赤鸟强烈钩曲的脚爪,则更可能是其树栖能力总体提高的一个重要组成部分。

头骨结构的适应通常与食性相关 (Wing, 1956)。波罗赤鸟的头骨具有的一个显著特征是嘴具利钩。这一特征与产于同一地点的华夏鸟存在明显的区别,而与掠夺性食肉鸟类较为相似。华夏鸟同始祖鸟一样,在前颌骨上还保留四枚牙齿。而在波罗赤鸟中,这几枚牙齿都没有保存,推测已经退化,如果事实如此,那么这些牙齿的退化,可能与钩状喙的形成有关,或者说是这一新的结构和适应的形成,加速了牙齿这一原始结构退化的过程。

此外,波罗赤鸟所具有的尖锐且强烈钩曲的脚爪,不仅表明这一鸟类具有较强树栖生活的能力,而且可能也是这一鸟类用于捕获猎物的工具。

除以上分析的特征外,根据本文作者对现生鸟类骨骼标本的观察和比较,多数猛禽类(如 Falconidae, Pandionidae, Tytonidae, Strigidae 等)在趾骨滑车的结构上还具有一些共同的特点,如第 II 趾骨滑车相对较宽,第 III 趾骨滑车的外支向后比较突出,第 IV 趾骨滑车向后突出等等。

波罗赤鸟的第 II 趾骨滑车也相对较宽,不仅稍宽于第 III 趾骨滑车,而且明显宽于第 IV 趾骨滑车。这一特征与多数猛禽类相似,而不同于多数其它类型的鸟类。除此特征外,波罗赤鸟的趾骨滑车结构还相当简单,不仅与猛禽类无法相比,而且在后肢结构等其它方面也都比所有现代鸟类原始。因此,尽管这一鸟类可能在一些结构的特征上,显示了与现代猛禽类的某些相似,并且可能也确已具备了掠食生活的习性,但其掠食的能力肯定还十分有限。因而,在严格的意义上,尚不能被称作真正的猛禽类。

但不管怎样,波罗赤鸟与同期的华夏鸟相比,毕竟代表了一种不同的适应类型。后者虽然也属于树栖鸟类,但头部并未出现钩状的喙。而另外一种也发现于同一地点的鸟类:朝阳鸟,则相对个体较大,也更加进步。但对于它的生活习性,目前还无从推知。总之,在辽宁发现的这一鸟类动物群中,多种不同类型的鸟类,以各自独特的方式适应环境。这在某种意义上也保证了这一动物群的繁荣。

本文作者衷心感谢孙艾玲、侯连海老师对本文的宝贵意见。张杰摄制图版,侯晋封帮助清绘插图,王昭制作标本印模,本文借此一并致谢。最后,还要特别感谢美国国家自然历史博物馆的 Storrs Olson 博士,为本文作者赴美比较现生鸟类标本,所作的许多努力。

简 字 说 明

cv	caudal vertebra	尾椎
de	dentary	齿骨
fem	femur	股骨
fem(r.)	right femur	右侧股骨
il(r.)	right ilium	右侧髂骨
isc	ischium	坐骨
ke	keel	龙骨突
lc	lateral condyle	外髁
lp	lateral process of sternum	胸骨的侧突
mc	medial condyle	内髁
mp	maxillar process of premaxilla	前颌骨的上颌突
na	nasal	鼻骨
np	nasal process of premaxilla	前颌骨的鼻突
pmx	premaxilla	前颌骨
pub	pubis	耻骨
pub(r.)	right pubis	右侧耻骨
py	pygostyle	尾综骨
r	rib	肋骨
ste	sternum	胸骨
sys	synsacrum	愈合荐椎
tbt	tibiotarsus	胫附骨
tmt	tarsometatarsus	跗蹠骨
I—IV	claw of digit I—IV	第 I—IV 趾爪
1—4	metatarsal I—IV	第 I—IV 蹠骨

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DISCOVERY OF A NEW ENANTIORNITHINE BIRD FROM THE EARLY CRETACEOUS OF LIAONING, CHINA

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Key words Liaoning; Early Cretaceous; Enantiornithes; habits

Summary

In September 1990, I collected three bird specimens from the Early Cretaceous of Liaoning, China. Among them, the best one (V9769) has been published and named *Cathayornis yandica* (Zhou et al., 1992); the second (V9941), with only a sternum impression, has not been referred to any known taxa yet; and the third (V9770), an incompletely articulated individual, is significantly different from either *Cathayornis* and *Chaoyangia* (Hou et Zhang, 1993) from the same site or any other known Early Cretaceous birds.

