

# 中国发现从始祖鸟到反鸟的 重要缺失环节<sup>1)</sup>

侯连海<sup>1</sup> 拉里·马丁<sup>2</sup> 周忠和<sup>1,2</sup> 艾伦·费多契亚<sup>3</sup>

1 中国科学院古脊椎动物与古人类研究所 北京 100044

2 美国堪萨斯大学生态学与系统学及自然历史博物馆 劳伦斯, 堪萨斯 66054

3 美国北卡罗来纳大学生物系 查佩尔希尔 27599-3280

**摘要** 最近在中国辽宁省北票地区中生代义县组地层中又发现了迄今最为原始的反鸟——始反鸟(*Eoenantiornis buhleri* gen. et sp. nov.)。在系统进化上,这一具有牙齿的反鸟介于始祖鸟和华夏鸟(*Cathayornis*)之间,后者也产于中国的同一地区的早白垩世九佛堂组中。这种过渡或转变突出地表现在其肩带上。新属与其他鸟类的牙齿具有共同的特征,这也说明该种齿型和其独特的植入和替换方式是所有已知中生代具牙齿鸟类的共同特征。该鸟小于始祖鸟和孔子鸟,但大于早白垩世的反鸟类。这表明在反鸟类的早期演化中,向小个体方向演化趋势所起的重要作用。

**关键词** 中国辽宁,中生代,原始反鸟类

**中图法分类号** Q915.864

**鸟纲** Aves Linnaeus, 1758

**蜥鸟亚纲** Sauriurae Haeckel, 1866

**反鸟次亚纲** Enantiornithes Walker, 1981

**始反鸟目** 新目 Eoenantiornithiformes ord. nov.

**始反鸟科** 新科 Eoenantiornithidae fam. nov.

**始反鸟属** 新属 *Eoenantiornis* gen. nov.

**属型种** 步氏始反鸟 *Eoenantiornis buhleri* sp. nov.

**特征** 吻短,具牙齿;上颌骨背突构成整个外鼻孔的后缘;颈椎11枚。“V”形叉骨,下突长;鸟喙骨相对较短,末端宽;胸骨顶端不强烈向后凹陷,胸骨具有单一、较短的后侧突;前肢爪不如华夏鸟的退化。腕掌骨短,第四掌骨扩展但不与第三掌骨末端愈合;第二指骨细长。尾综骨长。

1) 国家自然科学基金和中国科学院资源与生态环境研究重大项目(KZ2951-B1-410)资助。

收稿日期:1999-01-18

**步氏始反鸟 *Eoenantiornis buhleri* sp. nov.**

(图版 I: 图 1)

**正型标本** 一接近完整的个体, 中国科学院古脊椎动物与古人类研究所标本编号: V11537.

**产地和时代** 辽宁省北票市上园地区黑蹄子沟义县组底部泥岩夹层, 晚侏罗世或早白垩世。

**特征** 同属的特征。

**ARCHAEOPTERYX TO OPPOSITE BIRDS—MISSING LINK  
FROM THE MESOZOIC OF CHINA**HOU Lian-Hai<sup>1</sup> MARTIN, Larry D.<sup>2</sup> ZHOU Zhong-He<sup>1,2</sup> FEDUCCIA, Alan<sup>3</sup><sup>1</sup> Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044<sup>2</sup> Natural History Museum and the Department of Systematics and Ecology, University of Kansas Lawrence, KS 66045, USA<sup>3</sup> Department of Biology, University of North Carolina at Chapel Hill Chapel Hill, NC 27599-3280, USA

**Abstract** The Confuciusornis Fauna of northeastern China has produced the oldest known enantiornithine birds—*Eoenantiornis buhleri* Gen. et sp. nov. A new toothed form lies between *Archaeopteryx* and the Early Cretaceous enantiornithine, *Cathayornis*, from the same region of China. The transition is most marked in the shoulder girdle. The teeth of the new genus have the characteristics of other bird teeth and demonstrate that this tooth form along with its distinctive implantation and replacement is characteristic of all known toothed birds.

