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# A second Cretaceous ornithuromorph bird from the Changma Basin, Gansu Province, northwestern China

HAI-LU YOU, JESSIE ATTERHOLT, JINGMAI K. O'CONNOR, JERALD D. HARRIS, MATTHEW C. LAMANNA, and DA-QING LI



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Finely-bedded lacustrine deposits of the Aptian (Lower Cretaceous) Xiagou Formation exposed in the Changma Basin of Gansu Province, northwestern China, have yielded numerous fossil vertebrate remains, including approximately 100 avian specimens. Though the majority of these birds appear referable to the ornithuromorph *Gansus yumenensis*, a number of enantiornithine fossils have also been recovered. Here we report on a specimen consisting of a complete, three-dimensionally preserved sternum, furcula, and sternal ribs that represents a second ornithuromorph taxon from the Xiagou Formation at Changma. The fossil exhibits morphologies that distinguish it from all previously-known Xiagou birds and demonstrate that it represents a derived non-ornithurine member of Ornithuromorpha. Though it is morphologically distinct from the equivalent elements of all other described ornithuromorphs, the material is too incomplete to justify the erection of a new taxon. Nonetheless, it increases the taxonomic diversity of the Xiagou avifauna, thereby expanding our knowledge of Early Cretaceous avian diversity and evolution.

Key words: Aves, Ornithuromorpha, Aptian, Early Cretaceous, China.

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## Introduction

In recent decades, Lower Cretaceous deposits have yielded spectacular fossil discoveries that have provided critical insight into early avian evolution and diversification (Hou 1997a; Chiappe and Dyke 2002, 2006; Sanz et al. 2002; Zhou and Hou 2002; Zhou and Zhang 2006a). The majority of these fossils pertain to Enantiornithes, which is widely regarded as the dominant Cretaceous avian clade; Ornithuromorpha, the group that includes modern birds (Neornithes) and their nearest relatives, is much more poorly represented. Due to the relative scarcity of archaic ornithuromorph fossils, the paleoecological, temporal, and phylogenetic contexts of the origin and early diversification of this clade remain unclear. Consequently, new Early Cretaceous ornithuromorph material is important for an increased understanding of the early evolution of the modern bird lineage.

Most Early Cretaceous avian fossils have come from strata of the Jehol Group, which are primarily exposed in Liaoning and Hebei provinces of northeastern China. The Jehol avifauna is dominated in both numbers and diversity by basal (i.e., non-ornithothoracine) and enantiornithine taxa, but it has also yielded several basal ornithuromorphs, including *Archaeorhynchus spathula* (Zhou and Zhang 2006b), *Chaoyangia beishanensis* (Hou and Zhang 1993), *Hongshanornis longicresta* (Zhou and Zhang 2005), *Jianchangornis microdonta* (Zhou et al. 2009), *Longicrusavis houi* (O'Connor et al. 2010), *Songlingornis linghensis* (Hou 1997a), *Yanornis martini* (Zhou and Zhang 2001), and *Yixianornis grabaui* (Zhou and Zhang 2001).



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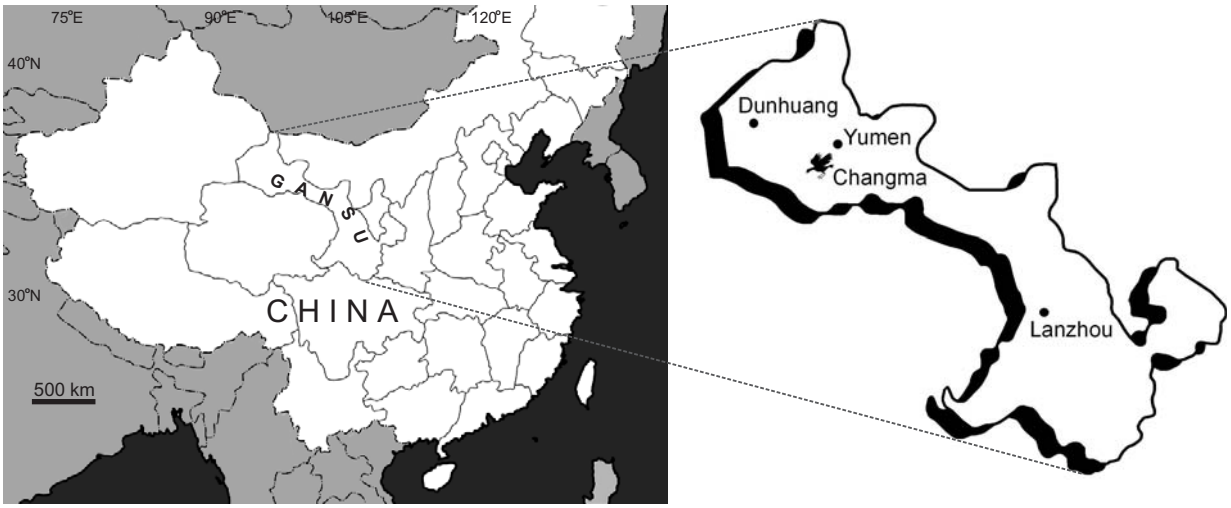



Fig. 1. Geographic location of the Changma Basin (indicated by avian silhouette), northwestern Gansu Province, China.

