

## A New Enantiornithine Bird from the Lower Cretaceous Jiufotang Formation in Jinzhou Area, Western Liaoning Province, China

LI Li\*, WANG Jinqi, ZHANG Xi and HOU Shilin

*Paleontology Institute, Shenyang Normal University, Shenyang, Liaoning 110034, China*

**Abstract:** A new Early Cretaceous enantiornithine bird from Liaoning Province of northeastern China, *Shengjingornis yangi*, gen. et sp. nov., is reported. This new bird possesses the following unique combination of features: a long rostrum, with some teeth in the front; short nasal; slender jugal; Y-shaped furcula, with expanded distal end of the hypocleidum; cake-like sternum, with a low and caudally distributed keel; strut-like and caudally concave coracoid. The derived features of the scapula and the wings suggest a powerful flapping flight capability.

**Key words:** Early Cretaceous, Jiufotang Formation, Enantiornithine, Liaoning Province

### 1 Introduction

The abundance of bird fossils discovered in Mesozoic, which are distinct in shape, body size, feeding habits and ecological habits, indicate that many species of birds had appeared at that time. Especially for members of the Enantiornithes, the abundant and diverse avialans, were quite different in size. Most of them were relatively small, some even as small as sparrows, while a few were giant, for example, *Pengornis* (Zhou et al., 2008). Many Enantiornithes fossils were discovered from Cretaceous northern China, Iberia Peninsula of Europe, Australia, and Argentina. Their widespread occurrence suggests that the Enantiornithes had high flight ability. Representatives of Enantiornithes include *Propteryx* and *Shenqiornis* (Zhang and Zhou, 2000; Wang et al., 2010) from the Early Cretaceous in Hebei Province, China; *Eoenantiornis* (Hou et al, 1999) from the Early Cretaceous Jiufotang Formation Beipiao, Liaoning Province, China, and *Iberomesornis* (Sanz and Bonaparte, 1992) from the Early Cretaceous of Cuenca, Spain, etc.

Most enantiornithine species fed on insects, but some had different feeding habits. For example, *Longipteryx*, which were quite similar to modern kingfishers, had a special feeding habit. They would sit in a tree by the waterside, and preyed on fish swimming in the water (Zhang et al., 2001). While according to the sharp rostrum and the beak with teeth on the tip, *Longirostravis* were believed to be filter feeding birds (Hou et al., 2004).

### 2 Systematic Paleontology

Aves Linnaeus, 1758

Pygostylia Chiappe, 2002

Enantiornithes Walker, 1981

Longipterygidae, Zhang et al. 2000

*Shengjingornis* gen. nov.

(Figs.1,2; Table 1)

**Etymology:** The generic name is derived from the ancient name of Shenyang, the capital city of Liaoning Province.

**Diagnosis:** As for the species.

*Shengjingornis yangi* sp. nov.

**Holotype:** PMOL (Liaoning Paleontological Museum) AB00179, a complete skeleton mostly exposed in ventral view. The specimen is stored in Shenyang Normal University.

**Etymology:** Specific name is dedicated to the fossil preparator of Mr. Yang Qiang.

**Type locality and horizon:** Toudaoyingzi, Jinzhou, Liaoning Province, northeastern China (Fig. 3). Early Cretaceous, Jiufotang Formation.

**Diagnosis:** A pigeon-sized enantiornithine bird with the following unique combination of features: long, tapering, and slightly curved beak; teeth in the front of mouth; nasal short; jugal slender; frontal high; furcula Y-shaped, expanded hypocleidum at the distal end; coracoids short; sternum with a low and caudally distributed keel; humerus nearly as long as ulna and radius; carpal and metacarpal fused, at least two manual unguals; head of femur developed; fibula nearly half the length of tibia; proximal

\* Corresponding author. E-mail: Lilishenyang1978@163.com



Fig. 1. Photograph of *Shengjingornis yangi*, gen. et sp. nov. (PMOL-AB00179).

metatarsus fused.

