

Articles

Cite this article: Clark A., Wang Y., Wang X., Zhang X., Wang X., Zheng X., Zhou Z., and O'Connor J. 2026. The plumage of *Longipteryx* (Aves: Enantiornithes). *Journal of Paleontology*, 1–9
<https://doi.org/10.1017/jpa.2026.10282>

Received: 03 March 2026 UTC

Revised: 21 July 2026 UTC

Accepted: 27 July 2026 UTC

Corresponding authors:

Alexander Clark and Yan Wang;

Emails: adclark@uchicago.edu;

wangyan6696@lyu.edu.cn

Handling Editor:

Daniel Ksepka

The plumage of *Longipteryx* (Aves: Enantiornithes)

Alexander Clark^{1,2} , Yan Wang³, Xiaoli Wang³, Xiangyu Zhang³, Xing Wang⁴, Xiaoting Zheng³, Zhonghe Zhou⁵ and Jingmai O'Connor²

¹Committee on Evolutionary Biology, University of Chicago, Chicago, IL, USA

²Negaunee Integrative Resource Center, Field Museum of Natural History, Chicago, Illinois, USA

³Linyi University, Linyi, China

⁴Institution of Geology and Paleontology, Linyi University, Linyi, China

⁵Institute of Vertebrate Paleontology and Paleoanthropology Chinese Academy of Sciences, Beijing, China

Abstract

The 121 Ma Jiufotang Formation in northeastern China contains the greatest avifaunal diversity of any known Mesozoic deposit. Enantiornithine birds dominate this formation with hundreds of exceptionally preserved specimens often bearing soft tissues such as feather traces. Of the described enantiornithines from these deposits, *Longipteryx* is the most abundant, easily identified by its elongate rostrum and distally restricted, proportionally large teeth. Although numerous specimens of this taxon have been described, data concerning its plumage is surprisingly lacking. Here, we qualitatively describe two new *Longipteryx chaoyangensis* specimens preserving feathers across the body, including the best evidence of wing feather (remex) morphology thus far for this taxon. The folded wing of *Longipteryx* has a predominantly linear trailing margin and primary feathers nearly twice the length of the secondaries. Based on remex lengths and the preserved position of the forelimbs, the outstretched wings of *Longipteryx* may have been intermediate (i.e., a wing profile between the broad morphology inferred for some enantiornithines and the elongate shape reconstructed for *Confuciusornis*), superficially resembling extant bird species whose wing profiles are associated with bounding, continuous-flapping, and flap-gliding flight. These flight strategies have been previously predicted for some enantiornithines based also on remex and skeletal morphometrics. Additionally, all known *Longipteryx* specimens lack traces or impressions of tail feathers (rectrices) altogether. Most enantiornithines with preserved rectrices have a pair of elongate ornamental feathers. It is thus unusual and notable that these appear to be absent in both sexes in *Longipteryx*.

Non-technical Summary

Of all Early Cretaceous enantiornithine birds (Aves: Ornithothoraces), *Longipteryx chaoyangensis*, from the 121-million-year-old Jiufotang Formation in northeastern China, has the greatest number of specimens attributable to it. *Longipteryx* is easily characterized by an elongate rostrum and rostrally restricted large dentition. Although numerous specimens of *Longipteryx* are present in collections, descriptions of soft tissue traces such as body and wing (remex) plumage, are largely absent in the literature. Here we describe two new specimens of *Longipteryx* with the best-preserved body and wing plumage thus far, revealing a wing profile likely more narrow than other enantiornithines with remex traces. Additionally, all *Longipteryx* specimens completely lack ornamental tail feathers despite preservation of other soft tissues. Given the number of described specimens with preserved soft tissues and yet no tail feathers, it is likely this taxon lacked them all together, regardless of sex.

Introduction

The Cretaceous enantiornithines were the most diverse group of Mesozoic birds (Chiappe and Witmer, 2002; O'Connor and Chiappe, 2011). The greatest portion of this known diversity comes from Lower Cretaceous deposits in northeastern China (ca. 121–131 Ma), which collectively yield the Jehol Biota, representing the cumulative organisms found across the Huajiyi, Yixian, and Jiufotang formations (Zhou and Wang, 2010, 2024; Pan et al., 2013). These volcanolacustrine deposits preserve numerous organisms, often with soft tissues, including non-avian dinosaurs, birds, squamates, and pterosaurs (Zhou and Wang, 2010). Of these organisms, enantiornithines are among the most numerous terrestrial vertebrates collected in these deposits (Zhou and Wang, 2010).

The exceptional preservation that characterizes fossils from these deposits provides insight into enantiornithine ontogeny (Chiappe et al., 2007; O'Connor et al., 2020; O'Connor, 2022) and diet (O'Connor et al., 2024), and allows direct observation of soft tissues (e.g., feathers, skin,

© The Author(s), 2026. Published by Cambridge University Press on behalf of Paleontological Society. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

JOURNAL OF
PALEONTOLOGY
A PUBLICATION OF THE
PALEONTOLOGICAL SOCIETY



CAMBRIDGE
UNIVERSITY PRESS



muscle traces) (O'Connor et al., 2012; Wang et al., 2021). Of these preserved soft tissues, feathers are the most common (O'Connor et al., 2012; Wang et al., 2021). Along with open pennaceous contour feathers, confuciusornithiforms and some enantiornithines preserve a pair of elongate, ornamental tail feathers with proportionally wide rachises (O'Connor et al., 2012; Hu et al., 2015; Wang et al., 2021). Based on their variable presence in individuals of the same species and their non-aerodynamic morphology, these rachis-dominated feathers (RDFs) are often considered sexually dimorphic, suggesting sexually selected pressures acted on enantiornithine plumage as early as 131 Ma (O'Connor et al., 2012; Wang et al., 2021). Although the number of enantiornithine specimens preserving body and tail feathers continues to increase, those preserving remiges that allow for morphological description (e.g., *Protopteryx*, *Eopengornis*) are comparatively uncommon (Wang et al., 2014; O'Connor et al., 2020). The paucity of specimens preserving remiges compared to contour feathers is unusual and may suggest taphonomic loss of these feathers during the early stages of post-mortem tissue breakdown.

Longipteryx is one of few Jehol avifauna taxa for which numerous specimens have been described (Zhang et al., 2001; Wang et al., 2015; O'Connor et al., 2024). This taxon is easily identified by its distinct elongate rostrum (~60% of the skull's length) and proportionally large, distally restricted dentition (Li et al., 2020; O'Connor et al., 2024). *Longipteryx* belongs to a diverse clade of enantiornithines known as the Longipterygidae, currently comprised of six taxa: *Longipteryx chaoyangensis* Zhang et al., 2001, *Chromeornis funkyi* O'Connor et al., 2025, *Boluochia zhengi* Zhou, 1995 (O'Connor et al., 2011), *Longirostravis hani* Hou et al., 2004, *Rapaxavis pani* Morschhauser et al., 2009, and *Shanweiniaio cooperorum* O'Connor et al., 2009. Although *Longipteryx* has been the subject of much previous research including investigations of its diet, dentition, and quadrate morphology (Stidham and O'Connor, 2021; Clark et al., 2023; Wang et al., 2023; O'Connor et al., 2024), the plumage of this taxon has yet to be described or discussed, due in part to the absence of significant soft-tissue preservation in previously described specimens. Here, we qualitatively describe two new *Longipteryx chaoyangensis* specimens that preserve traces of body feathers and remiges. These specimens allow for qualitative description-based interpretations of potential wing shape and suggest rectrices were entirely absent in this taxon.