Situated some 2000 km west of Jehol Group localities, outcrops of the Lower Cretaceous Xiagou Formation in the Changma Basin of Gansu Province in northwestern China (Fig. 1) have also yielded a significant assemblage of avian remains. The first bird fossil discovered in this basin was the holotypic distal pelvic limb of the ornithuromorph *Gansus yumenensis*, found in 1981 (Hou and Liu 1984). Renewed fieldwork in the Changma Basin beginning in 2002 has yielded approximately 85 partial to nearly complete ornithuromorph skeletons, as well as roughly a dozen enantiornithine fossils (You et al. 2005; Harris et al. 2006a; Lamanna et al. 2006b, 2009; unpublished data) representing at least two taxa (Lamanna et al. 2006b; unpublished data). A significant number of these specimens preserve carbonized remnants of soft-tissues, such as feathers, keratin, or skin. However, despite this wealth of material, until recently *Gansus* remained the only ornithuromorph taxon identified in the Xiagou Formation avifauna (You et al. 2006).

Recent preparation of many Xiagou avian specimens collected since 2004 has allowed their more precise identification and analysis. Among these is FRDC-05-CM-021, an associated sternum, furcula, and sternal ribs that are neither enantiornithine nor referable to *Gansus* (Fig. 2). Although the specimen is incomplete, it demonstrates that *Gansus* was not the only ornithuromorph taxon in the Xiagou avifauna. Compared to other currently known Early Cretaceous avian assemblages, as presently understood, that of the Xiagou Formation is unique in that fossils of ornithuromorphs numerically dominate over those of enantiornithines. With the addition of the taxon represented by FRDC-05-CM-021, the Xiagou avifauna can be shown to further differ from that of the Jehol Group in exhibiting subequal low-level taxonomic diversity within Enantiornithes and Ornithuromorpha.

*Institutional abbreviations*.—BPV, Beijing Natural History Museum, Paleovertebrate Collection, Beijing, China; CAGS-IG, Chinese Academy of Geological Sciences, Institute of Geology, Beijing, China; DNHM, Dalian Natural History Museum, Dalian, China; FRDC, Fossil Research and Development Center, Third Geology and Mineral Resources Exploration Academy, Gansu Provincial Bureau of Geo-Exploration and Mineral Development, Lanzhou, China; IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaan Bataar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LH, Las Hoyas Collection, Museo de Cuenca, Cuenca, Spain; LHV, Department of Land and Resources of Liaoning Province, Shenyang, China; NIGPAS, Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, Nanjing, China; PKUP, Peking University Paleontological Collection, Beijing, China; SMM, Sternberg Museum of Natural History, Fort Hays State University, Hays, USA; YPM, Peabody Museum of Natural History, Yale University, New Haven, USA.

# Geological setting

Mesozoic strata exposed in the Changma Basin pertain to the Lower Cretaceous Xiagou and Zhonggou formations, which together constitute the Xinminpu Group (Bureau of Geology and Mineral Resources of Gansu Province 1989, 1997; Editorial Committee of Chinese Stratigraphic Standard: Cretaceous 2000; Tang et al. 2001). The avian fossil described herein comes from laminated brownish-yellow shales of the Xiagou Formation. The Xiagou Formation has yielded numerous specimens of plants, bivalves, gastropods, ostracodes, conchostracans, insects, fishes (Ma 1993; Murray et al. 2010), a salamander, turtles, and birds (You et al. 2005, 2006; Harris et al. 2006a; Lamanna et al. 2006a, b, 2009; unpublished data). Though much of it has not yet been studied in detail, the fossil assemblage of the Xiagou Formation at Changma is generally perceived to be comparable to the *Eosestheria–Epicharmeropsis* (= *Ephemeropsis* sensu Huang et al. [2007])*–Lycoptera* fauna of the Jehol Biota of eastern Asia (Chang et al. 2003),

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though it lacks the latter taxon. However, the Chijinpu Formation, which underlies the Xiagou Formation, has reportedly produced specimens of *Lycoptera* (Editorial Committee of Chinese Stratigraphic Standard: Cretaceous 2000). Together with recent radiometric dates (Li and Yang 2004) and chemostratigraphic age estimates (Suarez et al. 2008), this evidence suggests that the Xiagou Formation is slightly younger than the Jehol Biota, probably pertaining to the lower or middle portion of the Aptian Stage of the Lower Cretaceous (~120–115 Mya; Ogg et al. 2008).

# Systematic paleontology

Aves Linnaeus, 1758

Ornithothoraces Chiappe, 1996

Ornithuromorpha Chiappe, 2002

Gen. et sp. indet.