#### Description:

**Skull.** The skull is badly crushed. However, some of its elements are articulated and in their natural places, which provides the possibility of identifying them.

The skull is mainly exposed in left lateral view. The rostrum (measured from the rostral margin of the orbit to the rostral margin of the premaxilla) constitutes 54% of the total skull length, distinctly less than the percentage in *Shanweinia* and *Longipteryx* (estimated at 62% and 64%, respectively). The premaxilla has an elongate nasal process and holds up to four teeth. The teeth are big and nearly conical in shape, and their crowns are constricted obviously at the base. The maxilla appears to lack teeth, although this is based on limited exposure of the ventral margin of the left maxilla. The rostral end of the dentary is distinctly curved and possesses four teeth, indicating that mandibular teeth, if present, were also restricted to the rostral portion of the dentary, as in *Longirostravis*. The proximally restricted teeth and elongated skull suggests that *Shengjingornis* may also have occupied the mudprobing niche of *Longirostravis* (Hou et al. 2004). The two nasals are not well preserved, but their preserved anterior parts seem short. The maxilla articulates posteriorly with the slender jugal. The frontal is large and domed.

The mandibles are curved, like *Longipteryx* and

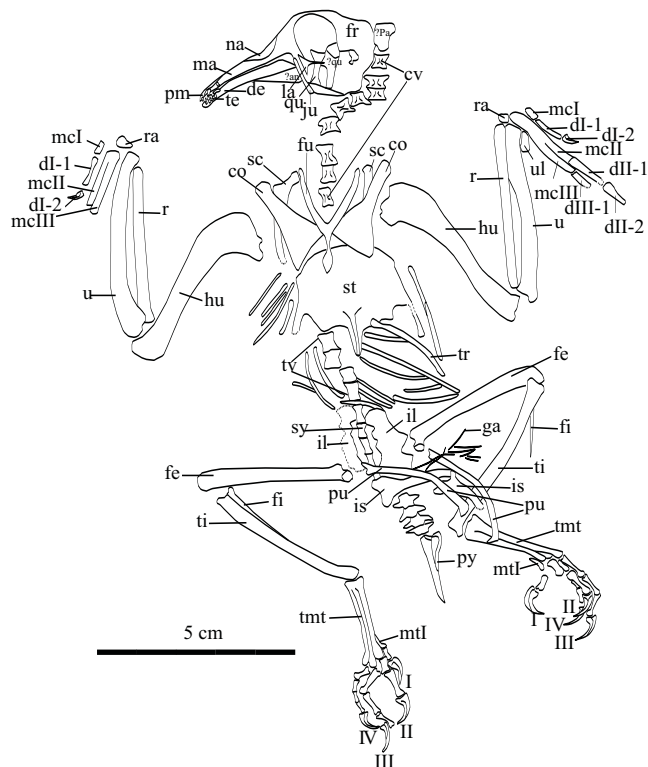


Fig. 2. Line drawing of the holotype of *Shengjingornis yangi* gen. et sp. nov. (PMOL-AB00179).

?an, angular; cv, cervical vertebrae; co, coracoid; de, dentary; dl-1, first phalanx of the alular digit; dl-2, second phalanx of the alular digit; dII-1, first phalanx of the major digit; dII-2, second phalanx of the major digit; dIII-1, first phalanx of the minor digit; fe, femur; fi, fibula; fr, frontal; fu, furcula; ga, gastralia; hu, humerus; il, ilium; is, ischium; ju, jugal; la, lacrimal; ma, maxilla; mcl-I-III, metacarpal I-III; mt I, metatarsal; na, nasal; ?pa, ?parietal; pm, premaxilla; pu, pubis; r, radius; ra, radiale; hu, humerus; u, ulna; ul, ulnare; sc, scapula; st, sternum; te, teeth; ti, tibiotarsus; tmt, tarsometatarsus; tr, thoracic rib; I-III, pedal digits.

