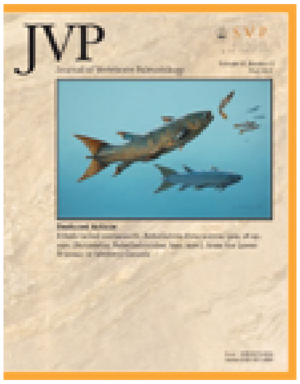

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A new enantiornithine bird from the Lower Cretaceous of Western Liaoning, China, and its implications for early avian evolution

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ARTICLE

A NEW ENANTIORNITHINE BIRD FROM THE LOWER CRETACEOUS OF WESTERN LIAONING, CHINA, AND ITS IMPLICATIONS FOR EARLY AVIAN EVOLUTION

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ABSTRACT—Recent studies have blurred the distinctness of two major avian groups: the Enantiornithes, a major radiation of early birds in the Cretaceous, and the Ornithuromorpha, the clade including extant birds. Here we describe a new enantiornithine bird from the Lower Cretaceous Jiufotang Formation of western Liaoning, China, *Xiangornis shenmi*, gen. et sp. nov., which further reduces the morphological gap between the two groups. *Xiangornis shenmi* has several enantiornithine features, including a furcula with a significantly elongated hypocleidium, a coracoid with a convex lateral margin, and a minor metacarpal that extends further distally than the major metacarpal. However, it also possesses some derived ornithurine features, such as a short alular metacarpal (about one-sixth as long as the major metacarpal) that is completely fused to the major metacarpal, a large extensor process on the alular metacarpal, proximal and distal fusion between the minor and major metacarpals, and an intermetacarpal space positioned significantly distal to the alular metacarpal. This new find indicates that a carpometacarpal morphology similar to that seen in modern birds probably evolved independently in enantiornithines and appeared earlier than in Ornithuromorpha, and demonstrates that character evolution in early birds was more complex than previously believed.

INTRODUCTION

Enantiornithes and Ornithuromorpha represent two major avian radiations. Enantiornithes is restricted to the Cretaceous, whereas Ornithuromorpha is the sister taxon to Enantiornithes and includes all living birds. The two groups were previously considered to differ in many aspects of their skeletal anatomy. However, new discoveries of basal birds (Norell and Clarke, 2001; Clarke and Norell, 2002), particularly some recent finds from the Lower Cretaceous Jehol Group of Liaoning Province, China (Zhou and Zhang, 2005, 2006; Zhou et al., 2008), have substantially reduced this morphological gap. During the 2005 field season, the partial postcranial skeleton of a new enantiornithine bird was discovered at the Dapingfang Locality, Chaoyang County, western Liaoning. This new taxon also exhibits some features normally present in derived ornithurines, further blurring the distinctness of the two groups.

Institutional Abbreviations—**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **PMOL**, Paleontological Museum of Liaoning, China; **PVL,** Paleontología de Vertebrados, Instituto Miguel Lillo, Tucuman, Argentina; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
ENANTIORNITHES Walker, 1981
XIANGORNIS SHENMI, gen. et sp. nov.
(Figs. 1, 2)

Etymology—Generic name from ‘xiang,’ the Mandarin word for ‘free flight,’ and ‘ornis,’ the Greek term for bird; specific name from ‘shenmi,’ the Mandarin word for mysterious.

Holotype—PMOL-AB00245, partial postcranial skeleton including nearly complete furcula, left coracoid, left carpometacarpus, and first phalanx of the left alular digit; partial sternum, and left humerus, ulna, and radius. These skeletal elements are damaged to varying degrees.

Horizon and Locality—Jiufotang Formation, Lower Cretaceous (Duan et al., 2006); Dapingfang Town, Chaoyang County, Liaoning Province, China.

Diagnosis—*Xiangornis* can be referred to Enantiornithes based on the following synapomorphies: ‘Y’-shaped furcula with elongated hypocleidium; coracoid with convex lateral margin and concave dorsal fossa; and minor metacarpal extending distally beyond major metacarpal. Differs from other enantiornithines in having the following unique combination of features: large size; coracoid with medially curved acrocoracoid process; proximally convex humeral head; carpometacarpus longer than coracoid and completely fused both proximally and distally; short alular metacarpal (about one-sixth of the length of major metacarpal) completely fused to major metacarpal; large flange-like extensor process; and intermetacarpal space positioned significantly distal to the alular metacarpal.

