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Jinfengopteryx Compared to *Archaeopteryx*, with Comments on the Mosaic Evolution of Long-tailed Avialan Birds

JI Shu'an* and JI Qiang
Institute of Geology, Chinese Academy of Geological Sciences, Beijing 100037

Abstract: *Jinfengopteryx* is a newly uncovered *Archaeopteryx*-like avialan bird outside Germany, which was found from the Jehol Biota of northern Hebei in northeastern China. It shares many characters only with *Archaeopteryx* by the possession of three fenestrae in the antorbital cavity, 23 caudal vertebrae and long tail feathers attached to all the caudal vertebrae. But the former differs from the latter in the relatively short and high preorbital region of skull, more and closely packed teeth, much shorter forelimb compared to hindlimb. Such differences indicate *Jinfengopteryx* is even slightly more primitive than *Archaeopteryx,* although both birds can be placed at the root position of the avialan tree based on cladistic analysis. *Shenzhouraptor* is suggested to be slightly more advanced than *Jinfengopteryx* + *Archaeopteryx,* supported by some derived features in teeth, shoulder girdles and forelimbs such as the reduction of tooth number, dorsolaterally directed glenoid facet, very long forelimb and comparatively short manus. Meanwhile, the tail of *Shenzhouraptor* shows more primitive characters than those of *Jinfengopteryx* and *Archaeopteryx,* e.g., the strikingly longer tail composed of more caudal vertebrae and the long tail feathers attached only to distal caudal segments. The mixed primitive and advanced characters reveal the evident mosaic evolution among long-tailed avialan birds.

Key words: *Jinfengopteryx, Archaeopteryx,* long-tailed avialans, mosaic evolution, Mesozoic

1 Introduction

Being regarded as the oldest and most primitive bird for 145 years, the Late Jurassic *Archaeopteryx* in Germany differs from nearly all other Mesozoic birds in having a distinctly long bony tail that consists of 21–23 caudal vertebrae (Elzanowski, 2002). In the past 10 years, several Cretaceous fossil birds were reported to possess a long skeletal tail, but some of them are still in dispute. A beaked bird *Confuciusornis* was reported from the Yixian Formation of western Liaoning, China in 1995. Unfortunately, it was mistakenly figured out to be an *Archaeopteryx*-level bird with long caudal series originally on the basis of the incompletely preserved and fragmentary material (Hou et al., 1995a, b). But the following finding of abundant specimens demonstrates that *Confuciusornis* has a pygostyle rather than a long bony tail (Hou et al., 1996; Martin et al., 1998; Chiappe et al., 1999). In 1998, an incomplete skeleton *Rahonavis* was reported from the Upper Cretaceous of Madagascar, and was regarded to be closely related with *Archaeopteryx* mostly based on the existence of a long bony tail in *Rahonavis* (Forster et al., 1998). It should be noted here that *Yandangornis*, a long-tailed animal found from the Upper Cretaceous of Zhejiang Province, China, most probably represents a maniraptoran theropod, although it was originally assigned to birds (Cai and Zhao, 1999).

The definite birds with long skeletal tails outside Germany have been erected on complete and well-preserved skeletons from the Early Cretaceous Jehol Biota in western Liaoning recently. *Shenzhouraptor* and *Jeholornis* were named by Ji et al. and by Zhou and Zhang respectively in mid 2002 (Ji et al., 2002a; Zhou and Zhang, 2002), but the further observation indicates that the latter is the junior synonym of the former (Ji et al., 2003). In late 2002, Ji et al. reported another long-tailed bird from western Liaoning, *Jixiangornis*, which resembles *Shenzhouraptor* in many respects (Ji et al., 2002b). More recently, a new genus *Dalianraptor* was named based upon a nearly complete skeleton (Gao and Liu, 2005), which shows some differences from *Shenzhouraptor* in the morphology and proportions of the forelimb. Fortunately, the long-tailed avialan bird has also been discovered from

* Corresponding author. E-mail: jishu_an@sina.com.

Fig. 1. Holotype of *Jinfengopteryx elegans* (CAGS-IG-04-0801).
Scale bar = 10 cm.

northern Hebei, where many typical Jehol fossils were excavated before. In early 2005, a new long-tailed bird *Jinfengopteryx*, unearthed from the Early Cretaceous Qiaotou Formation of Fengning County in northern Hebei, was briefly described (Ji et al., 2005). A large quantity of the similarities show *Jinfengopteryx* is the sister taxon of *Archaeopteryx*, thus *Jinfengopteryx* is very significant for our understanding the basal avialan evolution. In the present paper, we will focus on the comparative features between *Jinfengopteryx* and *Archaeopteryx*, and provide some viewpoints on the mosaic evolution of long-tailed avialan birds.

