

# Current Biology

## An Early Cretaceous enantiornithine bird with a pintail

### Highlights

- Wang et al. describe a new pengornithid enantiornithine from the Early Cretaceous
- The new enantiornithine specimen preserves a pintail indicative of sexual selection
- The exaggerated pintail of this fossil bird may arise from the handicap process
- Mesozoic enantiornithines and ornithuromorphs show contrasting tail morphotype

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### In brief

Wang et al. describe a new enantiornithine preserving a rectricial fan combined with an elongate central pair of fully pennaceous plumes, constituting a new tail morphotype unknown among nonavian dinosaurs and Mesozoic birds. Fossil evidence shows that stem birds repeatedly evolved extravagant structures driven by sexual selection in their history.



## Report

# An Early Cretaceous enantiornithine bird with a pintail

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## SUMMARY

Enantiornithes are the most successful group of Mesozoic birds, arguably representing the first global avian radiation,<sup>1–4</sup> and commonly resolved as the sister to the Ornithuromorpha, the clade within which all living birds are nested.<sup>1,3</sup> The wealth of fossils makes it feasible to comparatively test evolutionary hypotheses about the pattern and mode of eco-morphological diversity of these sister clades that co-existed for approximately 65 Ma. Here, we report a new Early Cretaceous enantiornithine, *Yuanchuavis kompsosoura* gen. et. sp. nov., with a rectricial fan combined with an elongate central pair of fully pennaceous rachis-dominated plumes, constituting a new tail plumage previously unknown among nonavian dinosaurs and Mesozoic birds but which strongly resembles the pintail in many neornithines. The extravagant but aerodynamically costly long central plumes, as an honest signal of quality, likely evolved in enantiornithines through the handicap process of sexual selection. The contrasting tail morphotypes observed between enantiornithines and early ornithuromorphs reflect the complex interplay between sexual and natural selections and indicate that each lineage experienced unique pressures reflecting ecological differences. As in neornithines, early avialans repeatedly evolved extravagant structures highlighting the importance of sexual selection in shaping the plumage of feathered dinosaurs, even early in their evolutionary history.

## RESULTS

### Systematic paleontology

Aves Linnaeus 1758.

Ornithothoraces Chiappe 1995.

Enantiornithes Walker 1981.

Pengornithidae Wang et al., 2014.

*Yuanchuavis kompsosoura* gen. et. sp. nov. (Figure 1)

### Etymology

The generic name is derived from Mandarin “yuanchu” (referring to a Chinese mythological bird) and Greek “avis” (bird). The specific name is derived from Greek “kompsos” (elegant) and “oura” (tail), referring to the elegant tail feathers.

### Holotype

IVPP V27883 (housed at the Institute of Vertebrate Paleontology and Paleoanthropology), an articulated partial skeleton with associated feathers (Table S1).

### Locality and horizon

Near the Xiaoyaogou site in Jianchang Country, near Huludao City, Liaoning Province, China; Early Cretaceous, Jiufotang Formation.<sup>5</sup>