DESCRIPTION AND COMPARISON

Furcula

The furcula is exposed in ventral view (Fig. 1). The furcula is ‘Y’-shaped, with a long hypocleidium as in other known enantiornithines (Martin, 1995; Chiappe and Walker, 2002; Zhou et al., 2008). The interclavicular angle and hypocleidium are approximately 65 degrees and one-half of the length of the clavicular ramus, respectively. This interclavicular angle is wider

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*Corresponding authors.

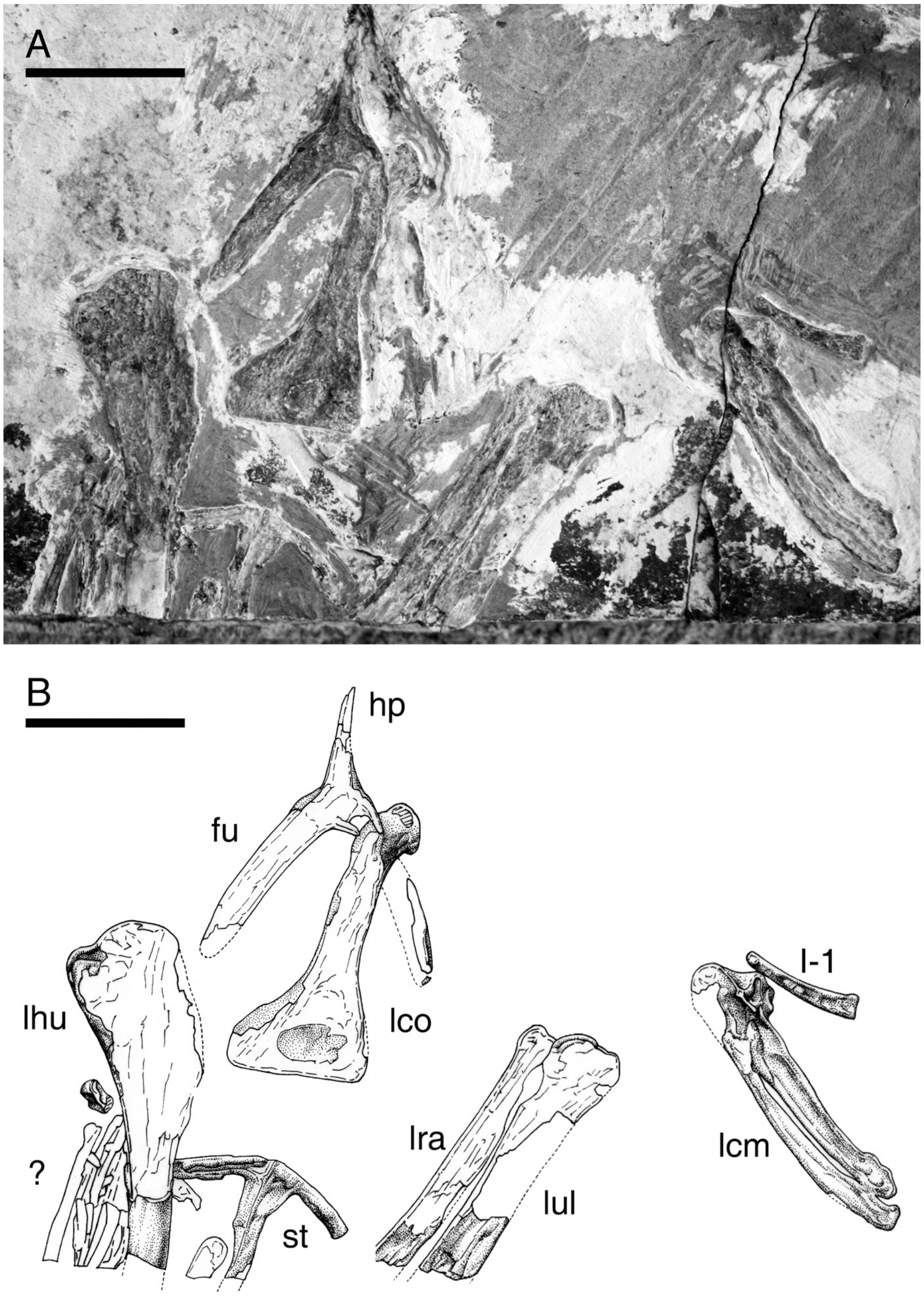

FIGURE 1. Holotype specimen of *Xiangornis shenmi*, gen. et sp. nov. (PMOL-AB00245). **A**, photograph; **B**, line drawing. **Abbreviations**: **fu**, furcula; **hy**, hypocleidium; **lcm**, left carpometacarpus; **lco**, left coracoid; **lhu**, left humerus; **lra**, left radius; **lul**, left ulna; **st**, sternum; **I-1**, first phalanx of the alular digit. Scale bars equal 20 mm.