*Longirostravis*. The left mandible is preserved in lateral, with a lateral groove paralleling the tomial edge marked (Fig. 4).

**Vertebral column.** The vertebral column is partly preserved and somewhat crushed. Cervical vertebrae are not well preserved, but near the foramen magnum of the skull, the atlas and axis are visible in lateral view. The thoracic ribs are the biceps ribs. The gastralia are slender. Synsacrum is composed of at least eight vertebrae as indicated by the transverse processes. Four caudal vertebrae are preserved. They are relatively wide, with slender and caudally directed transverse processes. The proximal end of the pygostyle is also present. Considering that the pygostyle usually becomes fused progressively from the distal to the proximal end, we estimate that *Shengjingornis* had a well-fused pygostyle, which is also true of *Longirostravis* and most other Early Cretaceous enantiornithine birds (Sanz et al., 1995).

**Sternum.** As in other enantiornithine birds (Zhang and Zhou, 2000; Zhang et al., 2001), the sternum is short and broad with the width and length of about equal size. The

**Table 1** Measurements of *Shengjingornis yangi* gen. et sp. nov. (PMOL-AB00161). (mm)

|                          |          |
|--------------------------|----------|
| Skull length             | 46.6†    |
| Coracoid length          | 18.7(l)  |
| Coracoid maximum width   | 13.7(r)‡ |
| Scapula length           | 25(r)‡   |
| Furcula total length     | 28.1(r)  |
| Sternum length           | 31.6     |
| Sternum width            | 28.5     |
| Humerus length           | 41(l)    |
| Ulna length              | 42(l)    |
| Radius length            | 43(l)    |
| Alular metacarpal length | 3.8(l)   |
| Phalanx 1 length         | 8.8(l)   |
| Claw length              | 5.1(l)   |
| Major metacarpal length  | 18.5(l)  |
| Phalanx 1 length         | 9.5(l)‡  |
| Phalanx 2 length         | 8(l)     |
| Minor metacarpal length  | 22.8(l)  |
| Phalanx 1 length         | 8.8(l)†  |
| Claw length              | 5.1(r)   |
| Femur length             | 37.5(l)  |
| Tibiotarsus length       | 44.1 (l) |
| Fibula length            | 21.2(l)  |
| Metatarsal I length      | 4.4(r)   |
| Phalanx 1 length         | 4.1(r)   |
| Phalanx 2 length         | 6.8(r)   |
| Metatarsal II length     | 21.1(r)  |
| Phalanx 1 length         | 5.3(r)   |
| Phalanx 2 length         | 6.7(r)   |
| Phalanx 3 length         | 7.6(r)   |
| Metatarsal III length    | 23.5(r)  |
| Phalanx 1 length         | 7.1(r)   |
| Phalanx 2 length         | 6.2 (r)  |
| Phalanx 3 length         | 6.5(r)   |
| Phalanx 4 length         | 7.5(r)   |
| Metatarsal IV length     | 22(r)    |
| Phalanx 1 length         | 3.8(r)   |
| Phalanx 2 length         | 3.1(r)†  |
| Phalanx 3 length         | 3.3(r)   |
| Phalanx 4 length         | 3.5(r)   |
| Phalanx 5 length         | 6.1(r)   |
| Pubis length             | 29.4(l)  |

†Estimated measurement; ‡Preserved measurement; l and r indicate left and right sides.

