



A new euornithine from the Lower Cretaceous (Aptian) of China reveals the first radiation of fish-eating birds



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ABSTRACT

A new euornithine bird, *Kunpengornis anhuimusei* gen. et sp. nov., is described based on a nearly complete skeleton from the Lower Cretaceous (Aptian) Jehol Biota in western Liaoning, China. The new taxon is characterized by possessing the unique combination of reduced maxillary ramus of premaxilla shorter than half the buccal margin of premaxilla, coracoid having a trapezoidal procoracoid process not expanded craniocaudally at its medial margin, sternum with blunt craniolateral process, drop-shaped distal end of lateral trabecula and reduced intermediate trabecula not enclosing a caudal fenestra, pubis lacking ossified distal symphysis and with gradually expanding distal end, resulting twice longer craniocaudally than at mid-shaft, but lacking an abrupt distinction between shaft and distal foot. The macerated fish bones preserved in the abdominal cavity provides direct evidence that *Kunpengornis* was piscivorous. Despite overall similarity with some yanornithids and other piscivorous euornithines, the phylogenetic analysis places *Kunpengornis* as sister taxon of *Piscivoravis* and closer to the "ornithur-omorph-gansuid" clade than Yanornithidae, a result which supports the hypothesis that a piscivorous "Yanornis-like" *bauplan* was a grade along the evolutionary sequence leading to the precursors of the modern avians. The acquisition of the fish-eating ecology and the exploitation of the aquatic environments represented key innovations for the successful radiation of the euornithine birds.

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1. Introduction

The Lower Cretaceous Jehol Biota in northeastern China has yielded abundant exquisitely preserved early birds, significantly enhancing our understanding of the early evolution of Avialae, including the basal long-tailed jeholornithiforms and the short-tailed pygostylians (Chiappe et al., 1999; Zhou Z-H, 2004, 2014; Wang M. et al., 2017, 2021; Wu S-Y et al., 2023; Wang X-L et al., 2024; Zhou and Wang, 2024; Wang X-R et al., 2025). Euornithes represents the diversified pygostylian group which led to the ancestry of modern birds later in the Cretaceous (Benito et al., 2022). The rich fossil record of Euornithes from the Jehol Biota

has provided novel insights into their diversity, ontogeny and ecology (Yu et al., 2021; Monfroy and Kundrát, 2021; Miller and Pittman, 2021; Wu Y. et al., 2023). Furthermore, some avialan specimens preserved with gut contents have offered direct evidence to elucidate their trophic habits (Hu et al., 2022; Clark et al., 2023; Wu Y. et al., 2023; O'Connor et al., 2024). To date, among Lower Cretaceous euornithines only *Yanornis*, *Abitusavis* and *Piscivoravis* (and possibly, *Jianchangornis*) have been reported preserved with macerated fish bones as direct evidence of a piscivorous diet (Zhou et al., 2014; Zhou Z-H, 2014; Zheng et al., 2014; Zhou S. et al., 2014; Wang M. et al., 2020). Here, we describe an almost complete Jehol Biota euornithine from Lama-dong Town (Jianchang County) in western Liaoning Province of China (Fig. 1). The unique skeletal morphology of the specimen supports the erection of a new euornithine genus and species, *Kunpengornis anhuimusei* gen. et sp. nov. Gut content demonstrates a piscivorous diet in this bird, the fourth case of this ecology among the Lower Cretaceous euornithines.

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Fig. 1. Map of Liaoning Province, China, showing the Lamadong locality at Jianchang County, Huludao City, where the holotype of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483) was recovered.

1.1. Geological background

The holotype of *Kunpengornis anhuimusei* gen. et sp. nov. was uncovered from the Lower Cretaceous Jiufotang Formation at the Lamadong locality, Jianchang County, Huludao City, Liaoning Province, China. The Jianchang Basin is located in the eastern part of the Yanshan Fold and Thrust Belt, and along the northern margin of the North China Craton (Zhang et al., 2012; Zhu et al., 2012). The Upper Mesozoic units are nearly completely and successively distributed in this basin, in ascending order, containing the Middle Jurassic Haifanggou/Jiulongshan Formation, the Upper Jurassic Tiaojishan Formation, the Upper Jurassic-Lower Cretaceous Tuchengzi Formation, and the Lower Cretaceous Yixian and Jiufotang formations. The Jiufotang Formation exposed at Lamadong locality is mainly composed of a series of yellow-green conglomerate (pebbly sandstone), grayish green tuffaceous fine sandstone, and grayish white tuffaceous siltstone, which can be subdivided into three parts and represented three sedimentary phases (Wang S-M et al., 2020). The fossil bird herein described was uncovered from the second part of the Jiufotang Formation (Fig. 2), representing shallow to moderately deep lacustrine conditions.

2. Material and methods

The material described here was uncovered by a local farmer from the Lower Cretaceous (Aptian) Jiufotang Formation at Lamadong Town in Jianchang County (40° 41' 32" N, 119° 47' 36" E), Liaoning Province, China. It was donated to Anhui Geological Museum for research in 2023. It is a nearly complete and articulated skeleton preserved in a single slab, and is housed at Anhui Geological Museum under collection number AGB15483.

We use standard sauropsid terminology for bone orientation (medial/lateral, dorsal/ventral, etc.), and apply the terms "cranial/caudal" for the postcranial skeleton instead of "anterior/posterior". The term "rostral" replaces "cranial" for the description of the cranium and mandible. Carpal bone homology and terminology follow the integrated paleontological and embryological framework of Botelho et al. (2014): the "*os carpi radiale*" and "*os carpi ulnare*" of Baumel and Witmer (1993) are homologous to,

respectively, the scapholunare (i.e., fused radiale + intermedium) and pisiform of other sauropsids.

Following the taxonomic emendations of Benito et al. (2022), the most inclusive clade containing crown birds but excluding the enantiornithines is called "Euornithes"; the name "Ornithur-omorpha" is used for the least inclusive clade containing crown birds and *Patagopteryx*. We follow Wang M. et al. (2020) who defined Yanornithidae as the most inclusive clade containing *Yanornis martini* and *Abitusavis lii*, but not *Yixianornis grabaui*, *Piscivoravis lii*, or *Passer domesticus*.