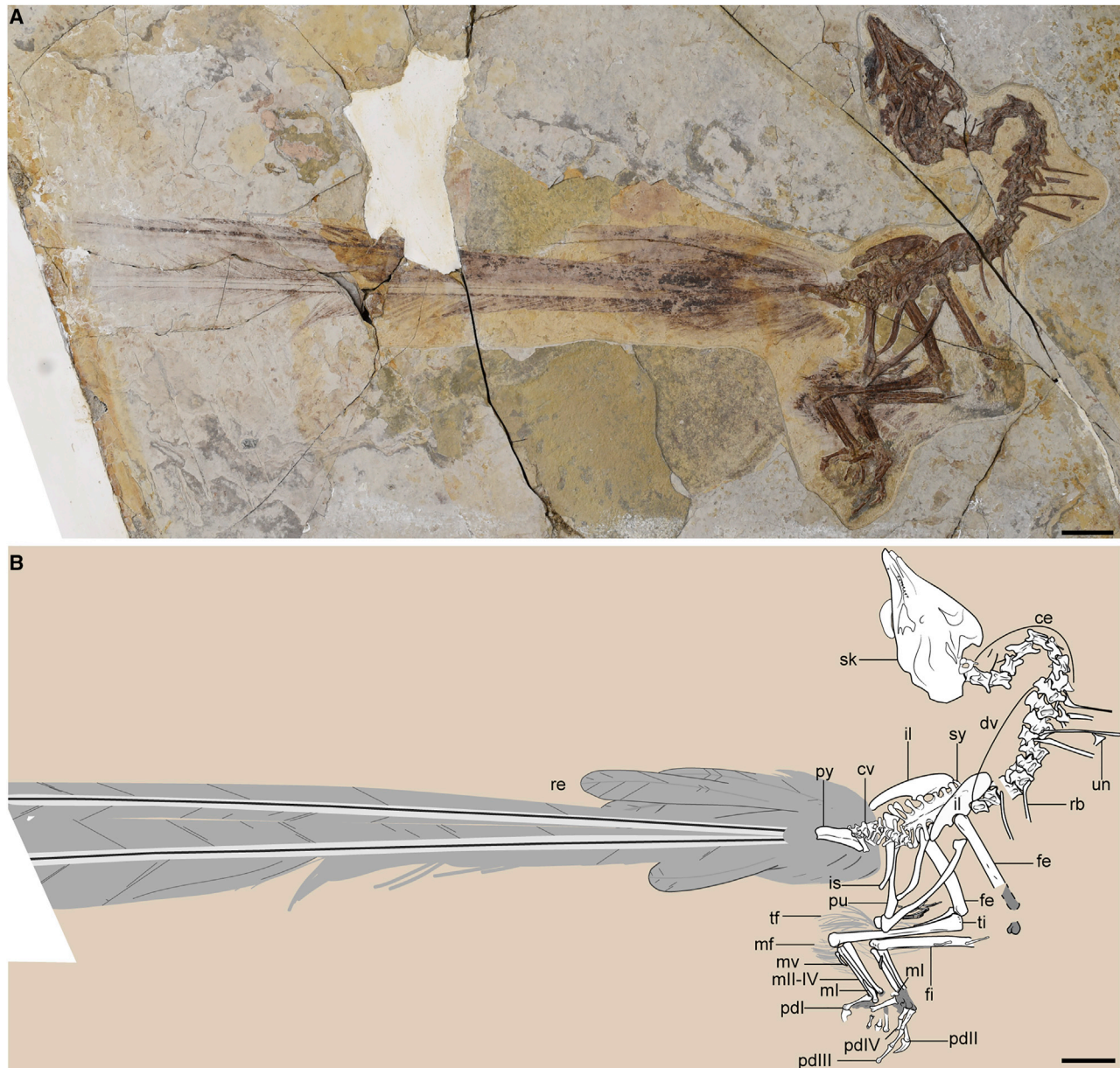
### Diagnosis

A large pengornithid (short and robust pygostyle; ischium without a dorsal process; elongate femur approximately 90% of tibiotarsus in length; metatarsal I longer than one-third of tarsometatarsus; metatarsal V present; and proximal phalanx of hallux longer than other non-ungual pedal phalanges) enantiornithine distinguishable from other pengornithids through the unique combination of features: premaxilla bearing five teeth with its rostral tip edentulous; lacrimal with reduced rostral and caudal rami; cranial dorsal vertebrae bearing well-developed hypapophyses; middle dorsal centra laterally excavated by broad fossa; and pygostyle with elongate ventrolateral processes and short dorsal processes.