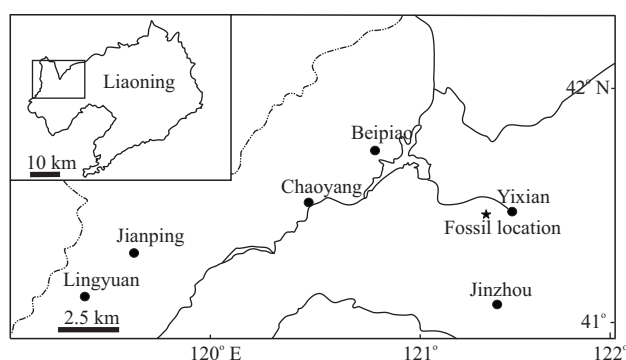


Fig. 3. Geographic position of Toudaoyingzi fossil location in western Liaoning, China.

keel is low and distributed only in the caudal part of the sternum as is typical of enantiornithine birds; the early ornithurine birds such as *Hongshanornis* and *Archaeorhynchus* all had a long keel extending along the full length of the sternum (Kurochkin, 1985; Zhou and Zhang, 2005; Zhou and Zhang, 2006). The cranial margin

of the sternum is round, and dorso-ventrally thin. The caudo-lateral processes are approximately parallel to each other. They have an expanded distal extremity, but lack a unique three-branched structure as in *Longirostriavis* (Hou et al., 2004). A pair of caudal processes lies between the lateral processes and the keel; they are small compared to that of *Longirostriornis*.

**Thoracic girdle.** The right scapula is well preserved and articulates with the coracoid, while the left scapula is more or less covered by the left coracoid. In the anterior end, the acromion and coracoid tuberosity are well developed. It cannot be judged whether the shaft is sagittally curved, as in modern birds. In agreement with other enantiornithines, the furcula is Y-shaped with a prominent hypocleidum. The clavicular ramus is robust with a thin and narrow epicleidum. In anterior view, the clavicular rami are slightly curved medially and separated by an angle of 50°. Unlike in other enantiornithines (Chiappe, 1996; Chiappe et al., 2002), the distal end of the hypocleidum is expanded in *Shengjingornis*. The coracoid is strut-like. It lacks the procoracoid that is present in all modern birds. The lateral margin of the coracoid is straight to slightly concave, not markedly convex as in some other Enantiornithes (Chiappe and Walker, 2002). The medial margin is concave and the sternal margin is straight.

**Forelimb.** The humerus is nearly as long as the ulna and the radius. The shaft of the humerus is slightly S-shaped. The head is typical of enantiornithine birds in having an internally slanting profile (Zhou, 1995). The head is flat, cranially concave and caudally convex as in *Longirostravis*. At the proximal end, the ventral and dorsal tubercles are developed. The pectoral crest is moderately expanded externally. The bicipital crest is bulbous as is typical of other enantiornithine birds, but is less expanded than in *Longirostravis*. At the distal end, the dorsal condyle is developed, but the ventral condyle is small and barely seen on the dorsal side. The olecranon fossa is low.

The ulna is bow-shaped. The proximal part of the ulna is slightly curved, and the olecranon seems slightly developed in caudoventral view. The radius is thin and straight, with the distal part slightly curved. The proximal end of the radius is slightly expanded and seems to have a simple articular face. The ulnare bone appears to be triangular. The radiale is a rather compressed bone with the distal articulation surfaces divided by a low ridge.

The carpometacarpus is fused only proximally. The alular metacarpal is close to the major metacarpal and seems not fused to it. The major metacarpal is straight and significantly thicker than the minor metacarpal. The minor metacarpal is slightly curved and extends somewhat more distally than the major metacarpal. The alular metacarpal is about one-fifth of the major metacarpal in length. The



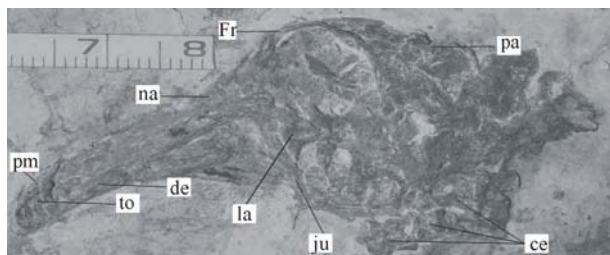


Fig. 4. Skull of *Shengjingornis yangi*, gen. et sp. nov. (PMOL-AB00179).

