

·特 稿·

# First avialian bird from China

## 中国发现世界上最原始的鸟类化石：

## 华美金凤鸟(新属、新种)

## (*Jinfengopteryx elegans* gen. et sp. nov.)

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**Abstract** *Archaeopteryx* has been recognized as the earliest known bird in the world for more than 140 years, and it is well documented from seven skeletons with feather impressions and an isolated feather. *Archaeopteryx* shows a combination of diapsid (“reptile-like”) plesiomorphies and the derived (“bird-like”) features. It provides the most important evidence for the hypothesis that birds originated from a dinosaurian ancestor. Since 1990s, the rich assemblage of taxonomically diverse and numerically abundant feathered theropods and primitive birds have been found from the Early Cretaceous Yixian Formation of western Liaoning, China. These findings further strengthen the hypothesis that birds were derived from small theropod dinosaurs. However, no avialian birds were found from China at that time. Until 2002, two avialian birds, *Shenzhouraptor sinensis* and *Jixiangornis orientalis*, were reported from the Early Cretaceous beds in western Liaoning, China. Here we describe a new well-preserved avialian bird from northern Hebei, China. Our phylogenetic analyses have placed it at the root of the avialian family tree. It sheds new light on the phylogenetic relationship between non-avian theropods and avian theropods (birds) and on the definition of birds.

**Key words**: avialian birds; definition of birds; Qiaotou Formation; Fengning, northern Hebei Province; China

**摘要** 始祖鸟的发现被认为是19世纪最重要的科学发现之一,迄今为止共发现了7枚保存骨骼、羽毛印痕的化石标本和1枚单根羽毛化石标本。由于始祖鸟既显示了明显的爬行动物的特征又保存了精美的羽毛,140多年来人们一直将其作为介于恐龙与鸟类之间的“中间环节”(“missing link”),但更倾向认为它是世界上最古老的鸟,或鸟类的始祖。由于始祖鸟化石稀少,加之地理分布十分局限,长期以来国际上一直围绕鸟类起源问题展开了激烈的争论,提出了各种各样的假说。直到20世纪90年代,在中国辽西晚中生代地层中发现了大量长羽毛的恐龙和原始鸟类化石,有力地支持了鸟类起源于小型兽脚类恐龙的学术观点,使赫

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胥黎140多年前提出的“假说”成为当今国际科学界占主流地位的学说和理论,基本解决了长期困扰国际科学界的鸟类起源问题。遗憾的是,在过去的几年中,中国一直没有发现与德国始祖鸟十分接近,或与德国始祖鸟处于同样进化水平的原始鸟类化石。这种缺憾使我们难以对鸟类定义问题进行深入的研究和探讨。2002年,笔者等在中国辽西早白垩世地层中发现了2种初鸟类化石,即中华神州鸟和东方吉祥鸟。通过比较解剖学研究和支序分析,这2种初鸟类要比始祖鸟略微进步一些,在研究鸟类的早期演化方面具有重要意义;但仍然难以对鸟类定义问题作进一步研究。本文首次报道了一件采自中国河北省丰宁县龙凤山桥头组的初鸟类化石——华美金凤鸟(新属、新种) (*Jinfengopteryx elegans* gen. et sp. nov.), 与其共生的化石有 *Lycoptera davidi*, *Peipiaosteus pani*, *Yanosteus longidorsalis* (鱼类); *Jibeinia luanhera*, *Protopteryx fengningensis* (鸟类); *Ephemeropsis trisetalis* (昆虫)及少量植物。支序分析表明,华美金凤鸟处于初鸟类谱系树的基部,比始祖鸟略微原始,与后者为姊妹群关系。奔龙等兽脚类恐龙是它们的外类群。金凤鸟、始祖鸟是中华神州鸟等原始鸟类的外类群。这说明华美金凤鸟处在恐龙向鸟类演化过程中一个非常关键的位置,是世界上迄今所发现的最原始的初鸟类。华美金凤鸟的发现对研究鸟类起源、鸟类飞行起源、恐龙-鸟类的系统关系等方面具有重要的科学意义。

关键词:初鸟类;鸟类定义;桥头组;丰宁;冀北;中国

中图分类号:Q915.865

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Northern Hebei-western Liaoning is one of the classic area for studying the late Mesozoic terrestrial strata and the Jehol Biota. In the past decade, the discoveries of the rich feathered non-avian theropods and primitive birds greatly promoted the study of the avian origin. In this paper, we describe a new exceptional avialian bird, which was unearthed from the dark gray thin-bedded tuffaceous silty mudstones of the middle part of the Qiaotou Formation in Waigoumen area, Fengning County, Hebei Province, China. The associated fossils are some common elements of the Jehol Biota, such as *Lycoptera davidi*, *Peipiaosteus pani* and *Yanosteus longidorsalis* (fishes), *Jibeinia luanhera* and *Protopteryx fengningensis* (birds), *Ephemeropsis trisetalis* (insects) and some plants<sup>[1,2]</sup>. The new finding provides further crucial information for our understanding the phylogenetic relationships of basal birds and the definition of birds.

## Systematic Palaeontology

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Avialae Gauthier, 1986

*Jinfengopteryx elegans* gen. et sp. nov.

**Etymology:** *Jinfeng* (Chinese): golden phoenix, the queen of birds in Chinese folklores; *-pteryx* (Greek): wing or feather; *elegans* (Greek): elegant.

**Holotype:** A complete skeleton with skull and feather impressions (Chinese Academy of Geological Sciences, Institute of Geology, Beijing:

CAGS-IG-04-0801).

**Locality and horizon:** Longfengshan Hill, Fengning County, Hebei Province, China. The holotype is from the middle part of the Qiaotou Formation, which is stratigraphically lower than the *Sinosauropteryx*-bearing beds of the Yixian Formation<sup>[2]</sup>.

**Geological age:** The age of the Qiaotou Formation is equivocal. It has been suggested to be Late Jurassic by some paleontologists, or Early Cretaceous by others<sup>[2]</sup>. The work

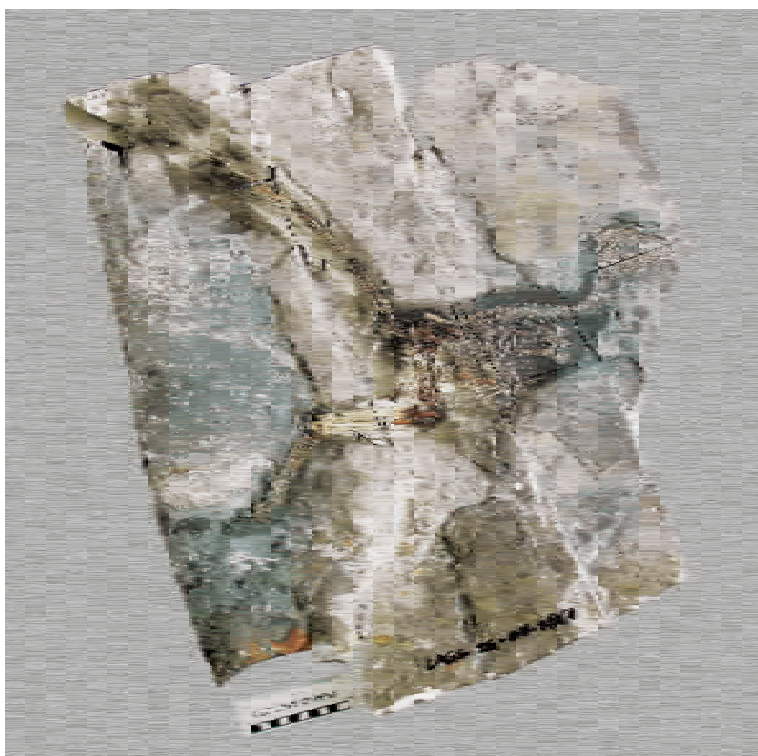


Fig.1 Holotype of *Jinfengopteryx elegans* gen. et sp. nov. (CAGS-IG-04-0801)

of the isotopic dating is in process.

**Diagnosis :** Large-sized avialian bird. It can be distinguished from *Archaeopteryx* in having more and closely packed teeth (18 teeth in the lower and upper jaws respectively), a relatively shorter and higher preorbital portion of the skull, relatively shorter metacarpal II in comparison to metacarpal I, and the comparatively longer and more robust hindlimb with the forelimb-to-hindlimb ratio of 0.62. It is different from *Shenzhouraptor*<sup>[3,4]</sup> and *Jixiangornis*<sup>[5]</sup> mainly in possessing much more teeth and much shorter forelimb compared to hindlimb. It also differs from troodontids in having fewer and unserrated teeth, and from dromaeosaurids in absence of the extremely long extensions of prezygapophyses of caudal vertebrae.