than in the furculae of most known enantiornithines, particularly the small taxa *Iberomesornis* (Sanz and Bonaparte, 1992), *Concornis* (Sanz et al., 1995), *Eoalulavis* (Sanz et al., 2002), *Noguerornis* (Chiappe and Lacasa-Ruiz, 2002), *Longirostravis* (Hou et al., 2004), *Vescornis* (Zhang et al., 2004), and *Shenqiornis* (Wang et al., 2010). Although a hypocleidium is also present in the ornithuromorph bird *Hongshanornis* (Zhou and Zhang, 2005) and the more basal bird *Sapeornis* (Zhou and Zhang, 2003), the furcula is 'U'-shaped or boomerang-shaped in both cases and bears only a short hypocleidium in *Hongshanornis* (Zhou and Zhang, 2005). The clavicular ramus is mediolaterally broad and dorsoventrally compressed as in the enantiornithines *Iberomesornis* (Sanz and Bonaparte, 1992), *Elsornis* (Chiappe et al., 2007), and *Pengornis* (Zhou et al., 2008), whereas the medial surface of each clavicular ramus gradually widens towards the omal end in the enantiornithines *Longipteryx* (Zhang et al., 2001) and *Bohaiornis* (Hu et al., 2011). However, the lateral margin of the clavicular ramus is prominently convex in *Iberomesornis* and *Pengornis*, but relatively straight in *Elsornis* and *Xiangornis*. The clavicular ramus appears to taper at the omal end, in contrast to the laterally expanded omal end seen in *Bohaiornis* (Hu et al., 2011).

Coracoid

The left coracoid is exposed in dorsal view. The coracoid is strut-like with a length/width ratio of 2.1; it is proportionally shorter than the coracoids of the enantiornithines *Concornis* (Sanz et al., 1995), *Eoalulavis* (Sanz et al., 2002), and *Enantiornis* (Walker and Dyke, 2010), in all of which the equivalent ratio is more than 2.5. Although the more basal bird *Confuciusornis* has also a strut-like coracoid, it has a length/width ratio of only 1.7 (Zhang et al., 2009) and is fused to the scapula. Proximally, the acrocoracoid process is prominent, and has a considerable medial curvature and a broad sulcus for the M. supracoracoideus, in contrast to a small and straight process in most known enantiornithines (Martin, 1995; Chiappe and Walker, 2002; Zhou et al., 2008). The acrocoracoid process is developed to a similar extent only in relatively derived ornithuromorphs such as *Gansus* (You et al., 2006) and *Ichthyornis* (Clarke, 2004). The presence of a procoracoid process and a distinct supracoracoid nerve foramen cannot be confirmed because the coracoid is damaged, but the latter feature is probably located in a depressed area adjacent to the medial margin. The sternal third of the lateral margin of the coracoid is significantly convex as in the enantiornithines *Concornis* (Sanz et al., 1995), *Eoalulavis* (Sanz et al., 2002), *Elsornis* (Chiappe et al., 2007), and *Pengornis* (Zhou et al., 2008), rather than slightly convex or straight as in the enantiornithines *Iberomesornis* (Sanz and Bonaparte, 1992), *Longipteryx* (Zhang et al., 2001), *Rapaxavis* (Morschhauser et al., 2009), and *Bohaiornis* (Hu et al., 2011). However, most known ornithuromorphs other than *Hongshanornis* have a concave lateral margin of the coracoid (Clarke et al., 2006). The lateral-most margin is more depressed as in *Pengornis* (Zhou et al., 2008), suggesting the presence of an incipient lateral process. The sternal third of the dorsal surface of the coracoid clearly forms a fossa for the M. sternocoracoideus as in most known enantiornithines (Martin 1995; Chiappe and Walker, 2002; Chiappe et al., 2007), in contrast to the flat or convex surface present in most known ornithuromorphs (Clarke et al., 2006).