### Description

The premaxilla bears subparallel maxillary and frontal processes, forming a shallower rostrum than in other pengornithids (Figure 2).<sup>6–8</sup> There are five premaxillary teeth (Figures S1A and S1B), whereas four are typical in enantiornithines, including other pengornithids. In contrast to other enantiornithines, such as *Parapengornis*, bohaiornithids, and longipterygids,<sup>7,9</sup> the rostral tip of the premaxilla is edentulous (Figure 2B)—a morphology also present in toothed ornithuromorphs, such as *Yanornis* and





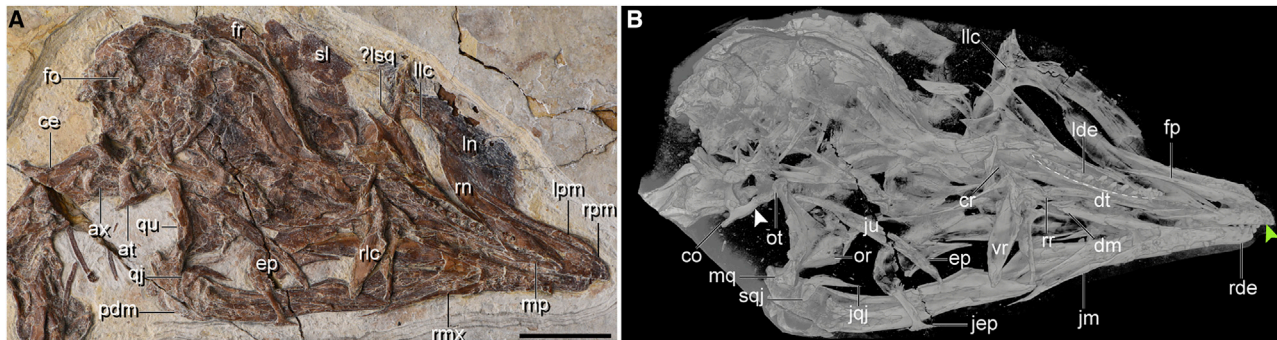
**Figure 1. *Yuanchuavis komposoura* holotype (IVPP V27883)**

(A) Photograph and (B) line drawing. ce, cervical vertebra; cv, caudal vertebra; dv, dorsal vertebra; fe, femur; fi, fibula; il, ilium; is, ischium; mf, metatarsal feather; ml-mV, metatarsals I-V; pdl-pdIV, pedal digits I-IV; pu, pubis; py, pygostyle; rb, rib; re, rectrices; sk, skull; sy, synsacrum; tf, tibiotarsus feather; ti, tibiotarsus; un, uncinat process. Scale bars, 20 mm. See also [Figures S1](#) and [S2](#) and [Table S1](#).

*Yixianornis*.<sup>10</sup> The triradiate maxilla has a large dorsal process as in other pengornithids<sup>7</sup> but lacks the foramina present in *Pengornis*.<sup>8</sup> The broad nasal lacks a ventral process and narrows at both ends. The T-shaped lacrimal differs greatly from that of other pengornithids in having reduced rostral and caudal rami. The stout ventral ramus rapidly tapers rostrocaudally along its distal half-shaft, giving itself blade-like outline laterally. The jugal and quadratojugal are unfused as in some enantiornithines, including *Parapengornis*.<sup>7</sup> The L-shaped quadratojugal consists of squamosal process that is twice as long as its jugal process ([Figure 2](#)).

The rarely preserved ectopterygoid is large with a hook-shaped jugal process that expands rostrocaudally ([Figure 2](#)), as in *Sapeornis*, *Archaeopteryx*, and nonavian theropods.<sup>11,12</sup> However, unlike those taxa, the medio-rostral end of the ectopterygoid body strongly projects rostrally, suggesting a broad surface contacting the pterygoid. As typical of pengornithids,<sup>7,8,13</sup> the dentary is packed with numerous, blunt, and low-crowned teeth; 12 teeth are preserved on the left side. The postdentary mandibular elements are fused with one another, forming a rostroventrally sloping articulation with the dentary.





**Figure 2. Cranial anatomy of *Yuanchuavis* (IVPP V27883)**

(A) Photograph. Scale bar represents 10 mm.