## Description and Comparison

The new avialian bird is relatively large, being approximately 54.8 cm from the rostrum to the end of tail (Table 1). The holotype is nearly complete except that some parts are preserved as impressions (Figs. 1, 2). The skeleton and associated feathers are exposed in lateral view. The skull is triangular in outline, with a relatively deep temporal region (Figs. 3, 4), similar to that of *Archaeopteryx lithographica*<sup>[6,7]</sup>. The premaxilla protrudes beyond the tip of the mandible. The long nasal processes of both premaxillae are displaced, implying that the two premaxillae are not fused. The maxillary process of premaxilla is unknown. The antorbital cavity is large, and consists of three fenestrae: the relatively large internal antorbital fenestra, large maxillary fenestra and small premaxillary fenestra. These fenestrae are nearly identical in proportion and topographical relationship to those in *Archaeopteryx lithographica*<sup>[8]</sup>. The paired nasals are elongated, and their external surface bears many striations. Within the nasals, an elongate cavity located on the posterior part of the nasal, which is tentatively interpreted to be a nasal sinus. The sutures between the frontals and the parietals are clear. The orbit is large and round in lateral view, and the scleral ring consists of 12 or 13 scleral plates, comparable

to *Archaeopteryx*, which has 11 to 12 scleral plates<sup>[7]</sup>.

The lingual aspect of left mandible is exposed, and bears 18 dentary teeth. The teeth are closely spaced, and there are no interdental plates between the dentary teeth, unlike the case in *Archaeopteryx lithographica*, which has interdental plates and the teeth are widely spaced<sup>[7,9]</sup>.

Two thread-like bones under the posterior part of the

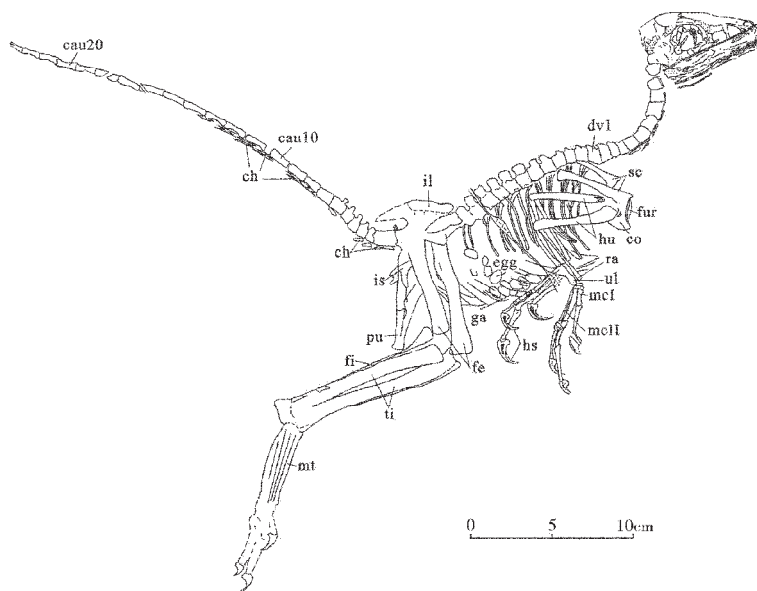


Fig.2 Line drawing of the holotype of *Jinfengopteryx elegans* gen. et sp. nov. (CAGS-IG-04-0801)

Abbreviations : cau10—the 10th caudal vertebra ; cau20—the 20th caudal vertebra ; ch—chevron ; co—coracoid ; dv1—the 1st dorsal vertebra ; fe—femur ; fi—fibula ; fur—furcula ; ga—gastralia ; hs—horny sheath ; hu—humerus ; il—ilium ; is—ischium ; mcl—metacarpal I ; mclII—metacarpals II ; mt—metatarsals ; ra—radius ; sc—scapula ; pu—pubis ; ti—tibia ; ul—ulna



Fig.3 Skull of *Jinfengopteryx elegans* gen. et sp. nov. (CAGS-IG-04-0801)

mandibles are hyoid bones. The two ends of these hyoid elements are slightly expanded.

The premaxilla has 4 teeth and the maxilla 14 teeth, the upper and lower teeth are very closely spaced (Figs. 3 A). By comparison, the lower teeth in *Archaeopteryx* are far fewer in number and have interdental plates<sup>[9,40]</sup>. Some teeth of the new taxon show a slight constriction at the base of the crown, but no strongly expanded root. These features are similar to the condition in *Archaeopteryx*<sup>[7]</sup>.

The vertebral column includes 23 presacral, unknown number of sacral and 23 caudal vertebrae. Although cervical vertebrae are preserved as impressions, the outlines of the cervical vertebrae are well-preserved and allow the identification of about 12 cervical vertebrae including the atlas and axis. The thread-like, elongated cervical ribs are present. The anterior dorsal vertebrae are preserved also as impressions. By the number of the associated ribs and the spines of the posterior dorsal vertebrae, 11 dorsal vertebrae can be recognized. The neural spines of the last five dorsal vertebrae are well preserved and have slightly expanded tips.

As in *Archaeopteryx*, *Rahonavis*<sup>[11]</sup>, *Shenzhouraptor*<sup>[12]</sup> and *Jixiangornis*<sup>[5]</sup>, the new avialian bird retains a long bony tail and lacks any evidence of pygostyle. The caudal series consists of 23 vertebrae, and this is very close to the count of caudal vertebrae of *Archaeopteryx* and *Caudipteryx*<sup>[13~15]</sup>. The caudal series is 27.3 cm long, occupying approximately 50% of the body length. Except for the first caudal, which is twice as long as the second, the second to fourth caudal vertebrae are short. At the fifth caudal vertebra, the centrum becomes markedly longer but more slender. Beyond the fifth caudal vertebra, the centra have almost the same length till the end of the tail, although they become successively thinner distally. A distinctive transitional point in the caudal series begins at the fifth and sixth caudal vertebrae. The anterior chevrons are elongate with anteroposteriorly short proximal end, similar to non-avian theropod dinosaurs. The chevrons articulated with the middle caudal vertebrae appear very low and long, nearly exceeding the length of the adjacent caudal centrum and being bifurcate at both ends.

No sternum is found associated with the skeleton, as in *Archaeopteryx* except the Munich specimen where a small and rectangular sternum was identified<sup>[16]</sup>. Like *Archaeopteryx*,

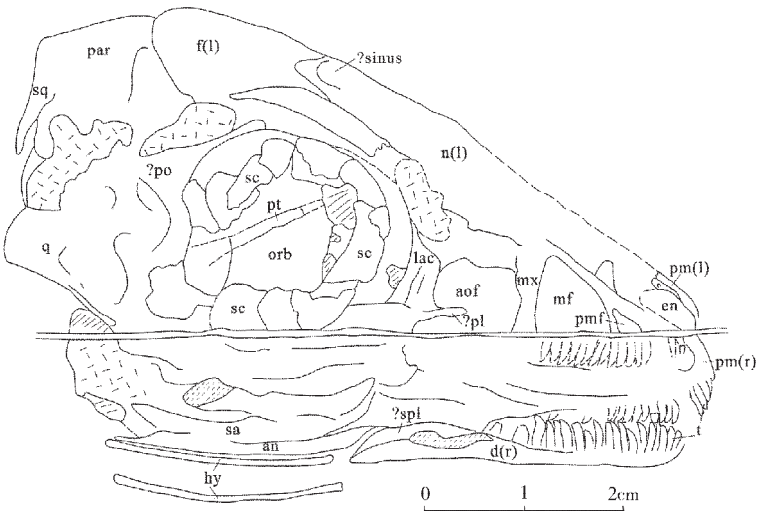


Fig.4 Line drawing of the skull of *Jinfengopteryx elegans* gen. et sp. nov.( CAGS-IG-04-0801 )

Abbreviations : an-angular ; aof-antorbital fenestra ; d(r)-right dentary ; en-external nasal opening ; f(l)-left frontal ; hy-hyoid ; lac-lacrimal ; mf-maxillary fenestra ; mx-maxilla ; n(l)-left nasal ; orb-orbit ; par-parietal ; ?pl- ? palatine ; pmf-promaxillary fenestra ; pn(l)-left premaxilla ; pn(r)-right premaxilla ; ?po- ? postorbital ; pt-pterygoid ; q-quadrate ; sa-surangular ; sc-scleral plate ? spl-? splenial ; sq-squamosal ; t-tooth

Table 1 Measurements of CAGS-IG 04-0801

	Length ( mm )	Shaft width ( mm )
Skull length	68 ( est. )	
Scapula	47.09	3.53
Humerus	49.22	4.13
Radius	42.44	1.52
Ulna	43.31	2.41
Metacarpal I	8.77	2.18
Phalanx 1/digit I	18.83	
Phalanx Ⅸ claw )/digit I	17.75	
Metacarpal II	21.37	
Phalanx 1/digit II	15.26	
Phalanx 2/digit II	21.07	
Phalanx Ⅸ claw )/digit II	17.32	
Metacarpal III	56.67 ( est. )	
Phalanx 1/digit III	10	
Phalanx 2/digit III	-	
Phalanx 3/digit III	12.95	
Femur	70.32	
Tibia	100.50	
Fibula	98.75	
Metatarsal + digit III	102.1	

Note : est. estimated length ; - , not preserved



the new bird possesses no uncinat e processes. But the quite complete gastral basket is composed of roughly 12 rows of slender gastralia. The lateral gastral elements are longer than the median elements.