Sternum

The preserved portion of the sternum appears approximately anchor-shaped, and a rounded segment of the margin is significantly thickened compared with the rest of the bone. If this fragment is interpreted as the anterior portion, then the sternum is similar to those of most known enantiornithines such as *Eoenantiornis* (Zhou et al., 2005) and *Bohaiornis* (Hu et al., 2011) in having a rounded and thickened anterior margin for the articulation with the coracoid. The posterior margin of the sternum also appears to be rounded in some ornithuromorphs such as *Songlingornis* (Hou, 1997), *Yanornis*, and *Yixianornis* (Zhou and Zhang, 2001). However, the posterior half of the sternum normally bears a carina in basal birds, and the posterior margin is not especially thick. The absence of a carina and the thickened margin of the preserved sternal fragment of *Xiangornis* probably indicate that the fragment is anterior. A suture runs along the midline of the sternal fragment, suggesting that the left and right plates of the sternum are incompletely fused together.

Humerus

The proximal half of the left humerus is present, and its anterior surface is exposed. The head of the humerus obviously projects further proximally than the deltopectoral crest, as in most ornithuromorphs such as *Hongshanornis* and *Archaeorhynchus* (Zhou and Zhang, 2005, 2006) and the enantiornithine *Pengornis* (Zhou et al., 2008), whereas the central portion of its proximal margin is concave in most known enantiornithines, such as *Bohaiornis* (Hu et al., 2011). The humeral head is separated by a shallow notch from the bicipital crest, which is proximodistally elongated and projects slightly ventrally. An incompletely preserved transverse groove, probably representing the sulcus ligamentum transversum, occurs near the proximal end of the bicipital crest. The deltopectoral crest is proximodistally long, and about as wide as the humeral shaft. It is not perforated, in contrast to the condition in the more basal birds *Confuciusornis* (Martin et al., 1998) and *Sapeornis* (Zhou and Zhang, 2003).

Ulna and Radius

The distal halves of the left ulna and radius are preserved, but little can be said about their morphology except that the radius is much more slender than the ulna.

Manus

Most of the left manus is preserved, although the proximal carpals and most of the phalanges are absent. The semilunate carpal and metacarpals are completely fused both proximally and distally to form a carpometacarpus (Fig. 2). This element is exposed in ventral view. *Xiangornis* resembles ornithuromorphs, but differs from other enantiornithines, in that the carpometacarpus is longer than the coracoid (Table 1). The semilunate carpal is laterally positioned, with a small contact with the dorsal portion of the proximal surface of the alular metacarpal. The carpal trochlea is strongly convex transversely.

The alular metacarpal is only about one-sixth as long as the major metacarpal, approaching the condition in the Late Cretaceous enantiornithine *Martinavis* (Walker and Dyke, 2010) and the derived ornithurine *Iaceornis* (Clarke, 2004). The alular metacarpal is about one-fourth of the length of the major metacarpal in most Early Cretaceous ornithothoracines, including *Bohaiornis* (Hu et al., 2011) and *Yanornis* (Zhou and Zhang, 2001). In *Xiangornis* the alular metacarpal is completely fused to the major metacarpal as in the Late Cretaceous enantiornithines *Enantiornis* and *Martinavis* (Walker and Dyke, 2010) and derived ornithurines such as *Apsaravis* (Clarke and Norell, 2002) and *Ichthyornis* (Clarke, 2004), but a short groove is visible along the distal part of the suture between the two metacarpals. In other Early Cretaceous ornithothoracines, including *Yanornis* and *Yixianornis* (Zhou and Zhang, 2001), the alular metacarpal is not fused to the major metacarpal distally. The alular metacarpal has a weakly ginglymoid distal end; the medial condyle is much narrower transversely than the lateral condyle, but extends further distally. The most unusual feature of the alular metacarpal is the presence of a flange-like extensor process, a feature otherwise unknown in Early Cretaceous birds and Late Cretaceous enantiornithines. The process is formed by the rounded, prominent

TABLE 1. Measurements (mm) and proportions of the coracoid, carpometacarpus, and first phalanx of the alular digit of *Xiangornis*, gen. et sp. nov. (PMOL -AB00245) compared with those of some early birds.