ce, cervical vertebrae; de, dentary; fr, frontal; ju, jugal; la, lacrimal; na, nasal; pa, parietal; pm, premaxilla; to, tooth.

alular digit bears two phalanges. The first phalanx is slender and long; the ungula phalanx is shorter than that of the major digit. The major digit bears three phalanges. The second phalanx is shorter than the first one. The minor digit bears two phalanges. The first phalanx is compressed; the ungula phalanx is not preserved.

**Pelvic girdle.** Some portions of the pelvis are also relatively well preserved. Both ilia are preserved, with the left ilium overlapping much of the right. The ilium is mainly dorsoventrally extended, and it has a wide and cranially rounded preacetabular wing and a shorter and narrow postacetabular. The proximal end of the right ischium is expanded. The ischium is short, with a prominent ascending process that contacts the posterior end of the ilium. The pubis is thick, long, and curved caudally; the iliac process of the pubis is slightly wider than that of the pubic body. The pubic foot is perpendicular to the pubic body.

**Hind limb.** The hind-limb elements are preserved in almost complete articulation. The femur is robust, nearly straight, and shorter than the tibiotarsus. It has a distinct neck and a prominent ball-shaped head, which lacks a capital fossa. The greater trochanteric is poorly developed, as in many other Mesozoic taxa, including the enantiornithines. The distal end has a distinct popliteal fossa that seemingly is separated from the intercondylar groove by a transverse ridge. The tibiotarsus is straight, and about 120% of the length of the femur. There is no anterior cnemial crest, unlike in extant birds. The proximal articulation appears to be round as in other enantiornithine birds and it has a well-developed fibular crest. The fibula is long, thin and about 45% of the tibiotarsus. The proximal fibula is lateromedially flat, and its proximal articular facet is slightly convex.

The tarsometatarsus is only fused proximally as in enantiornithines and other basal birds (Chiappe and Witmer, 2002). It is about half the length of the tibiotarsus and its midshaft is slightly more compressed. Among the three major metatarsals, metatarsal III is the longest, and IV the second, and II the shortest. Distally, the trochleae for

metatarsals II and IV are higher than that of metatarsal III. The first metatarsal is short and attaches to the distal part of the shaft of metatarsal II. Similar to those of other birds, the phalangeal formula of the foot is 2-3-4-5. The second digit is the strongest toe, while the third is the longest. The hallux is long and strong. All phalanges have well-developed flexor tubercles. The claw phalanges are long and moderately recurved, resembling that of a perching bird more than one that lives on the ground.

#### Phylogenetic analysis:

The phylogenetic position of *Shengjingornis yangi* was determined using a modified version of the O'Connor et al. (2009) dataset. Twenty-three taxa were scored for 242 characters. Neornithes was represented by *Anas platyrhynchos* and *Gallus gallus*, and *Archaeopteryx* was used as the outgroup. The matrix was run using NONA (Goloboff, 1993); optimal trees were identified using five random addition sequence replications of taxa, each followed by Tree Bisection Reconnection (TBR) branch-swapping and 100 iterations of jackknife ratchet, collapsing the trees on TBR rearrangements. The result was six most parsimonious trees of 526 steps. The trees differ within the relative placement of taxa within the enantiornithine and ornithuromorph clades.