Fig. 2.

*Material*.—FRDC-05-CM-021, a complete, associated sternum and furcula, with sternal ribs and possible thoracic rib fragments.

*Description*.—FRDC-05-CM-021 remains embedded in the matrix in which it was found; the dorsal surface of the sternum has been exposed via preparation, and the furcula is exposed in cranial view. All elements are preserved in three dimensions with minimal crushing and distortion. The furcula has been displaced from its position in life to lie obliquely on the cranial portion of the sternum; the preserved sternal ribs have been disarticulated from their corresponding costal facets and rest in the dorsal concavity of the sternum just caudal to the furcula.

Ribs: The ribs are slender elements, triangular in cross section proximally and rounding to a more oval cross section distally. It appears that all preserved ribs and rib fragments are of sternal ribs, though it is possible that some of the smaller, thinner fragments pertain to thoracic ribs.

Furcula: The furcula is exposed in cranial view. The general morphology of the element is reminiscent of that in many basal ornithuromorphs such as *Archaeorhynchus spathula* (IVPP V14287; Zhou and Zhang 2006b), *Gansus yumenensis* (CAGS-IG-04-CM-003, CAGS-IG-04-CM-004; You et al. 2006), *Jianchangornis microdonta* (IVPP V16708; Zhou et al. 2009), and *Yanornis martini* (IVPP V12558, V13358; Zhou and Zhang 2001; Zhou et al. 2002, 2004). It is narrow (having a low interclavicular angle), U-shaped, and lacks a hypocleideum. The latter morphology is characteristic of most non-neornithine ornithuromorphs, including *Archaeorhynchus*, *Gansus*, *Jianchangornis*, *Yanornis*, *Yixianornis grabaui* (IVPP V12631 [Zhou and Zhang 2001; Clarke et al. 2006]), and probably *Ichthyornis dispar* (YPM 1755 [Marsh 1880; Clarke 2004]), but it differs from the small hypocleideum present in Hongshanornithidae (*Hongshanornis longicresta* + *Longicrusavis houi*; O'Connor et al. 2010) and is highly distinct from the hypertrophied hypocleideum of enantiornithines such as *Eoalulavis hoyasi* (LH 13500; Sanz et al. 1996, 2002)