	Co	Cm	I-1	Co/Cm	I-1/Cm
Enantiornithes					
Eoenantiornis (IVPP V11537)	15.8	13.8	5.4	1.14	0.39
Bohaiornis (LPM-B00167)	23	22.7	9.5	1.01	0.42
Pengornis (IVPP V15336)	37.9	34.3	—	1.10	—
Xiangornis (PMOL–AB00245)	35	38.5	15.2	0.92	0.39
Ornithuromorpha					
Yanornis (IVPP V12558)	30	35	17	0.86	0.49
Yixianornis (IVPP V12631)	23	25	11	0.92	0.44
Jianchangornis (IVPP V16708)	32	36	29	0.88	0.80

Abbreviations: **Co**, coracoid; **Cm**, carpometacarpus; **I-1**, first phalanx of the alular digit; **—**, missing values.

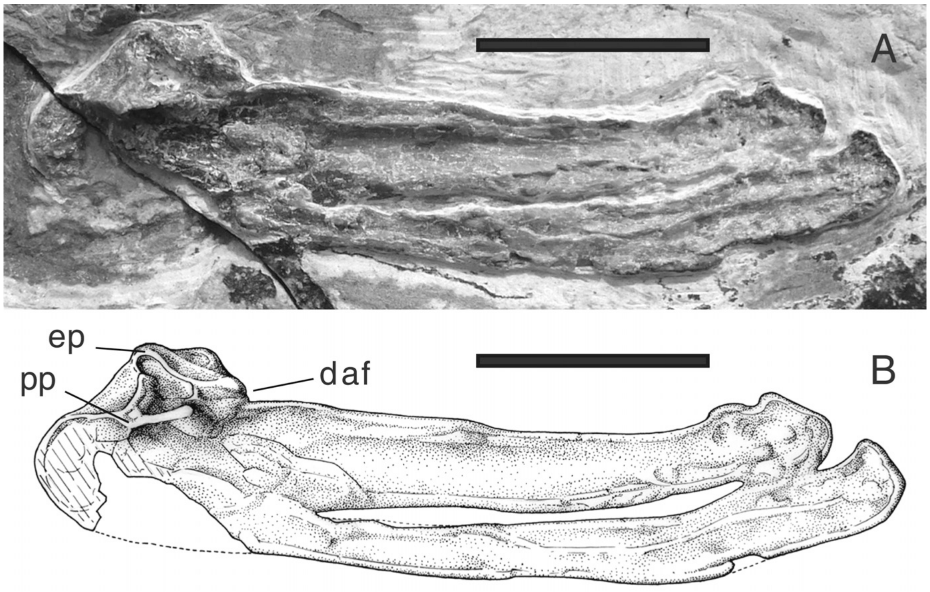

FIGURE 2. Close-up photograph and line drawing of left carpometacarpus of *Xiangornis shenmi*, gen. et sp. nov. (PMOL-AB00245). **Abbreviations**: **daf**, distal articular facet (of alular metacarpal); **ep**, extensor process; **pp**, pisiform process. Scale bars equal 10 mm.

proximomedial corner of the metacarpal plus an additional convexity located further distally on the medial edge. There is neither a sharp distinction between the extensor process and the shaft of the alular metacarpal nor a sharp proximal embayment between the extensor process and the trochlear articular surface of the carpometacarpus, in contrast to modern birds and to the ornithurines *Apsaravis* (Clarke and Norell, 2002) and *Ichthyornis* (Clarke, 2004). Its length covers about four-fifths of the medial margin of the alular metacarpal and its width is slightly greater than that of the distal end of the bone.

The major metacarpal is robust and slightly bowed laterally, but this might be a preservational artifact. A prominence that probably represents the pisiform process is present on the boundary with the alular metacarpal and has the form of an approximately longitudinal crest, but only the medial surface is clearly preserved. A distinct ridge arises from near its midpoint and extends transversely to the proximal end of the extensor process. A deep fossa containing a shallow muscle scar is present on the proximal surface of this ridge.

The minor metacarpal is strongly bowed laterally and extends distally beyond the major metacarpal as in other known enantiornithine birds (Martin, 1995; Chiappe and Walker, 2002; Zhou et al., 2008). It is fused to the major metacarpal both proximally and over a short interval near the distal end, in contrast to only the proximal fusion in all known enantiornithines. The proximal and distal fusion of the major and minor metacarpals is present only in the early ornithuromorphs *Yanornis* and *Yixianornis* (Zhou and Zhang, 2001) and most derived ornithurines (Clarke, 2004), and the major and minor metacarpals of all known enantiornithines exhibit proximal fusion. A narrow intermetacarpal space is present between the two regions of fusion, likely terminating proximally at a level considerably distal to the end of the alular metacarpal as in modern birds.