(B) CT rendering. The white arrowhead indicates the fused atlantal arch, and the green arrowhead indicates the edentulous rostral margin of the premaxilla. at, atlas; ax, axis; co, costal process; cr, caudal ramus of lacrimal; dm, dorsal process of maxilla; dt, dentary teeth; ep, ectopterygoid; fo, foramen magnum; fp, frontal process of premaxilla; fr, frontal; jep, jugal process of ectopterygoid; jm, jugal process of maxilla; jqj, jugal process of quadratojugal; ju, jugal; lde, left dentary; llc, left lacrimal; ln, left nasal; lpm, left premaxilla; ?lsq, possible left squamosal; mp, maxillary process of premaxilla; mq, mandibular process of quadrate; or, orbital process of quadrate; ot, otic process of quadrate; pdm, postdentary mandible; qj, quadratojugal; qu, quadrate; rde, right dentary; rlc, right lacrimal; rmx, right maxilla; rn, right nasal; rpm, right premaxilla; rr, rostral ramus of lacrimal; sl, sclera ossicle; sqj, squamosal process of quadratojugal; vr, ventral ramus of lacrimal. See also [Figure S1](#).

The vertebral column consists of ten cervicals, ten dorsals, a fused sacrum composed of eight vertebrae, seven free caudal vertebrae, and a completely fused pygostyle ([Figures S1 and S2](#); see [Methods S1](#) for morphological description of vertebral column and pelvis).

Like other pengornithids,<sup>7</sup> the elongate femur measures approximately 90% of the tibiotarsus in length and the two bones are equally robust ([Table S1](#)). The fibula extends distally and nearly contacts the lateral condyle ([Figure S2](#)), a plesiomorphy among enantiornithines that is only retained in pengornithids.<sup>6,14</sup> The proximal-most portions of metatarsals III–V are weakly ankylosed, but metatarsal II remains free. As in other pengornithids,<sup>7,13</sup> metatarsal I is proportionately long, measuring approximately 40% the length of metatarsal II. The proximal half of the shaft tapers proximally, and its distal portion is deflected plantarly, indicating a fully reversed hallux. Metatarsal II is the most robust, approaching the combined width of metatarsals III and IV at the midshaft. Metatarsal III is the longest and slightly more robust than metatarsal IV. The presence of metatarsal V is another plesiomorphy in ornithothoracines only present in pengornithids and *Vorona* ([Figure S2](#)).<sup>3,7,14</sup> Metatarsal V is short, measuring 1/4 the length of metatarsal IV; the distal half is tapered and weakly deflected cranially. The proximal phalanx of the hallux is the longest, but that of digit II is the most robust, as in other pengornithids.<sup>8,13</sup> The ungual phalanges are strongly recurved and bear deep medial and lateral grooves as in other enantiornithines,<sup>2</sup> suggesting an arboreal lifestyle.

The tail plumage appears to be complete or nearly so ([Figure 3](#)). The tail consists of eight rectrices. The central pair of rectrices are elongate, and their preserved length (30 cm) measures approximately 1.3 times the snout-vent length of the bird. The fully pennaceous central rectrices have a proportionately wide rachis with a longitudinal dark stripe preserved throughout its length ([Figures 3B and 3G](#)), resembling the rachis-dominated feathers (RDFs) in *Eopengornis* and *Parapengornis*.<sup>7,14</sup> A tail consisting of a pair of RDFs is commonly