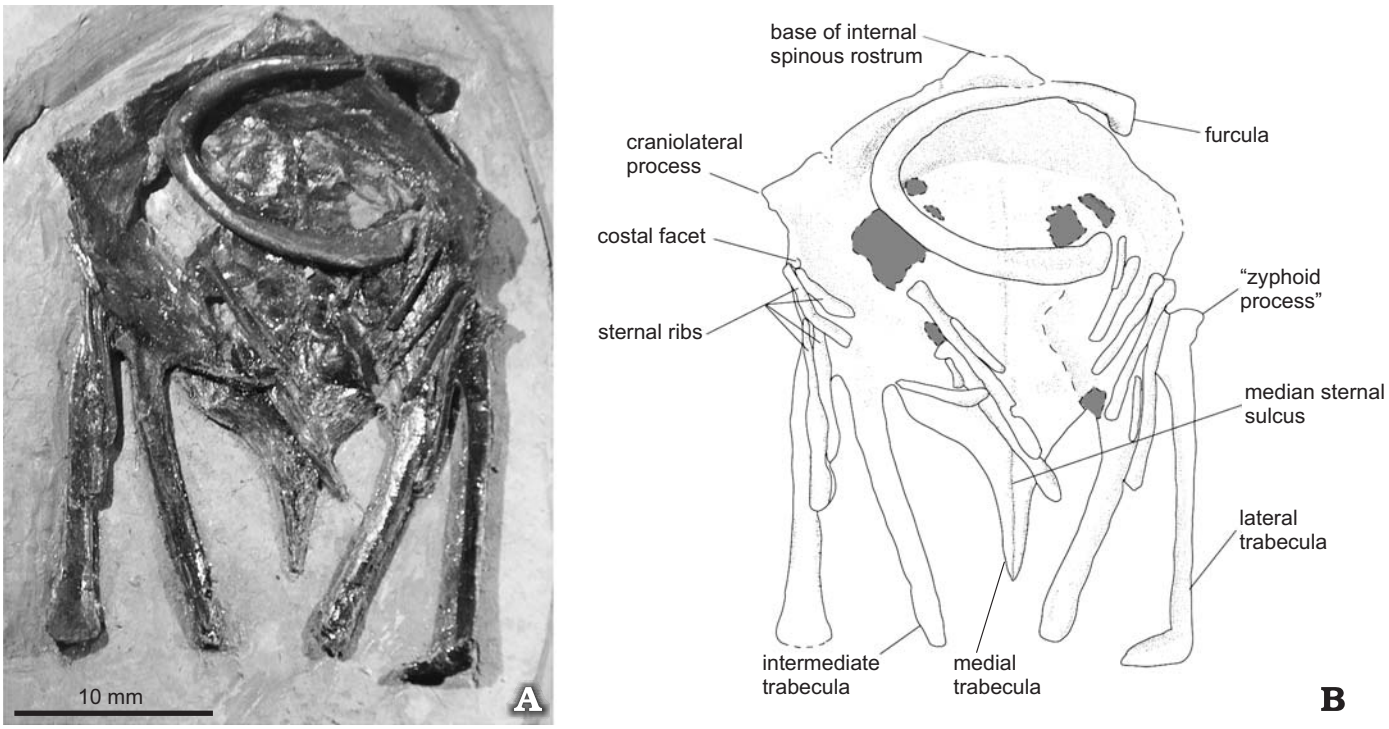



Fig. 2. Ornithuromorpha gen. et sp. indet. (FRDC-05-CM-021) from the Early Cretaceous of the Changma Basin, northwestern Gansu Province, China: associated furcula (in cranial view), sternum (in dorsal view), and ribs. Photograph (**A**), interpretive drawing (**B**). Dashed lines in B represent points of breakage; gray areas represent holes.

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and *Sinornis santensis* (BPV 538; Sereno and Rao 1992; Sereno et al. 2002). The sternal extremity is convex in cranial view, as opposed to the straighter margins present in *Gansus* and *Yixianornis*. The rami are oval in cross-section at midshaft, with the long axis oriented obliquely such that the caudal margin lies in a plane medial to that of the cranial margin. Omally, the rami curve and expand caudally as in *Gansus* and modern birds. The rami gently increase in size caudally over their omal one-third; the omal tips also expand medially. Due to the essentially two-dimensional preservation of most other Cretaceous ornithuromorphs, we are unable to determine whether or not most of these morphologies are present in other taxa, though medial expansions are lacking in *Gansus*, *Ichthyornis* (SMM 2503; Clarke 2004), and *Yixianornis*. The interior of the furcula, visible in a break at midshaft of the right ramus (Fig. 2), is apneumatic.

Sternum: The sternum is exposed in dorsal view, with much of its morphology preserved in three dimensions (Fig. 2). It is comparable in size to a small (presumably juvenile or subadult) *Gansus* sternum, FRDC-06-CM-011 (Fig. 3), which demonstrates that FRDC-05-CM-021 does not represent an early stage in the ontogeny of that genus. The cranial margin bears deep, mediolaterally wide sulci for the articulation of the coracoids. This suggests that the sternal margin of the coracoid was also wide, as in most other basal ornithuromorphs (e.g., *Gansus*, *Songlingornis linghensis* [IVPP V10913; Hou 1997a], *Yanornis*) but in contrast with the narrower coracoidal sternal margins of *Apsaravis ukhaana* (IGM 100/1017 [Norell and Clarke 2001; Clarke and Norell 2002]) and most enantiornithines. The coracoidal sulci meet craniomedially, with the left and right margins of the sternum intersecting at an angle of approximately 100°, constituting an unusually sharp craniomedial apex. This morphology is similar to those of *Archaeorhynchus*, *Jianchangornis*, *Songlingornis*, and the probable basal ornithuromorph *Aberratiodontus wui* (LHV 0001; Gong et al. 2004). Conversely, in *Apsaravis* and *Gansus*, the cranial margin of the sternum lacks this "peaked" appearance because the coracoidal sulci meet at a much greater angle (approximately 160° in *Gansus*; Fig. 3B). The dorsal margin of each coracoidal facet projects cranially relative to the ventral margin, as in *Yixianornis*. The cranial midline of the sternum is abraded and was almost certainly flattened during diagenesis, but the broad base of an internal spinous rostrum (Baumel and Witmer 1993) is preserved. It appears to have been more robust than those of *Apsaravis* or *Archaeorhynchus*, but similar to that present in *Jianchangornis*.

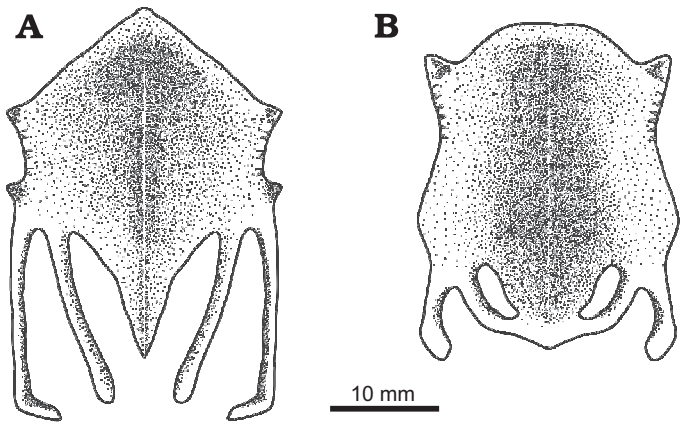



Fig. 3. Early Cretaceous ornithuromorph birds from the Changma Basin, northwestern Gansu Province, China: reconstructed sterna in dorsal view. **A**. Ornithuromorpha gen. et sp. indet. (FRDC-05-CM-021). **B**. *Gansus yumenensis* (FRDC-06-CM-011, small [presumably juvenile or subadult] individual).