Methods

Longipteryx specimens STM 8-28 and STM 8-132 (Fig. 1) were collected Jianchang county, Liaoning Province, China, by an amateur fossil collector and donated to the Shandong Tianyu Museum of Nature (Pingyi, China) where they are now housed. These specimens are referable to *Longipteryx* based on: rostral length (~60%); dental arrangement (distally restricted); dental morphology (proportionally large, labiolingually compressed, and recurved); humerus morphology (weakly developed but proximodistally long deltopectoral crest); and metatarsal proportions (metatarsal IV longer than metatarsals III and II) (Zhang et al., 2001). Photos of the fossil were edited in Adobe Photoshop version 24.3.0 to increase contrast, improve clarity, and correct color balance. Anatomical nomenclature primarily follows Baumel et al. (1993) using the English equivalents of the Latin terminology. All measurements used for description and comparisons were taken in ImageJ (Schneider et al., 2012), utilizing the scale measuring tool calibrated to in-photo scales.

Repositories and institutional abbreviations. BMNH – Beijing Museum of Natural History; DNHM – Dalian Natural History Museum; HGM – Henan Geological Museum; PMOL – Paleontological Museum of Liaoning; SG – Shenyang Institute of Geology and Mineral Resources; STM – Shandong Tianyu Museum; IVPP – Institute of Paleontology and Paleoanthropology.

Results

Specimen STM 8-28. The individual is preserved in a single slab in ventral aspect (Fig. 1). Based on humeral length (~33.4 mm), estimated body mass is 75.5–89.1 g, similar in size to extant icterids (e.g., *Sturnella*) (Field et al., 2013). Although much of the skeletal elements are poorly preserved, soft tissue traces are prevalent, surrounding the entire skeleton except for the rostrum and feet. Contour feathers, which are better preserved than the remiges, extend from the rostral margin of the antorbital fenestra to the dorsal and ventral margins of the neck, across the shoulders, around the pectoral girdle and ribcage, underneath each wing radiating outwards from the ulna, down the legs to the distal end of the tibiotarsi, and around the pygostyle. The body contour feathers and remiges can be differentiated based on their lengths and open-pennaceous (body) and closed-pennaceous (wing) morphologies, respectively. The contour feathers are all darkly preserved and range in length from 8–10 mm across the head and neck region, 10–13 mm around the pectoral girdle, and 5–17 mm surrounding the pelvic girdle and pygostyle. The layer of dark-colored underwing feather traces on the right wing are likely contour feathers, based both on their position relative to the remiges and their nonuniform lengths, which measure 12–25 mm. Those extending off the caudal margin of the pygostyle tend to be shorter (~5–8 mm), projecting just beyond the distal tip of the bone.

Both wings are partially folded, although to a lesser degree in the right wing in which the remiges traces are more complete. The right humerus:radius angle measures ~30.6°, and the radius:carpometacarpus angle measures ~58.2°. These same angles on the left wing measure ~27.3° and ~8.9°, respectively. In contrast to the contour feathers, the remex traces are much fainter and not as consistently preserved, with only the mid to distal portions consisting of dark-colored traces. A darker patch of feathers preserved above the right manus with a smooth leading edge is tentatively interpreted as the alula. It projects from the proximocranial surface of the alular metacarpal on the right wing with a preserved length of 25 mm. Of the two major preserved primary remex traces of the right wing, one demarcates the outer margin of the wing with the other more medially positioned. Following the outer trace to its proximal origin suggests this remex (or remiges) may have attached near the distoventral end of the second phalanx of the major digit. This feather is ~98 mm long, from the area of probable articulation to the distal tip of the dark-colored trace. Similarly, the second primary trace, with an estimated length of 94 mm, appears to have attached near the midpoint of the minor metacarpal. However, precise location of articulation is difficult to determine due to poor preservation of the proximal region. The number of primaries cannot be determined due to poor preservation and overlap caused by the folded position of the wing.

The secondary remiges are very faintly preserved. Total length can only be estimated for a single secondary feather that attaches at the proximocaudal surface of the ulna and measures approximately 55 mm (Fig. 1). This feather appears to be symmetrically vaned with a rounded distal margin. The trailing margin of the wing formed by