The fused scapula and coracoid is L-shaped in lateral view and forms an angle of about 90° between the two bones. These features are very similar to those of *Archaeopteryx* and dromaeosaurids such as *Sinornithosaurus* and *Microaptor*<sup>[17–19]</sup>. The scapula is slightly shorter than humerus ; its shaft is long , narrow and strap-like ; and its posterior end is slightly expanded. The scapula has a prominent acromial process. The coracoid is relatively large , plate-like. Its outline is similar to that of *Archaeopteryx*. The sternal margin of the coracoid is round. The biceps tubercle is present and the supracoracoid foramen is below the biceps tubercle. Their relative positions are similar to those of *Archaeopteryx*. The right clavicle is a very thin and rod-like bone found between the right scapula and coracoid. Because the other clavicle is unknown , it is not clear if clavicles are fused to form the furcula.

The proximal end of the left humerus is preserved as an impression. The long , high and well-defined deltopectoral crest is continuous with the head. There is no indication of external or internal tuberosities. The shaft is slightly curved.

The ulna is bowed , much wider and slightly longer than the radius , and the radius is straight , leaving a large gap between the two bones. The distal end of the ulna is round and slightly expanded , but its proximal end is not clear.

Two carpals are preserved in the left wrist. The larger of the two is the semilunate carpal , which is centered on the metacarpal II and contact the medial part of the metacarpal I but not fused with the metacarpal I. The proximal and smaller carpal is the radiale that lies between the semilunate carpal and the radius. The proximal end of the

metacarpal III does not reach the semilunate carpal as in *Archaeopteryx*.

Metacarpal I is short but relatively robust. Metacarpals II and III are sub-equal in length , but metacarpal III is slender and bowed laterally. Metacarpal II is about 2.5 times the length of metacarpal I. This proportion is different from that of *Archaeopteryx* , in which metacarpal II is more than 3 times the length of metacarpal I<sup>[6]</sup>.

The manual digit I is the shortest , digit II is the longest and digit III is intermediate in length. The phalangeal formula is 2–3–4. The penultimate phalanx is the longest in each finger. The first and the second phalanges of the digit III appear to be fused. The manual unguals of digits I and II are nearly same in size , but the ungual of digit III is relatively smaller. All unguals bear distinct flexor tubercles and are strongly curved , with a pointed tip and developed horny sheath preserved as impression. The manual unguals are more curved than the pedal unguals , similar to condition in *Archaeopteryx*<sup>[7]</sup>. The intramembral ratio of the forelimb and the ratio ( 100% ) of the femur to the tibia are similar to that of the smallest specimen of *Archaeopteryx* ( Eichstätt specimen ) ( Table 2 ).

The pelvic girdle is crashed. The posterior part of the ilium is missing , but its outline is represented by impression. The dorsal margin of the ilium is convex and its postacetabular process tapers to the end , similar to that of *Archaeopteryx*. The ischium is poorly preserved. Both pubes are preserved , and they slightly rotated about a vertical axis. They are oriented at about 110° to the posterior dorsal vertebrae , similar to that of *Archaeopteryx*<sup>[6]</sup>. The pubis is preserved down to its distal end and the ventral margin of the pubic foot is straight. The femur is slightly curved and convex anteriorly , and the structures of its proximal and distal ends are not clear. It is shorter than the tibia. The tibia is almost straight , but its two ends are not well preserved. The fibula extends from the knee to the tarsus , and it is

Table 2 Intramembral ratios ( % ) between *Jinfengopteryx* and different specimens of *Archaeopteryx*

Specimen	Hu + Ul + McII = 100 %	Fe + Ti + MtIII = 100 %	Hu/Ul	Fe/Ti
<i>Jinfengopteryx</i>	43.2 + 38.2 + 18.6	( 30.9 + 44.2 + 24.9 )	113.6	70.0
Eichstätt	43.3 + 38.1 + 18.6	30.8 + 44.1 + 25.1	113.7	69.8
Munich	( 41.4 + 39.8 + 18.8 )	( 29.3 + 45.1 + 25.6 )	( 103.8 )	( 65.0 )
Berlin	42.8 + 38.2 + 19.0	( 32.6 + 44.3 + 23.1 )	112.1	73.5
London	42.5 + 38.0 + 19.5	( 32.6 + 43.9 + 23.5 )	111.9	( 74.4 )

This table is from Elzanowski ( 2002 ) with the new taxon added. Paraentheses mark ratios based on at least one approximate measurement. Abbreviations : Fe , femur ; Hu , humerus ; McII , metacarpal II ; MtIII , metatarsal III ; Ti , tibia ; Ul , ulna

not fused to the tibia. Its proximal end is wide and plate-like. Its shaft is thin and rod-like. The distal end is slightly expanded. The structures of the metatarsals are not clear.

Feather impressions are clearly preserved around the neck, the body, the hips, the upper hindlimbs, the tail, and near the manus. The feathers attaching to the neck, body, hips, and upper legs are relatively short and have simple structure, like those in *Sinosauropteryx*, *Protarchaeopteryx* and some dromaeosaurids. Two patches of feathers are preserved with the right fingers, but enough to show that no primaries are preserved. The long and vaned tail feathers are beautifully preserved around the middle and distal caudals. The feathers become increasingly longer distally, like those in *Archaeopteryx* and *Microraptor gui*<sup>[19]</sup>. The distal tail feathers are very long and have symmetrical vanes that show distinct barbs.

*Jinfengopteryx* also had some oval structures preserved within the posterior part of the gastral basket (Figs. 1 2). According to our observation, 10 or more oval structures can be recognized. They are small and smooth, most of which are approximately less than 10 mm in axial length. The structures are somehow reddish yellow in color, markedly distinctive from the surrounding rocks in dark color. The posterior dorsal ribs and gastralia lie over the surfaces of them, indicating that the structures are within the body cavity. Although small and numerous eggs were also reported in one specimen of *Sinosauropteryx*<sup>[20]</sup> and *Compsognathus*<sup>[21]</sup>, we are still not sure that the oval structures in *Jinfengopteryx* are eggs based on our observation. Maybe they are small eggs, developing follicles, seeds or nuts. If these oval structures in *Jinfengopteryx* are small eggs or developing follicles, it is possibly the first evidence for the reproductive biology of avialian and other basal birds.

## Discussion

Our phylogenetic analysis (Fig. 5) shows that *Jinfengopteryx* and *Archaeopteryx* are sister taxa, which are sister group to the clade (*Shenzhouraptor* + *Pygostylia*) (Fig. 5). *Jinfengopteryx* is more similar to *Archaeopteryx* than any other non-avian theropods and avialian birds in having the

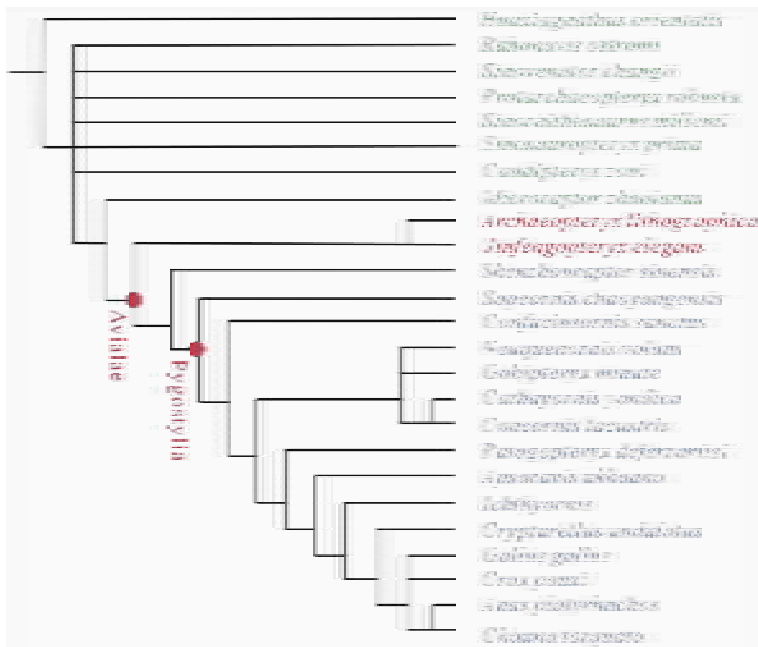


Fig.5 Strict consensus of 60 most parsimonious trees shows that

*Jinfengopteryx* and *Archaeopteryx* form a sister group

Tree length=384, consistency index (CI)=0.6404, homoplasy index (HI)=0.3594, CI excluding uninformative characters=0.6167, HI excluding uninformative characters=0.3833, retention index (RI)=0.8107, rescaled consistency index (RC)=0.5194

triangular skull outline, basically conical tooth without serrations, in the markedly shortened caudals 2–5, in the thin cervical ribs longer than the cervical centra, and in the extensive contact of the semilunate carpal to metacarpal I. All these characters strongly suggest that *Jinfengopteryx* is the sister genus to *Archaeopteryx*. Compared to *Archaeopteryx*, *Jinfengopteryx* also shows such primitive characters as the relatively large number of lower jaw teeth, short metacarpal II compared to the metacarpal I, smaller ratio of the forelimb to hindlimb, relatively small nasal openings, and a short rostrum. It is implied that *Jinfengopteryx* is the earliest avialian bird in the world up to now.