The strict consensus tree (Fig. 5) places *Shengjingornis* within Enantiornithes. *Jeholornis* and *Archaeopteryx* from consecutive outgroups of Pygostylia with the confuciusornithid clade and *Sapeornis* as basalmost pygostylians. A large ornithothoracine clade is formed by Enantiornithes and Ornithuromorpha. The “longirostrine” enantiornithines (*Longipteryx*, *Shanweiniao*, *Longirostravis*, *Shengjingornis*) form a basal clade within enantiornithines, with *Longirostravis* and *Shengjingornis* forming a more exclusive relationship within this large clade. Remaining enantiornithine taxa form a large clade in which *Concornis* and Eoenantiornis are successive outgroups to a polytomy formed by *Neuquenornis*, *Iberomesornis*, *Gobipteryx*, *Eoalulavis*, and *Vescornis* (Elzanowski, 1974; Sanz et al., 1988; Chiappe, 1991; Sanz et al., 1996; Zhang et al., 2004).

The remaining ornithuromorph relationships largely agree with previous work (Chiappe, 2002; Clarke et al., 2006; Zhou and Zhang, 2006). *Ichthyornis* is placed as sister taxon to Neornithes, whereas *Hesperornis*, *Gansus*, *Yixianornis*, *Yanornis* and *Hongshanornis* form a series of successive outgroups (Fig. 5).

### 3 Discussions and Conclusions

A number of derived features support the inclusion of *Shengjingornis yangi* in the Enantiornithes clade, including the Y-shaped furcula; the sternums with two large

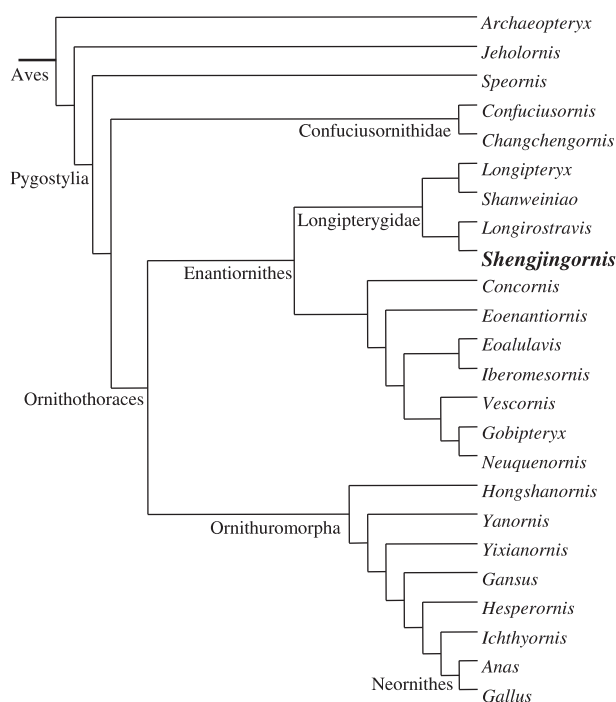


Fig. 5. Phylogeny of *Shengjingornis yangi* gen. et sp. nov. Tree length: 526 steps, consistency index = 0.53, retention index = 0.74, the cladogram is based on the strict consensus tree from 70 most parsimonious trees.

branches, that are similar to other Enantiornithes; minor metacarpal which is longer than major metacarpal, minor metacarpal which bends toward major metacarpal, and proximal portion of ischium that have significant back processes.

The elongate rostrum of *Shengjingornis*, along with the teeth restricted to the premaxilla and rostral-most dentary and the straight lateral margin of the coracoid, place it firmly within Longipterygidae (O'Connor et al., 2009). *Shengjingornis* also possesses a curving rostrum in common with *Longirostravis*. This indicates that within this group, the two taxa are fairly closely related, in keeping with the findings of O'Connor et al., 2009. However, we can also find many differences between them: *Shengjingornis* has a larger body size and more sturdy rostral with slightly curved tip. The teeth are blunt and coarse in *Shengjingornis*, while the teeth are small in *Longirostravis*. Lateral process of the sternum has different shapes: *Shengjingornis* has no triangle structure that exists in *Longirostravis*. Heads of femur are very developed in *Shengjingornis*. In addition, the distal end of the hypocleidum of furcula is expanded in *Shengjingornis*, and pygostyles are shorter in *Shengjingornis* than in *Longirostravis*.