The cranial and craniolateral margins of the sternum bound the concave dorsal surface. The craniolateral corners of the margin form sharp processes, as in some other basal ornithuromorphs (e.g., *Jianchangornis*, *Songlingornis*, *Yanornis*). In *Gansus* (e.g., FRDC-05-CM-005), these processes are proportionally more robust and may have projected dorsolaterally (Fig. 3B). The lateral margin of the sternum bears at least four costal facets separated by spaces approximately 1.5 times greater in craniocaudal length than the facets themselves. The total number of costal facets may have been higher: five sternal ribs are preserved on each side, but the obscured caudal portion of the left costal articular region makes an exact facet count difficult. *Gansus* (FRDC-04-CM-020) appears to possess six costal facets (contra Harris et al. 2006b); the cranial two facets are shallow and not as well-defined as the caudal four. Furthermore, the facets are almost directly adjacent, as opposed to the widely separated facets of FRDC-05-CM-021. Immediately caudal to the costal region, and visible only on the right side of the sternum, the lateral margin appears to be attenuated into a laterally projecting, triangular process (the "zyphoid process" of Clarke et al. 2006). Similar processes are present in *Gansus* (Fig. 3B), *Songlingornis* (Hou 1997a), and *Yixianornis* (Clarke et al. 2006), but are larger and more rounded in these genera.

Caudally, the sternum is deeply excavated by four V-shaped incisures bounded by elongate, strap-like lateral, intermediate, and medial trabeculae. The incisures are much deeper than in other known basal ornithuromorphs, with the exception of *Archaeorhynchus* (Zhou and Zhang 2006b). In this latter taxon, however, the transverse distance between the lateral trabeculae is considerably greater than the width of the sternal body at its craniocaudal midpoint, while this intertrabecular space is approximately as wide as the sternal body in FRDC-05-CM-021. In addition, *Archaeorhynchus* appears to lack intermediate trabeculae (Zhou and Zhang 2006b: fig. 3).

Though the total craniocaudal length of the sternum of FRDC-05-CM-021 is comparable to those of other basal ornithuromorphs (Table 1), the sternal body is comparatively much shorter than in most of these taxa. Indeed, this relatively short sternal body with long trabeculae is reminiscent of the morphology observed in some enantiornithines (e.g., *Longipteryx chaoyangensis* [IVPP V12325; Zhang et al. 2001], *Vescornis hebeiensis* [NIGPAS 130722; Zhang et al. 2004]). We hypothesize that, in life, the lateral trabeculae projected caudodorsally as in modern birds, but that they were broken and flattened during diagenesis. The lateral and

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Table 1. Measurements (mm) of pectoral elements in selected Early Cretaceous Chinese basal ornithuromorphs: Ornithuromorpha gen. et sp. indet. (FRDC-05-CM-021), *Gansus yumenensis* (CAGS-IG-04-CM-003), *Songlingornis linghensis* (IVPP V10913; Hou 1997a: table 17), *Yanornis martini* (IVPP V12558; Zhou et al. 2002: supplementary information), and *Yixianornis grabaui* (IVPP V12631; Clarke et al. 2006: table 1).

| | | FRDC-05-CM-021 | *Gansus* | *Songlingornis* | *Yanornis* | *Yixianornis* |
|---|---|---|---|---|---|---|
| Furcula | length of clavicular ramus | 14.9 | 16.6 | 25.0 | – | 20.5 |
| | distance between rami | 6.6 | 10.9 | 12.0 | 5.0 | 4.2 |
| | shaft diameter | 1.5 | 1.1 | – | – | 2.2 |
| Sternum | length (along midline) | 28.9 | 40.0 | 35.0 | 48.4 | 43.1 |
| | width (between "zyphoid processes") | 23.2 | 30.7 | – | – | – |
| | length of lateral trabecula | 19.2 | 14.3 | – | – | – |