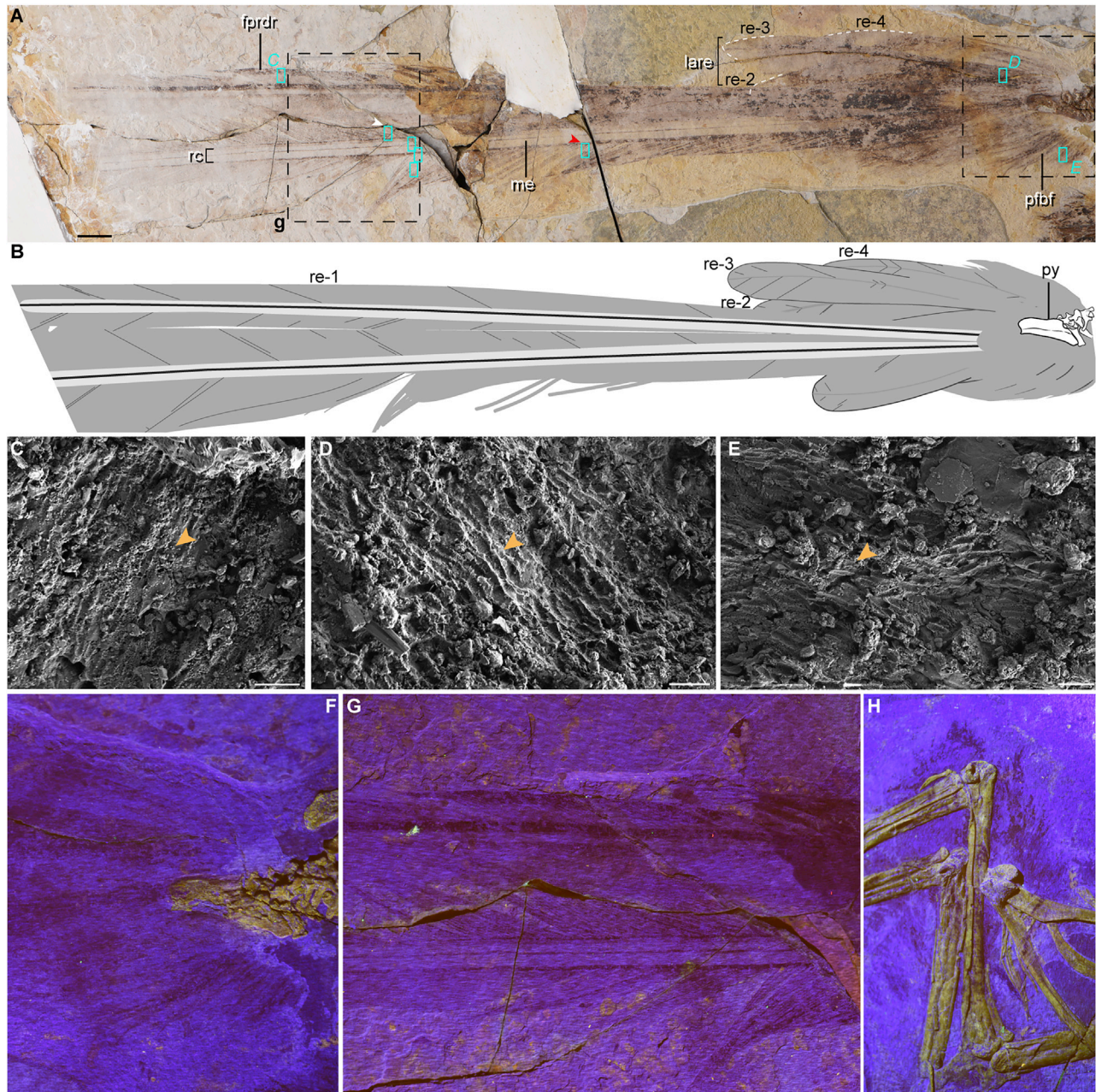
preserved in enantiornithines and the Confuciusornithiformes, but in nearly all specimens, the pennaceous portion is distally restricted, forming distally pennaceous RDFs (dPRDFs).<sup>14,15</sup> The fully pennaceous RDFs (fPRDFs) morphology is only observed in pengornithids like *Yuanchuavis*. The proportionately much shorter (~1/3 the length of central rectrices) lateral three pairs of rectrices have narrow rachises and asymmetrical vanes (medial vane wider than the lateral vane) with rounded distal margins. The lateral rectrices decrease in length laterally, forming a highly graduated tail fan, proximally surrounded by filamentous body feathers ([Figure 3F](#)). In enantiornithines, a rectricial fan is only otherwise present in *Chiappeavis*, in which the fan is similarly highly graduate but estimated to consist of five pairs of rectrices.<sup>6</sup> Eight samples from different regions of the rectrices were analyzed using scanning electron microscope, revealing rod-like sub-micrometric impressions interpreted as molds of fossilized eumelanosomes in following recent studies ([Figures 3C–3E and S3](#)).<sup>16,17</sup> The eumelanosomes in the fPRDFs and the base of the shorter rectrices forming the fan (which may be overlapped by body feathers) are statistically different in geometry ( $p < 0.01$ ; [Table S2](#)), implying they formed different *in vivo* colors (but see Vinther<sup>16</sup> for uncertainty of color reconstructing based on melanosome shape). Comparison with modern feather data suggests the shorter feathers were gray and the fPRDFs were black ([Figure S3G](#)).