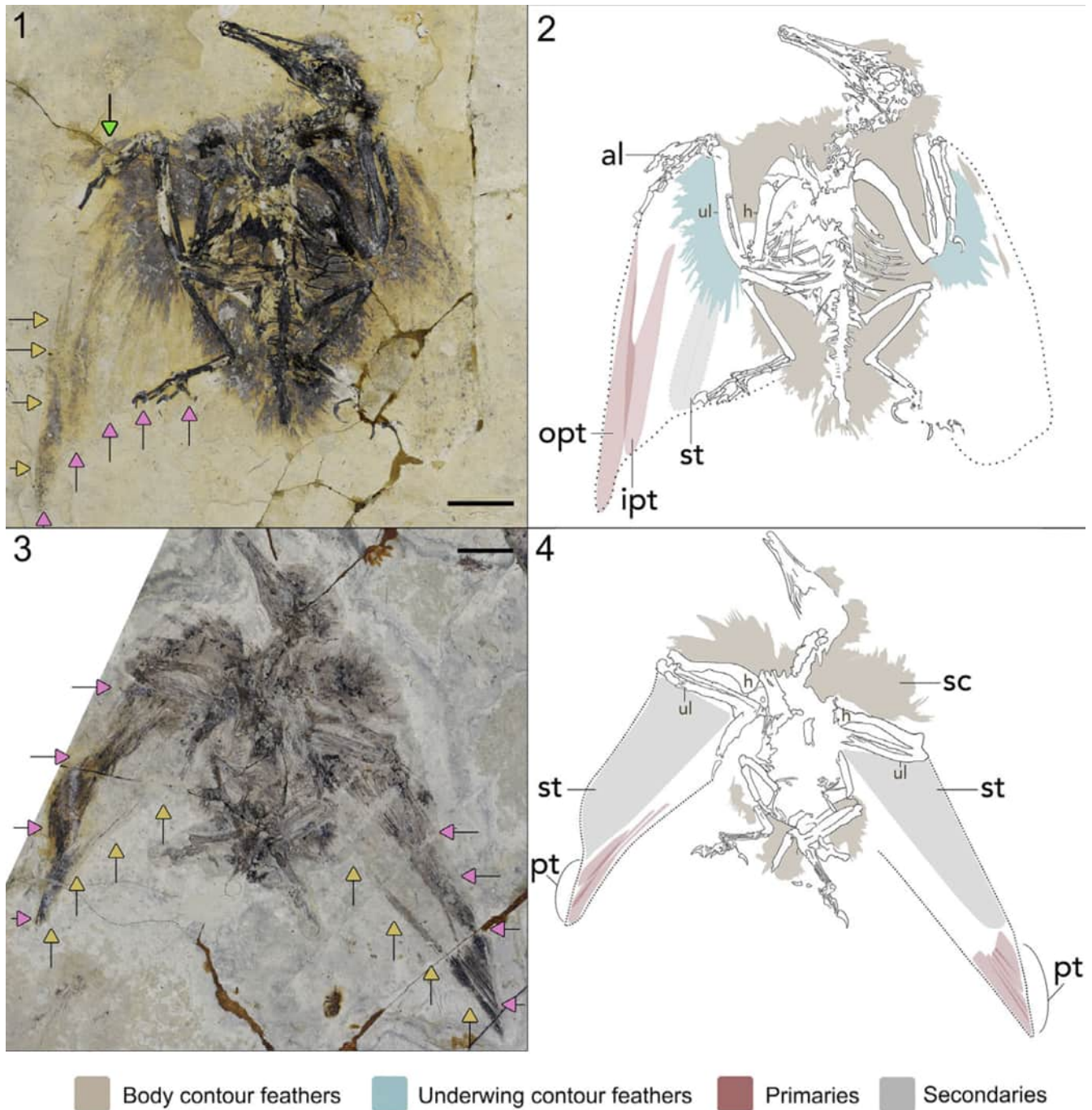


Figure 1. Specimens STM 8-28 (**1, 2**) and STM 8-132 (**3, 4**). Soft tissue traces of the body and contour feathers and are preserved in both specimens, although to a greater degree in STM 8-28. Dotted lines denote the area of preserved remex traces in (**2**) and (**4**). Green arrow, probable alula; yellow arrows, the leading edge of the wings post-wrist joint; pink arrows indicate the trailing edge of the wing. Abbreviations: al = alula; h = humerus; ipt = inner primary trace; opt = outer primary trace; pt = primary trace; sc = potential scapular feathers; st = secondary trace; ul = ulna. Scale bars in (**1, 3**) equal 20 mm.

the secondaries is faint but appears linear. STM 8-28 does not preserve any trace of rectrices.

Specimen STM 8-132. The individual is primarily preserved in a single slab in ventral aspect preserving body contour feather and remex traces (Fig. 1). Based on the humeral length (~33.7 mm), the estimated body mass of the individual is 76.7–90.9 g, which is similar to STM 8-28 (Field et al., 2013). Both forelimbs are preserved in an unusual position, partially folded and rotated cranially,

such that the dorsal aspect of both wings is exposed from the elbow joint. Most of the skeletal elements are either missing or very poorly preserved, being heavily crushed throughout. The body contour feathers begin near the midline of the antorbital fenestra and extend across the neck, torso, upper tibiotarsi, around the pelvic region, and surround the pygostyle. These contour feathers range in length from 8–12 mm across the head and neck region, to 15–18 mm around the pelvic girdle and legs. Those that immediately surround the pygostyle are comparatively shorter (4–8 mm) than the contour

feathers that surround the rest of the body, similar to what is observed in STM 8-28. Two longer (16–26 mm) fan-like tracts of contour feathers extend from the shoulder area and likely represent scapular feathers folded upwards and cranially due to the unusual position on the forelimbs (Fig. 1.4).

As in STM 8-28, the distal portions of the primary feathers consist of dark-colored traces, whereas the proximal portions leave little to no trace. On the right wing, the primary feather traces appear to originate from the caudal surface of the distal portion of the major digit, and measure 85–90 mm from the points of probable articulation to the distal margins of the dark-colored traces. On the left wing, the major digit is not preserved, making estimated length of the discernable primary traces equivocal. However, using the preserved portions of the right manus to estimate remex lengths, those of the left would measure approximately 95–120 mm. This discrepancy suggests the traces of the right wing are distally incomplete. The secondary feathers on both wings are seemingly overlapping and clumped together distally, originating along the caudal margin of the ulna. The shortest secondary feather traces measure 25.7 mm and 28.9 mm on the right and left wings, respectively. The longest secondary feather traces measure 70.3 mm and 71.8 mm on the right and left wings, respectively. Like STM 8-28, STM 8-132 does not preserve any trace or impression of rectrices.

Discussion

Longipteryx is known from 19 specimens—more than any other enantiornithine (Zhang et al., 2001; Li et al., 2010; Wang et al., 2015; Chiappe and Meng, 2016; O'Connor et al., 2024), and many preserve soft tissue structures (Table 1). Although preserved body contour feathers in specimens attributable to *Longipteryx* are relatively common, preserved remiges are quite rare. The two new *Longipteryx* specimens described here provide new information on the plumage of this distinctive Early Cretaceous enantiornithine.

In STM 8-28 and 8-132, both specimens preserve extensive traces of contour feathers which surround most of the body except for the rostrum distal to the caudal margin of the antorbital fenestra and below the ankle joint. These observations are in alignment with observations in *Longipteryx* IVPP V12325 and BMNH Ph930B (Zhang et al., 2001; Chiappe and Meng, 2016). These featherless areas of body are also present in most enantiornithines (Chiappe and Witmer, 2002; Chiappe et al., 2020; Liu et al., 2019, 2022), except for some Late Cretaceous amber-encased taxa, which show feathers extending around the pedal digits (Xing et al., 2019).

Notably, although difference in the maximum estimated body mass between STM 8-28 and STM 8-132 is minimal (~2% difference), the longest measurable preserved primary traces differ by approximately 18%, suggesting either individual or sexually

dimorphic variation in wing chord length. Alternatively, it could suggest differences in preserved completeness (STM 8-132 being more complete) (Table 2). Although feathers are preserved throughout the body in these two *Longipteryx* specimens and others (Table 1), there is a notable absence of rectrices in all described specimens. Therefore, we suggest that this taxon entirely lacked rectrices—both ornamental RDFs, which are more common in other enantiornithines, as well as feathers constituting a rectricial fan (Table 1). Here we discuss the implications of the discernable remex morphology and the significance of the lack of RDFs within the genus *Longipteryx*.

Potential wing profile supports previous hypotheses for enantiornithine flight strategies. Even in the best enantiornithine specimens preserving traces of remiges (e.g., *Protopteryx*, *Eopengornis*), the wings are always folded to some degree, confounding observations of the full wing profile and subsequent inferences regarding flight strategies and ecology (Wang et al., 2014; O'Connor et al., 2020). However, some observable patterns in the remiges of living birds can help elucidate probable enantiornithine wing profile morphology despite these preservational obstacles. Among extant birds, those with proportionally longer primaries compared to their secondaries (~30–40% that of longest primary) have blade-like, high aspect ratio wings characterized by the presence of a distinctive cranially excavated notch along the trailing edge of the wing when folded (Fig. 2.1) (e.g., anatids, falconids, pandionids, lariids) (Lovette et al., 2016). In contrast, when the lengths of the secondaries are subequal to those of the primaries, the wing profile is broad with a low-aspect ratio and, importantly, has a reduced or absent notch when the wing is folded (Fig. 2.2). This pattern is consistent across birds—as the secondary:primary ratio increases, so too does the broadness of the wing profile.