*Shengjingornis* shows great differences with *Longipteryx*, *Shanweinia* and *Rapaxavis* (Zhang et al., 2000; Morschhauser et al., 2009; O'Connor et al., 2009).

First, *Longipteryx* has a longer and burlier mouth with large hook-like curved teeth, their forelimbs are significantly longer than hind. Second, *Shanweinia* preserved an elongated rostrum that is about 60% or more of the skull in length (54% in *Shengjingornis*). It has a small individual with reduced or weakened bones, and preserved an elongate tail composed of at least four closely aligned rectrices. Third, *Rapaxavis* has many unique characteristics: (1) caudolateral processes of the sternum with two prominent branches and a smaller third branch, (2) a pair of triangular thoracic elements, (3) and the combination of six sacral vertebrae and six free caudal vertebrae.

There are many differences between *Shengjingornis* and other Enantiornithes. For example *Cathayornis* (Zhou et al., 1992; Zhang et al., 2004), which has a short but stout mouth with numerous reduced teeth, and long sternums which bear developed lateral processes. *Boluochia* has hooked anterior end of premaxilla and their three major metatarsals are about the same in length. There are also many big differences between the primitive *Protopteryx* and *Shengjingornis*. First, *Shengjingornis* has a bigger individual. Second, *Protopteryx* has many scale-like structures on both sides of tail which are quite similar to reptiles, and it also has alular structures bearing on phalanges. Based on the above comparisons, we conclude that *Shengjingornis* represents a new genus and species.

## Acknowledgements

We thank Mr Hou L.H. for reading the manuscript and providing valuable support. This study was supported by the director foundation item of experiment center of Shenyang Normal University (Grant No. sy201101), National Natural Science Foundation of China (No. 41202014).

Manuscript received Jan. 27, 2011

accepted July 11, 2012

edited by Fei Hongcai

## References

- Chiappe, L.M., 1991. Cretaceous avian remains from Patagonia shed new light on the early radiation of birds. *Alcheringa*, 15:333–338.
- Chiappe, L.M., 1996. Late Cretaceous birds of southern South America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi*. In: Arratia G. (ed.), *Contributions of southern South America to vertebrate paleontology*. Munchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie 30, Verlag Dr. Friedrich Pfeil, Munich, Germany. 203–224.
- Chiappe, L.M., 2002. Basal bird phylogeny: problems and solutions. In: Chiappe, L.M., and Witmer, L. (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California