The hindlimbs are covered by short filamentous feathers that extend down to the distal third of the metatarsals ([Figures 3H and S2](#)), as in some enantiornithines.<sup>18</sup> Although their precise lengths cannot be measured, the feathers decrease in length distally along the hindlimb.

## DISCUSSION

Our phylogenetic analysis confirms a close affinity between *Yuanchuavis* and other pengornithids, recovering all purported pengornithids together in a clade, the monophyletic





### Figure 3. Plumages of *Yuanchuavis* (IVPP V27883)

(A) Photograph with boxes indicating the locations of the feather samples.

(B) Line drawing of the tail feathers.

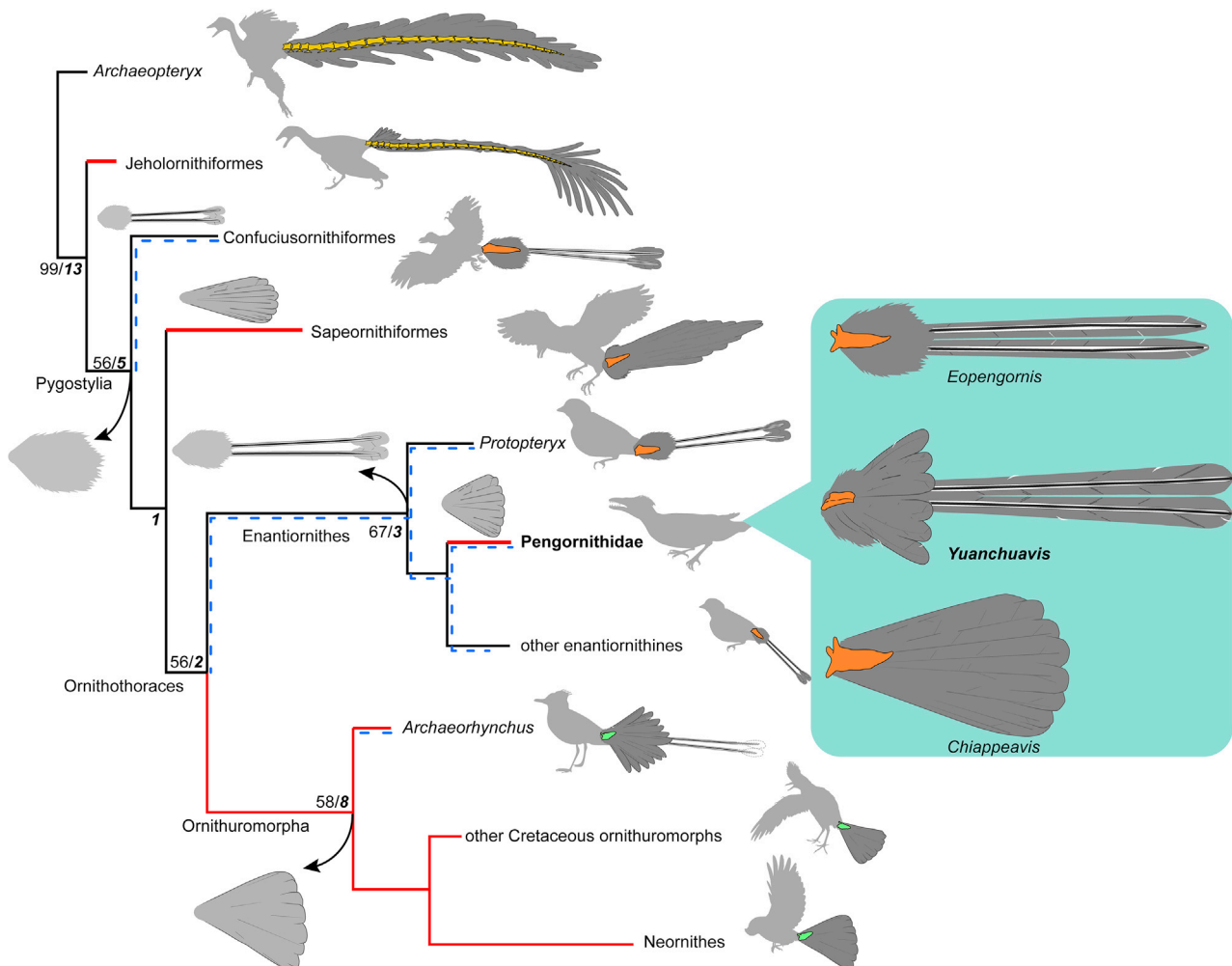
(C–E) Scanning electron microscopy (SEM) images showing the melanosomes preserved in different regions of the tail feathers denoted in (A). See [Figure S3](#) for SEM images of the feather sampled in locations denoted by the red and white arrowheads in (A).