No other vertebrate fossil taxon has had a larger impact on the evolutionary biology of vertebrates and development of biological thought<sup>[22,23]</sup>. The discovery of *Jinfengopteryx* from China greatly extended the known palaeogeographic distribution of this important avialian group. *Jinfengopteryx* had the relatively strong hindlimb, indicating that it is a fast-running forager. The new finding provides more information for the locomotory adaptation of avialian birds,

strengthening the hypothesis about the cursorial origin of avian flight<sup>[2, 24-26]</sup>. The discovery of *Jinfengopteryx* also enriches the diversity of non-avian feathered theropods and primitive Birds of the Mesozoic Jehol biota in China.

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## References :

- [1]Chang M M, Chen P J, Wang Y Q, et al. The Jehol Biota[M]. Shanghai: Shanghai Scientific & Technical Publishers, 2003. 1–208.
- [2]Ji Q, et al. Mesozoic Jehol Biota of Western Liaoning, China [M]. Beijing: Geological Publishing House, 2004. 1–375.
- [3]Ji Q, Ji S A, You H L, et al. Discovery of an avialae bird—*Shenzhouraptor sinensis* gen. et sp. nov.—from China[J]. Geol. Bull. China, 2002, 21(7): 363–369.
- [4]Zhou Z H, Zhang F C. A long-tailed, seed-eating bird from the Early Cretaceous of China[J]. Nature, 2002, 418: 405–409.
- [5]Ji Q, Ji S A, Zhang H B, et al. A new avialian bird—*Jixiangornis orientalis* gen. et sp. nov.—from the Lower Cretaceous of western Liaoning, NE China[J]. J. Nanjing Univ. (Nat. Sci.), 2002, 38(6): 723–736.
- [6]Ostrom J H. *Archaeopteryx* and the origin of birds[J]. Biol. J. Linn. Soc., 1976, 8: 91–182.
- [7]Elzanowski A. Archaeopterygidae (Upper Jurassic of Germany)[A]. In: Chiappe L M, Witmer L M, eds. Mesozoic Birds: above the Heads of Dinosaurs[C]. Berkeley: Univ. California Press, 2002. 129–159.
- [8]Witmer L M. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity[J]. Soc. Vert. Paleont. Memoir, 1997, 3: 1–73.
- [9]Elzanowski A, Wellnhofer P. Cranial morphology of *Archaeopteryx*: evidence from the seven skeleton[J]. J. Vert. Paleont., 1996, 16(1): 81–94.
- [10]Wellnhofer P. A new specimen of *Archaeopteryx* from the Solnhofen Limestone[J]. Nat. Hist. Mus. Los Angeles County Sci. Ser., 1992, 36: 3–23.
- [11]Forster C A, Sampson S D, Chiappe L M, et al. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar[J]. Science, 1998, 279: 1915–1919.
- [12]Ji Q, Ji S A, You H L, et al. An Early Cretaceous avialian bird, *Shenzhouraptor sinensis* from western Liaoning, China[J]. Acta Geol. Sin. (English Edition), 2003, 77(1): 21–27.
- [13]Ji Q, Currie P J, Norell M A, et al. Two feathered dinosaurs from northeastern China[J]. Nature, 1998, 393: 753–761.
- [14]Zhou Z H, Wang X L. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China [J]. Vert. Palasiat., 2000, 38(2): 111–127.
- [15]Zhou Z H, Wang X L, Zhang F C, et al. Important features of *Caudipteryx*—evidence from two nearly complete new specimens[J]. Vert. Palasiat., 2000, 38(4): 241–254.
- [16]Wellnhofer P. Das siebte exemplar von *Archaeopteryx* aus den Solnhofener Schichten[J]. Archaeopteryx, 1993, 11: 1–47.
- [17]Xu X, Wang X L, Wu X C. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China [J]. Nature, 1999, 401: 262–266.
- [18]Xu X, Zhou Z H, Wang X L. The smallest known non-avian theropod dinosaur[J]. Nature, 2000, 408: 705–708.
- [19]Xu X, Zhou Z H, Wang X L, et al. Four-winged dinosaurs from China[J]. Nature, 2003, 421: 335–340.
- [20]Chen P J, Dong Z M, Zhen S N. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China [J]. Nature, 1998, 391: 147–152.
- [21]Griffiths P. The question of *Compsognathus* eggs[J]. Rev. Paleobiol. Spec. Issue, 1993, 7: 85–94.
- [22]Mayr E. Agassiz, Darwin, and evolution[A]. In: Appleman P, ed. Darwin[C]. New York: Norton, 1970. 299–307.
- [23]Hecht M K. The biological significance of *Archaeopteryx*[A]. In: Hecht M K, Ostrom J H, Viohl G, et al. eds. The Beginnings of Birds[C]. Eichstätt: Freunde des Jura-Museums, 1985. 199–207.
- [24]Williston S W. Are birds derived from dinosaurs[J]. Kansas City Rev. Sci., 1879, 3: 457–460.
- [25]Ostrom J H. The cursorial origin of avian flight[J]. Mem. California Acad. Sci., 1986, 8: 73–81.
- [26]Burgers P, Chiappe L M. The wing of *Archaeopteryx* as a primary thrust generator[J]. Nature, 1999, 399: 60–62.

## Supplementary Information

### Part I. Character description :

Analysis of the phylogenetic relationship of *Jinfengopteryx elegans* to all other maniraptoriforms was based on a matrix of 205 characters by 25 taxa. Many of the systematic characters used in this analysis were adopted from several previous studies , including : Zhou and Zhang ( 2002 ) and Norell and Clarke ( 2001 ). We also added several new features specifically aimed to resolve the relationship of *Jinfengopteryx elegans* , in addition to the characters used by others. Also in this analysis , we use *Shenzhouraptor* instead of *Jeholornis* because the fossil material of *Shenzhouraptor* is better preserved and available for our comparative study ( Ji et al. , 2003 ). In this analysis , all multi-state characters are unordered.

1. Premaxillae : (0) unfused in adults ; (1) fused anteriorly in adults ; (2) fused posteriorly as well as anteriorly.

2. Premaxillary teeth : (0) present ; (1) absent.

3. Maxillary teeth : (0) present ; (1) absent.

4. Dentary teeth : (0) present ; (1) absent.

5. Tooth crown , ornamentation : (0) serrations ; (1) serrations vestigial or absent.

6. Dentaries : (0) joined proximally by cartilage ; (1) joined in osseous symphysis.

7. Mandibular symphysis , two strong grooves forming an anteriorly-opening " v " in ventral view : (0) absent ; (1) present.

8. Facial margin : (0) primarily formed by the maxilla , with the maxillary process of the premaxilla restricted to the anterior-most extreme ; (1) maxillary process of the premaxilla extending 1/2 facial margin ; (2) maxillary process of the premaxilla extending most of facial margin.

9. Nasal process of the premaxilla : (0) short ; (1) long , posteriorly approaching the frontals.

10. Nasal process of the maxilla , dorsal ramus : (0) prominent , exposed medially and laterally ; (1) absent or reduced to slight medial , and no lateral , exposure.

11. Nasal process of the maxilla , participation of ventral ramus in anterior margin of antorbital fenestra in lateral view : (0) present ; (1) absent.

12. Osseous external nares : (0) considerably smaller than the antorbital fenestrae ; (1) larger.

13. Ectopterygoid : (0) present ; (1) absent.

14. Articulation between the vomer and pterygoid : (0) present ; (1) reduced , narrow process of pterygoid passes dorsally over palatine to contact vomer ; (2) absent , pterygoid and vomer do not contact.

15. Palatine and pterygoid : (0) long anteroposteriorly overlapping contact ; (1) short primarily dorsoventral contact.

16. Palatine contacts : (0) maxillae only ; (1) premaxillae and maxillae.

17. Vomer contacts premaxilla : (0) present ; (1) absent.

18. Coronoid ossification : (0) present ; (1) absent.

19. Basisphenoid articulation with the pterygoid developed as a process : (0) present ; (1) absent.

20. Basispterygoid processes : (0) elongate ; (1) short , articulation with pterygoid sub-equal to longer than amount projected from the basisphenoid rostrum.

21. Basisphenoid , pterygoid articulations : (0) located basal on basisphenoid ; (1) located markedly anterior on basisphenoid (" parasphenoid ") such that the articulations are subadjacent on narrow rostrum.

22. Basisphenoid/pterygoid articulation : (0) anteroventral ; (1) mediolateral ; (2) entirely dorsoventral.

23. Pterygoid , articular surface for basisphenoid : (0) concave " socket " , or short groove enclosed by dorsal and ventral flanges ;

(1) flat to convex ; (2) flat to convex facet , stalked , variably projected.

24. Pterygoid , kinked : (0) present , surface for basisphenoid articulation at a high angle to the axis of the palatal process of the pterygoid ; (1) absent , articulation in line with axis of pterygoid.