The third specimen is described here as a new genus and species: *Boluochia zhengi*, and further referred to Enantiornithes as at least four enantiornithine syna-

pomorphies can be recognized in this specimen: (1) intercondylar fossa of tibiotarsus narrow, medial condyle of tibiotarsus with fairly flat anterior margin in distal view; (2) metatarsus IV reduced; (3) slender lateral process of sternum with expanded distal end; and (4) presence of a peculiar dorsal process on proximal ischium.

Boluochia is believed to be a new enantiornithine bird from the Early Cretaceous of China, since *Cathayornis* from the same site had previously been proposed to be included in Enantiornithes (Zhou, in press). *Boluochia* is distinguished from *Cathayornis* in many respects, such as (1) skull with hooked bill; (2) presence of a concave surface between main body and nasal process of premaxilla; (3) lateral process of sternum only slightly expanded distally; (4) trochanter of femur relatively developed; and (5) trochleas for digits 2—4 close in height.

Finally, comparisons between *Boluochia* and extant birds in the skull and hindlimb structures also indicate that *Boluochia* is probably a bird with not only strong perching capability but also somewhat raptorial habit, although the primitiveness of many of its structures rules out the possibility of its being a raptorial bird in strict modern sense.

Systematics

Class Aves Linnaeus, 1758

Subclass Enantiornithes Walker, 1981

Order and Family indet.

Genus *Boluochia* gen. nov.

Species *Boluochia zhengi* sp. nov.

Diagnosis Small-sized bird. Beak hooked. Tooth probably absent on premaxilla. Sternum with very low incipient keel, lateral process of sternum with slightly expanded distal end. Ilium significantly reduced posteriorly, dorsal process present on ischium near its proximal end, pubis retroverted and strongly curved with a small pubic foot. Intercondylar fossa of tibiotarsus narrow, medial condyle of tibiotarsus with relatively flat anterior margin in distal view. Tarsometatarsus fused only proximally, midshaft of tarsometatarsus medio-laterally compressed and constricted, three digital trochleas of tarsometatarsus close in height. Pedal claws strongly curved and sharply pointed distally. Pygostyle markedly longer than tarsometatarsus.

Holotype an incompletely articulated individual. Preserved skeleton includes: the anterior portion of the skull, partial sternum, some crushed vertebrae, a complete pygostyle, fairly complete hindlimbs as well as pelvic girdles. Skeleton is preserved mostly as impression. Institute of Vertebrate Paleontology and Paleoanthropology Specimen Collection V9770.

Locality and horizon Boluochi, Chaoyang County, Liaoning Province, northeast China; Bluish-grey mudstone, Jiufotang Formation (Neocomian).

Etymology The generic name is derived from the locality of the holotype; the species name is dedicated to Professor Zheng Zuoxin, who is the doyen of Chinese Ornithology.

Description The description is based mainly on a cast from the natural mold. The skull is preserved only rostrally. The premaxilla is nearly complete; its

nasal process is straight, slender, and slightly dorso-ventrally compressed and it becomes thinner anteriorly. The main body (anterior portion) of the premaxilla bears no tooth on its ventral margin (there appears to be no evidence suggesting that the teeth were lost post-mortem), The main body of the premaxilla is also obviously convex dorsally, thus there exists a concave dorsal surface between the main body and the nasal process of the premaxilla. The bill is hooked. The maxillary process of the premaxilla tapers posteriorly. The putative lower jaw appears robust, but unfortunately is not completely preserved, only one tooth is found in the lower jaw. The tooth is nearly conical in shape, and its crown is constricted at the base. The two nasals are not well preserved, but their preserved anterior parts seem to be meeting along the midline. The maxillary part of the skull is fragmentary, it is difficult to know whether it is morphologically reduced or partly lost simply as a result of poor preservation.

The vertebral column is partly preserved and somewhat crushed, the vertebrae anterior to the synsacrum could not be recognized at all. The incomplete synsacrum, composed of unknown number of vertebrae, is well fused. A long flat crest is found on its dorsal side. The free caudal vertebrae are mostly crushed and inarticulated, therefore its total number remains uncertain. The pygostyle is completely preserved, and is markedly longer than the tarsometatarsus (Table 1); the crest on the dorsal side of the pygostyle is long and generally flat.

The sternum is preserved posteriorly. There seem to exist two pairs of sternal notches. The lateral process is long and slender, it is nearly parallel to the keel and slightly expanded at the distal extremity. The posterior process is short. The incipient sternal keel is low and ridge-shaped, its distribution is limited to the posterior part of the sternum.