**Key words** Liaoning, China, Mesozoic, primitive enantiornithine

The discovery of the Enantiornithes by C. Walker (1981) was one of the most important ornithological events of this century. Over half of all avian evolution during its first 80,000,000 years concerns these birds. A dichotomy between the Enantiornithes and the modern radiation is widely accepted (Hou *et al.*, 1996). The relationship of *Archaeopteryx* with the Enantiornithes is more controversial, ranging from inclusion in an extinct subclass Sauriurae (Wellnhofer, 1993) to consideration of *Archaeopteryx* as the common ancestor of all later birds. The *Confuciusornis* fauna of the Liaoning province in northeastern China is the most important fauna bearing on this question as it includes the next oldest birds to *Archaeopteryx*. A new bird from this fauna provides a link between *Archaeopteryx* and more advanced enantiornithines. The preservation of the bastard wing (alula) on the new specimen represents the evidence of this modern

avian structure. It also provides the best preserved examples of avian teeth after *Archaeopteryx* and before the Late Cretaceous, demonstrating that all birds share a uniform tooth morphology presently unknown in adult or juvenile dinosaurs. *Eoenantiornis* is smaller than *Archaeopteryx* and *Confuciusornis*, but larger than Early Cretaceous enantiornithine birds (Martin, 1995), indicating a trend towards smaller body size played an important role in the early evolution of enantiornithine birds.

**Class Aves Linnaeus, 1758**

**Subclass Sauriurae, Haeckel, 1866**

**Infraclass Enantiornithes Walker, 1981**

**Order Eoenantiornithiformes ord. nov.**

**Family Eoenantiornithidae fam. nov.**

**Genus *Eoenantiornis* gen. nov.**

**Type species** *Eoenantiornis buhleri* sp. nov.

**Diagnosis** Moderate sized toothed bird with a short rostrum; deep skull; dorsal maxillary process forming the entire posterior margin of narial opening; and long neck with 11 cervicals. "V" shaped furcula with a long hypocleidum. Coracoids broad at base and relatively short. Single, short postero-lateral process on the sternum. Claws on wings less reduced than in *Cathayornis*. Carpometacarpus short with outer metacarpal (IV) extending past but not fused to the distal end of the middle metacarpal (III). Manual digit II slender and long. Pygostyle long. Sternum not strongly emarginate posteriorly. Possible fragments of gastralia present.

***Eoenantiornis buhleri* sp. nov.**

(pl. I; fig. 1)

**Holotype** A nearly complete skeleton but lacking the right wing. Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) Collection V11537.

**Horizon and locality** Yixian Formation (Late Jurassic–Early Cretaceous); Shihetun, Beipiao, Liaoning, China.

**Diagnosis** as for the genus.

**Etymology** Eo, greek dawn; enantiornis, opposite bird; buhleri, for the late Paul BÜhler, a distinguished German functional morphologist and paleornithologist.

**Measurements**(in mm) skull length, 22; sternum length, 22; sternum width, 16; Cervical vertebrae,  $\approx$  29; coracoid length, 12.5, coracoid (base) width, 6.0; wing, 94; humerus length, 29.5; ulna length, 31; carpometacarpus length, 12; femur length, 26.5; tibiotarsus length 31; tarsometatarsus length, 22.3.