Compared to other enantiornithines preserving remiges, STM 8-28 and STM 8-132 have relative secondary:primary lengths (as percentages) similar to that of *Orienantius*, being approximately 56–59% (Table 2). The same percentages in *Eopengornis* and *Junornis* measure 73% and 87%, respectively, suggesting these two enantiornithines had comparatively broader wing profiles than *Longipteryx* and *Orienantius* (Wang et al., 2014; O'Connor et al., 2020) (Fig. 3). Although folding of the wings in all these enantiornithine specimens hinders observation of the wing profile, there is a clear absence of an inter-remex notch on the trailing edge of the wing, which is particularly clear in *Longipteryx* (Fig. 1). Instead, in STM 8-28, the trailing-edge margin of the secondaries is linear with the wing partially folded. In contrast, the basal pygostylian bird *Confuciusornis*, with its elongate primaries and relatively shorter secondaries, preserves a clear notch between the primary and secondary feather tracts (Falk et al., 2016) (Fig. 3). Reconstruction

Table 1. Comparative remex lengths among enantiornithines—as the ratio between the longest secondary and primary feathers increases, so does the aspect ratio of the outstretched wing

Taxon	Catalog	Source	Humerus	Hum:Prime	Longest primary	Longest secondary	Sec:Prime
<i>Longipteryx</i>	STM 8-28	this publication	33.4	0.3408163	98	55	0.56122449
<i>Longipteryx</i>	STM 8-132	this publication	33.7	0.2808333	120	71.8	0.59833333
<i>Orienantius</i>	BMNH Ph 1154	Chiappe et al., 2019	28.5	0.3294798	86.5	51.1	0.59075145
<i>Protopteryx</i>	BMNH Ph 1158	Liu et al., 2019	30.87	0.3631765	85	59.6	0.70117647
<i>Eopengornis</i>	STM 24-1	Wang et al., 2014	38.8	0.4110169	94.4	68.6	0.72669492
<i>Junornis</i>	BMNH Ph 919a	Liu et al., 2017	25.9	0.352381	73.5	63.6	0.86530612

Table 2. Fossil specimens attributable to *Longipteryx* and the presence or absence of various soft tissues

Specimen	Source	Soft Tissues Present	Remiges	Body Feathers	Rectrices
BMNHC Ph 1071	Chiappe and Meng, 2016	x	x	x	—
BMNHC Ph 826	Chiappe and Meng, 2016	x	x	x	—
BMNHC Ph 930B	Chiappe and Meng, 2016	x	—	x	—
DNHM-D2889	Wang et al., 2015	x	—	x	—
HGM-41HIII0319	Chiappe and Meng, 2016	x	—	x	—
IVPP V12325	Zhang et al., 2001	x	—	x	—
IVPP V12552	personal photo	x	—	x	—
IVPP V16067	personal observation STM	x	—	x	—
IVPP V21702	personal photo	—	—	—	—
PMOL-AB00179	Li et al., 2012 (<i>Shengjingornis</i>)	—	—	—	—
SG2005-B1	Li et al., 2010 (<i>Camptodontus</i>)	—	—	—	—
STM8-112	O'Connor et al., 2024	—	—	—	—
STM8-132	this publication	x	x	x	—
STM8-134	personal observation STM	x	—	x	—
STM8-138	personal observation STM	x	—	x	—
STM8-28	this publication	x	x	x	—
STM8-36	personal observation STM	x	—	x	—
STM8-38	personal observation STM	x	—	x	—
STM8-86	O'Connor et al., 2024	—	—	—	—

of the unfolded wing reveals a high aspect ratio morphology (approximately 1:2.5) unlike any extant neornithine, with the lengths of the secondary feathers being only ~19% that of the primaries (Falk et al., 2016) (Fig. 3.3). Based on the clear absence of a notch between the primaries and secondaries in the folded wings of these enantiornithine taxa (e.g., *Longipteryx*, *Eopengornis*, *Junornis*, *Orienantius*), we suggest they had comparatively broader wings than *Confuciusornis*. Among neornithines, similar wing profiles, in which the inter-remex notch is absent or reduced when the wing is folded, are present among families that primarily utilize continuous or flap-gliding flight styles, such as parulids, fringillids and turdids (del Hoyo et al., 1992, 1999; Lovette et al., 2016). Using predicted wing-loading models, previous findings have suggested that the Early Cretaceous enantiornithines (*Protopteryx*, *Eoalulavis*, *Junornis*, *Concornis*) utilized bounding or flap-gliding flight strategies (Liu et al., 2017; Serrano et al., 2018; Chiappe et al., 2020). Remex feather traces of *Longipteryx* support this interpretation, indicating that gliding or soaring flight strategies were unlikely in this taxon.

Although fossilized soft tissues help elucidate how enantiornithines flew, the underlying skeletal remains must also be considered when interpreting potential flight strategies. Osteological correlates, such as the morphology of the humerus' deltopectoral crest [which anchors some of the primary flight muscles (e.g., mm. *pectoralis major* and *deltoideus major*)] previously have been associated with certain flight strategies among extant birds—and previously have been invoked in support of inferences regarding enantiornithine flight style (Chiappe et al., 2020; Wang et al., 2024). Proximodistally short, but dorsoventrally deep deltopectoral crests (similar to *Confuciusornis*) are typically associated with extant birds that use burst flight or rapid continuous flapping (e.g., alacids,

apodids) (Serrano et al., 2020). In contrast, long, weakly developed deltopectoral crests are often seen in birds with low wing beat frequency flight strategies such as soaring or gliding (e.g., procellariids, cathartids) (Serrano et al., 2020).

Although the potential wing profile of *Longipteryx*, based on proportional remex lengths and pattern of the trailing edge with the wing folded, does not suggest low frequency wing beat strategies (i.e., gliding, soaring), the proximodistally long and cranially shallow deltopectoral crests of their humeri do. Although bounding and intermittent flap-gliding remain plausible energy-efficient flight strategies for enantiornithines, the combination of these traits observed in *Longipteryx* suggests this taxon, and other enantiornithines, may have utilized a flight style unrepresented by modern birds. This is further supported by the unusual semi-lunate morphology of the humeral head, which suggests a more limited range of dorsoventral motion during the flight stroke compared to neornithines, and the caudally restricted and weakly developed sternal keel indicating a relatively reduced m. *pectoralis major* (Baumel et al., 1993). The unique skeletal differences present in the flight apparatus of enantiornithines compared to neornithines suggests direct comparison to crown birds, with regards to locomotor behaviors, may not only result in inaccurate predictions but may also fail to capture the significance of this important radiation for understanding the early evolutionary refinement of avian flight (Lo Coco et al., 2025).

Complete absence of rectrices in an enantiornithine. Enantiornithine rectrices, when present, typically consist of RDFs—an extinct feather morphotype characterized by a proportionally wide rachis with a C-shaped cross-section that contrasts with the hollow tube-like rachis present in extant feathers (O'Connor et al., 2012; Xing