intermediate trabeculae project caudally past the caudal end of the medial trabecula, and are of approximately equal length (the lateral trabeculae are slightly longer). Many other basal ornithuromorphs (e.g., *Gansus*, *Songlingornis*, *Yanornis*, *Yixianornis*), in contrast, are characterized by a single set of free trabeculae (the lateral pair), while the strap-like intermediate trabeculae curve toward the sternal midline to contact and fuse with the medial trabecula, enclosing caudal fenestrae. Like FRDC-05-CM-021, *Hongshanornis* and *Jianchangornis* also exhibit intermediate trabeculae that do not merge with the medial trabecula; in these taxa, however, the intermediate trabeculae are much shorter than the lateral trabeculae. In FRDC-05-CM-021, the lateral trabeculae are craniocaudally oriented and straight, while the intermediate trabeculae project caudomedially, approaching the midline but remaining distinct from the medial trabecula. The lateral trabeculae appear to have been moderately expanded at their caudal tips, but this is uncertain because the caudal morphologies of the two trabeculae differ: the right trabecula exhibits an expansion in the shape of a sharp, reverse L-shaped "boot" that tapers medially, but on the left side, the expansion is much more subtle. Additionally, the caudal margin of the left expansion appears to be excavated by a groove (although this is possibly an artifact resulting from damage to a morphology more similar to that preserved in the right lateral trabecula). Caudal expansions of the lateral trabeculae are common among enantiornithines and present in some basal ornithuromorphs (e.g., *Jianchangornis*, *Songlingornis*, *Yanornis*, *Yixianornis*) but absent in others (e.g., *Archaeorhynchus*, *Hongshanornis*). The medial trabecula is laterally convex cranially, but sharply tapers caudally into a narrow, pointed, V-shaped process. The median sternal sulcus is visible along the length of the sternum, and is especially prominent along the medial trabecula (likely emphasized by crushing here). This midline groove is also present in some specimens of *Gansus* (e.g., FRDC-05-CM-005, FRDC-06-CM-011) and in modern birds.

*Stratigraphical and geographical range*.—Near the town of Changma, in the Changma Basin, Gansu Province, northwestern China (Fig. 1). Precise locality information is available to qualified researchers upon request. Lower Cretaceous (lower–middle? Aptian) Xiagou Formation, lower unit of the Xinminpu Group.

# Phylogenetic analysis

A phylogenetic analysis was performed using the dataset of O'Connor et al. (2009), with the deletion of *Longicrusavis houi* and *Rapaxavis pani* (presented therein as PKUP V1069 and DNHM D2522, respectively) and the addition of FRDC-05-CM-021, *Archaeorhynchus spathula*, *Liaoningornis longidigitris*, *Songlingornis linghensis*, and three undescribed Xiagou Formation enantiornithine specimens (see Supplementary Online Material at http://app.pan.pl/acta55/app55-You_etal_SOM.pdf). The large number of enantiornithine taxa incorporated into the analysis was intended to provide a substantial representation of this avian clade so as not to bias FRDC-05-CM-021 toward Ornithuromorpha on the basis of morphological inferences. Neornithes was represented by *Anas platyrhynchos* and *Gallus gallus*; Dromaeosauridae was scored as the outgroup. A matrix of 214 characters (31 ordered; 28 uninformative characters removed from data set of 242, see Supplementary Online Material 2) and 34 taxa was evaluated using NONA ver. 2.0 (Goloboff 1993); optimal trees were identified by a heuristic search implementing 1000 replicates of the Tree Bisection and Reconnection (TBR) algorithm, retaining the 10 shortest trees from each replication. Additional TBR branch-swapping was not required.

The analysis resulted in two most parsimonious trees (MPTs) of 592 steps, the strict consensus of which (Fig. 4) supports FRDC-05-CM-021 as a member of Ornithuromorpha. Within this clade, *Patagopteryx deferrariisi* and *Archaeorhynchus* are recovered as successive outgroups to a large polytomy formed by *Hongshanornis longicresta*, *Gansus yumenensis*, *Apsaravis ukhaana*, FRDC-05-CM-021, a *Yixianornis grabaui* + (*Songlingornis* + *Yanornis martini*) clade, and Ornithurae (*Hesperornis regalis* + [*Ichthyornis dispar* + Neornithes]). The *Yixianornis* + (*Songlingornis* + *Yanornis*) clade differs in structure from previous analyses (Clarke et al. 2006) in that *Yanornis* and *Songlingornis* share a more exclusive relationship with each other than either does with *Yixianornis*; this pairing is supported by three synapomorphies (char. 62: 1→2; char. 109: 1→0; char. 111: 1→2). In the analysis of Clarke et al. (2006), *Songlingornis* was recovered as more closely related to *Yixianornis* than to *Yanornis*.

The two MPTs differ only in the placements of FRDC-05-CM-021, *Apsaravis*, and *Gansus* (see Supplementary Online Material 1). In both trees, *Hongshanornis* is basal to these taxa

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and the *Yixianornis* + (*Songlingornis* + *Yanornis*) clade. In one tree, *Apsaravis* and FRDC-05-CM-021 form a polytomy with Ornithurae, with *Gansus* as the outgroup. This large clade forms a dichotomy with the *Yixianornis* + (*Songlingornis* + *Yanornis*) clade, to which *Hongshanornis* is the outgroup. In the second tree, *Apsaravis* and *Gansus* form successive outgroups to Ornithurae. This clade forms a dichotomy with the *Yixianornis* + (*Songlingornis* + *Yanornis*) clade. Specimen FRDC-05-CM-021 and *Hongshanornis* together constitute a clade that falls outside this large dichotomy.