(F–H) Laser stimulated fluorescence (LSF) imaging of the proximal filamentous body feathers (F), middle portion of the elongate central paired rectrices (G), and the feathers attached to the hindlimb (H).

fpdr, fully pennaceous rachis-dominant rectrices; lare, lateral asymmetrical pennaceous rectrices; me, medial stripe of the rachis; pbf, proximal filamentous body feather; rc, rachis; re-1 to r-4, rectrices 1–4. Scale bars, 10 mm (A) and 2  $\mu$ m (C–E). See also [Figure S3](#) and [Table S2](#).

Pengornithidae ([Figures 4](#) and [S4](#)). With five taxa, it is the most diverse enantiornithine family after the Bohaiornithidae and the only lineage that persisted through the entirety of the Jehol Biota (131–120 Ma).<sup>19</sup> As the second earliest diverging enantiornithine lineage, the pengornithids preserve a suite of plesiomorphic

features, including the presence of ectopterygoid, metatarsal V, and elongate fibula that are eventually lost in more derived enantiornithines. Pengornithids also display several morphological characters that are unusual within the Enantiornithes and may at first appear to be derived, such as heterocoelic cervical



**Figure 4. Phylogenetic position of the Pengornithidae and the evolution of tail feathers in stem avialans**

The cladogram is simplified from the strict consensus tree of the phylogenetic analysis (see Figure S4 for complete result). The elongate central rectrices are independently evolved along branches subtending to Confuciusornithiformes, Enantiornithes, and *Archaeorhynchus* (blue dashed lines), which are lost in more crownward Mesozoic ornithuromorphs. The rectricial fan was convergently evolved in sapeornithids, ornithuromorphs, and derived members of pengornithids (red lines). The pygostyle colored in orange denotes the primitive rod-like pygostyle morphology and in green denotes the derived plough-shaped form. Silhouettes and rectrix reconstructions of *Archaeopteryx*, Jeholornithiformes, and Sapeornithiformes were modified from literature.<sup>9,18</sup> See also Figure S4 and Methods S2.

vertebrae, globose humeral head, and proportionately short pygostyle, but may in fact also be plesiomorphic to enantiornithines.<sup>18</sup>

Most enantiornithines lack pennaceous rectrices, instead preserving a halo of filamentous body feathers surrounding the pygostyle.<sup>20</sup> In specimens that preserve pennaceous rectrices, most commonly a single pair of RDFs is present, which are most racket-plumes (pennaceous portion distally restricted), but in pengornithids, they are fully pennaceous. RDFs are proportionately elongate and regarded as ornamental structures (e.g., display and species recognition).<sup>14</sup> They are generally hypothesized to be sexually dimorphic and present only in males (other function is also possible, such as acting as a stabilizer or rudder).<sup>14,21</sup> The combination of a proportionately short, plough-shaped pygostyle and rectricial fan was initially thought to have exclusively coevolved in ornithuromorphs.<sup>10,22</sup> However,

the subsequent discoveries of the enantiornithine *Cruralispennia* preserving a plough-shaped pygostyle but lacking rectricial fan<sup>23</sup> and the tail fan present in *Sapeornis* and two pengornithids, *Chiappeavis* and now *Yuanchuavis*, which all lack a plough-shaped pygostyle,<sup>6</sup> indicate that these two structures have independent origins in at least some lineages of early avialans (Methods S1).