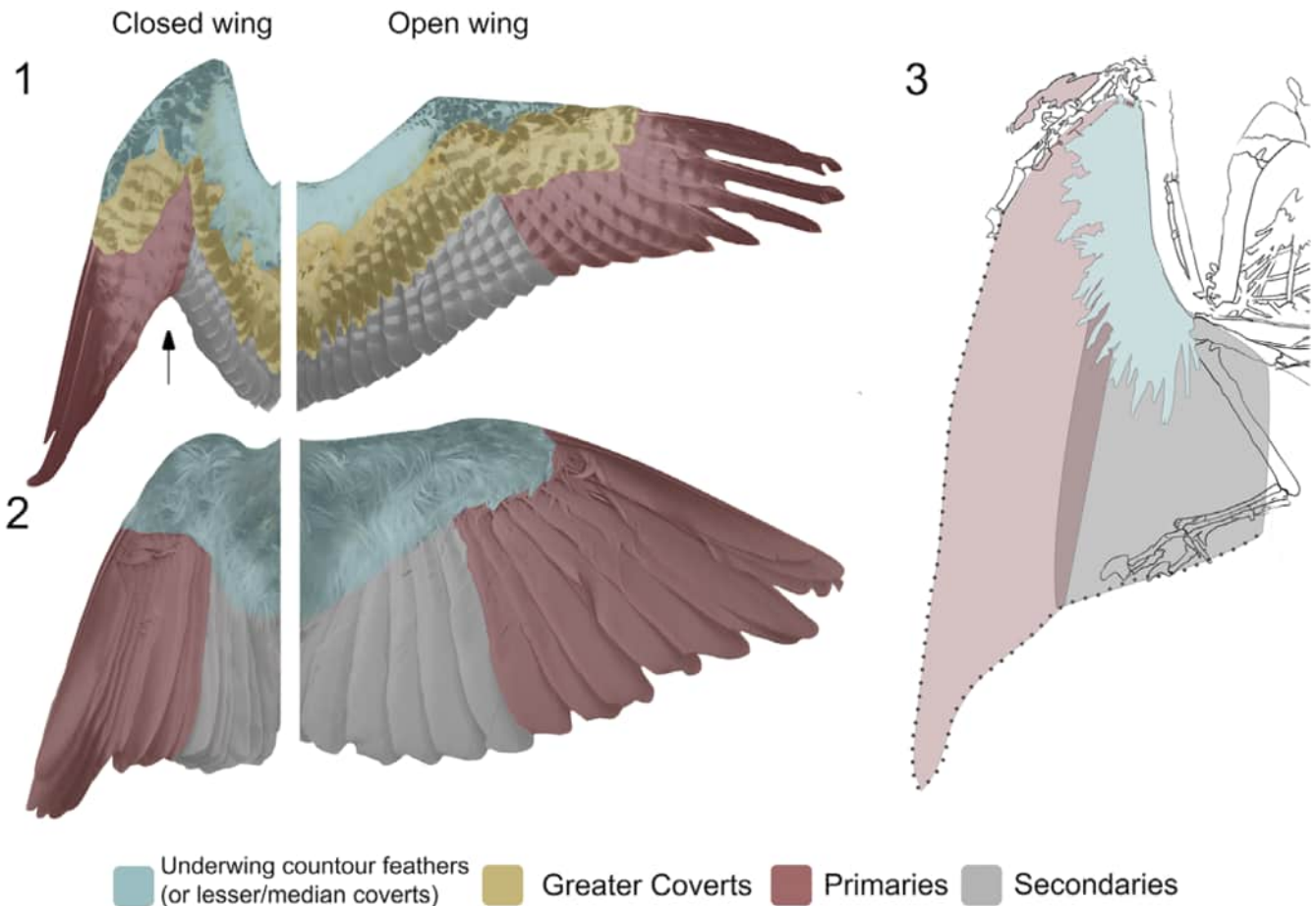


Figure 2. Change in wing profile morphology. Major feather tract regions of the wing in ventral aspect are given colored labels (figure legend). (1) A high aspect wing—*Pandion haliaetus* (Linnaeus, 1758), family Pandionidae—presenting the dorsally excavated notch (indicated by the black arrow) between the primaries and secondaries when the wing is bent. In contrast, (2) low-aspect ratio wings—*Junco hyemalis* (Linnaeus, 1758), family Passerellidae—lack this notch and present primaries subequal in length to the secondaries. (3) The right forelimb and remex traces of STM 8-28 as preserved, with hypothetical positioning, and areas of overlap between the primary and secondary feathers.

et al., 2018; Carroll et al., 2019; Wang et al., 2021). These feathers vary between taxa in terms of proportional length and extent of the pennaceous vane (streamers vs. racket-plumes) and, when the vane is distally restricted, the shape and proportion of the racket. Due to their ornamental (i.e., not forming a lift producing aerodynamic surface) morphology, their variable preservation (e.g., two out of five feather-bearing specimens of *Protopteryx* preserve RDFs), and the presence of analogous structures in some sexually dimorphic extant birds, these feathers are widely considered to be sexually dimorphic and present only in males (O'Connor et al., 2012, 2016; Wang et al., 2021; Clark et al., 2026). RDF racket plumes are also variably present in confuciusornithiforms (e.g., in a sample of 106 *Confuciusornis* specimens preserving soft tissues, 62% have RDFs) and similarly widely interpreted as sexually dimorphic (Chinsamy et al., 2013; Zhou et al., 2024; Zhou and Wang, 2024).

In contrast, multiple soft-tissue-bearing specimens of *Longipteryx* have now been recovered and none preserves evidence of rectrices (Table 2). It should be noted that preserved remiges in *Longipteryx* specimens are also rare, which may suggest potential taphonomic bias for the loss of heavier feathers (e.g., remiges, rectrices) during the early stages of post-mortem tissue breakdown. However, even in instances where remiges and extensive body feathers are preserved, such as in STM 8-28 and 8-132, traces or impressions of tail feathers are unambiguously absent (Table 2;

Figs. 1.1, 3). This strongly suggests that this species was characterized by the complete absence of rectrices, regardless of sex, which is a condition absent among all extant birds (Lucas and Stettenheim, 1972). Female enantiornithines and *Confuciusornis* have been long hypothesized to lack rectrices entirely (pygostyle surrounded by body contour feathers), and the implications on flight this would have had has only been briefly discussed (O'Connor et al., 2016).

Although aerodynamic or maneuver-assisting tail feathers are not essential for flight in neornithines, as evinced from aerial locomotion in individuals that lack tail feathers due to molting (e.g., flight after shock-molt (Møller et al., 2006)), rectrices nevertheless help facilitate navigation, take-off, and changes in speed (Thomas, 1993; Terrill and Shultz, 2023). Although spreading and pivoting of the rectrices aids in steering, some genera (e.g., *Neafrapus*, *Mearnsia*, *Pitta*) demonstrate that sustained and maneuverable flight is still achievable with greatly reduced (shortened), though not absent, rectrices (Winkler et al., 2020, 2024). Movement of the rectrices during flight (e.g., raising, lowering, and fanning) are all facilitated by the underlying rectricial muscles (e.g., mm. levator caudae, depressor caudae, lateralis caudae) (Baumel et al., 1993; Clark et al., 2025). Currently, evidence from both preserved potential rectricial muscles and RDF morphologies, suggest that enantiornithines may have lacked similar levels of rectricial control compared to modern birds, but were likely able to move