The largely incomplete nature of FRDC-05-CM-021 makes it difficult to resolve its phylogenetic position relative to other taxa, and support for the consensus tree is weak (see Supplementary Online Material). However, the placement of the new specimen within Ornithuromorpha, as suggested by the morphology of its furcula, is confirmed. *Gansus* is recovered as earlier diverging than in the analysis of You et al. (2006), where this taxon was hypothesized as a member of Ornithurae. The revised position of *Gansus* proposed here may reflect our incorporation of previously unavailable morphological information gleaned from newly prepared specimens of this genus, the inclusion of a greater diversity of basal ornithuromorph taxa in our analysis, or both.

# Discussion

The recent surge in discovery of Early Cretaceous ornithothoracine fossils has resulted in an improved understanding of basal ornithuromorph sternal anatomy, since most recently-described specimens preserve this element (e.g., the holotypes of *Archaeorhynchus spathula*, *Hongshanornis longicresta*, *Jianchangornis microdonta*, *Longicrusavis houi*, *Songlingornis linghensis*, *Yanornis martini*, *Yixianornis grabaui*, and new specimens of *Gansus yumenensis*). As presently understood, the morphology of archaic ornithuromorph sterna is fairly conservative, with several taxa (*Gansus*, *Songlingornis*, *Yanornis*, *Yixianornis*) exhibiting caudal fenestrae and craniocaudally abbreviate lateral trabeculae. The sternum of FRDC-05-CM-021 represents one of the most distinctive departures from this morphology yet observed within basal Ornithuromorpha.

The revised phylogenetic position of the Early Cretaceous Chinese bird *Liaoningornis longidigitris* proposed here (Fig. 4) is a striking reflection of our increased knowledge of early ornithothoracine sternal morphology and diversity. At the time that the only known, incomplete *Liaoningornis* specimen was described (Hou 1997b), with the sternum as its best-preserved and only truly diagnostic element, just a few definitive Early Cretaceous ornithuromorph fossils had been discovered (e.g., the holotypes of *Ambiortus dementjevi* [Kurochkin 1982], *Chaoyangia beishanensis* [Hou and Zhang 1993], and *Gansus* [Hou and Liu 1984]), none of which included well-preserved sternal material, thus rendering meaningful morphological comparisons difficult. *Liaoningornis* was placed within Ornithurae (Hou 1997b), though the distribution of the character states used to support this assignment (e.g., the presence of a sternal carina) is now known to extend beyond this clade.

If the position of *Liaoningornis* within Ornithurae, or even the more inclusive group Ornithuromorpha, were to be strongly supported, then the morphology of this genus would represent a significant divergence from that of other ornithuromorphs. Instead, the skeleton of *Liaoningornis* closely resembles that of the bizarre Spanish Early Cretaceous enantiornithine *Eoalulavis hoyasi* (Sanz et al. 1996) while simultaneously lacking clear ornithuromorph morphologies such as the presence of two cnemial crests or a well developed intercotylar eminence on the proximal tarsometatarsus. In our analysis (Fig. 4), *Eoalulavis* and *Liaoningornis* form a clade within Enantiornithes, supported by a single character state (char. 117: 2→3) that reflects the similar morphology of the caudal half of the sternum in both genera. This position of *Liaoningornis* within Enantiornithes differs from those retrieved by previous studies, which also vary widely in the placement of this taxon. One analysis resolved *Liaoningornis* as a basal ornithuromorph (Zhou and Zhang 2006b), consistent with the original description of the taxon, while another postulated this genus as outside of Pygostylia (You et al. 2006). Nevertheless, the position recovered by the present study is currently the most strongly supported by empirical morphological comparisons with other birds. As demonstrated by *Liaoningornis*, when combined with detailed analyses of existing specimens, the discovery of additional Cretaceous ornithothoracine fossils such as FRDC-05-CM-021 can significantly affect systematic assessments of previously-described taxa.

The phylogenetic positions of FRDC-05-CM-021 and *Gansus* emphasize the importance of the Xiagou Formation avifauna for deciphering the early evolution and diversification of Ornithuromorpha, and, ultimately, of the extant avian clade Neornithes. In the Jehol Group, representatives of Enantiornithes are both numerically and taxonomically dominant over their ornithuromorph counterparts. In contrast, ornithuromorph fossils from the Xiagou Formation greatly outnumber those of enantiornithines, suggesting that, in the Xiagou paleoecosystem, representatives of the former clade were more common than those of the latter. Until the discovery of FRDC-05-CM-021, however, it appeared that the taxonomic diversity of Xiagou enantiornithines was higher than that of sympatric ornithuromorphs, with probably two enantiornithine taxa (Lamanna et al. 2006b: 430; unpublished data) to only one ornithuromorph (*Gansus*) recorded. Because it pertains to a second Xiagou ornithuromorph taxon, the specimen described here tentatively suggests that enantiornithines and ornithuromorphs were of comparable diversity in the paleoecosystem of this unit. This, in turn, constitutes further evidence that this unit may record the initial stages of the eventual rise of ornithuromorphs to taxonomic and numerical dominance over enantiornithines (You et al. 2006).