2.1. Phylogenetic analysis

We tested the phylogenetic affinities of *Kunpengornis* gen. nov. using a modified version of the analysis of Cau (2024) which integrates ontogenetic and morphological diversity in the reconstruction of Mesozoic theropod relationships. The original taxon sample has been here restricted to members of Avialae (118 taxa), using *Anchiornis* as the outgroup. Character statements were based on Cau (2024) (see Supplementary Material). We included the recently named *Baminornis* (Chen et al., 2025) in the taxon sample. Yet, the purported presence of a pygostyle in the latter taxon is ambiguous, since the fused vertebrae interpreted as the distal end of the tail by Chen et al. (2025), could alternatively be partial remnants of the sacral series (e.g., the "pygostyle" in figure 2a of Chen et al., 2025, closely recalls the shape and morphology of the lateral side of the avialan synsacrum shown in figure 2c of O'Connor, 2019. See also <https://theropoddatabase.blogspot.com/2025/02/no-pygostyle-for-baminornis.html>). Accordingly, the character statements describing the caudal vertebrae in the data string of *Baminornis* were coded conservatively as unknown pending unambiguous confirmation of the pygostyle in that taxon (note that this conservative coding strategy was followed also by Wang X-R et al., 2025, for the fused vertebrae in the pelvic region of *Shuilingornis angelai*). We performed 1000 "New Technology" analyses in TNT (Goloboff and Catalano, 2016) followed by a series of "Traditional search" analyses exploring the tree islands found during the first round. The most unstable "wildcard" taxa were pruned *a posteriori* from the consensus topology used as evolutionary framework. We calculated the nodal support using the Bremer Support function in TNT sampling all topologies up to ten steps longer than the shortest trees found.

2.2. Nomenclatural act

The electronic version of this article in portable document format will represent a published work according to the International Code of Zoological Nomenclature, and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>.

This publication:

LSIDurn:lsid:zoobank.org:pub:B537092C-7486-421A-9120-75F530157707.

Genus *Kunpengornis*:

LSIDurn:lsid:zoobank.org:act:5FE3F342-4F9D-4BEE-8FA2-4B5B8334331F.

Species *Kunpengornis anhuimusei*:

LSIDurn:lsid:zoobank.org:act:46FCBA09-7D8E-48FD-9B3F-D34EC415EDB5.

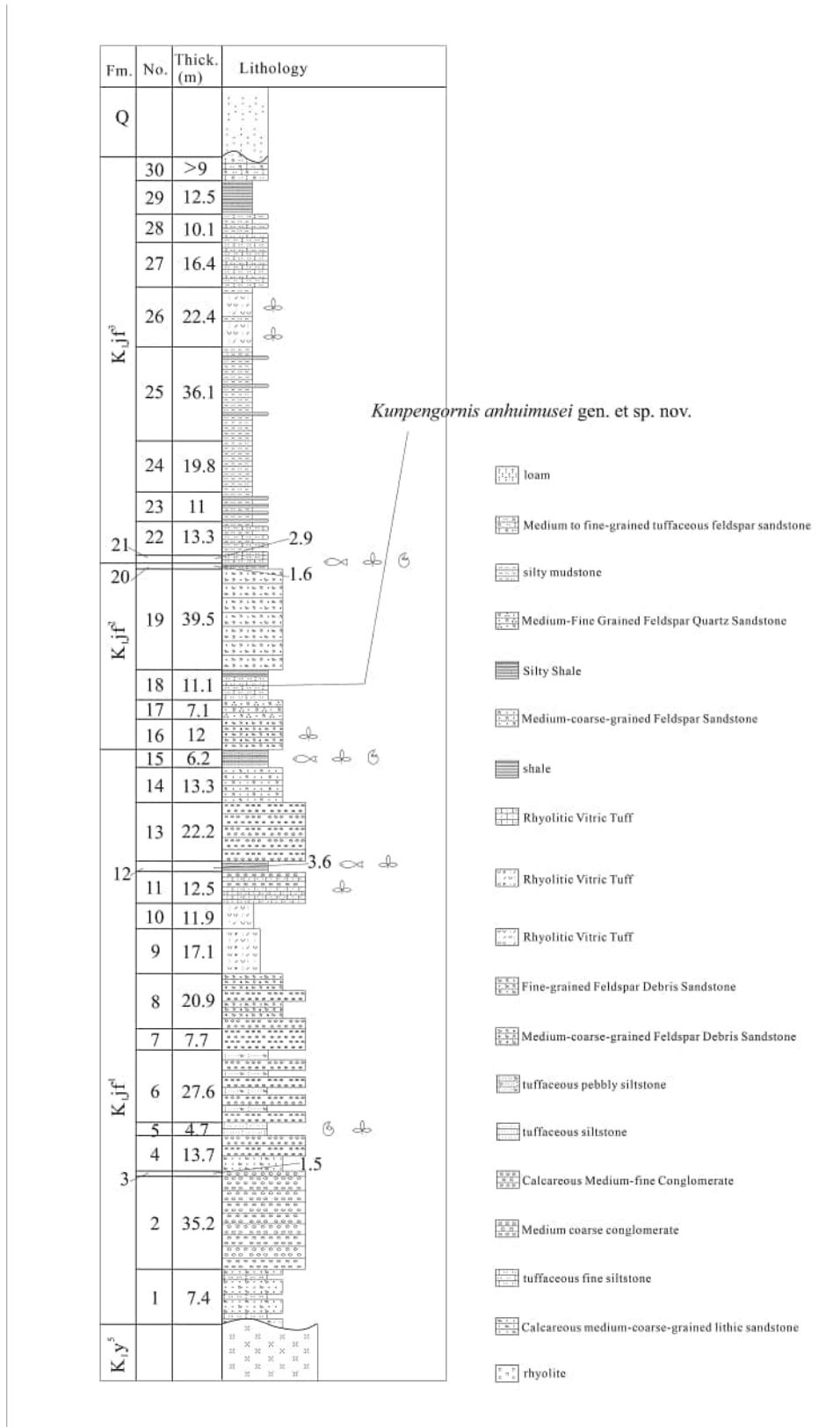


Fig. 2. Stratigraphic column of the Jiufotang Formation at the Lamadong locality.

3. Systematic paleontology

Avialae Gauthier, 1986.
 Pygostylia Chiappe, 2002
 Euornithes Sereno, 1998
 (Fig. 3, Table 1)

Kunpengornis anhuimusei gen. et sp. nov.

Etymology. The genus name is composed of Chinese “Kunpeng” (an animal in ancient Chinese myth) and Greek “ornis” (bird). The species name indicates that the type specimen is housed at Anhui Geological Museum.

Locality and horizon. Lamadong Town, Jianchang County, Huludao City, Liaoning Province, China; Jiufotang Formation, Lower Cretaceous (Aptian) (Yu et al., 2021).

Diagnosis. Longirostrine euornithine bird with reduced maxillary ramus of premaxilla shorter than half the buccal margin of premaxilla; premaxillary body shorter than the maxillary preantorbital ramus; premaxilla with five teeth restricted to the caudal half of the occlusal margin; nasal with acuminate frontal ramus and blunt rounded maxillary (subnasial) ramus; postorbital ramus of frontal rounded in dorsal view and abruptly projected from orbital margin of bone; coracoid having a trapezoidal

Table 1

Selected measurements of the holotype *Kunpengornis anhuimusei* gen. et sp. nov. (AGB15483). Abbreviations: L, left; R, right; # indicates preserved length.