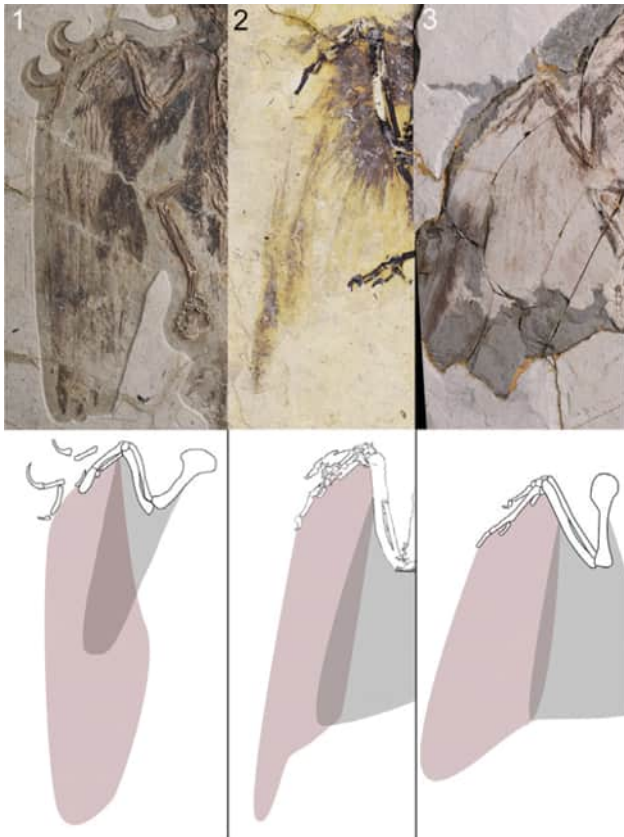


Figure 3. Remex comparisons with other Mesozoic birds. Colors of major feather tract regions of the wing continued from Figure 2. Approximate outlines of the primary and secondary flight feather tracts of (1) *Confuciusornis sanctus* Hou et al., 1995 (IVPP V1315) (photo courtesy of Gao Wei), (2) *Longipteryx chaoyangensis* (STM 8-28), and (3) *Eopen-gornis maratini* Wang et al., 2014 (STM 24-1) (photo courtesy of Xiaoli Wang). Note the varying degrees of differences between the primary and secondary lengths across the three taxa, showing distinct differences from proportionally long primaries (*Confuciusornis*) to primaries and secondaries of similar length (*Eopen-gornis*). These two represent rather high- and low-aspect ratio wing profiles in vivo, respectively, whereas *Longipteryx* may have had a wing profile somewhere in-between.

the tail, and the corresponding RDFs, along a dorsoventral plane (Clark et al., 2026). Therefore, interpretations of *Longipteryx* and other described enantiornithines, suggest they must have utilized fundamentally different methods of approaching and landing on surfaces compared to modern birds. This adds to growing evidence from humeral and sternal morphology that enantiornithines utilized flight strategies not directly analogous those present in any living bird (Zheng et al., 2012; Liu et al., 2017; Chiappe et al., 2020; O'Connor, 2022). However, with the diversity of enantiornithines likely far exceeding what is represented by the fossil record, it should be noted that clade-wide conclusions are potentially erroneous.

Conclusion

Though discoveries from the Jehol deposits continue to increase known enantiornithine diversity, information pertaining to remex morphology remains relatively scant. The two new *Longipteryx* specimens described here provide the first evidence of wing shape in this important taxon. Comparative lengths of the remiges and their overall shapes with the wing folded suggest an aspect ratio that is lower than most previously described enantiornithines, but

potentially similar to *Orienantius*. Additionally, the aspect ratio of the wing of enantiornithines, now including *Longipteryx*, was also much lower than that predicted for *Confuciusornis*. Currently there are 19 known specimens of *Longipteryx*, a majority of which preserve some trace of soft tissue with none preserving rectrices, suggesting that if this taxon exhibited integumentary sexual dimorphism, it did not do so via ornamental tail feathers as is predicted for some enantiornithines like *Protopteryx* (O'Connor et al., 2012; Wang et al., 2014; O'Connor et al., 2016).

Acknowledgments. Thanks to B. Marks, D. Willard, S. Hackett, and J. Bates, of the Field Museum (Chicago, IL USA), for access to bird collections. We thank S. Yin, X. Yin, and X. Zhang for facilitating our visit to the STM. We thank the editor and two reviewers for their helpful and constructive comments.

Funding. This research was in part funded by the Taishan Scholars Program of Shandong Province (Ts20190954) and the National Natural Science Foundation of China (NSFC) grant number (42572027, 42288201).

Competing interests. The authors declare no competing interests.

References

- Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., and Vanden Berge, J.C., 1993, *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 2nd edition: Cambridge, Nuttall Ornithological Club, 779 p.
- Carroll, N.R., Chiappe, L.M., and Bottjer, D.J., 2019, Mid-Cretaceous amber inclusions reveal morphogenesis of extinct rachis-dominated feathers: *Scientific Reports*, v. 9, 18108. <https://doi.org/10.1038/s41598-019-54429-y>.
- Chiappe, L.M., Di, L., Serrano, F.J., Yuguang, Z., and Meng, Q., 2019, Anatomy and flight performance of the early enantiornithine bird *Protopteryx fengningensis*: information from new specimens of the early cretaceous Huajiyang Formation of China: *The Anatomical Record*, v. 303, p. 716–731, <https://doi.org/10.1002/ar.24322>.
- Chiappe, L., and Meng Q., 2016, *Birds of Stone: Chinese Avian Fossils from the Age of Dinosaurs*: Baltimore, Johns Hopkins University Press. <https://doi.org/10.1353/book.48019>.
- Chiappe, L.M., and Witmer, L.M., eds., 2002. *Mesozoic Birds: Above the Heads of Dinosaurs*: Berkeley, University of California Press, 532 p.
- Chiappe, L.M., Shu'an, J., and Qiang, J., 2007. Juvenile birds from the Early Cretaceous of China: implications for enantiornithine ontogeny: *American Museum Novitates*, v. 3594, p. 1–46, [https://doi.org/10.1206/0003-0082\(2007\)3594\[1:JBFTFC\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2007)3594[1:JBFTFC]2.0.CO;2).
- Chiappe, L.M., Di, L., Serrano, F.J., Yuguang, Z., and Meng, Q., 2020, Anatomy and flight performance of the early enantiornithine bird *Protopteryx fengningensis*: information from new specimens of the Early Cretaceous Huajiyang Formation of China: *The Anatomical Record*, v. 303, p. 716–731, <https://doi.org/10.1002/ar.24322>.
- Chinsamy, A., Chiappe, L.M., Marugán-Lobón, J., Chunling, G., and Fengjiao, Z., 2013., Gender identification of the Mesozoic bird *Confuciusornis sanctus*: *Nature Communications*, v. 4, 1381, <https://doi.org/10.1038/ncomms2377>.
- Clark, A.D., Hu, H., Benson, R.B., and O'Connor, J.K., 2023, Reconstructing the dietary habits and trophic positions of the Longipterygidae (Aves: Enantiornithes) using neontological and comparative morphological methods: *PeerJ*, v. 11, e15139, <https://doi.org/10.7717/peerj.15139>.
- Clark, A.D., Atterholt, J., Clark, S.J., and Seward, N.W., 2025, Courtship display behavior influences tail myology in *Centrocerus minimus* (Gunnison sage-grouse): *Journal of Anatomy*, Early View, <https://doi.org/10.1111/joa.70089>.
- Clark, A.D., O'Connor, J.K., Price, T., Pruett-Jones, S., Wang X., Zhang X., Wang X., Zheng X., and Zhou Z., 2026. Hyperelongate ornamental tail feathers in a new Early Cretaceous bird: *PLoS ONE*, v. 21, e0347641, <https://doi.org/10.1371/journal.pone.0347641>.
- del Hoyo, J., Elliott, A., Sargatal, J., and Cabot, J., eds., 1992, *Handbook of the Birds of the World*. Volume 2. Barcelona, Lynx Edicions.