2 Anatomical Comparison between *Jinfengopteryx* and *Archaeopteryx*

Only the holotype of *Jinfengopteryx elegans* has been discovered and briefly described to date (Ji et al., 2005). It is nearly completely preserved (Fig. 1), and shows many features similar to *Archaeopteryx*. Detailed comparisons of *Jinfengopteryx* to *Archaeopteryx* can provide us important ideas about the definition of birds, the phylogenetic relationships of non-avian theropods and avialans, and the diversity and mosaic evolution of avialan birds.

2.1 Skull, mandible and teeth

The lateral outline of the skull of *Jinfengopteryx* is more or less triangular, as in *Archaeopteryx* (Martin, 1991). But *Jinfengopteryx* has a relatively shorter and higher preorbital portion, different from that of *Archaeopteryx*, whose preorbital portion is distinctly long and low (Fig. 2). The external nasal opening is small in *Jinfengopteryx*, and the snout is remarkably blunt. Compared to those, the external nasal opening is very large and the snout pointed in *Archaeopteryx*. The antorbital cavity is large in both genera, and composed of three fenestrae: large antorbital fenestra, maxillary fenestra and very small promaxillary

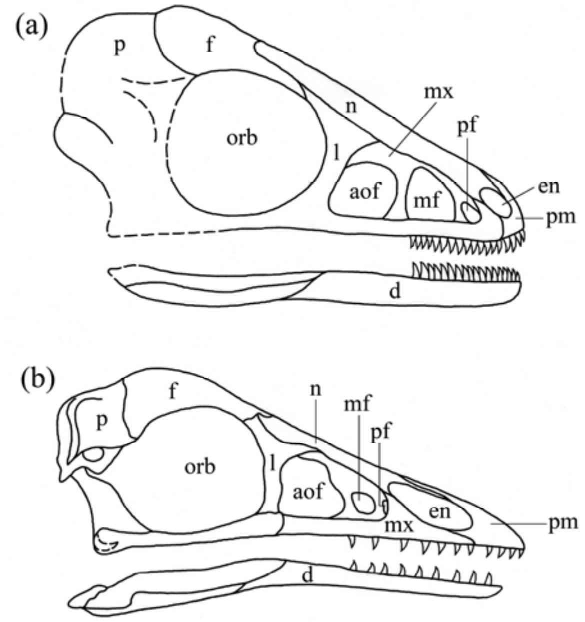

Fig. 2. Comparison of the skulls between *Jinfengopteryx elegans* and *Archaeopteryx lithographica*.

(a) Restoration of the skull of *J. elegans* (based on the holotype specimen CAGS-IG-04-0801); (b) Restoration of the skull of *A. lithographica* (after Martin, 1991, fig. 10). Not to scale.

Abbreviations: aof – antorbital fenestra; d – dentary; en – external nasal opening; f – frontal; l – lacrimal; mf – maxillary fenestra; mx – maxilla; n – nasal; p – parietal; pm – premaxilla; orb – orbital opening; pf – promaxillary fenestra.

fenestra. It is noteworthy that the maxillary fenestra in *Jinfengopteryx* is proportionally much larger than that in *Archaeopteryx* (Witmer, 1990; Martin, 1991; Mayr et al., 2005). The other major difference of the skull is that the nasal is relatively longer in *Jinfengopteryx* than in *Archaeopteryx*.

The tooth crown is conical and unserrated in both *Jinfengopteryx* and *Archaeopteryx*, unlike the laterally compressed and serrated tooth in dromaeosaurids although the reduction of serration occurred to some extent such as in *Microraptor zhaoianus* (Xu et al., 2000). The tooth similarities of these two long-tailed birds also include the uniform-shaped crowns and a slight constriction at the base of crown in some teeth. The most remarkable difference of the dentitions between *Jinfengopteryx* and *Archaeopteryx* is the tooth number and its arrangement. In *Jinfengopteryx*, there are 4 premaxillary teeth, 14 maxillary teeth, and 18 dentary teeth (Ji et al., 2005). But *Archaeopteryx* possesses 4 premaxillary teeth, only 8 maxillary teeth in the Berlin and Eichstätt specimens (Wellnhofer, 1992), and 12 dentary teeth as shown in the Munich specimen (Elzanowski and Wellnhofer, 1996), much less than those in *Jinfengopteryx*. By comparison, the upper teeth are completely lost in *Shenzhouraptor* (= *Jeholornis*), and only 2 or 3 small teeth retain at the anterior end of dentary (Zhou and Zhang, 2003, Zhou, 2004). All the teeth are very closely packed in *Jinfengopteryx*, while the upper and lower teeth in *Archaeopteryx* are widely spaced with the interdental spaces average more or less one tooth diameter. Furthermore, the length of the upper tooth series is very short in *Jinfengopteryx*, occupying just 1/4 the whole skull length, proportionally shorter than that in *Archaeopteryx* (>1/3).