The pelvic girdle on the left side is well preserved. The pubis is articulated and probably fused to some extent with the ischium proximally. The pubis is slender and strongly curved, it is also obviously retroverted. Although the pubic foot is still partially covered in the matrix, it is most probably small, triangle-shaped and dorsally directed. The ischium tapers posteriorly, there is a dorsal process near its proximal end. The pelvic girdle on the right side is fragmentary, with only an incomplete ilium and a questionable partial pubis preserved. The ilium posterior to the acetabulum is markedly reduced.

The distal half of the femur is well preserved on the left side, the distal end does not appear to be markedly wider than the shaft, a deep longitudinal groove is present near the distal end of the femur on anterior side. The right femur is slightly curved. Proximally, the head is round and well-produced, the trochanter is relatively developed with a convex lateral margin.

The left tibiotarsus is straight and well preserved. Proximally, no cnemial crest is formed; distally, the two condyles are less produced anteriorly. The anterior margin of the medial condyle appears fairly flat in distal view, the medial condyle does not seem to be markedly wider than the lateral one, the intercondylar fossa is narrow. The supratendinal bridge is undeveloped. The posterior side of the distal tibiotarsus is revealed on the right tibiotarsus, the internal ligamental prominence is developed.

The tarsometatarsus is completely preserved. Metatarsi II—IV are fused only proximally. Distal tarsi are fused into a big tarsal cap, which is also fused to the three main metatarsi. Metatarsal II is relatively straight, IV is slightly curved and reduced. The mid-shaft of the tarsometatarsus is medio-laterally compressed and strongly constricted. The three trochleas for digits 2—4 are close in height. The trochlea for digit 3 is almost as high as that for digit 4, both of them are only slightly lower than that for digit 2. The trochlea for digit 2 is slightly wider than that for digit 3, and both of them are obviously wider than that for digit 4, which is also slightly laterally deviated. The structures of the three trochleas for digits are all simple, with no obvious posterior projection, therefore they are nearly on the same plane. Metatarsal I is reversed J-shaped.

Most of the pedal phalanges and claws are preserved, but unfortunately not well articulated. The unguis phalanges are longer than the other ones, the sheathed claws are strongly curved and sharply pointed distally. The flexor tubercle is absent.

Comparison and discussion

Among the reported Early Cretaceous birds from China, *Chaoyangia* and *Gansus* (Hou et Liu, 1984) are relatively advanced types, and strikingly different from both *Cathayornis* and *Sinornis* (Sereno et Rao, 1992). *Boluochia* is slightly larger than *Cathayornis*, but less well preserved. It possesses some of the enantiornithine characters, which indicate that it represents undoubtedly another early member of the avian subclass: Enantiornithes. These characters include: (1) intercondylar fossa of tibiotarsus narrow (Walker, 1981; Molnar, 1986); medial condyle of tibiotarsus with a fairly flat anterior margin in distal view; (2) metatarsus IV reduced (Chiappe, 1992); (3) slender lateral process of sternum with expanded distal end (Zhou, in press); (4) presence of a peculiar dorsal process on proximal ischium (Martin, 1983; Zhou, in press).

Among the aforementioned characters, the character [(1) merits some explanation. The medial condyle of the tibiotarsus in *Boluochia* does not seem to be markedly wider than the lateral condyle as seen in *Nanantius* and other enantiornithine birds, this is surely a primitive condition. But in *Boluochia* the anterior margin of the medial condyle in distal view appears fairly flat, this feature is quite consistent with those found in other enantiornithine birds. As this feature is neither known in other birds nor reported in any putative avian ancestors, it is proposed here as another synapomorphy for Enantiornithes. The character "medial condyle markedly wider than lateral condyle" is thus regarded as a synapomorphy diagnosing a more specific enantiornithine group.

Elzanowski (in press) proposed that the lack of teeth might be another synapomorphy for Enantiornithes. This is surely not true, as both *Cathayornis* and *Boluochia* retained certain teeth, although the degeneration of teeth might well be a evolutionary trend in the subclass of Enantiornithes.

So far, in Early Cretaceous time, in addition to *Nanantius* (Molnar, 1986) from Australia, *Cathayornis* and *Sinornis* from China, the three Spanish birds: *Nogueroornis* (Lacasa, 1989; 1991), *Concornis* (Sanz et al., 1992) and *Iberomesornis* (Sanz et

al., 1992) may all be finally referred to *Enantiornithes* too.

It should also be noted that Dong (1993) reported an unnamed enantiornithine bird from the Ordos Basin of Inner Mongolia, China. It only includes pectoral girdle and forelimb elements and can not be directly compared *Boluochia*. Dong's reference of its being an enantiornithine bird does seem acceptable, although he did not provide precise and convincing character analysis and discussion supporting his conclusion.