Element	Length (in mm)
Skull	73.35
Coracoid	R 34.47
Scapula	R 64.02
Humerus	R 82.93
Ulna	L 83.39
Radius	R 79.15 [#]
Metacarpal I	L 7.40
Manual digit I-1	L 16.91
Manual digit I-2	L 9.29
Metacarpal II	L 31.69
Manual digit II-1	L 19.11
Manual digit II-2	L 17.45
Manual digit II-3	L 8.83
Metacarpal III	L 29.64
Manual digit III-1	L 7.96
Synsacrum	36.29
Femur	L 58.25
Tibia	L 76.60
Tarsometatarsus	L 40.53

procoracoid process not expanded craniocaudally at its medial margin; robust minor metacarpal with shaft broader than half of major metacarpal; sternum with blunt craniolateral process, drop-shaped distal end of lateral trabecula and reduced intermediate trabecula not enclosing a caudal fenestra; pubis lacking ossified distal symphysis and with gradually expanding distal end, resulting in a distal tip twice longer craniocaudally than at mid-shaft, but lacking an abrupt distinction between shaft and distal foot (autopomorphy); intermembranal index = 1.12.

Description and comparisons. The skull is preserved in right lateral view with most elements remaining in articulation (Fig. 4). The ratio of skull length/height is approximately 2.6, which exceeds that in *Yixanornis*, *Yanornis* and *Similiyanornis* (Clarke et al., 2006; Wang M. et al., 2020). The rostrum occupies nearly 60 % of the skull length, similar to the condition in the enantiornithine longipterygids (O'Connor and Chiappe, 2011) and some “Gansus-like” taxa (Huang et al., 2016). This is greater than the proportion (approximate 50 %) in *Yixianornis*, *Yanornis* and *Similiyanornis* (Clarke et al., 2006; Wang M. et al., 2020), and smaller than the proportion in *Xinghaiornis* (67 %) and *Dingavis* (63 %) (Wang X-R et al., 2013; O'Connor et al., 2016). The premaxilla is straight ventrally and tapered rostrally. The frontal process of the premaxilla is very long, nearly contacting the frontal, approximately 6 times the maxillary process length. The maxillary process of the premaxilla is much shorter than the premaxillary corpus, and tapers caudally, similar to the condition in *Similiyanornis* but contrary to that in *Yanornis* (Wang M. et al., 2020). The maxillary process is less than half the length of the premaxilla, different from that in *Yanornis* and *Similiyanornis*. As in *Yanornis* and *Yixianornis*, the premaxillary corpus does not possess a foramen, which is present in *Similiyanornis* (Wang M. et al., 2020). Five teeth can be observed on the right premaxilla, which are similar in size and morphology. As in *Yixianornis*, *Yanornis* and *Similiyanornis*, the rostral fourth of the premaxilla is edentulous (Clarke et al., 2006; Wang M. et al., 2020). The conical premaxillary teeth are not as closely packed as in yanornithids, with the interalveolar space subequal to the crown width. The maxilla is poorly preserved and overlain by the right premaxilla rostrally and by the nasal caudally, preventing the observation of detailed characteristics. Yet, based on the position of the articulated nasal, which bounds a relatively short antorbital fenestra with its caudoventral margin, the preantorbital ramus of the maxilla is inferred to be longer than the premaxillary body, differing from the condition seen in some

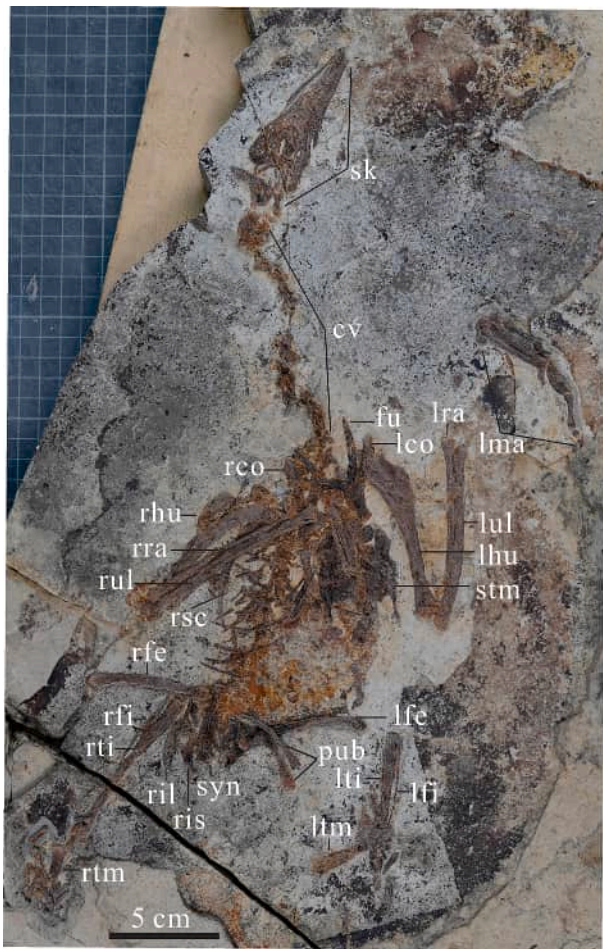


Fig. 3. Holotype of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Abbreviations: cv, cervical vertebrae; fu, furcula; lco, left coracoid; lfe, left femur; lfi, left fibula; lhu, left humerus; lma, left manus; lra, left radius; lti, left tibia; ltm, left tarsometatarsus; lul, left ulna; pub, pubis; rco, right coracoid; rfe, right femur; rfi, right fibula; rhu, right humerus; ril, right ilium; ris, right ischium; rra, right radius; rsc, right scapula; rti, right tibiotarsus; rtm, right tarsometatarsus; sk, skull; stm, sternum; syn, synsacrum. Scale bar = 5 cm.

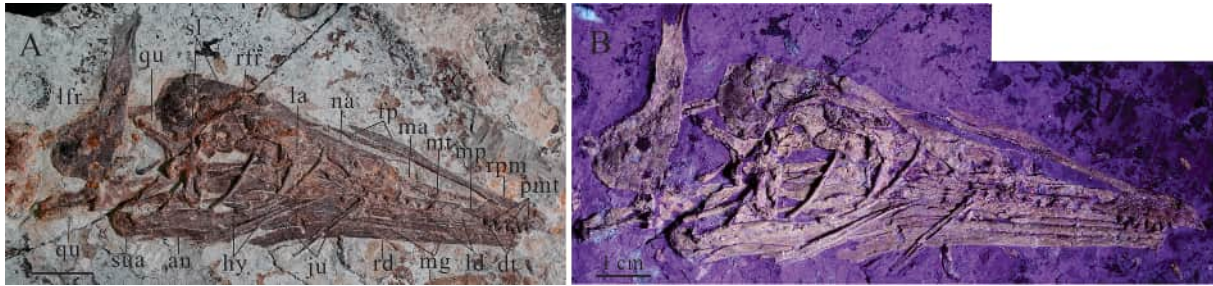


Fig. 4. Skull of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483) under normal light (A) and UV light (B). Abbreviations: an, angular; dt, dentary teeth; fp, frontal process of premaxilla; ju, jugal; la, lacrimal; ld, left dentary; lfr, left frontal; ma, maxilla; mg, Meckel's groove; mp, maxillary process of premaxilla; mt, maxillary teeth; na, nasal; qu, quadrate; rd, right dentary; rfr, right frontal; rpm, right premaxilla; sl, scleral bones; sua, surangular. Scale bar = 1 cm.