The one preserved phalanx is identified as manual phalanx I-1 (Fig. 1). This phalanx is about 39% of the length of the carpometacarpus, comparable to the equivalent value in most known enantiornithines. In most basal ornithuromorphs from Liaoning, however, phalanx I-1 is proportionally longer (Table 1). In *Xiangornis* the proximal end of phalanx I-1 is much deeper than the distal end, and the distal part of the phalanx has a considerable ventral curvature. The distal end appears not to be ginglymoid, but is robust enough to indicate the presence of an additional phalanx of the alular digit.

DISCUSSION

Phylogenetic Position

Xiangornis displays the following enantiornithine synapomorphies: 'Y'-shaped furcula with long hypocleidium; coracoid with convex lateral margin and concave dorsal fossa; and minor metacarpal extending distally beyond major metacarpal (Martin 1995; Chiappe, 2002; Chiappe and Walker, 2002). These features strongly support the identification of *Xiangornis* as an enantiornithine. However, *Xiangornis* also displays the following character states previously considered diagnostic of Ornithuromorpha: coracoid with medially curved acrocoracoid process; proximally convex humeral head; carpometacarpus completely fused both proximally and distally; short alular metacarpal (about one-sixth of the length of the major metacarpal) completely fused to major metacarpal; large extensor process; and intermetacarpal space positioned significantly distal to alular metacarpal. The holotype of *Xiangornis shenmi* is the first specimen to display this combination of features.

We conducted a phylogenetic analysis using the software package TNT (Goloboff et al., 2008) on a recently published data set (Zhou et al., 2008) with *Xiangornis* added, and our analysis confirms the placement of *Xiangornis* within Enantiornithes (Fig. 3A). It is notable that the analysis places *Protopteryx* (Zhang and Zhou, 2000) in a position basal to the Enantiornithine-Ornithuromorph split. Accordingly, the morphological evidence provided by *Xiangornis* further weakens the support for a monophyletic Enantiornithes, at least as traditionally conceived (Norell and Clarke, 2001; Zhou et al., 2008). Four character states were optimized by our analysis as unambiguous synapomorphies of a monophyletic Enantiornithes, including humeral distal margin angling strongly ventrally (124.1), ulnar distal end with dorsal condyle significantly extended on posterior margin (134.1), metacarpal III extending further distally than metacarpal