Discoveries of additional specimens referable to the ornithuromorph taxon presently represented solely by FRDC-

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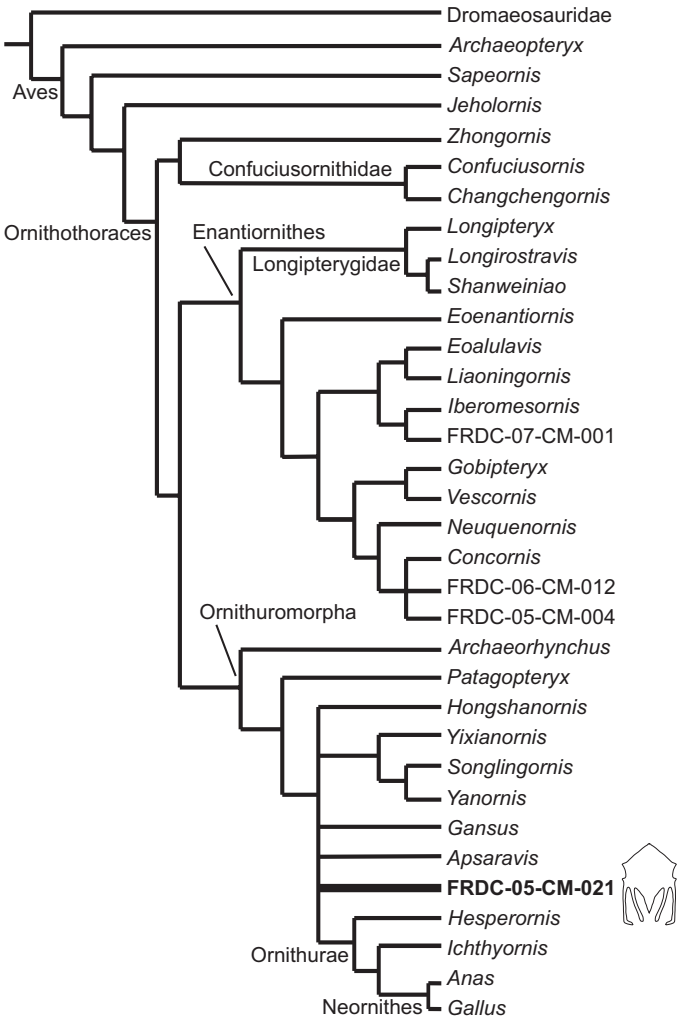



Fig. 4. Hypothesized phylogenetic position of Ornithuromorpha gen. et sp. indet. (FRDC-05-CM-021 [indicated by sternum]) from the Early Cretaceous of the Changma Basin, northwestern Gansu Province, China. Strict consensus of two most parsimonious trees of 592 steps (CI = 47; RCI = 47; RI = 67) recovered by cladistic analysis. FRDC-07-CM-001, FRDC-06-CM-012, and FRDC-05-CM-004 are as-yet undescribed enantiornithine fossils in the FRDC collection.

05-CM-021 would provide additional phylogenetic and ecomorphological information regarding the early evolution and diversification of Ornithuromorpha, and potentially the origins of Ornithurae. For instance, an important aspect of the paleobiology of *Gansus* is its presumed aquatic or semi-aquatic lifestyle, which has been inferred from its prominent, proximally-projecting cnemial crest on the tibiotarsus, proximal position of the metatarsal II trochlea, and elongate, webbed pedal digits (You et al. 2006; Hinic-Frlog 2007). Coupled with the phylogenetic position of *Gansus* as an advanced non-ornithurine ornithuromorph or basal ornithurine, this was considered to support the hypothesis that Cretaceous ornithuromorphs may have been largely aquatic in habits, and that neornithines may have originated in water-based niches (You et al. 2006). Whether or not the taxon represented by FRDC-05-CM-021 possessed similar aquatic adaptations can only be determined by the discovery of more complete specimens, because no sternal or furcular characters have yet been determined to be indicative of an aquatic ecology. It is interesting to note, however, that sterna with short bodies and long trabeculae bordering deep incisures (closed in vivo by fibrous membranes) convergently occur in terrestrial, largely cursorial galliforms. Furthermore, a similar sternal morphology is also observed in the Mongolian Late Cretaceous enantiornithine *Elsornis keni* (Chiappe et al. 2006), a taxon hypothesized (based on its pectoral limb proportions) to have been terrestrial, and possibly flightless. This does not imply that such sternal morphology is present in all terrestrial birds (many other landbirds—excepting ratites—have more typical sternal morphologies), though the association of this morphology with reduced flight capabilities is noteworthy.

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