yanornithids which have a relatively shorter preantorbital ramus of the maxilla (e.g., *Similiyanornis*, Wang M. et al., 2020). This peculiar elongation of the maxillary participation to the rostrum closely recalls some "Gansus-like" euornithines (e.g., *Changzuiornis*, *Iteravis*; Huang et al., 2016; Ju et al., 2021), and differs from the extant birds which display a marked reduction of the whole maxilla and have acquired a more relevant participation of the premaxilla in the rostrum (Huang et al., 2016). Three conical teeth can be observed at the rostral end of the right maxilla. The nasal is forked rostrally and tapered caudally. The frontals are preserved separately, which indicates that they are not fused together, as in other early-diverging euornithines. The rostral half of the right frontal is rectangular and contacts the distal end of the right nasal. The ventral margin of the frontal is domed due to the expansion of the caudal half. The lacrimal is overlain by the nasal and scleral bones, with only the descending ramus exposed. The jugal is rod-like and tapered distally. The hyoid is also rod-like and moderately robust, similar to *Changzuiornis* (Huang et al., 2016). The quadrate is strut-like. No predentary is preserved. Yet, the rostral end of the dentary is blunt and shows a large lateral pit, a combination of features compatible with the predentary facet observed in many euornithines (Zhou and Martin, 2011). The dentary is extremely long and about 60 % the skull length, with a relatively wide and deep Meckel's groove at the middle portion. The dorsal and ventral margins of the dentary are subparallel for most of the rostral portion, and slightly curved caudoventrally. The rostral end of the right dentary possesses three conical teeth, which are similar in size and morphology to the premaxillary teeth, differing from the hypertrophied first dentary tooth diagnostic of *Similiyanornis* (Wang M. et al., 2020). Seven spaced teeth are preserved in the middle portion of the left dentary, much less numerous than the approximately 20 densely placed teeth in *Yanornis* (Wang M. et al., 2020). The angular is strap-like and preserved between the dentary and surangular.

Eleven cervical vertebrae are completely preserved in ventral view, including the atlas and axis (Fig. 5). As in the *Yixianornis*, *Yanornis*, *Piscivoravis* and *Abitusavis*, for the fifth to ninth cervical vertebrae, the centrum is more than 2 times longer than

mediolaterally wide (Clarke et al., 2006; Zhou S. et al., 2014; Wang M. et al., 2020). Like *Similiyanornis*, the craniolaterally projected prezygapophyses are much longer than the laterally projected postzygapophyses in the middle elongated cervical vertebrae, opposite to the condition in *Yanornis* and *Abitusavis* (Wang M. et al., 2020). Only three articulated thoracic vertebrae are exposed in dorsal view, which are rectangular craniocaudally. As in many euornithines, including *Yanornis*, *Piscivoravis* and *Similiyanornis*, the lateral surface of the thoracic centra are excavated by a large elliptical fossa in the middle (Zhou S. et al., 2014; Wang M. et al., 2020). The syncsacrum is completely fused and composed of 9 vertebrae, and is approximately 63 % of the femoral length. A prominent ventral groove can be observed in the middle portion as in *Abitusavis* and *Yanornis*. The cranial end of the syncsacrum is expanded laterally and forms a flat articular facet (Fig. 6).

The furcula is "U" shaped without a hypocleidium, as in most Mesozoic euornithine birds (Fig. 7), and lacks the flattened sternal margin seen in *Songlingornis* and *Yixianornis* (Hou, 1997; Clarke et al., 2006; Zhou S. et al., 2014). The two clavicular rami slightly taper towards the omal ends, as in *Yanornis*. Both strut-shaped coracoids are preserved in ventral view, with the craniocaudal length about 1.7 times the straight sternal margin (Fig. 7), similar to that of *Yanornis*, *Yixianornis*, *Similiyanornis* and *Abitusavis*, but less elongate than that of *Piscivoravis* (Zhou S. et al., 2014; Wang M. et al., 2020). The procoracoid process is trapezoidal, different from the rectangular process in *Ambiortus*, *Yixianornis*, *Yanornis* and *Abitusavis*, or from the triangular process in *Similiyanornis* (O'Connor and Zelenkov, 2013; Wang M. et al., 2020). Furthermore, the procoracoid process projects medially and does not expand craniocaudally, differing from the craniomedially-projected processes in *Yanornis* and *Abitusavis*, or that medially tapered one in *Similiyanornis*. The acrocoracoid process is slightly expanded cranially. The sternolateral process is rectangular, and lacks the cranial hook present in *Gansus* (Ju et al., 2021). Both scapulae are partly overlapped by other bones, but the scapular shaft is long and curved based on the exposed portion. The rectangular sternum is ventrally exposed, with the middle portion partly overlain by the right manus (Fig. 8). The cranial margin of the sternum is



Fig. 5. Cervical vertebrae of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Abbreviations: pr, prezygapophyses; po, postzygapophyses; 1–11, the first to eleventh cervical vertebra. Scale bar = 1 cm.



Fig. 6. Synsacrum and pelvic girdle of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Abbreviations: gr, groove of synsacrum; is, ischium; lilm, left ilium; poa, postacetabular process of ilium; pra, preacetabular process of ilium; pub, pubis; rilm, right ilium; syn, synsacrum; 1-9, the first to ninth sacral of synsacrum. Scale bar = 1 cm.



Fig. 8. Sternum of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Abbreviations: clp, craniolateral process; imt, intermediate trabecula; lt, lateral trabecula; zp, zyphoid process. Scale bar = 1 cm.