2.2 Axial skeleton

About 12 cervical vertebrae including the atlas and axis, and 11 dorsal vertebrae are recognized in the unique specimen of *Jinfengopteryx*. But they do not give us more information in comparison to *Archaeopteryx* because of their poor preservation. The sacral vertebrae are not exposed in *Jinfengopteryx*, so the nature of them remains unknown.

As in *Archaeopteryx*, *Rahonavis*, *Shenzhouraptor* and *Jixiangornis*, the avialan *Jinfengopteryx* has an unreduced, long bony tail and lacks any evidence of pygostyle. The number of caudal vertebrae measures 23 in *Jinfengopteryx*, which lies in the same range of caudal segments as in *Archaeopteryx* (21–23). This is one of the major evidences supporting the sister relationship between the two taxa. In contrast, the tail of *Shenzhouraptor* includes up to 27 caudal vertebrae (Zhou and Zhang, 2003; Zhou, 2004), more than that of *Jinfengopteryx* and any specimen of *Archaeopteryx*. The bony tail is approximately half the total skeletal length of *Jinfengopteryx*, close to about 0.45 in *Archaeopteryx*. Moreover, the tail is roughly as long as the hindlimb in *Jinfengopteryx*; however, the tail is slightly shorter than hindlimb in *Archaeopteryx*. In contrast, the bony tail is comparatively much longer in *Shenzhouraptor*, occupying 0.57 of its total skeletal length and 1.58 of its hindlimb length respectively. In the caudal series, the proximal six caudal vertebrae are short in *Jinfengopteryx*; and the transition point is proximally placed at the seventh caudal vertebra, which makes the number of the elongated caudal vertebrae to be 17. Such situation is close to that in *Archaeopteryx*, but different from that in *Shenzhouraptor*, which has more than 20 elongated caudal vertebrae.

In *Jinfengopteryx*, the chevrons attached to the elongated caudal vertebrae are considerably long anteroposteriorly and bifurcate at their both ends. In this aspect, it is dissimilar to *Archaeopteryx*, which bears relatively short and weak chevrons articulated with the middle caudal vertebrae.

The sternum is unknown in *Jinfengopteryx*, as in all specimens of *Archaeopteryx*. It should be noted that the small and rectangular "sternum" recognized in the Munich

Table 1 Comparative ratios of some skeletal element lengths in *Jinfengopteryx*, *Archaeopteryx* and *Shenzhouraptor*

	Jinfengopteryx elegans [1]	*Archaeopteryx lithographica* [2]	*Shenzhouraptor sinensis* [3]
Skull preorbital portion/whole skull	0.43	0.54	-
Tail/whole skeleton	0.50	0.45	0.57
Tail/hindlimb	1.00	0.94	1.58
Forelimb/hindlimb	0.62	1.00–1.02	1.26
Humerus/femur	0.70	1.19–1.24	1.52
Ulna/humerus	0.88	0.87	1.02
Manus/ulna	1.73	1.40–1.46	1.06
First metacarpal/second metacarpal	0.41	0.22–0.28	0.22
Tibia/femur	1.43	1.28–1.33	1.19

1. Based on the holotype CAGS-IG-04-0801; 2. mainly based on the Solnhofen, London and Berlin specimens (Wellnhofer, 1992); 3. mainly based on the specimen IVPP V13353 (Zhou and Zhang, 2003).