- Press, Berkeley, California. 448–472.
- Chiappe, L.M., and Walker, C.A., 2002. Skeletal morphology and systematics of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes). In *Mesozoic birds: above the heads of dinosaurs*. Edited by Chiappe L M and Witmer L M. University of California Press, Berkeley, Calif., pp.240–267.
- Chiappe, L.M., and Witmer, L., 2002. *Mesozoic birds: above the heads of dinosaurs*. University of California Press, Berkeley, Calif.
- Chiappe, L.M., Lamb, J.P. Jr., and Ericson, P.G.P., 2002. New enantiornithine bird from the marine Upper Cretaceous of Alabama. *Journal of Vertebrate Paleontology*, 22: 170–174.
- Clarke, J.A., Zhou, Z.H., and Zhang, F.C., 2006. Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of Yixianornis grabaui. *Journal of Anatomy*, 208: 287–308.
- Elzanowski, A., 1974. Preliminary note on the palaeognathous bird from the Upper Cretaceous of Mongolia. *Paleontologica Polonica*, 30: 103–109.
- Hou, L.H., Chiappe, L.M., Zhang, F.C., Chuong, C., 2004. New Early Cretaceous fossil from China documents a novel trophic specialization for Mesozoic birds. *Naturwissenschaften*, 91: 22–25.
- Kurochkin, E.N., 1985. A true carinate bird from Lower Cretaceous deposits in Mongolia and other evidence of Cretaceous birds in Asia. *Cretaceous Res.*, 6: 271–278.
- Hou, L.H., Martin, L.D., Zhou, Z.H., Feduccia, A., 1999. *Archaeopteryx* to opposite birds-missing link from the Mesozoic of China. *Vertebrata Palasiatica*, 37(2): 88–95.
- Morschhauser, E.M., David, J., Gao, C.L., Gao, C.L., Liu, J.Y., Wang, X.R., Cheng, X.D. and Meng, Q.J., 2009. Anatomy of the Early Cretaceous Bird *Rapaxavis Pani*, A New Species From Liaoning Province, China. *Journal of Vertebrate Paleontology*, 545–554.
- O'Connor, J.K., Wang, X.R., Chiappe, L.M. Cao, C.L., Meng, Q. J., Cheng, X.D. and Liu, J.Y., 2009. Phylogenetic support for a specialized clade of Cretaceous Enantiornithine birds with in formation from a new species. *Journal of Vertebrate Paleontology*, 29(1): 188–204.
- Sanz, J.L., Bonaparte, J.F., and Lacasa, A., 1988. Unusual Early Cretaceous birds from Spain. *Nature*, 331: 433–435.
- Sanz, J.L., and Buscalioni, A.D., 1992. A new bird from the Early Cretaceous of Las Hoyas, Spain. *Paleontology*, 35: 829–845.
- Sanz, J.L., Chiappe, L.M., and Buscalioni, A.D., 1995. The osteology of *Concornis lacustris* (Aves: Enantiornithes) from the Lower Cretaceous of Spain and a reexamination of its phylogenetic relationships. *Amer. Mus. Novitates*. 3133:1–23.
- Sanz, J.L., Chiappe, L.M., Perez-Moreno, B.P. Buscalioni, A.D., Moratalla, J.J., Ortega, F. and Poyato-Ariza, F.J., 1996. An Early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature*, 382: 442–445.
- Walker, C. A., 1981. New subclass of birds from the Cretaceous of South America. *Nature*, 292: 51–53.
- Wang, X.R., O'Connor, J.K., Zhao, B., Luis, M.C., Gao C.L., and Chang, X.D., 2010. New species of Enantiornithes (Aves: Ornithothoraces) from the Qiaotou formation in Northern Hebei, China. *Acta Geologica Sinica* (English version), 84(2): 247–256.
- Zhang, F.C., and Zhou, Z.H., 2000. A primitive enantiornithine bird and the origin of feathers. *Science*, 290: 1955–1959.
- Zhang, F.C., Zhou, Z.H., Hou, L.H., and Gu, G., 2001. Early diversification of birds: evidence from a new opposite bird. *Chinese Science Bulletin* (English version), 46: 945–949.
- Zhang, F.C., Ericson, P.G. and Zhou, Z.H., 2004. Description of a new enantiornithine bird from the Early Cretaceous of Hebei, northern China. *Canadian Journal of Earth Sciences*, 41: 1097–1107.
- Zhou, Z.H., 1995. The discovery of Early Cretaceous birds in China. In: Peters, D.S. (ed.), *Acta Palaeornithologica*, 3 Symposium SAPE; 5 Internationale Senckenberg -Konferenz 22–26 Juni 1992. Courier Forschungsinstitut Senckenberg, 181. Frankfurt. 9–22.
- Zhou, Z.H. and Zhang F.C., 2005. Discovery of a new ornithurine bird and its implication for Early Cretaceous avian radiation[J], *Proceedings of the National Academy of Sciences of the United States of America*, 102(52): 18998–19002.
- Zhou, Z.H., and Zhang, F.C., 2006. Mesozoic birds of China-A synoptic review. *Vertebrata Palasiatica*, 44(1): 74–98.
- Zhou, Z.H., Clarke, J., and Zhang, F.C., 2008. Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. *Journal of Anatomy*, (212): 565–577.