**Discussion** The skull (fig. 1, A) as compared to either *Archaeopteryx* or

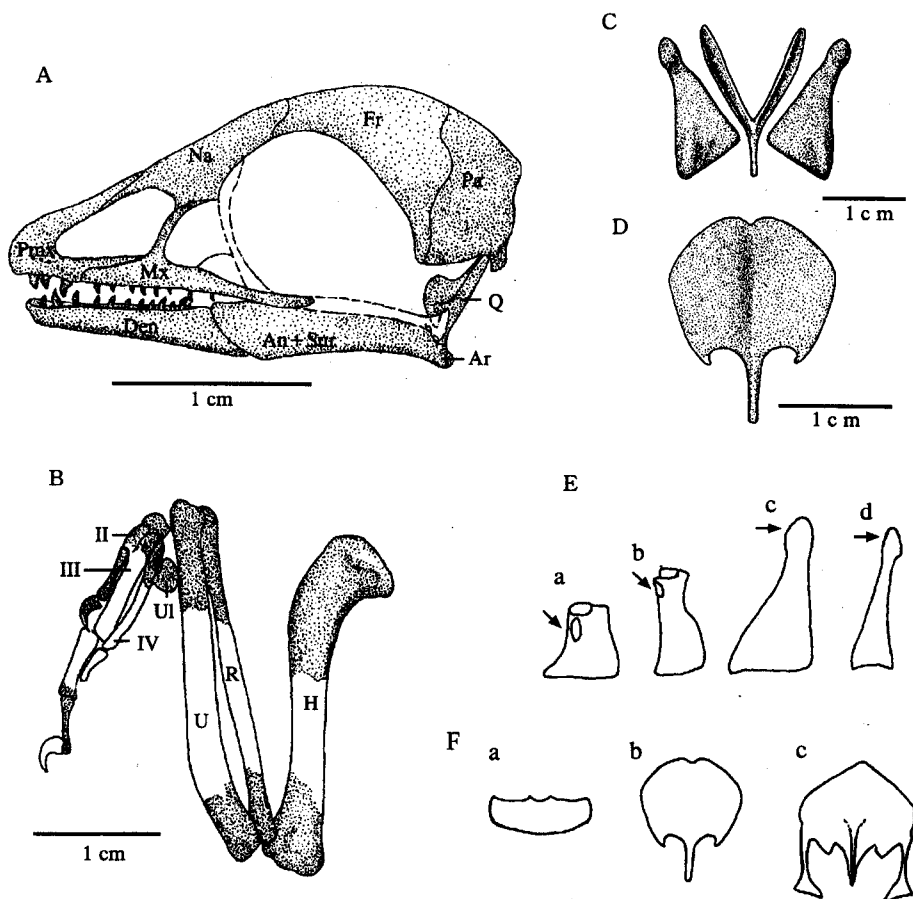


图 1 A. 步氏始反鸟头骨复原; B. 步氏始反鸟翼的左背面; C. 步氏始反鸟的叉骨和乌喙骨后面复原; D. 步氏始反鸟胸骨背面复原; E. 早期鸟类乌喙骨比较: a. 印板石始祖鸟, b. 巴伐利亚始祖鸟, c. 步氏始反鸟, d. 反鸟(箭头指示 a~b 中二头肌结节的发育和 c~d 中乌喙骨顶部的变化); F. 胸骨比较: a. 巴伐利亚始祖鸟, b. 步氏始反鸟, c. 燕都华息鸟

Fig. 1 A. Reconstruction of the skull of *Eoenantiornis buhleri*; B. Left dorsal view of the wing of *Eoenantiornis buhleri*; C. Reconstruction of a posterior view of the furcula and coracoids of *Eoenantiornis buhleri*; D. Reconstruction of a dorsal view of the sternum of *Eoenantiornis buhleri*; E. Hypothetical transformation showing anterior views of right coracoids going from older to younger: a. *Archaeopteryx lithographica*; b. *A. bavarica*; c. *Eoenantiornis buhleri*; d. *Eanatiornis* sp. (arrow shows biceps tubercle in a~b and acrocoracoid in c~d.); F. Hypothetical transformation series of sterna: a. *Archaeopteryx bavarica*; b. *Eoenantiornis buhleri*; c. *Cathayornis yandica*

简字说明 Abbreviations: An + Sur, angular and surangular 隅骨和上隅骨; Ar, articular 关节骨; Den, dentary 齿骨; Fr, frontal 额骨; H, humerus 肱骨; Mx, maxilla 上颌骨; Na, nasal 鼻骨; Pa, parietal 顶骨; Pmx, premaxilla 前颌骨; Q, quadrate 方骨; R, radius 挠骨; U, ulna 尺骨; UI, ulnare 尺腕骨; II, metacarpal II 第 2 掌骨; III, metacarpal III 第 3 掌骨; IV, metacarpal IV 第 4 掌骨

*Cathayornis* (Martin and Zhou, 1997) is remarkably short and deep with a reduction of the anterior part of the anteorbital fenestra and the development of a very long, slender dorsal process of the maxilla. There is no evidence of subsideray divisions of the antorbital fenestra as seen in *Archaeopteryx* and *Cathayornis* and there seems to be no room for them. The maxillary teeth as preserved are smaller than those of the premaxilla (fig. 1, A). The nasals meet at the midline. They are short and broad. The posterior jaw is preserved in such a way that it is viewed from a dorso-interior aspect and we have not been able to make it out in detail but it seems to lack a mandibular fenestra. The teeth are set in a groove as in *Hesperornis*. *Eoenantiornis* provides a remarkable intermediary between *Archaeopteryx* and more advanced flying enantiornithines like *Sinornis* (Serenio and Rao, 1992) and *Cathayornis* (Zhou *et al.*, 1992). The anterior edge of the sternum is grooved by coracoidal sulci along its entire width, accommodating wide coracoidal bases. The short coracoids are intermediate between those of *Archaeopteryx bavarica* (Wellnhofer, 1993) and *Enantiornis* (fig. 1, E). The coracoid is thus more advanced than *Archaeopteryx* or *Confuciusornis* (Hou *et al.*, 1995) but less so than in *Cathayornis* and *Enantiornis* (fig. 1, E). The sternum is more elongated than in *Archaeopteryx bavarica* (Wellnhofer, 1993) and has the long posterior process that forms most of the keel as in *Cathayornis* (fig. 1, F). Unlike *Cathayornis* and other advanced enantiornithine birds, the posterior margin of the sternum is not double notched (fig. 1, F). The furcula has the typical "V" shaped form (fig. 1, F) found in other enantiornithine birds with a long hypocleidium, and the dorsal (posterior) surface grooved down its entire length as in *Archaeopteryx* and *Confuciusornis*, giving it a different cross section from that of ornithurine birds.