- del Hoyo, J., Elliott, A., Sargatal, J., and Cabot, J., eds., 1999, *Handbook of the Birds of the World*. Volume 5. Barcelona, Lynx Edicions.
- Falk, A.R., Kaye, T.G., Zhou, Z., and Burnham, D.A., 2016, Laser fluorescence illuminates the soft tissue and life habits of the Early Cretaceous bird *Confuciusornis*: *PLoS ONE*, v. 11, e0167284, <https://doi.org/10.1371/journal.pone.0167284>.
- Field, D.J., Lynner, C., Brown, C., and Darroch, S.A.F., 2013, Skeletal correlates for body mass estimation in modern and fossil flying birds: *PLoS ONE*, v. 8, e82000, <https://doi.org/10.1371/journal.pone.0082000>.
- Hou, L., Chiappe, L.M., Zhang, F., and Chuong, C.-M., 2004, New Early Cretaceous fossil from China documents a novel trophic specialization for Mesozoic birds: *Naturwissenschaften*, v. 91, p. 22–25, <https://doi.org/10.1007/s00114-003-0489-1>.
- Hou, L., Zhou, Z., Gu, Y., and Zhang, H., 1995, *Confuciusornis sanctus*, a new Late Jurassic sauriurine bird from China: *Chinese Science Bulletin*, v. 40, p. 1545–1551.
- Hu, H., O'Connor, J.K., and Zhou, Z., 2015, A new species of Pengornithidae (Aves: Enantiornithes) from the Lower Cretaceous of China suggests a specialized scansorial habitat previously unknown in early birds: *PLoS ONE*, v. 10, e0126791, <https://doi.org/10.1371/journal.pone.0126791>.
- Li, L., Gong, E., Zhang, L., Yang, Y., and Hou, L., 2010, A new enantiornithine bird (Aves) from the Early Cretaceous of Liaoning, China: *Acta Paleontologica Sinica*, v. 49, p. 524–531.
- Li, L., Jinqi, W., Xi, Z., and Shilin, H., 2012, A new enantiornithine bird from the Lower Cretaceous Jiufotang Formation in Jinzhou area, western Liaoning Province, China: *Acta Geologica Sinica—English Edition*, v. 86, p. 1039–1044, <https://doi.org/10.1111/j.1755-6724.2012.00729.x>.
- Li, Z., Wang, C.-C., Wang, M., Chiang, C.-C., Wang, Y., Zheng, X., Huang, E.-W., Hsiao, K., and Zhou, Z., 2020, Ultramicrostructural reductions in teeth: implications for dietary transition from non-avian dinosaurs to birds: *BMC Evolutionary Biology*, v. 20, 46, <https://doi.org/10.1186/s12862-020-01611-w>.
- Linnaeus, C., 1758, *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Tomus I. Editio decima, reformata: Holmiae, Laurentii Salvii.
- Liu, D., Chiappe, L.M., Serrano, F., Habib, M., Zhang, Y., and Meng, Q., 2017, Flight aerodynamics in enantiornithines: information from a new Chinese Early Cretaceous bird. *PLoS ONE*, v. 12, e0184637, <https://doi.org/10.1371/journal.pone.0184637>.
- Liu, D., Chiappe, L.M., Zhang, Y., Serrano, F.J., and Meng, Q., 2019, Soft tissue preservation in two new enantiornithine specimens (Aves) from the Lower Cretaceous Huajiyang Formation of Hebei Province, China: *Cretaceous Research*, v. 95, p. 191–207, <https://doi.org/10.1016/j.cretres.2018.10.017>.
- Liu, D., Chiappe, L.M., Wu, B., Meng, Q., Zhang, Y., Qiu, R., Xing, H., and Zeng, Z., 2022, Cranial and dental morphology in a bohaiornithid enantiornithine with information on its tooth replacement pattern: *Cretaceous Research*, v. 129, 105021, <https://doi.org/10.1016/j.cretres.2021.105021>.
- Lo Coco, G.E., Motta, M.J., Agnolín, F.L., and Novas, F.R., 2025, Reconstruction of pectoral musculature in non-avian paravians and basal birds: implications in the acquisition of flapping flight: *BMC Ecology and Evolution*, v. 25, 113, <https://doi.org/10.1186/s12862-025-02454-z>.
- Lovette, I., 2016, *Cornell Lab of Ornithology's Handbook of Bird Biology*. Third Edition: Chichester, John Wiley & Sons.
- Lucas, S.G., and Stettenheim, P.R., 1972, *Avian Anatomy: Integument part I: Agriculture Handbook 361*, U.S. Department of Agriculture, Washington, D.C.
- Møller, A.P., Nielsen, J.T., and Erritzøe, J., 2006, Losing the last feather: feather loss as an antipredator adaptation in birds: *Behavioral Ecology*, v. 17, p. 1046–1056, <https://doi.org/10.1093/beheco/arl044>.
- Morschhauser, E.M., Varricchio, D.J., Chunling, G., Jinyuan, L., Xuri, W., Xiadong, C., and Qingjin, M., 2009, Anatomy of the Early Cretaceous bird *Rapaxavis pani*, a new species from Liaoning Province, China: *Journal of Vertebrate Paleontology*, v. 29, p. 545–554, <https://doi.org/10.1671/039.029.0210>.
- O'Connor, J., 2022, Enantiornithes: *Current Biology*, v. 32, p. R1166–R1172, <https://doi.org/10.1016/j.cub.2022.07.074>.
- O'Connor, J.K., and Chiappe, L.M., 2011, A revision of enantiornithine (Aves: Ornithothoraces) skull morphology: *Journal of Systematic Palaeontology*, v. 9, p. 135–157, <https://doi.org/10.1080/14772019.2010.526639>.
- O'Connor, J.K., Wang, X., Chiappe, L.M., Gao, C., Meng, Q., Cheng, X., and Liu, J., 2009, Phylogenetic support for a specialized clade of Cretaceous enantiornithine birds with information from a new species. *Journal of Vertebrate Paleontology*, v. 29, p. 188–204, <https://doi.org/10.1080/02724634.2009.10010371>.
- O'Connor, J.K., Chiappe, L.M., Chuong, C., Bottjer, D.J., and You, H., 2012, Homology and potential cellular and molecular mechanisms for the development of unique feather morphologies in early birds. *Geosciences*, v. 2, p. 157–177, <https://doi.org/10.3390/geosciences2030157>.
- O'Connor, J.K., Wang, X., Zheng, X., Hu, H., Zhang, X., and Zhou, Z., 2016, An Enantiornithine with a fan-shaped tail, and the evolution of the rectricial complex in early birds: *Current Biology*, v. 26, p. 114–119, <https://doi.org/10.1016/j.cub.2015.11.036>.
- O'Connor, J.K., Zheng, X., Pan, Y., Wang, X., Wang, Y., Zhang, X., and Zhou, Z., 2020, New information on the plumage of *Protopteryx* (Aves: Enantiornithes) from a new specimen: *Cretaceous Research*, v. 116, 104577, <https://doi.org/10.1016/j.cretres.2020.104577>.
- O'Connor, J., Clark, A., Herrera, F., Yang, X., Wang, X., Zheng, X., Hu, H., and Zhou, Z., 2024, Direct evidence of frugivory in the Mesozoic bird *Longipteryx* contradicts morphological proxies for diet: *Current Biology*, v. 34, p. 4559–4566.e1, <https://doi.org/10.1016/j.cub.2024.08.012>.
- O'Connor, J., Wang, X., Clark, A., Kuo, P., Davila, R., Wang, Y., Zheng, X., and Zhou, Z., 2025, A new small-bodied longipterygid (Aves: Enantiornithes) from the Aptian Jiufotang Formation preserving unusual gastroliths: *Palaeontologia Electronica*, n. 28.3.a53, <https://doi.org/10.26879/1589>.
- Pan, Y., Sha, J., Zhou, Z., and Fursich, F.T., 2013, The Jehol Biota: definition and distribution of exceptionally preserved relicts of a continental Early Cretaceous ecosystem: *Cretaceous Research*, v. 44, p. 30–38, <https://doi.org/10.1016/j.cretres.2013.03.007>.
- Pan, Y., Zheng, W., Moyer, A.E., O'Connor, J.K., Wang, M., Zheng, X., Wang, X., Schroeter, E.R., Zhou, Z., and Schweitzer, M.H., 2016, Molecular evidence of keratin and melanosomes in feathers of the Early Cretaceous bird *Eoconfuciusornis*: *Proceedings of the National Academy of Sciences U.S.A.*, v. 113, p. E7900–E7907, <https://doi.org/10.1073/pnas.1617168113>.
- Schneider, C., Rasband, W., and Eliceiri, K., 2012, NIH Image to ImageJ: 25 years of image analysis: *Nature Methods*, v. 9, p. 671–675, <https://doi.org/10.1038/nmeth.2089>.
- Serrano, F.J., Chiappe, L.M., Palmqvist, P., Figueirido, B., Marugán-Lobón, J., and Sanz, J.L., 2018, Flight reconstruction of two European enantiornithines (Aves, Pygostylia) and the achievement of bounding flight in Early Cretaceous birds: *Palaeontology*, v. 61, p. 359–368, <https://doi.org/10.1111/pala.12351>.
- Serrano, F.J., Costa-Pérez, M., Navalón, G., and Martín-Serra, A., 2020, Morphological disparity of the humerus in modern birds: *Diversity*, v. 12, 173, <https://doi.org/10.3390/d12050173>.
- Stidham, T.A., and O'Connor, J.K., 2021, The evolutionary and functional implications of the unusual quadrate of *Longipteryx chaoyangensis* (Avialae: Enantiornithes) from the Cretaceous Jehol Biota of China: *Journal of Anatomy*, v. 239, p. 1066–1074, <https://doi.org/10.1111/joa.13487>.
- Terrill, R.S., and Shultz, A.J., 2023, Feather function and the evolution of birds: *Biological Reviews*, v. 98, p. 540–566, <https://doi.org/10.1111/brv.12918>.
- Thomas, A.L.R., 1993, On the aerodynamics of birds' tails: *Philosophical Transactions of the Royal Society B*, v. 340, p. 361–380, <https://doi.org/10.1098/rstb.1993.0079>.
- Wang, M., O'Connor, J.K., Zhao, T., Pan, Y., Zheng, X., Wang, X., and Zhou, Z., 2021, An Early Cretaceous enantiornithine bird with a pintail: *Current Biology*, v. 31, p. 4845–4852.e2, <https://doi.org/10.1016/j.cub.2021.08.044>.
- Wang, X., O'Connor, J.K., Zheng, X., Wang, M., Hu, H., and Zhou, Z., 2014, Insights into the evolution of rachis dominated tail feathers from a new basal enantiornithine (Aves: Ornithothoraces): *Biological Journal of the Linnean Society*, v. 113, p. 805–819, <https://doi.org/10.1111/bij.12313>.
- Wang, X., Shen, C., Liu, S., Gao, C., Cheng, X., and Zhang, F., 2015, New material of *Longipteryx* (Aves: Enantiornithes) from the Lower Cretaceous Yixian Formation of China with the first recognized avian tooth crenulations: *Zootaxa*, v. 3941, p. 565–578, <https://doi.org/10.11646/zootaxa.3941.4.5>.
- Wang, X., Clark, A.D., O'Connor, J.K., Zhang, X., Wang, X., Zheng, X., and Zhou, Z., 2024, First edentulous enantiornithine (Aves: Ornithothoraces) from the Lower Cretaceous Jehol avifauna: *Cretaceous Research*, v. 159, 105867, <https://doi.org/10.1016/j.cretres.2024.105867>.