25. Osseous interorbital septum ( mesethemoid ) : (0) absent ; (1) present.

26. Osseous interorbital septum ( mesethemoid ) : (0) restricted to posterior or just surpassing premaxillae/frontal contact in rostral extent , does not surpass posterior edge of external nares in rostral extent ; (1) extending rostral to posterior extent of the frontal processes of the premaxillae and rostral to posterior edge of external nares.

27. Eustachian tubes : (0) paired and lateral ; (1) paired , close to , cranial midline ; (2) paired and adjacent on midline or single anterior opening.

28. Eustachian tubes ossified : (0) absent ; (1) present.

29. Squamosal , ventral or " zygomatic " process : (0) variably elongate dorsally enclosing the dorsal process and extending anteroventrally along shaft of quadrate , dorsal head of quadrate not visible in lateral view ; (1) short , head of quadrate exposed in lateral view.

30. Orbital process of quadrate , pterygoid articulation : (0) pterygoid broadly overlapping medial surface of orbital process ; (1) restricted to anteromedial edge of process.

31. Quadrate , orbital process : (0) pterygoid articulates with anterior-most tip ; (1) pterygoid articulation does not reach tip ; (2) pterygoid with no extent up orbital process.

32. Quadrate/ pterygoid contact : (0) as a facet , variably with slight anteromedial projection cradling base ; (1) condylar , with a well-projected tubercle on the quadrate.

33. Quadrate , well-developed tubercle on anterior surface of dorsal process : (0) absent ; (1) present.

34. Quadrate , quadratojugal articulation : (0) overlapping ; (1) peg and socket articulation.

35. Quadrate , braincase articulation : (0) with squamosal only ; (1) with squamosal and prootic.

36. Quadrate , dorsal process , development of intercotylar incisure between prootic and squamosal cotylae : (0) absent , articular surfaces not differentiated ; (1) two distinct articular facets , incisure not developed ; (2) incisure present , " double headed " .

37. Quadrate , ventral process : (0) bicondylar articulation with mandible ; (1) tricondylar articulation , additional posterior condyle or broad surface.

38. Quadrate , pneumaticity : (0) absent ; (1) present.

39. Quadrate , cluster of pneumatic foramina on posterior surface of the tip of dorsal process : (0) absent ; (1) present.

40. Quadrate , large single pneumatic foramen : (0) absent ; (1) posteromedial surface of dorsal process.

41. Articular pneumaticity : (0) absent ; (1) present.



42. Dentary , strongly forked posteriorly : ( 0 ) unforked ; ( 1 ) forked.

43. Splenial , anterior extent : ( 0 ) splenial stops well posterior to mandibular symphysis ; ( 1 ) extending to mandibular symphysis , though non-contacting ; ( 2 ) extending to proximal tip of mandible , contacting on midline.

44. Mandibular symphysis , dorsal surface : ( 0 ) concave ; ( 1 ) flat to convex.

45. Mandibular symphysis , symphyseal foramina : ( 0 ) absent ; ( 1 ) present.

46. Mandibular symphysis , symphyseal foramina : ( 0 ) single ; ( 1 ) paired.

47. Mandibular symphysis , symphyseal foramina : ( 0 ) opening on posterior edge of symphysis ; ( 1 ) opening on dorsal surface of symphysis.

48. Meckel's groove : ( 0 ) open , conspicuous ; ( 1 ) not exposed medially.

49. External mandibular fenestra : ( 0 ) absent ; ( 1 ) present.

50. Jugal/postorbital contact : ( 0 ) present ; ( 1 ) absent.

51. Frontoparietal suture ( 0 ) open ; ( 1 ) closed.

52. Cervical vertebrae : ( 0 ) dorsoventrally compressed amphicoelous ; ( 1 ) anterior surface heterocoelous , posterior surface flat ; ( 2 ) both anterior and posterior surfaces heterocoelous.

53. Thoracic vertebrae ( with " true " ribs , articulating with the sternum ) , one or more with prominent hypapophyses : ( 0 ) absent ; ( 1 ) present.

54. Dorsal vertebrae ( with free , ventrally projecting free ribs ) , count : ( 0 ) 12 or more ; ( 1 ) 11 ; ( 2 ) 10 ; ( 3 ) 9 or less.

55. Thoracic vertebrae , at least part of series heterocoelous : ( 0 ) absent ; ( 1 ) present.

56. Dorsal vertebrae , parapophyses : ( 0 ) rostral to transverse processes ; ( 1 ) directly ventral to transverse processes , close to mid-point of vertebrae.

57. Dorsal vertebrae , centra markedly longer than wide : ( 0 ) absent ; ( 1 ) present.

58. Dorsal vertebrae , lateral excavations : ( 0 ) absent or slight indentations ; ( 1 ) present , deep , emarginate excavations.

59. Thoracic vertebrae with ossified connective tissue connecting transverse processes : ( 0 ) absent ; ( 1 ) present.

60. Notarium : ( 0 ) absent , ( 1 ) present.

61. Sacral vertebrae , number ankylosed : ( 0 ) less than 7 ; ( 1 ) 7 ; ( 2 ) 8 ; ( 3 ) 9 ; ( 4 ) 10 ; ( 5 ) 11 or more ; ( 6 ) 15 or more.

62. First sacral vertebra , anterior vertebral articulation : ( 0 ) approximately equal in height and width ; ( 1 ) wider than high.

63. Free caudal vertebrae , number : ( 0 ) more than 8 ; ( 1 ) 8 or less.

64. Caudal vertebrae , ( chevron ) , fused on at least one anterior or caudal : ( 0 ) present ; ( 1 ) absent.

65. Anterior ( free ) caudals , length of transverse processes on caudals : ( 0 ) approximately the vertebral width ; ( 1 ) significantly

shorter than vertebral width.

66. Anterior ( free ) caudal vertebrae : ( 0 ) well developed pre/post-zygopophyses ; ( 1 ) pre/post-zygopophyses short.

67. Distal caudals : ( 0 ) unfused ; ( 1 ) fused into a pygostyle.

68. Pygostyle : ( 0 ) long , more than the length of 4 caudal vertebrae ; ( 1 ) short less than the length of 4 caudal vertebrae ; ( 2 ) less than 2 caudal vertebrae in length.

69. Ossified uncinate processes : ( 0 ) absent ; ( 1 ) present ; ( 2 ) fused to ribs.

70. Gastralia : ( 0 ) present ; ( 1 ) absent.

71. Ossified sternal plates : ( 0 ) unfused ; ( 1 ) fused ; ( 2 ) fused , with slightly raised midline ridge ; ( 3 ) fused with projected carina.

72. Carina : ( 0 ) restricted to posterior half of sternum ; ( 1 ) approaches anterior limit of sternum.

73. Sternum , dorsal surface , central pneumatic foramen : ( 0 ) absent ; ( 1 ) present.

74. Sternum , midline ridge from anterior edge : ( 0 ) absent ; ( 1 ) present.

75. Sternum , deep coracoidal sulci : ( 0 ) present ; ( 1 ) absent.

76. Sternum , coracoidal sulci spacing on anterior edge : ( 0 ) widely separated mediolaterally ; ( 1 ) adjacent ; ( 2 ) crossed on midline.

77. Sternal costal processes : ( 0 ) three ; ( 1 ) four ; ( 2 ) five ; ( 3 ) six ; ( 4 ) seven ; ( 5 ) eight.

78. Sternum : raised , paired intermuscular ridges parallel to sternal midline : ( 0 ) absent ; ( 1 ) present.

79. Clavicles : ( 0 ) fused into a furcula ; ( 1 ) unfused.

80. Interclavicular angle ( clavicles elongate ) : ( 0 ) greater than 90 degrees ; ( 1 ) less than 90 degrees.

81. Furcula , hypocleideum : ( 0 ) absent ; ( 1 ) a tubercle ; ( 2 ) an elongate process.

82. Furcula , laterally excavated : ( 0 ) absent ; ( 1 ) present.

83. Scapula and coracoid : ( 0 ) sutured ; ( 1 ) free.

84. Scapula and coracoid articulation : ( 0 ) pit shaped scapular cotyla developed on the coracoid , and coracoidal tubercle developed on the scapula ( " ball and socket " articulation ) ; ( 1 ) scapular cotyla of the coracoid convex ; ( 2 ) flat facet.

85. Coracoid , procoracoid process , ( 0 ) absent ; ( 1 ) present.

86. Coracoid : ( 0 ) height approximately equal mediolateral dimension ; ( 1 ) height more than twice the mediolateral , coracoid " strut like " .

87. Coracoid , lateral margin in ventral view : ( 0 ) straight to slightly concave ; ( 1 ) convex.

88. Coracoid , dorsal surface : ( 0 ) strongly concave ; ( 1 ) flat to convex throughout majority of shaft.

89. Coracoid , dorsal surface , deep fossa : ( 0 ) absent ; ( 1 ) present.

90. Coracoid : ( 0 ) solid ; ( 1 ) hollow , pneumatized.

91. Coracoid : ( 0 ) pneumatic foramen proximal ; ( 1 ) distal.

92. Coracoid , lateral process : ( 0 ) absent ; ( 1 ) present.

93. Coracoid, ventral surface, distal fossa and lateral intermuscular line: (0) absent; (1) faint impressions; (2) well developed depression and ridge.