Ostrom (1976) proposed a hypothetical transformation series leading from *Archaeopteryx* to a modern flying bird (*Cathartes*). His scheme can now be substantiated to a remarkable degree for enantiornithine birds (fig. 1, E) including the transformation of the "biceps tubercle" into the acrocoracoid. The formation of the triosseal canal in enantiornithine birds is so different from that in ornithurine birds that it seems likely that this transformation series occurred independently in the two avian lineages (Sauriurae; Ornithurae). As might be expected, the sternum shows a parallel transformation series (fig. 1, F) to that of the coracoids. The sternum begins as little more than a crossbrace between the coracoids (*Archaeopteryx bavarica*) and elongates (*Eoenantiornis*), and finally forms a posterior keel and emarginations (*Cathayornis*). The sternum in modern birds begins developmentally as parallel extensions from the coracoids. In ornithurine birds it includes a central interclavicle component that may be absent in the sterna of the Sauriurae.

*Eoenantiornis* (pl. I) has a relatively long neck when compared to *Confuciusornis*

and *Archaeopteryx*. It is composed of some 11 cervical vertebrae. The synsacrum is fused and probably composed of 6~8 vertebrae. The pygostyle is similar to that of *Cathayornis*, but slightly shorter than *Confuciusornis*. It tapers distally like in other enantiornithine birds.

The humerus (fig. 1, B) has a flat deltoid crest and an internally slanted head, which are typical of enantiornithine birds. The humerus is about 95% the length of the ulna, and in *Cathayornis* it is 94%. In *Archaeopteryx* the humerus is almost the same length as the ulna (103% of the ulna). In *Confuciusornis sanctus*, the humerus is 106% of the ulna in length. The occurrence of a relative long ulna as compared to humerus represents a general evolutionary trend in early avian evolution. In modern birds the ulna is generally longer than the humerus. The carpometacarpi are short in *Eoenantiornis* and *Cathayornis* (44% and 47% of the ulnae respectively), they are longer in *Confuciusornis* (63%) and most modern birds.

The hand of *Eoenantiornis* (fig. 1, B) also shows transition from *Archaeopteryx* to Early Cretaceous enantiornithine birds (*Cathayornis*). There are two claws on each wing. The middle metacarpal (III) and the middle digit are more robust than the other two. The first manual digit (II) is relatively longer than in *Cathayornis*, but shorter than in *Archaeopteryx* and *Confuciusornis*. The first phalange of the middle digit (III) is robust, but its distal end is not as expanded as in *Cathayornis*. The second phalange of the middle digit is relatively slender and longer than in *Cathayornis*, but it is shorter than in *Archaeopteryx* and *Confuciusornis*. Like in *Cathayornis*, the outer digit (IV) has only one phalange compared with three phalanges in *Archaeopteryx* and *Confuciusornis*, although it is less reduced than in *Cathayornis*. The claw on the outer digit may also be lost. The hand of *Eoenantiornis* is generally much reduced compared with *Archaeopteryx* and *Confuciusornis*, but it still has large enough claws to give some assist in climbing.

Previously the oldest known record of a bastard wing (alula) was from *Eoalulavis* of the Early Cretaceous of Spain (Sanz *et al.*, 1996). The impression of the bastard wing was also preserved in the specimen of *Eoenantiornis* (pl. I), showing that this unique modern avian structure appeared during the early development of modernized flight structures in the Enantiornithes.

The tarsometatarsus is fused proximally, as in all other sauriurine birds. The reflexed hallux claw is not hypertrophied as in other enantiornithines and the pedal claws are not as recurved.