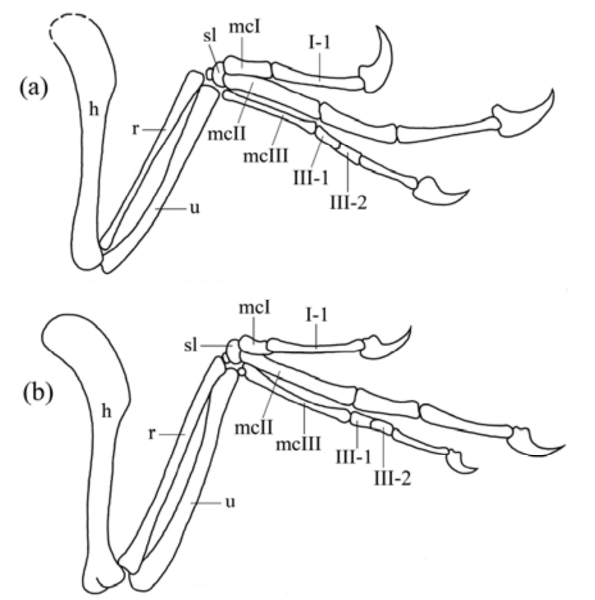

Fig. 3. Comparison of the forelimbs between *Jinfengopteryx elegans* and *Archaeopteryx lithographica*.
(a) Restoration of the forelimb of *J. elegans* (based on the holotype specimen CAGS-IG-04-0801); (b) Forelimb of *A. lithographica* (modified after Wellnhofer, 1992, fig. 11). Not to scale.
Abbreviations: h – humerus; mcI – metacarpal I; mcII – metacarpal II; mcIII – metacarpal III; r – radius; sl – semilunate carpal; u – ulna; I-1 – first phalanx of the digit I; III-1 – first phalanx of the digit III; III-2 – second phalanx of the digit III.

specimen is now proved to be a portion of the coracoid (Wellnhofer, 1993; Wellnhofer and Tischlinger, 2004). So the sternum in *Archaeopteryx* remains also unknown. Both *Jinfengopteryx* and *Archaeopteryx* possess no uncinate processes, but these structures are present in *Shenzhouraptor* (Ji et al., 2002a, 2003), basal pygostylian birds *Confuciusornis* (Chiappe et al., 1999), and in some maniraptoran groups such as dromaeosaurids (Hwang et al., 2002; Xu et al., 2003; Liu et al., 2004) and oviraptorosaurs (Clark et al., 1999).

2.3 Girdles and limbs

The scapula and coracoid are fused at an angle of about 90° between them in *Jinfengopteryx*, thus showing L-shape in lateral view, as in *Archaeopteryx* and Liaoning dromaeosaurids (Ostrom, 1976; Xu et al., 1999; Liu et al., 2004). No evidence can we obtain about the glenoid in *Jinfengopteryx* owing to the bad preservation of this portion. The very weak furcula of *Jinfengopteryx* is preserved in lateral view, so its clavicular angle is uncertain. In some basal birds such as *Archaeopteryx*, *Shenzhouraptor*, *Confuciusornis* and some dromaeosaurids, the furcula is robust and boomerang-shaped in anterior view.

One of the most striking dissimilarities of *Jinfengopteryx* from *Archaeopteryx* is the proportionally short, slender forelimb and the obviously long, robust hindlimb in *Jinfengopteryx*. Its length ratio of forelimb to hindlimb is only 0.62 (Table 1), much less than about 1 in *Archaeopteryx* (Padian and Chiappe, 1998), 1.26 in *Shenzhouraptor* (Zhou and Zhang, 2003), and even less than ≥ 0.80 in some non-avialan dromaeosaurids *Sinornithosaurus* and *Microraptor* (Xu et al., 1999; 2003; Liu et al., 2004). Short and slender forelimb indicates the primitive features related to flight adaptation.

The first metacarpal is comparatively long in *Jinfengopteryx* with the length ratio of metacarpal I to metacarpal II about 0.41. This ratio is just 0.22–0.28 in *Archaeopteryx* (Wellnhofer, 1985, 1992). Within the forelimb, the manus is evidently longer than the ulna in *Jinfengopteryx* and *Archaeopteryx*, as in many maniraptoran theropods; whereas the manus nearly equals the ulna in length in *Shenzhouraptor*, as in more advanced enantiornithine and ornithurine birds. The first manual digit is relatively longer in *Jinfengopteryx* than in *Archaeopteryx*. The first phalanx of the first digit goes greatly beyond the distal end of the second metacarpal in *Jinfengopteryx* (Fig. 3), but the distal ends of these two bones lie almost at the same level in *Archaeopteryx* (Wellnhofer, 1985, 1992). In *Jinfengopteryx*, the first and second phalanges of manual digit III show a tendency to fuse each other, although the suture between them seems invisibly present. In some *Archaeopteryx* specimens, the joint of these two phalanges appear to be solid and inflexible (Wellnhofer, 1985, 1992). In this aspect, the two birds show the similarity to some extent. All the manual claws, together with the preserved horny sheathes, are strongly curved with pointed pits in both birds.