94. Coracoid, glenoid facet: (0) dorsal to acrocoracoid process/ "biceps tubercle"; (1) ventral to acrocoracoid process.

95. Coracoid, acrocoracoid: (0) straight; (1) hooked medially.

96. Coracoid, n. supracoracoideus passes through coracoid, foramen marking its passage: (0) present; (1) absent.

97. Coracoid, passage of foramen n. supracoracoideus opening into a medial groove: (0) absent; (1) present.

98. Coracoid, medial surface, area of exit of the foramen n. supracoracoideus (when developed): (0) strongly depressed; (1) flat to convex.

99. Angle between coracoid and scapula at glenoid: (0) more than 90 degrees; (1) 90 degrees or less.

100. Scapula, (0) posterior end as wide or wider than proximal dorsoventral width; (1) tapering distally.

101. Scapular shaft: (0) straight; (1) dorsoventrally curved.

102. Scapular shaft: (0) mid-part of scapular blade expanded to approach width of anterior end; (1) mid-shaft approximately constant width, narrow.

103. Scapula, acromium process: (0) blunt; (1) tapering to a point.

104. Scapula, acromium process: (0) straight; (1) hooking laterally.

105. Humerus and ulna, length: (0) humerus longer; (1) ulna and humerus approximately the same length; (2) ulna significantly longer than humerus.

106. Humerus, proximal view, head in anterior or posterior aspect: (0) strap-like, articular surface flat, no proximal midline convexity; (1) head domed proximally.

107. Humerus: (0) projected farther proximally dorsally; (1) midline projected farthest proximally.

108. Humerus, capital incisure: (0) absent; (1) present.

109. Humerus, capital incisure: (0) an open groove; (1) capital incisure closed by a muscular tubercle associated with an insertion just distal to humeral head.

110. Humerus, anterior surface, well-developed fossa on midline making the proximal articular surface appear v-shaped in proximal view: (0) absent; (1) present.

111. Humerus, ventral tubercle: (0) absent; (1) present.

112. Humerus, "transverse groove": (0) absent; (1) present, developed as discreet depressed scar on proximal surface of bicipital crest or slight transverse groove.

113. Humerus, deltopectoral crest: (0) projected dorsally (in line with long axis of humeral head; (1) projected anteriorly (at an angle to long axis of the humeral head).

114. Humerus, deltopectoral crest: (0) less than shaft width; (1) approximately the same measure; (2) dorsoventral width greater

than shaft width.

115. Humerus, deltopectoral crest, proximal, posterior surface: (0) flat to convex; (1) concave.

116. Humerus, bicipital crest, scar/fossa for muscular attachment on cranial or distal surface: (0) absent; (1) present.

117. Humerus, bicipital crest, pit shaped fossa for muscular attachment: (0) anterodistal on bicipital crest; (1) directly ventrodistal at tip of bicipital crest; (2) posterodistal, variably developed as a fossa.

118. Humerus, bicipital crest: (0) little or no cranial projection; (1) developed as a cranial projection relative to shaft surface in ventral view; (2) hypertrophied, rounded tumescence.

119. Humerus, proximal end, one or more pneumatic foramina: (0) absent; (1) present.

120. Humerus, distal condyles: (0) developed distally; (1) developed on the anterior surface of the humerus.

121. Humerus, long axis of dorsal condyle (0) angling proximoventrally at low angle to the humeral axis, overall more proximodistally oriented; (1) at high angle to the humeral axis, almost transversely oriented.

122. Humerus, distal condyles: (0) sub-round, bulbous; (1) weakly defined, "strap-like".

123. Humerus, distal margin: (0) approximately perpendicular to long axis of humeral shaft; (1) ventrodistal margin projected significantly distal to dorsodistal margin, distal margin angling strongly ventrally, sometimes described as a well-projected flexor process.

124. Humerus, distal end, compressed anteroposteriorly and flared dorsoventrally at its distal extreme: (0) absent; (1) present.

125. Humerus, brachial fossa: (0) absent; (1) present, developed as a flat scar or as a scar-impressed fossa.

126. Humerus, ventral condyle: (0) length of long axis of condyle less than the same measure of the dorsal condyle; (1) same or greater.

127. Humerus, distal end, posterior surface, groove for passage of m. scapulotriceps: (0) absent; (1) present.

128. Humerus, m. humerotricipitalis groove: (0) absent; (1) present as a well developed ventral depression contiguous with the olecranon fossa and demarcating a posteroventral ridge.

129. Ulna, cotylae: (0) dorsoventrally adjacent; (1) widely separated by a deep groove.

130. Ulna, dorsal cotyla convex: (0) absent; (1) present.

131. Ulna, distal end, dorsal condyle, dorsal trochlear surface developed as a semilunate ridge: (0) absent; (1) present.

132. Ulna, distal end, dorsal condyle, dorsal trochlear surface, extent along posterior margin: (0) less than transverse measure of dorsal trochlear surface; (1) equal; (2) greater than this measure.

133. Ulna, bicipital scar: (0) absent; (1) present as a slightly raised scar; (2) present as a prominent tubercle.

134. Ulna, brachial scar: (0) absent; (1) present.

135. Radius , ventroposterior surface : ( 0 ) smooth ; ( 1 ) with muscle impression along most of surface ; ( 2 ) deep longitudinal groove.

136. Ulnare : ( 0 ) absent ; ( 1 ) present.

137. Ulnare : ( 0 ) bulky , “ heart-shaped ” little differentiation into short dorsal and ventral rami ; ( 1 ) V-shaped , well-developed dorsal and ventral rami.

138. Ulnare , ventral ramus ( “ crus longum ” , Baumel and Witmer , 1993 ) : ( 0 ) shorter than dorsal ramus ( “ crus breve ” ) ; ( 1 ) same length as dorsal ramus ; ( 2 ) longer than dorsal ramus.

139. Semilunate carpal and metacarpals : ( 0 ) no fusion ; ( 1 ) incomplete proximal fusion ; ( 2 ) complete proximal fusion ; ( 3 ) complete proximal and distal fusion.

140. Semilunate carpal , position relative to metacarpal I : ( 0 ) over entire proximal surface ; ( 1 ) over less than 1/2 proximal surface.

141. Metacarpal III , anteroposterior diameter as a percent of same dimension of Metacarpal II : ( 0 ) approximately equal or greater than 50% ; ( 1 ) less than 50%.

142. Metacarpal I , extensor process : ( 0 ) absent , no antero-proximally projected muscular process ; ( 1 ) present.

143. Metacarpal I , anterior surface : ( 0 ) roughly hourglass shaped proximally at least moderately expanded anteroposteriorly and constricted just before the flare of the articulation for phalanx I ; ( 1 ) anterior surface broadly convex.

144. Metacarpal I , distal articulation with phalanx I : ( 0 ) gyn-glimoid ; ( 1 ) shelf.

145. Pisiform process : ( 0 ) absent ; ( 1 ) present.

146. Carpometacarpus , ventral surface , supratrochlear fossa , deeply excavating proximal surface of pisiform process : ( 0 ) absent ; ( 1 ) present.

147. Intermetacarpal space ( between metacarpals II and III ) : ( 0 ) reaches proximally as far as the distal end of metacarpal I ; ( 1 ) terminates distal to end of metacarpal I.

148. Carpometacarpus , distal end , metacarpals II and III , articular surfaces for digits : ( 0 ) metacarpal II sub-equals or surpasses metacarpal III in distal extent ; ( 1 ) metacarpal III extends farther.

149. Intermetacarpal process or tubercle : ( 0 ) absent ; ( 1 ) present as raised scar ; ( 2 ) tubercle or flange.

150. Manual digit II , phalanx 1 : ( 0 ) subcylindrical to subtriangular ; ( 1 ) strongly dorsoventrally flattened.

151. Manual digit II : ( 0 ) phalanx 1 shorter than phalanx 2 ; ( 1 ) longer.

152. Manual digit II , phalanx 2 : ( 0 ) subcylindrical to subtriangular ; ( 1 ) strongly depressed posteriorly.

153. Ilium , ischium , pubis , proximal contact : ( 0 ) unfused ; ( 1 ) fused in adult.

154. Ilium/ischium , distal fusion , closure of the “ ilioischiatic fenestra ” : ( 0 ) absent ; ( 1 ) present.

155. Ischium : ( 0 ) forked ; ( 1 ) straight , no dorsal process.

156. Ischium and pubis : ( 0 ) not subparallel ; ( 1 ) subparallel and posteriorly directed ; ( 2 ) posteriorly directed and appressed.

157. Laterally projected process on ischiadic peduncle/an-titrochanter : ( 0 ) directly posterior to acetabulum ; ( 1 ) posterodorsal to acetabulum.

158. Preacetabular tubercle , “ pectineal process ” : ( 0 ) absent ; ( 1 ) present as a small tubercle or flange ; ( 2 ) extremely well developed.

159. reacetabular ilii : ( 0 ) approach on midline , open , or cartilaginous connection ; ( 1 ) coossified , dorsal closure of “ iliosynsacral canals ”.