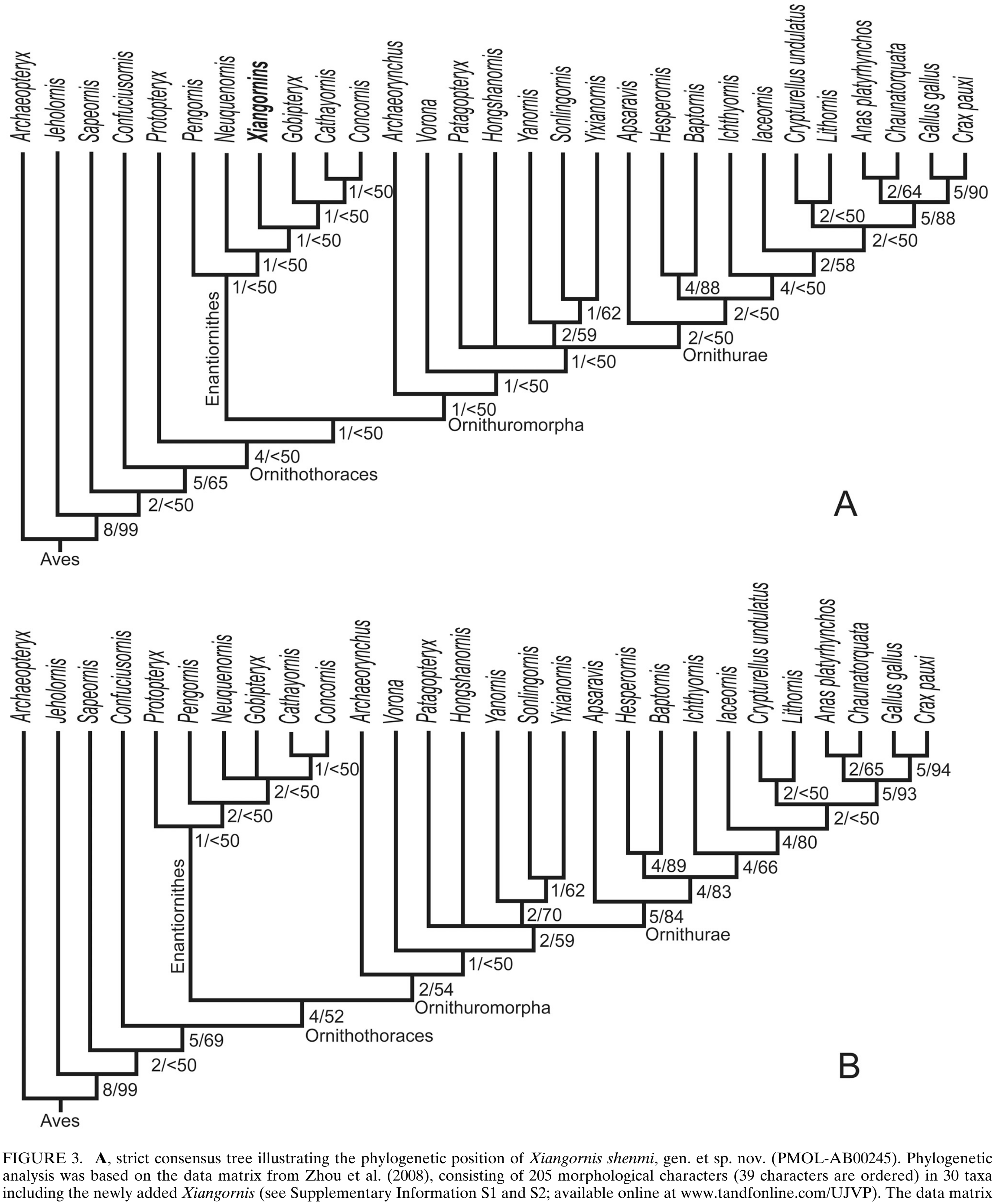

FIGURE 3. **A**, strict consensus tree illustrating the phylogenetic position of *Xiangornis shenmi*, gen. et sp. nov. (PMOL-AB00245). Phylogenetic analysis was based on the data matrix from Zhou et al. (2008), consisting of 205 morphological characters (39 characters are ordered) in 30 taxa including the newly added *Xiangornis* (see Supplementary Information S1 and S2; available online at www.tandfonline.com/UJVP). The data matrix was analyzed using a traditional search strategy in TNT, with default settings apart from the following: 10,000 maximum trees in memory and 1000 replications. Three most parsimonious trees (tree length = 478 steps, consistency index [CI] = 0.55, retention index [RI] = 0.79) were recovered by the analysis, and their strict consensus is shown here. **B**, strict consensus resulting from the same phylogenetic analysis using the original matrix excluding *Xiangornis* (tree length = 469 steps, CI = 0.56, RI = 0.80). Bremer and bootstrap support values computed in TNT for the nodes of the consensus trees were labeled adjacent to their respective nodes to the left and right.