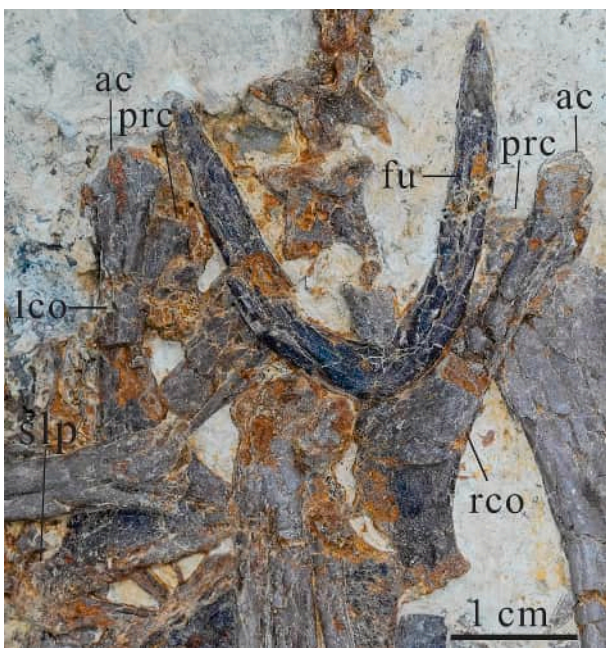


Fig. 7. Furcula and coracoids of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Abbreviations: ac, acrocoracoid process of coracoid; fu, furcula; lco, left coracoid; prc, procoracoid process of coracoid; rco, right coracoid; slp, sternolateral process of coracoid. Scale bar = 1 cm.

parabolic. The craniolateral process is not as pointed as that in *Yanornis* and *Similiyanornis* (Wang M. et al., 2020). The zyphoid process is similar to those in *Yanornis*, *Similiyanornis* and *Abitusavis*. The lateral trabecula is parallel to the long axis of the sternal plate and its distal end expands more medially than laterally. The intermediate trabecula projects distally and does not curve medially neither fuse with the xiphoidal process: accordingly, the sternum is caudally notched but lacks the pair of fenestrae present in *Yanornis* and some other euornithines (Clarke et al., 2006; Wang M. et al., 2020). The distal end of the xiphoidal process is underlain by the right metacarpals, preventing the observation of detailed length and morphology.

The forelimbs are nearly completely preserved with the intermembral index (humerus + ulna)/(femur + tibiotarsus) of 1.12, same as that of *Similiyanornis* but less than that of *Yanornis* (1.27) and *Abitusavis* (1.20) (Wang M. et al., 2020). The humerus bears a large deltopectoral crest that reaches approximately half the humeral shaft length. A prominent supracondylar process protrudes proximolaterally from the lateral condyle, as in *Archaeornithura*, *hongshanornithids*, *Ichthyornis*, *Abitusavis* and *Yanornis* (Wang M. et al., 2020). The ulna is subequal to the humerus in length and slightly longer than the radius. Three carpals can be observed in the left manus, which are not fused with the metacarpals (Fig. 9). The pisiform is separately preserved, with a deeply concave articular facet. The scapholunare is laterally articulated with the proximal end of the minor metacarpal. The semilunate carpal covers the proximal ends of the major and minor metacarpals. The alular digit terminates at the distal end of the major metacarpal as in *Yanornis* and *Similiyanornis*, shorter than in *Jianchangornis* and *Piscivoravis* (Zhou Z-H et al., 2009; Zhou S. et al., 2014; Wang M. et al., 2020). The ungual phalanx of the alular digit is larger than

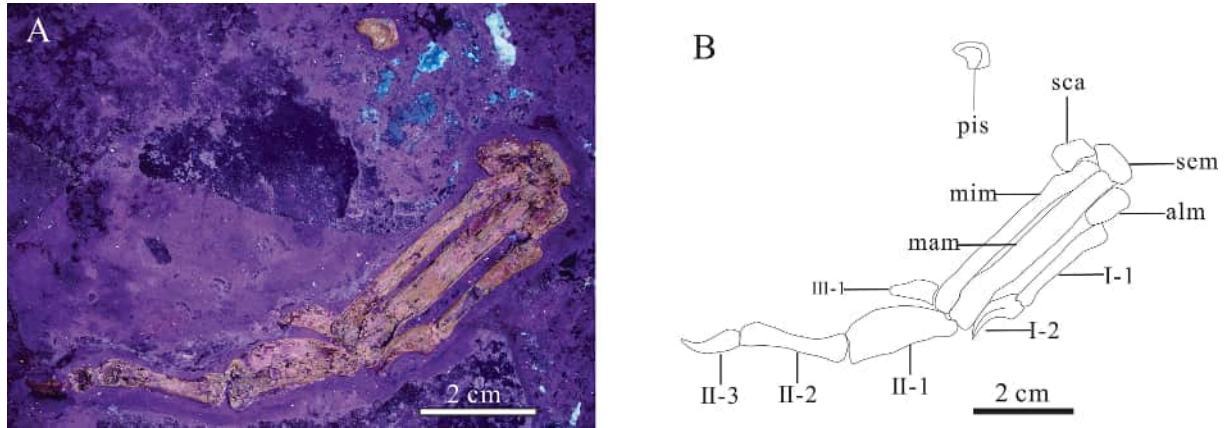


Fig. 9. Photo under UV light (A) and line drawing (B) of left manus of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Abbreviations: alm, alular metacarpal; mam, major metacarpal; mim, minor metacarpal; pis, pisiform; sca, scapholunare; sem, semilunate carpal; I-1, 2, manual digit I-1, 2; II-1, 2, 3, manual digit II-1, 2, 3; III-1, manual digit III-1. Scale bar = 2 cm.

that of the major digit (Fig. 9), a common feature among the Mesozoic birds (O'Connor et al., 2011). As in *Yixianornis* and *Piscivoravis*, the unguis phalanx of the alular digit possesses a semi-circular flexor process, different from the step-like projection without a flexor process seen in *Yanornis* and *Similiyanornis* (Wang M. et al., 2020). The major metacarpal and minor metacarpal are subequal in length and not fused with the alular metacarpal proximally. Compared to the major metacarpal, the first phalanx of the major digit is intermediate in elongation between *Yanornis* and *Similiyanornis* (i.e. 59 %, compared to, respectively, 48 % and 67 % in the other taxa) and expands ventrally. The second phalanx of the major digit is shorter than the first phalanges of both alular and major digits. The minor digit includes only one small phalanx that tapers distally.

The right pelvic girdle is relatively well preserved and the pelvic elements are all completely fused together based on the exposed right pelvic girdle, and form a round enclosed acetabulum (Fig. 6). The preacetabular process of the ilium is partly overlain by the right tibiotarsus, but the ventral margin is exposed and straight. The postacetabular process is subequal to the preacetabular process in length and also bears a straight ventral margin. The ventral margin of the ilium is convex in *Yanornis*, *Yixianornis*, *Piscivoravis* and *Similiyanornis* (Clarke et al., 2006; Zhou S. et al., 2014; Wang M. et al., 2020). The dorsal margin of

the ilium is flat in the middle portion and slightly declined caudoventrally. The ischium is incompletely preserved, with the distal portion broken. The pubis is long and slightly curved distally, different from the strongly curved condition in *Abitusavis*. The distal ends of the pubes are gradually expanded distally forming a gently spatulate end but do not form a symphysis as in *Abitusavis* and other early-diverging euornithines.

The femur is relatively long, with a femur/tibiotarsus length ratio of 0.74, greater than in *Yanornis* (0.68), less than in *Piscivoravis* (0.79) and *Similiyanornis* (0.85) (Wang M. et al., 2020). The fibula seems to extend almost to the distal end of the tibiotarsus, different from the more reduced shaft in many other euornithines. The tarsometatarsus is completely fused (Fig. 10). Metatarsal III is the longest. Metatarsal IV is slightly longer than Metatarsal II. The pedal digits are not articulated, preventing direct comparisons. The preserved pedal unguis phalanges are similar in size and morphology, which taper distally but are not as curved as the manual unguis phalanges.