160. Preacetabular ilii extend cranial to first sacral vertebra : ( 0 ) no free ribs overlapped , no parapophyseal facets on sacral ribs ; ( 1 ) one or more ribs overlapped.

161. Postacetabular ilii : ( 0 ) dorsoventrally oriented ; ( 1 ) mediolaterally oriented.

162. Postacetabular ilii , ventral surface , renal fossa developed : ( 0 ) absent ; ( 1 ) present.

163. Ilium , *m. cuppedicus* fossa as broad mediolaterally oriented surface directly anteroventral to acetabulum : ( 0 ) present ; ( 1 ) surface absent , insertion variably marked by a lateral fossa anterior to acetabulum.

164. Ischium , distinct proximal anteroventral process ( 0 ) absent ; ( 1 ) present developed as a small flange or raised scar contacting / fused with pubis and demarcating the obturator foramen distally.

165. Pubis : ( 0 ) sub-oval in cross section ; ( 1 ) compressed mediolaterally.

166. Pubes , distal contact : ( 0 ) contacting , variably coossified into a symphysis ; ( 1 ) non-contacting.

167. Distal end of pubes : ( 0 ) expanded , flared ; ( 1 ) straight , subequal in proportions with rest of pubis.

168. Femur , fossa for insertion of *lig. capitis femoris* : ( 0 ) absent ; ( 1 ) present.

169. Femur , posterior trochanter : ( 0 ) present ; ( 1 ) absent.

170. Femur , posterior trochanter and lateral ridge ( Norell and Makovicky , 1999 ) : ( 0 ) weakly projected muscular ridges ; ( 1 ) hypertrophied “ shelf-like ” conformation ; ( 2 ) not present.

171. Femur , lesser and greater trochanters : ( 0 ) separated by a notch ; ( 1 ) developed as a single trochanteric crest.

172. Femur , intercondylar groove ( “ patellar groove ” of other authors , but see Baumel and Witmer , 1993 ) : ( 0 ) developed only distally ; ( 1 ) extending around distal end and onto posterodorsal surface.

173. Femur : ( 0 ) ectocondylar tubercle and lateral condyle separated by deep notch ; ( 1 ) ectocondylar tubercle and lateral condyle form single trochlear surface.

174. Femur , posterior projection of the lateral border of the distal end , continuous with lateral condyle : ( 0 ) absent ; ( 1 ) present.

175. Laterally projected fibular trochlea : ( 0 ) absent ; ( 1 )

shelf-like projection.

176. Femur, popliteal fossa: (0) a groove open distally and bounded medially and laterally by narrow condyles; (1) closed distally by expansion of both condyles (primarily the medial).

177. Calcaneum and astragalus: (0) unfused to each other or tibia in adult; (1) fused to each other, unfused to tibia; (2) complete fused to each other and tibia.

178. Tibiotarsus, cnemial crest(s): (0) one; (1) two.

179. Tibia: (0) medial condyle projecting farther anteriorly than lateral; (1) equal in anterior projection.

180. Tibia, extensor canal: (0) absent; (1) an emarginate groove; (2) groove bridged by an ossified supratendinal bridge.

181. Tibia/tarsal formed condyles, *tuberositas retinaculi extensoris* (Baumel and Witmer, 1993) indicated by short medial ridge or tubercle proximal to the condyles close to the midline and a more proximal second ridge on the medial edge: (0) absent; (1) present.

182. Tibia/tarsal formed condyles, mediolateral widths: (0) medial condyle wider; (1) approximately equal; (2) lateral condyle wider.

183. Tibia/tarsal formed condyles: (0) gradual sloping medial constriction of condyles; (1) no medial tapering of either condyle.

184. Tibia/tarsal formed condyles, intercondylar groove: (0) mediolaterally broad, approximately 1/3 of the width of anterior surface; (1) less than 1/3, of the total anterior surface.

185. Tibiotarsus, extension of the articular surface for distal tarsals/tarsometatarsus: (0) no posterior extension of trochlear surface or restricted to distal-most edge of the posterior surface; (1) well-developed posterior extension, *sulcus cartilaginis tibialis* of Aves (Baumel and Witmer, 1993); distinct surface extending up the posterior surface of the tibiotarsus; (2) with well-developed, posteriorly projecting medial and lateral crests.

186. Tibia and proximal tarsals, distal-most mediolateral width: (0) wider than mid-point of shaft giving distal profile a weakly developed triangular form; (1) approximately equal to shaft width, no distal expansion of whole shaft though condyles may be variably splayed mediolaterally.

187. Fibula: (0) reaches tarsal joint articulating into distinct socket formed between the proximal tarsals and the tibia; (1) reduced in length, does not reach tarsal joint.

188. Distal tarsals and metatarsals, fusion: (0) distal tarsals fuse to metatarsals; (1) distal tarsals fuse to metatarsals and proximal metatarsals coossify; (2) distal tarsals as well as proximal and distal coossification of metatarsals; (3) extreme distal fusion, distal vascular foramen closed.

189. Metatarsal V: (0) present; (1) absent.

190. Metatarsal III: (0) proximally in plane with II and IV; (1) proximally pinched between II and IV.

191. Tarsometatarsus, intercondylar eminence: (0) absent or very weakly protuberant; (1) well developed, globose.

192. Tarsometatarsus, hypotarsus: (0) absent; (1) developed as a posterior projection with a flat posterior surface; (2) projection, with distinct crests and grooves; (3) at least one groove enclosed by bone posteriorly.

193. Tarsometatarsus, proximal vascular foramen(a): (0) absent; (1) one, between metatarsals III and IV; (2) two.

194. Metatarsal I: (0) straight; (1) "J shaped" (Chiappe, 1993).

195. Metatarsal I: (0) curved or distally deflected but not twisted, ventral surface convex; (1) deflected and twisted such that medioventral surface is concave proximal to trochlear surface for phalanx I.

196. Metatarsal II, dorsal surface, tubercle: (0) absent; (1) present.

197. Metatarsal II, distal plantar surface, "fossa for metatarsal I": (0) absent; (1) present.

198. Metatarsal II, articular surface for first phalanx: (0) ginglymoid; (1) rounded.

199. Metatarsals, comparative mediolateral width: (0) metatarsal IV approximately the same width as metatarsals II and III; (1) metatarsal IV narrower than MII and MIII.

200. Metatarsals, comparative trochlear width: (0) II approximately the same size as III and IV; (1) II broader than III and IV.

201. Distal vascular foramen: (0) simple, passing dorsoplantarly; (1) forked, two exits, plantar and distally between metatarsals III and IV.

202. Shaft of cervical ribs: (0) slender and longer than vertebra to which they articulate; (1) broad and shorter than vertebra (Hwang et al., 2004).

203. Caudal vertebral count: (0) more than 27; (1) 22–26; (2) fewer than 21 (modified from Chiappe, 2002).

204. Anterior six caudals: (0) second centrum nearly equal or longer than the first centrum; (1) fewer than half of the first centrum (new).

205. Tooth morphology: curved tips with sharp anterior and posterior cutting edges (0); conical tooth with D shaped in cross-section (1) (new).

## Part II. PAUP Matrix (Character distribution):

Characters and data matrix: character state 0 is plesiomorphic; character state 1–6 are apomorphic; "?" is either not preserved or unknown; [ ] means two or more character states included.

### *Anas platyrhynchos*

2111?10211111111?10112211[01]211121111111011000111101121310  
1010601100112131110131011010110100?1111101111000[01]11100111  
00120110000101011111112311101101011111?1111101111111211  
101121021100211311122?1010001120?

### *Chauna torquata*

1111?102111111[12]1111010221101112111111011000111111213101  
00060110011113100015001?1011010111110101111000211100111001  
201100001011011011112311101101111111?1111111111111211101

121021200211311122?1011001120 ?

*Gallus gallus*

1111 ?102111112111101122110111111111111011000110101121310101  
161100111[12]13101012101201211010111211101111000111110111001  
20110000101101101111113111011001211111?21211111111111211101  
121021100211311132?1011001120?

*Crax pauxi*

2111?10211111211?10112211011111111111111011000110101121310101  
16111011121310101210120121101011121110111100011111011100120  
11000010110110111111311101101121111 ?211111111111121110112  
1021100211311132?1011001?20 ?

*Crypturellus undulatus*

2111?11211111[01]0101000111110101[01]00110111111110011102131

0101161101112213111012001001211010101[12]1110111100011111011  
1001201100001101011011111031110110111111012120110111111121  
1101121021100211311122?101[01]001?20 ?

*Ichthyornis*

110010 ?11 ???????1 ??????1 ???11101110100102 ???011 ??[01] ??  
0011 ??6010001 ???31110220 ???10110100 ?12110011110[01]0111100  
110111101000010000111211 ???31110111000111100[12]1 ?[01] ?01 ?  
11?11211101121111100211311121??011000??00

*Patagopteryx deferrariisi*

??????????????20?0?1 ??????00 ?1 ???10?0 ?????????201000000  
[45]0 ??1 ???[23] ???0 ??????10010 ?0?00101 ?1 ?100100 ???[01] ??  
10 ???0100000?0001 ?[12]00 ??3?0 ??????00?10000?00?01[01]011 ?  
12?0 ?? ?120?0?000[12]1131001100000?001?0 ?