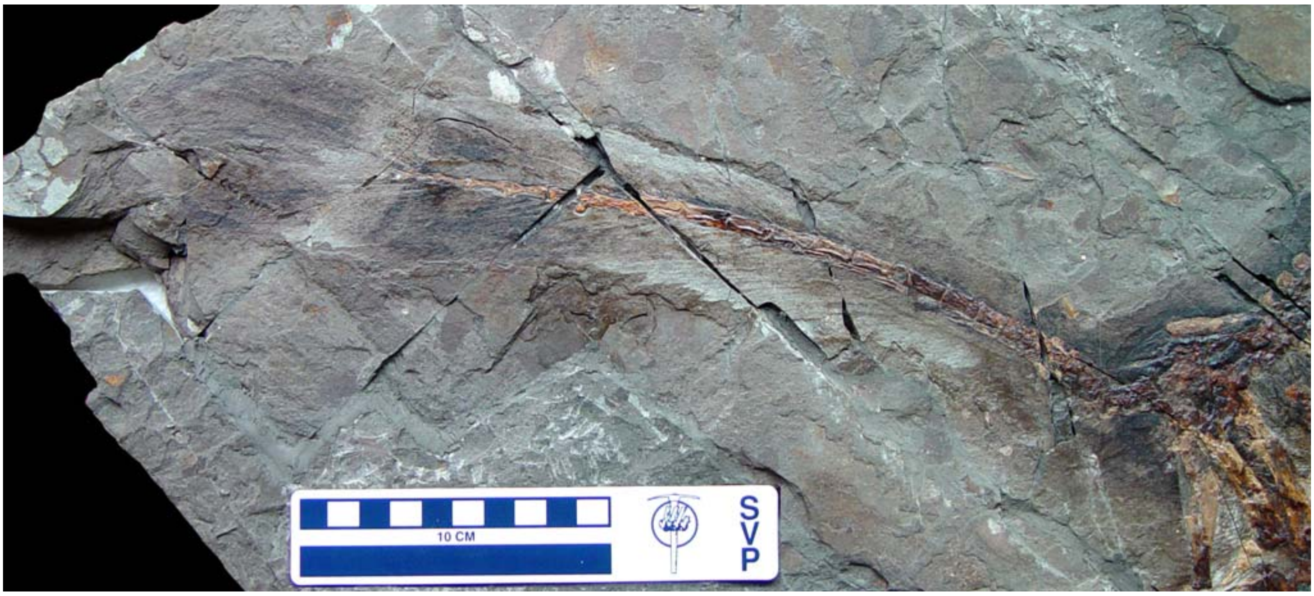

Fig. 4. Tail feathers of *Jinfengopteryx elegans* (holotype specimen CAGS-IG-04-0801), showing their attaching to all the caudal vertebrae.
Scale bar = 10 cm.

The pelvis of *Jinfengopteryx* is basically similar to that of *Archaeopteryx* in the retroverted pubes. The pubic symphysis appears relatively short and its distal margin is distinctly straight in *Jinfengopteryx*, comparable to *Archaeopteryx*, in which the pubic symphysis has a typical expansion distally and forms a spoon-shaped pubic foot (Wellnhofer, 1985).

The very strong hindlimb in *Jinfengopteryx* shows its powerful running ability, different from that in *Archaeopteryx*. The femur and tibia are comparatively much more robust in *Jinfengopteryx* than in *Archaeopteryx*. Although in *Jinfengopteryx* the fibula is slender, its distal end reaches the tarsus, as in *Archaeopteryx*. Unfortunately, we can not draw the detailed comparison of foot between *Jinfengopteryx* and *Archaeopteryx* because of the unclear preservation of the former bird.

2.4 Flight and tail feathers

Although two patches of feathers are preserved attached to the right fingers, there is no trace of preservation of any flight feathers in *Jinfengopteryx* unfortunately. We cannot give any suggestion about the wing feathers of *Jinfengopteryx*; but this bird is not a good flier or glider according to its very short forelimb. In *Archaeopteryx* and *Shenzhouraptor*, however, the flight feathers are long and asymmetrical, showing their powerful capabilities of flight. Such asymmetrical feathers also exist in non-avian dromaeosaurid *Microraptor* (Xu et al., 2003).