A cluster of disarticulated and fragile fish vertebrae and ribs can be recognized in the abdominal cavity (Figs. 11A–B). The fish bones were preserved within an oval cluster, consistent with a stomach content (O'Connor et al., 2015). Furthermore, the fish ribs have smooth surfaces but no sharp ends, indicating they were digested and macerated in the stomach.

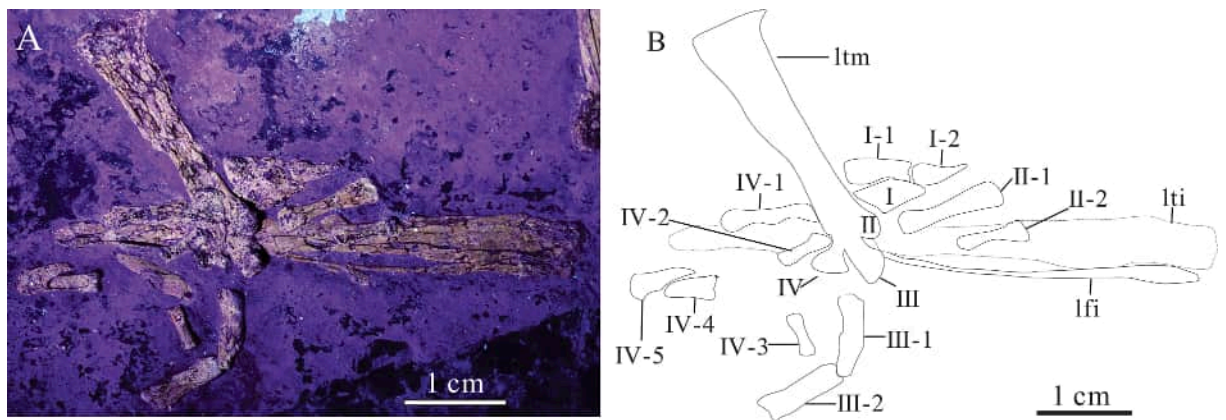


Fig. 10. Photo under UV light (A) and line drawing (B) of left foot of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Abbreviations: lfi, left fibula; lti, left tibiotarsus; ltm, left tibiotarsus; I, II, III, IV, metatarsal I, II, III, IV; I-1, 2, pedal digit I-1, 2; II-1, 2, pedal digit II-1, 2; III-1, 2, pedal digit III-1, 2; IV-1, 2, 3, 4, 5, pedal digit IV-1, 2, 3, 4, 5. Scale bar = 1 cm.

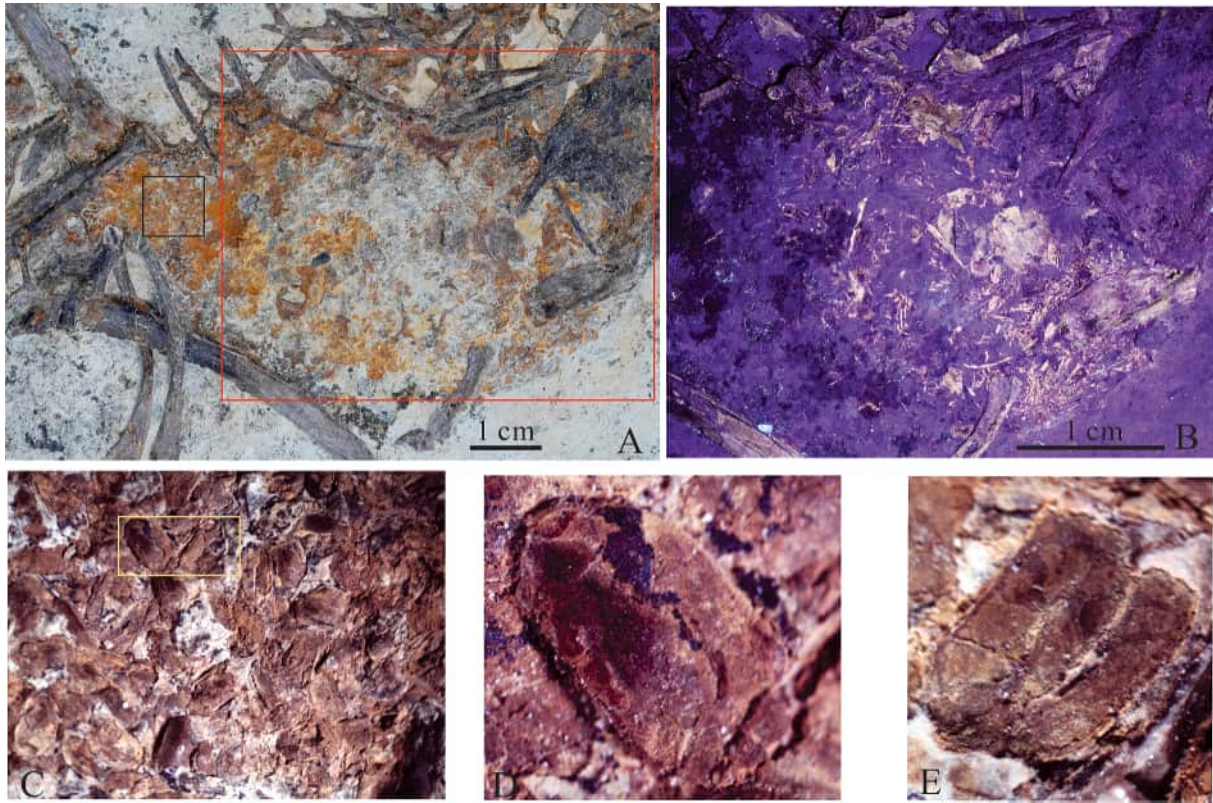


Fig. 11. Photo of the abdomen under normal light (A), the detailed macerated fish bones in the red box under UV light (B), the detailed ostracods in the black box (C), and the separate ostracods in the yellow box (D, E) of *Kunpengornis anhuimusei* gen. et sp. nov. (AGB 15483). Scale bar = 1 cm.

Lots of ostracods were preserved in the abdominal area (Fig. 11C) and also in the fossil-bearing rocks. Based on the morphologies of the well preserved ostracods, *Limnocypridea* is the dominant genus (Figs. 11D-E) (Wang Y-Q. et al., 2016).