*Cathayornis yandica*

[01]0?010?0 ???  
111 ?3?1?0010 ?[23]0 ??[12] ?01211101 ??????10 ??1?0 ?01001011 ?  
0[01]?10[12]0?111?0 ???? ?1 ?? ?2 ?? ?21001?1?01?0110000 ???? 0 ? 0 ?  
00 ?? 011???11[12]0?0?0?[01]1????????????1200

*Concornis lacustris*

??  
0111 ?2 ????10 ?30 ?01?0012111011 ?0?0010???1 ??????00 ?1110 ??  
1021?1??10??1???2 ??????????????????010 ??????????????0011 ????????  
20?0?00??111?00?00??[01]1?1 ???

*Neuquenornis volans*

??  
110 ?????????????31 ??????01111 ?011010 ?001 ?0101 ?01 ??1 ?????  
1 ?01 ????? ???? ??????1 ??????? ?001 ???01 ?????????????????  
01?0?1?1?0?????1?[01]?0??10?0111?1 ???

*Gobipteryx minute*

1111?100100002001?1?0?10?????????????????0??1 ?????????????????  
1????????????12?11010010?0??010110?00 [12]00??11?011???0?????????1?  
121??[012]?0?????1?0?0?0?????0?001????0??1?10?00111111000?101?11  
??1 ???

*Apsaravis ukhaana*

???1 ?0 ??????????????????????????????????????? ?0 ??????? ?0010 ?  
[01][345]?10011???[23] ??101 ??????10010010 ??01]100101111011111 ?

01101110[12]01111110?01011021[01]10?[23]11101100?[01]1??10121[01]?  
010111111??1110??2?101211211311011??001000 ???? ?

*Rahonavis ostromi*

???  
4?0?000?????????????1?????????????????00110 ??????????????????  
???0 ??????????????????????00 ????00?0?0100?00?1???101?001000?1??  
0000100?000???0 ?

*Confuciusornis sanctus*

1111?[01]001001??????????0??00??001200???1?011??100100001100001?  
0010102000?2000[01]00?010010?0010000000000000?000020??001000  
0000001002101011110100?000000000100000?00001101101?112000100  
01111000011010100?120 ?

*Sapeornis chaoyangensis*

?? 10 ??  
010001???0010?0 ???????00000?000?????10?0?0100002000 ?000110 ??  
001000000??0 ?000 ?0 ???1110000 ?000000000 ?0 ?0 ?00001 ?0010 ??  
102000?100?101000??00100?1200

*Archaeopteryx lithographica*

000010 ?000000000 ??000110 ??00 ?0 ??000 ?00 ????00 ?000000  
[01]00[01] ??00000 ?00 ???????00000 ?000000 ?00000000000000000 ?  
0001100 ?0 ???000 ?0001000000 ??0000000 ?0000000001000?0 ?00000 ?  
000000?000?00?0?[01]?0100000000?100?0111

*Shenzhouraptor sinensis*

??10110??1000?0 ??????????????0??00?00?0000?0??10?01 ??0010000 ?  
000000 ????000 ??000000?0110?001010000?101 ?01000 ?0001100 ?001 ?  
00000??01000001011100000?00000000?1000?0?0000?00??0100000010  
0101100000?00100?100 ?

*Jinfengopteryx elegans*

00001 ??00 ??0 ??????1 ???????????????????????????0 ??????0 ?0 ?00 ???  
0 ?0 ?011 ?0 ?00 ??????????????0 ?00 ??????0 ?00 ???000000000 ?????  
110 ?????????????????????????10?000?00?00?0000 ??????????????0 ?????  
????????????????0????????????0111

*Microraptor zhaoianus*

?00001 ?00 ??0 ???  
0000?00?00?100?????100[01]0?0?000??0????0000000000?0?00000001?  
000?000???????10?010??0?000?000001?0??0?01100?0000???20?0????0000  
?????00000?1000

*Sinovenator changii*

000001?00000 ???????0 ??????????0?0?0?101?0?11000 ?????1 ?00 ?0 ?  
00?0?000 ??????????????????1 ?00000 ?020 ???00101001 ??????000 ???  
01 ?000 ?1 ??????????????0 ??00 ??????????0011 ????? ?00000 ?00000 ??  
0[01]1???????0?00000?0?0?0?1000

*Protarchaeopteryx robusta*

?0000 ???  
???0???0??0 ??????0010 ?????????????????????????????????????  
?????????????????????????????????????0 ??????0 ?00 ??????????0  
?????????????????????????????????????1000

*Huaxiagnathus orientalis*

?00000?00000 ??000 ???  
0??01?00?00 ???????00000?000??000?0 ?????000000 ????????????????



?????????????10 300 ???0 30000 3000010 ???30 30 30000 ???  
00???????00???0?0000?1000  
*Sinornithosaurus millenii*  
000000 300000 ??????????????????????0 ??????10 ?????300 301000 ?  
0 300 301000 ???0 ?10 ???2010001 ?1000 300000001 ?1001000000000000 ?  
0 ?30 ??????????????????10 ??????300000000000100 300 30 ?30000 ???  
??1??0???????000000?00000?1000  
*Sinosauropteryx prima*  
000000 300000 ??????????????????????????1 ??????????0 ?30 ?????  
0 ?????1 300 ?30 ??????????????10000 ??????0 ?????3000000 3000000 ?  
?????????????????????10 ??????30 ?????300000000 ??????????30 ?30 ??  
???00???????0?000???0?000?1000  
*Caudipteryx zoui*  
000010 3000010 ?????0 ??????????10 ?0 30000 ?0 ???11 ??????100300 ?  
0?00?00000?100?0?0 ????0 ???00000?0?0?000 ????100100000?0 30000 ???  
00 ??????????30 30 ??????10 301 30 30 ????000000000 30 ?30 ?10 ?10 ??????????  
0?????????00000?0000?000?1100

Part III. Search Settings and Results :

P A U P\*  
Version 4.0b10 for Macintosh ( PPC/Altivec )  
Saturday , October 2 , 2004 12 54 PM  
This copy registered to : Z-X Luo  
Carnegie Institute  
( serial number = B414746 )

NOTICE

This is a beta-test version. Please report any crashes , apparent calculation errors , or other anomalous results. There are no restrictions on publication of results obtained with this version , but you should check the WWW site frequently for bug announcements and/or updated versions.  
See the README file on the distribution media for details  
Processing of file "Sino10-3-04" begins...  
Data matrix has 25 taxa , 205 characters  
Valid character-state symbols : 0123456  
Missing data identified by " ? "  
\*\*\*Skipping " MacClade " block  
Processing of file " Sino10-3-04 " completed.  
Outgroup status changed :  
1 taxon transferred to outgroup  
Total number of taxa now in outgroup = 1  
Number of ingroup taxa = 24  
Branch-and-bound search settings :  
Optimality criterion = parsimony  
Character-status summary :  
Of 205 total characters :

All characters are of type'unord'  
All characters have equal weight  
3 characters are constant  
21 variable characters are parsimony-uninformative  
Number of parsimony-informative characters = 181  
Gaps are treated as " missing "  
Multistate taxa interpreted as uncertainty  
Initial upper bound : unknown ( compute heuristically )  
Addition sequence : furthest  
Initial 'MaxTrees' setting = 100  
Branches collapsed ( creating polytomies ) if maximum branch length is zero  
'MulTrees' option in effect  
Topological constraints not enforced  
Trees are unrooted  
Branch-and-bound search completed :  
Score of best tree found = 384  
Number of trees retained = 60  
Time used = 00 02 58.2

Part IV. References to Supplementary Information :

Baumel J J, Witmer L M. Osteologia[A]. In: Baumel J J, ed. Handbook of Avian Anatomy: Nomina Anatomica Avium, 2nd edition[C]. Cambridge: Nuttall Ornithological Club, 1993. 45-132.  
Chiappe L M. Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of northwestern Argentina[J]. Amer. Mus. Novit., 1993, 3083: 1-27.  
Chiappe L M. Basal bird phylogeny: problems and solutions[A]. In: Chiappe L M, Witmer L M, eds. Mesozoic Birds: above the Heads of Dinosaurs[C]. Berkeley: Univ. California Press, 2002. 448-472.  
Hwang S H, Norell M A, Ji Q, et al. A large compsognathid from the Early Cretaceous Yixian Formation of China[J]. J. System. Palaeont., 2004, 2(1): 13-30.  
Ji Q, Ji S A, You H L, et al. An Early Cretaceous avialian bird, *Shenzhouraptor sinensis* from western Liaoning, China[J]. Acta Geol. Sin. (English Edition), 2003, 77(1): 21-27.  
Norell M A, Clarke J A. Fossil that fills a critical gap in avian evolution[J]. Nature, 2001, 409: 181-184.  
Norell M A, Makovicky P. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*[J]. Amer. Mus. Novit., 1997, 3282: 1-45.  
Zhou Z H, Zhang F C. A long-tailed, seed-eating bird from the Early Cretaceous of China[J]. Nature, 2002, 418: 405-409.