The excellent preservation of the teeth (pl. I) is important as they show the typical short, unserrated crowns with waisted bases and expanded roots of other bird teeth. This establishes beyond reasonable doubt that this type of tooth is uniform across the Class Aves where teeth occur. The form of bird teeth, their implantation

and replacement are a formidable obstacle to the widely held hypothesis of a dinosaurian origin for birds. Teeth of this type can be closely duplicated in crocodylians but are still unknown in adult and juvenile dinosaurs in the 17 years since the salient features of bird teeth were first elucidated (Martin *et al.*, 1980). Key features found in *Archaeopteryx* and *Eoenantiornis* but not in theropod dinosaurs include: no intermandibular joint in the lower jaw; the furcula grooved unlike the supposed furcula of *Velociraptor*; the scapula–coracoid forms a 90° angle as in all known volant bird; the hand is composed of digits 2–3–4 and the semilunate bone sets on metacarpal III as in modern birds; ischium and pubis reflected posteriorly and having features for pubic–breathing, and a reflexed hallux, a condition still undemonstrated for any theropod.

Birds with the most primitive flight apparatus (*Archaeopteryx*, *Confuciusornis*) are about the size of a crow. Slightly larger size is useful for gliders and primitive powered flight where gravity provides part of the energy required. Taking off from flat surfaces is more demanding and all the energy for lift comes from the wing stroke. In this case it is useful to decrease wing–loading by simply decreasing body size. *Eoenantiornis* is the oldest enantiornithine bird showing advanced features needed to take off from the ground, but may not have perfected this capability as the wing claws used for climbing are still well developed. It is about half the size of *Confuciusornis* or about the size of a robin. The more advanced Early Cretaceous birds that were fully capable of flight from the ground up (*Sinornis*, *Cathayornis*) had so reduced their size that they were no bigger than a sparrow. The Ornithurine birds went through this size bottleneck earlier and had begun to regain body size by the Early Cretaceous.

**Acknowledgments** We thank D. Miao for his kind help; the Chinese Natural Science Foundation (no, 49672088); the National Geographic Society (U. S.); and the 95 Grand Project of the Chinese Academy of Sciences for supporting fieldwork; Mary Tanner for drawings and John Chorn for the photographs. The manuscript was critically read by J. Chorn and D. Miao.

### References

- Feduccia A, 1996. The Origin of Evolution of Birds. New Haven and London: Yale University Press. 1~194
- Hou L H, Martin L D, Zhou Z H *et al.*, 1996. Early adaptive radiation of birds: evidence from fossils from northeastern China. *Science*, **274**:1164~1167
- Hou L H, Zhou Z H, Gu Y C *et al.* 1995. *Confuciusornis sanctus*, a new late Jurassic saucurine bird from China. *Chinese Sci Bull*, **40**(8):726~729(in Chinese)
- Hou L H, Zhou Z H, Martin L D *et al.* 1995. A beaked bird from the Jurassic of China. *Nature*, **377**:616~618
- Martin L D, 1995. The Enantiornithes: Terrestrial birds of Cretaceous in avian evolution. *Courier Forschungsinst*

- Senckenberg, 181:23~36
- Martin L D, Stewart J D, Whetstone K N, 1980. The origin of birds: structure of the tarsus and teeth. *Auk*, 97: 86~93
- Martin L D, Zhou Z H, 1997. *Archaeopteryx*-like skull in Enantiornithes bird. *Nature*, 389:556
- Ostrom J, 1976. Some hypothetical anatomical stages in the evolution of avian flight. *Smith Contr Paleobio*, 27: 1~21
- Sanz J L, Chiappe L M, Perez-Moreno B P *et al.*, 1996. An early cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature*, 382:442~445
- Sereno P C, Rao C G, 1992. Early evolution of avian flight and perching new evidence from the lower cretaceous of China. *Science*, 255:845~848
- Walker C A, 1981. New subclass of birds from the Cretaceous of South America. *Nature*, 292:51~53
- Wellnhofer P, 1993. Das siesta Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. *Archaeopteryx*, 11:1~47
- Zhou Z H, Jin F, Zhang J Y, 1992. Preliminary report on a Mesozoic bird from liaoning, China. *Chinese Sci Bull*, 37(16):1365~1368

### Explanations of Plate I

Holotype of *Eoenantiornis buhleri*, IVPP V11537,  $\times 1.2$