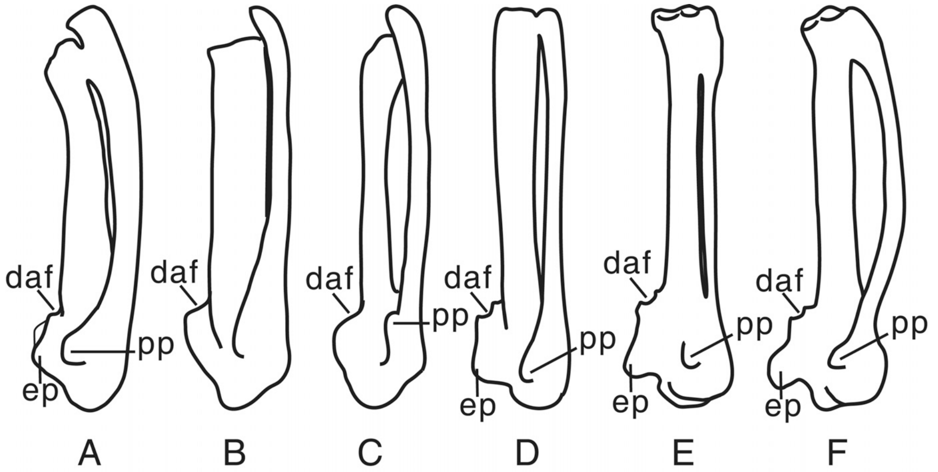

FIGURE 4. Comparison of carpometacarpii of **A**, *Xiangornis shenmi*, gen. et sp. nov. (PMOL-AB00245); **B**, Early Cretaceous enantiornithine *Cathayornis* (IVPP V9769) (Zhou and Hou, 2002); **C**, Late Cretaceous enantiornithine *Enantiornis leali* (PVL-4049) (Chiappe and Walker, 2002); **D**, Early Cretaceous ornithuromorph *Yixianornis* (IVPP V12631); **E**, Late Cretaceous ornithurine *Ichthyornis* (YPM 1724) (Clarke, 2004); and **F**, modern bird *Apterornis defossor*. **Abbreviations**: **daf**, distal articular surface; **ep**, extensor process; **pp**, pisiform process. Not to scale.

II (150.1), and manual phalanx II-1 longer than II-2 (153.1). Each of these character states is also convergently present in some other taxa, however. Re-running the analysis with *Xiangornis* excluded, a monophyletic Enantiornithes including *Protopteryx* was recovered (Fig. 3B). The unambiguous synapomorphies supporting this clade include furcula with a long hypocleidium (82.2), furcula laterally excavated (83.1), and scapular articular surface of coracoid convex (87.1), with the last two character states being unique to the group. We also used TNT to run Bremer support and bootstrap analysis (1000 replicates) on the two matrices with and without *Xiangornis*. Both the bootstrap and Bremer values for Enantiornithes and Ornithuromorpha are lower in the analysis with *Xiangornis* (Fig. 3A, B), and therefore confirm that the discovery of *Xiangornis* has weakened the support for the monophyly of both Enantiornithes and Ornithuromorpha.

Xiangornis is very similar to *Pengornis* (Zhou et al., 2008), in size and various other morphological features such as the proximally convex humeral head and the prominently convex lateral margin of the coracoid, and both are from the same locality and horizon. However, *Xiangornis* is clearly different from *Pengornis* in having a straight lateral margin of the clavicular ramus, a distinctly curved acrocoracoid process, a carpometacarpus exceeding the length of the coracoid, and a crest-like pisiform process on the ventral surface of the carpometacarpus between the alular and major metacarpals.

Manus Evolution

The discovery of *Xiangornis* suggests that a derived, ornithurine-type carpometacarpus evolved independently within Enantiornithines, and in fact appeared earlier in this group than in Ornithuromorpha (Fig. 4). The large extensor process and high degree of fusion in the carpometacarpus of *Xiangornis* are also potential indicators of a degree of flight adaptation exceeding that seen in other enantiornithines. Fusion of the carpometacarpus presumably strengthens the manus against aerodynamic forces. In extant birds, the extensor process serves as a point of attachment for the M. extensor metacarpi radialis and for a branch of the propatagial ligament that extends from the shoulder region to the wrist within the leading edge of the wing, joined prior to its insertion by a tendon from the biceps (Vazquez, 1994). The M. extensor metacarpi radialis is the primary muscle involved in adduction ('extension') of the avian wrist joint.

Ostrom (1976) proposed that a large extensor process might either reduce the amount of energy required to counteract the force of the airstream that tends to flex or fold the wing extremity, or allow rapid unfolding of the wing. The former function is highly plausible. The extensor process would increase the moment arms of the propatagial ligament and M. extensor metacarpi radialis with respect to adduction of the wrist, allowing them to generate large torques that would resist the tendency of drag on the feathered manus to abduct the wrist and collapse the wing. However, the increased moment arm would conversely reduce the ability of the M. extensor metacarpi radialis to bring about rapid rotation at the wrist joint, so the large extensor process seen in *Xiangornis* and derived ornithurines cannot be interpreted as an adaptation for rapid wing unfolding. The large extensor process and distal fusion between the major and minor metacarpals both seem to relate, in different ways, to stabilization of the distal wing during flight, implying that *Xiangornis* was converging on ornithurine birds in some functionally significant aspects of its wing structure.

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