- Wang, Y., Li, Z., Wang, C.-C., Bailleul, A.M., Wang, M., et al., 2023. Comparative microstructural study on the teeth of Mesozoic birds and non-avian dinosaurs: *Royal Society Open Science*, v. 10, 230147, <https://doi.org/10.1098/rsos.230147>.
- Winkler, D.W., Billerman, S.M., and Lovette, I.J., 2020, Pittas (Pittidae), version 1.0, in Billerman, S.M., Keeney, B.K., Rodewald, P.G., and Schulenberg, T.S., eds., *Birds of the World*: Ithaca, NY, Cornell Lab of Ornithology, <https://doi.org/10.2173/bow.pittid1.01>.
- Winkler, D.W., Billerman, S.M., and Lovette, I.J., 2024, Swifts (Apodidae), version 2.0, in Billerman, S.M., Keeney, B.K., Rodewald, P.G., and Schulenberg, T.S., eds., *Birds of the World*: Ithaca, NY, Cornell Lab of Ornithology, <https://doi.org/10.2173/bow.apodid1.02>.
- Xing, L., O'Connor, J.K., McKellar, R.C., Chiappe, L.M., Bai, M., Tseng, K., Zhang, J., Yang, H., Fang, J., and Li, G., 2018. A flattened enantiornithine in mid-Cretaceous Burmese amber: morphology and preservation: *Science Bulletin*, v. 63, p. 235–243, <https://doi.org/10.1016/j.scib.2018.01.019>.
- Xing, L., McKellar, R.C., O'Connor, J.K., Bai, M., Tseng, K., and Chiappe, L. M., 2019, A fully feathered enantiornithine foot and wing fragment preserved in mid-Cretaceous Burmese amber: *Scientific Reports*, v. 9, 927, <https://doi.org/10.1038/s41598-018-37427-4>.
- Zhang, F., Zhou, Z., Hou, L., and Gu, G., 2001, Early diversification of birds: evidence from a new opposite bird: *Chinese Science Bulletin*, v. 46, p. 945–949. <https://doi.org/10.1007/BF02900473>.
- Zheng, X., Wang, X., O'Connor, J., and Zhou, Z., 2012, Insight into the early evolution of the avian sternum from juvenile enantiornithines: *Nature Communications*, v. 3, 1116, <https://doi.org/10.1038/ncomms2104>.
- Zhou, Y., Pan, Y., Wang, M., Wang, X., Zheng, X., and Zhou, Z., 2024, Fossil evidence sheds light on sexual selection during the early evolution of birds: *Proceedings of the National Academy of Sciences U.S.A.*, v. 121, e2309825120, <https://doi.org/10.1073/pnas.2309825120>.
- Zhou, Z., 1995, [Discovery of a new enantiornithine bird from Early Cretaceous of Liaoning, China]: *Palaeontologia Sinica*, v. 33, p. 99–113. [in Chinese with English abstract]
- Zhou, Z., and Wang, M., 2024, Cretaceous fossil birds from China: *Geological Society, London, Special Publications*, v. 544, p. 477–499, <https://doi.org/10.1144/SP544-2023-129>.
- Zhou, Z., and Wang, Y., 2010, Vertebrate diversity of the Jehol Biota as compared with other Lagerstätten: *Science China Earth Sciences*, v. 53, p. 1894–1907, <https://doi.org/10.1007/s11430-010-4094-9>.