4. Results

The phylogenetic analysis found 10,000 shortest trees of 2754 steps each (Consistency Index excluding uninformative characters = 0.2485, Retention Index = 0.5169). The strict consensus of the shortest trees found after the *a posteriori* pruning of 21 "wilcard" OTUs (i.e., CAGS-IG 04-CM-023, *Dapingfangornis*, *Dunhuangia*, *Enantiophoenix*, *Enantiornis*, *Eoalulavis*, *Eocathayornis*, *Eoenantiornis*, *Fortunguavis*, *Fumicollis*, *Gargantuavis*, "cf. *Gargantuavis*" UBB V649, *Halimornis*, *Houornis*, *Iaceornis*, *Jiuquanornis*, *Mirarce*, *Paraprotopteryx*, *Pterygornis*, *Vorona*, and *Yungavolucris*) is well-resolved (Fig. 12). A noteworthy result of the analysis is the placement of *Baminornis* in all shortest trees found as sister-taxon of "Jeholornithiformes + Pygostylia", a placement also obtained by the independently-developed data set used by Chen et al. (2025). Since in our analysis *Baminornis* was conservatively coded as "unknown" about the states of the pygostyle characters, this result suggests that the affinities of that taxon among early-diverging avialans are not significantly biased by the interpretation of the "fused vertebrae" as a pygostyle vs a sacral series. In all shortest trees found, *Kunpengornis* is placed as sister taxon of *Piscivoravis*, and closer to the "gansuid-ornithur-omorph" clade than Yanornithidae or any other "Yanornis-like" euornithine. The yanornithids and the "Yanornis-like" forms (like *Yixianornis*) resulted a speciose grade placed more crown-ward than the hongshanornithids. Two features unambiguously support the sister taxon relationship between *Kunpengornis* and

Piscivoravis: the proportionally broad and short sternum, less elongate than in the majority of late-diverging euornithines (where it is usually longer than 150 % its maximum width), and the presence of a ventrally curved alular ungual. The sister taxon relationship between *Kunpengornis*-*Piscivoravis* clade and more crown-ward euornithines with the exclusion of the other "Yanornis-like" taxa is supported by the rostral ramus of maxilla longer than the premaxillary oral margin, the maxillary teeth widely spaced, and the intermediate trabeculae of the sternum not enclosing a caudal fenestra (homoplastic among some gansuid-like forms). Yet, *Kunpengornis* retains several "Yanornis-grade" features and is excluded from the "gansuid-ornithur-omorph" group because it retains a proportionally shorter subnarial ramus of the nasal, an open interfrontal suture, a distinct labial groove of a dentary, the premaxillary teeth, an extensively developed deltopectoral crest, the pollex which reaches the level of the distal end of the major metacarpal, a shallow acuminate postacetabular process, and a smaller tibiotarsus-to-femur ratio.

5. Discussion

The completely fused pelvic elements and tarsometatarsus combined with unfused metacarpals indicate that the holotype of *Kunpengornis* gen. nov. probably represents a subadult stage of somatic development at the time of death (O'Connor et al., 2015; Wang and Zhou, 2016; Wang M. et al., 2017). *Kunpengornis* gen. nov. possesses several typical euornithine synapomorphies, such as the "U"-shaped furcula, craniocaudally elongate sternum, metacarpal II and metacarpal III subequal in length, a robust and craniocaudally expanded first phalanx in the second manual digit, a reduced third finger, and a completely fused tarsometatarsus. *Kunpengornis* gen. nov. differs from all other Cretaceous

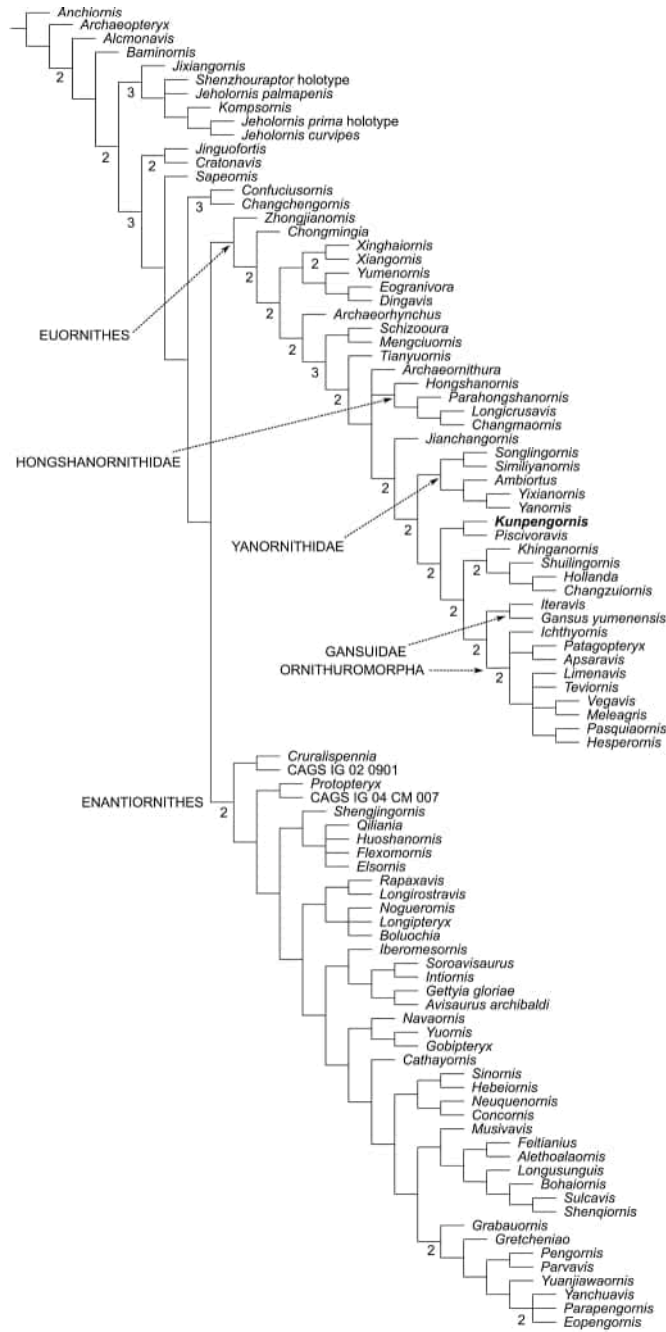


Fig. 12. Reduced strict consensus of the shortest trees found by the phylogenetic analysis, after the *a posteriori* pruning of 21 "wildcard" OTUs (listed in main text). Values at nodes indicate the Bremer Support >1 calculated in TNT from 131,417,986 sampled trees up to tensteps longer than the most parsimonious topologies.

euornithine birds in the coracoid having a trapezoidal procoracoid process not expanded craniocaudally at its medial margin, and in the spatulate shape of the pubis which gradually expands distally. The phylogenetic analysis supports *Kungpengornis* gen. nov. within a grade of euornithines more crown-ward than the hongshanornithids but less crown-ward than the "Gansus-like" forms (e.g., Wang X-R et al., 2020, 2025). This result is consistent with several previous phylogenetic analyses, which reconstructed most of the mentioned taxa in a "yanornithid/songlingornithid" cluster of Euornithes (Clarke et al., 2006; O'Connor and Zhou., 2013; Zhou S. et al., 2014; Wang M. et al., 2019, 2020; Wang X-R et al., 2020,