The tibiotarsus structure in *Nanantius* is clearly more specialized than in *Boluochia*, as the medial condyle had become markedly wider than the lateral condyle in the former.

Except *Nanantius*, all known Early Cretaceous enantiornithine birds are from Neocomian. These birds are generally known as sharing a very similar combination of primitive and derived characters, but how they were differentiated and phylogenetically related have yet to be explored.

Boluochia can be easily distinguished from *Sinornis* in the structure of the distal tarsometatarsus (Fig. 4).

Boluochia is significantly different from *Cathayornis* in at least following characters: (1) presence of a hooked bill; (2) presence of a concave surface between main body and nasal process of premaxilla; (3) lateral process of sternum only slightly expanded distally; (4) trochanter of femur relatively developed; (5) trochleas for digits 2—4 close in height. Additionally, the absence of teeth on the premaxilla might be another striking difference.

The detailed difference between *Boluochia* and all other enantiornithine birds are not discussed here. The notable structures in the skull and hindlimbs of this bird are not only distinctive features from other birds but also indicative of certain adaptational significance.

The pes claws are strongly curved in *Boluochia*, and the arc curvature of its third pes claw is about 130. This feature is in agreement with those of modern birds with strong perching capability (see Feduccia, 1993).

A comparison of the relative height of the trochleas for digits 2—4 of *Boluochia* with those of extant birds observed by the present author comes to the same conclusion. In modern avian groups, those with less height difference among these trochleas are usually perching birds. Furthermore, in some terrestrial orders like Galliformes and Gruiformes, a few families with perching habits are found, in comparison with other ones, to have a less difference of relative trochlea height. Therefore, the reduction of the trochlea height difference can probably be considered as a useful indication of tree life. In *Boluochia*, the trochleas for digits 3 and 4 are nearly of the same height and both of them are only slightly lower than that for digit 2. This is therefore believed to be another evidence for the perching habit of *Boluochia*. If the strongly curved claws of *Archaeopteryx* are only an adaptative compensation for overall weak perching ability (Feduccia, 1993), then the strongly curved pes claws in *Boluochia* should be viewed as evidence for overall improvement of perching capability.

The adaptation in the head structure of birds are generally associated with feeding habits (Wing, 1956). A distinctive feature in the head of *Boluochia* is the

presence of a hooked bill. This structure bears much resemblance to those of predatory birds. The simultaneous absence of teeth on the premaxilla (if not due to preservational loss) is supposed to be at least related to the appearance of a hooked bill, and is therefore a significant difference from *Cathayornis*, which is still primitive in retaining four teeth on the premaxilla like *Archaeopteryx*.

The strongly curved pes claw not only indicates a strong perching capability but may also act as a fierce tool in its predatory life.

According to my observation on the synoptic specimen of modern avian skeletons housed in the National Museum of Natural History in Washington, D.C., many raptorial birds (like Falconidae, Pandionidae, Tytonidae, Strigidae, etc.) also share a few distinctive characters in the structure of the digital trochleas of the tarsometatarsus. They include: (1) trochlea for digit 2 relatively wide; (2) trochlea for digit 4 protruding more posteriorly; and (3) external rim of trochlea for digit 3 projecting more posteriorly. Among these characters, only character (1) is shared by *Boluochia*, in which the trochlea for digit 2 is slightly wider than the trochlea for digit 3, and both of them are obviously wider than the trochlea for digit 4. This is very similar to those in many raptorial birds, and is different from most other birds. On the other hand, all the three digital trochleas of the tarsometatarsus are very simple in structure and have no obvious posterior projection. Besides, this extinct bird is deemed to be a poorer flyer compared with extant volant birds in view of its primitiveness in many structural features. Although it may in fact have some raptorial habit similar to modern predatory birds, it can not yet be categorized as a predatory bird in strict modern sense.

The author is grateful to Prof. Sun Ai-lin, Li Jin-ling and Hou Lian-hai for their critical review and comments on the manuscript. The author wish to thank the Office of the Fellowships and Grants of the Smithsonian Institution for providing me a grant that supported my visit to the U.S.A. I am also especially indebted to Dr. Storrs Olson and Helen James for facilitating my visit in many ways and allowing me to live with their family during my stay in Washington, D.C., where I was able to examine the modern avian skeleton extensively. I also benefitted from discussions with Larry Martin and Alan Feduccia. The English summary is also greatly improved by Miao Desui. My thanks are also extended to Mr. Hou Jin-feng for making the drawings and Mr. Zhang Jie for preparing the photos.

图版说明 (Explanation of plate)

郑氏波罗赤鸟 *Boluochia zhengi* gen. et sp. nov. (V9770), $\times 1.7$