The long and symmetrically-vaned tail feathers are well preserved in *Jinfengopteryx*, which seem to attach to nearly all the caudal vertebrae in a way similar to that of *Archaeopteryx* although their exact paired number is difficult to be determined (Fig. 4). It is distinctly different from *Shenzhouraptor* and even some non-avian theropods like *Caudipteryx* and *Microraptor*, in which the long tail feathers concentrate on the distal caudal vertebrae and form some fan-shaped rectrices at tail tip (Ji et al., 1998, 2002a; Zhou and Zhang, 2002, 2003; Xu et al., 2003).

3 Mosaic Evolution of Basal Long-tailed Avialans

According to cladistic analyses, *Jinfengopteryx* and *Archaeopteryx* constitute the sister taxa that occupy the most basal position of the avialan tree (Ji et al., 2005). *Shenzhouraptor* is probably just slightly more derived than (*Jinfengopteryx* + *Archaeopteryx*) and *Rahonavis*, while it is just more primitive than the most basal pygostylian birds *Sapeornis* and *Confuciusornis* (Zhou, 2004; Ji et al., 2005). Thus, *Jinfengopteryx* represents one of the most important findings of long-tailed birds because of its closest relationship with *Archaeopteryx*. As compared above, *Jinfengopteryx* is more similar to *Archaeopteryx* than to any other avialans in having the triangular skull outline, three fenestrae in the antorbital cavity, the same number of caudal vertebrae, and in the long tail feathers attached to all caudal vertebrae. Meanwhile, *Jinfengopteryx* shows some more primitive characters such as the short and high rostrum, relatively large number of teeth, much shorter forelimb proportionally compared to hindlimb and so on.

Let's turn to *Shenzhouraptor*. Several complete specimens made this avialan bird to be well-understood too (Ji et al., 2002a, 2003; Zhou and Zhang, 2002, 2003). *Shenzhouraptor* possesses some more advanced features than *Jinfengopteryx* and *Archaeopteryx*. Firstly, the teeth in *Shenzhouraptor* are remarkably reduced (Ji et al., 2002a, 2003; Zhou and Zhang, 2003), showing the derived character on the avian evolution. Secondly, the glenoid facet in *Shenzhouraptor* is dorsolaterally directed unlike the laterally pointed glenoid facet in *Archaeopteryx* (Ostrom, 1976; Jenkins, 1993), the forelimb is much longer than hindlimb in *Shenzhouraptor*, and the manus of *Shenzhouraptor* is about as long as the ulna as in most enantiornithine and ornithurine birds. Such characters are suitable for flight. In contrast, *Shenzhouraptor* has some more primitive characters than *Jinfengopteryx* and *Archaeopteryx*. The most striking one is that the tail of *Shenzhouraptor* is proportionally longer than those in *Jinfengopteryx* and *Archaeopteryx*, and consists of up to 27 caudal vertebrae, much more than 23 in the latter two. The other one is that the long tail feathers only attaches to the distal caudal vertebrae in *Shenzhouraptor* (Ji et al., 2002a, 2003; Zhou and Zhang, 2002, 2003), different from *Jinfengopteryx* and *Archaeopteryx* in which the long tail feathers are connected with nearly all caudal vertebrae. The long feathers limiting at distal caudal vertebrae possibly represents a primitive condition of avialan birds, and such condition is also shown in some non-avian maniraptorans *Caudipteryx* and *Microraptor* (Ji et al., 1998; Xu et al., 2003). The mixed primitive features and advanced characters occurring in different avialans reveal that the mosaic evolution is common among basal avialan birds.

4 Conclusions

The long-tailed *Jinfengopteryx* represents the only known bird more primitive than *Archaeopteryx* in the avialan tree. These two basal birds are the sister genera because they share the same or similar characters in the respects of skull, tooth, caudal vertebrae and tail feathers. But *Jinfengopteryx* is slightly more primitive than *Archaoepteryx* in the relatively large number of teeth, short and high preorbital region, and comparatively small length ratio of the forelimb to hindlimb.

In comparison with *Jinfengopteryx* and *Archaeopteryx*, another avialan *Shenzhouraptor* possesses the distinct derived and primitive characters together. The remarkable advanced features include the reduced teeth, dorsolaterally facing glenoid facet, forelimb longer than hindlimb, and the relatively short manus. The primitive features contain the great number of caudal vertebrae, and the long tail feathers only attached to the distal caudal vertebrae. Such mixed characters reveal the evident mosaic evolution among long-tailed avialan birds.

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