2025). Yet, our analysis does not support the placement of all these taxa, including *Kungpengornis*, among Yanornithidae (sensu Wang M. et al., 2020), a result which suggests that part of the "Yanornis-like" features are widespread euornithine homoplasies or symplesiomorphies of the larger euornithine clade excluding the earliest-diverging forms and the hongshanornithids. In particular, *Kungpengornis* is recovered as sister taxon of *Piscivoravis*; yet, this node is currently supported by only two homoplastic features, the reversals to conditions lost among the majority of late-diverging euornithines (sternum broad and relatively short, and curved alular unguis), and should be considered as tentative. The currently known record of the Yanornis-like grade including *Kungpengornis* is distributed from the Hauteriverian-Barremian Andaikhudag Formation of the Central Mongolian Altai (*Ambior-tus*), the Aptian Yixian Formation of western Liaoning and neighboring Inner Mongolia of China (*Abitusavis*), to the very rich diversity of the Aptian Jiufotang Formation in western Liaoning (*Jianchangornis*, *Kungpengornis*, *Piscivoravis*, *Similiyanornis*, *Songlingornis*, *Yanornis*, *Yixianornis*, see Hou, 1997; Clarke et al., 2006; O'Connor, 2019; Zhou S. et al., 2014; Wang et al., 2020a). It is noteworthy that the stratigraphic range of this grade broadly overlaps with that of the "Gansus-like" forms, the other Jehol Biota euornithine grade with a potentially aquatic ecology (Wang X-R et al., 2025).

A cluster of macerated fish bones preserved in the abdomen of *Kungpengornis* gen. nov. provides direct evidence of a piscivorous diet. After *Yanornis*, *Abitusavis* and *Piscivoravis*, this is the fourth direct documentation of a non-ornithurine euornithine bird eating fish (Zhou Z-H et al., 2014; Zhou S. et al., 2014; Zheng et al., 2018). Zhou Z-H et al. (2009) reported fish remains preserved near the left femur and tibiotarsus of the holotype of *Jianchangornis* (another member of the "Yanornis-like" grade in our phylogenetic result), and suggested that this bird probably was piscivorous. O'Connor (2019) suggested that the holotype of *Jianchangornis* could be chimaerical, and questioned the interpretation of piscivory in the latter taxon. Although the dentition of the yanornithids and of *Jianchangornis* has been considered adapted to a piscivorous diet (Zhou Z-H et al., 2009; Zheng et al., 2014), it is controversial how accurately the tooth morphology in Cretaceous birds is strictly related with their diet (e.g., Zhou et al., 2021; Wu Y. et al., 2023; Miller et al., 2024; O'Connor et al., 2024). In the absence of gut contents the trophic condition of a taxon should be considered as tentative.

The ostracods preserved in the abdominal area and fossil-bearing rocks indicate they were not digested but deposited concurrently with other fossils and rocks. *Limnocypridea* is an extinct ostracod genus and mainly distributed in the Jiufotang Formation in western Liaoning (Wang Y-Q, 2012; Wang Y-Q et al., 2015). Furthermore, *Limnocypridea* mainly lived in fresh water lake environments (Wang Y-Q, 2012). Therefore, the ostracods provide more solid evidence that *Kungpengornis* gen. nov. was uncovered from the Jiufotang Formation and deposited in lacustrine conditions).

The direct evidence of a piscivorous diet among at least four members of the "Yanornis-like" grade (pending a revision of *Jianchangornis*) is thus a strong support to the hypothesis that the trophic exploitation of the aquatic environments drove the diversification of that part of the euornithine radiation. *Kungpengornis* gen. nov. is comparable to *Yanornis*, *Jianchangornis*, *Piscivoravis*, *Similiyanornis* and *Abitusavis* in body size, and larger than *Ambior-tus*, *Songlingornis* and *Yixianornis* (Table 2). It is noteworthy that gut contents are so far known only among the largest species of the "Yanornis-like" grade, all from the Jiufotang Formation. The lack of direct evidence of piscivory among the smallest species of this grade is puzzling: it may indicate a genuine ecological signal linking

Table 2

Selected measurements of the genera closely related to *Kunpengornis anhuimusei* gen. et sp. nov. (AGB15483).# indicates preserved length;/indicates missing data.

Element length (mm)	<i>Kunpengornis</i> (AGB15483)	<i>Songlingornis</i> (IVPP V10913)	<i>Yixianornis</i> (IVPP V12558)	<i>Jianchangornis</i> (IVPP V16708)	<i>Yanornis</i> (IVPP V12558)	<i>Piscivoravis</i> (IVPP V17.78)	<i>Similiyanornis</i> (IVPP V13278)	<i>Abitusavis</i> (IVPP V14606)
Humerus	82.93	/	49.3	76	85.31	74	66.23	75.19
Ulna	83.39	28#	50.3	83	90.32	77	67.94	76.56
Radius	79.15	21	48	81	85.97	75	65.38	72.22
Femur	58.25	11#	42	60	55.77	56	54.97	54.76
Tibiotarsus	76.60	/	52.8	76	82.42	71	64.36	71.44
Tarsometatarsus	40.53	/	27	37	37.87	35	34.37	37.28

body size and diet in these birds, or may instead be a preservation artifact negatively impacting the palaeoecological record among the small-bodied taxa. In the latter case, any future inference about the distribution of piscivory among the Mesozoic birds should incorporate information about the body size and the original depositional setting of the discussed specimens.

6. Conclusion

In this paper, we describe and erect a new genus and species of euornithine bird, *Kunpengornis anhuimusei* gen. et sp. nov., from the Lower Cretaceous (Aptian) Jehol Biota of western Liaoning, China. *Kunpengornis* gen. nov. is the fourth direct documentation of a Mesozoic euornithine bird eating fish. The completely fused pelvic elements, tarsometatarsus and unfused metacarpals indicate that the holotype of *Kunpengornis* gen. nov. probably had reached the subadult stage of somatic development at the time of death. Phylogenetically, *Kunpengornis* gen. nov. is nested among a speciose radiation of non-ornithuromorph euornithines, which also includes the genera *Abitusavis*, *Ambiortus*, *Jianchangornis*, *Piscivoravis*, *Similiyanornis*, *Songlingornis*, *Yanornis*, and *Yixianornis*. So far, all direct evidence of piscivory among Early Cretaceous euornithines is restricted to this grade, revealing the first radiation of piscivorous birds in the Early Cretaceous, at least twenty million years before the immediate ancestors of the modern birds (Ornithurae).

CRediT authorship contribution statement

Jiandong Huang: Writing – original draft, Supervision, Resources, Investigation, Conceptualization. **Xuri Wang:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Andrea Cau:** Writing – original draft, Software, Methodology, Investigation, Conceptualization. **Lei Mao:** Visualization, Investigation. **Yichuan Liu:** Visualization, Investigation, Formal analysis, Conceptualization. **Yang Wang:** Validation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2025.106244>.