*Yuanchuavis* preserve a rectricial fan combined with a pair of elongate fPRDFs—a pintail similar to that in extant male sunbirds.<sup>24,25</sup> Among Mesozoic birds, this morphology was previously only recognized in the early diverging ornithuromorph *Archaeorhynchus*;<sup>26</sup> this is the first documented occurrence of a pintail in enantiornithines. Notably, the morphology preserved in *Yuanchuavis* essentially represents a combination of the two tail morphologies previously recognized in pengornithids. *Eopengornis*, the oldest and earliest diverging pengornithid, preserves fPRDFs,



suggesting that this morphology is plesiomorphic within the Pengornithidae. Our parsimony-based ancestral state reconstruction for tail morphology across stem avialan phylogeny shows four convergent evolutions of rectricial fan, the Jeholornithiforms, saepeornithids, ornithuromorphs, and derived members of pengornithids (Figures 4 and S4; Methods S1). The absence of a tail fan in *Parapengornis* may be secondarily lost or due to sexual, ontogenetic, or seasonal dimorphism.

The pintail has evolved repeatedly in neornithines.<sup>27,28</sup> Although the exact morphology observed in *Yuanchuavis*, with its fPRDFs, has not been previously reported in any Cretaceous bird, it is similar to the pintail in the earliest diverging ornithuromorph *Archaeorhynchus* (STM7-11), in which presumably dPRDFs were present.<sup>26</sup> Given that the pintail morphology is not widespread in either enantiornithines or early ornithuromorphs, it is likely that the pintail evolved independently multiple times in early avialans, as in Neornithes.<sup>25,27</sup> This hypothesis is supported by ancestor-state reconstructions, which shows that the elongate central paired plumes evolved independently along branches subtending to confuciusornithiforms, enantiornithines, and *Archaeorhynchus* but is absent in more crownward Mesozoic ornithuromorphs (Figure S4).

The neornithine tail fan is functionally integrated into the flight apparatus, not only providing lift but more critically increasing stability, agility, and maneuverability.<sup>27–30</sup> However, aerodynamic performance is not the only driving force that shapes avialan tails, attesting to the enormous diversity of tail plumes in extant birds, many of which exhibit aerodynamically costly extravagant forms, colors, and ornaments, which inspired Darwin to first introduce the subject of sexual selection.<sup>25,27,28,31,32</sup> The growing fossil record of feathered dinosaurs (including birds) documents numerous instances in which the preserved plumage on the tail and other regions of the body appear to have been shaped through sexual selection,<sup>33</sup> such as the pennaceous rectrices in *Caudipteryx*,<sup>34</sup> the ribbon-like tail feathers in *Epidexipteryx*,<sup>35</sup> and the RDFs in enantiornithines and the Confuciusornithiformes.<sup>15,21</sup> The discovery of *Yuanchuavis* contributes to the diversity of enantiornithine tail morphologies and reinforces hypotheses that sexual selection was a major driving force shaping the tail plumage in enantiornithines.<sup>14,26</sup>

Exaggerated phenotypes are most commonly produced through sexual selection and play an important role in speciation and extinction.<sup>33,36</sup> The Fisherian runaway and the handicap principle mechanisms of sexual selection have been extensively studied,<sup>36–39</sup> which differ in their assumptions and predications about the cost of the secondary sexual traits. fPRDFs in *Yuanchuavis* extend well beyond the point of the maximum continuous width of the tail fan, indicating that they produce little lift but increase drag and the moment of inertia substantially,<sup>29,30</sup> consequently lowering the lift:drag ratio. Compared with the dPRDFs in other enantiornithines and Confuciusornithiformes where the pennaceous portions are distally located,<sup>15,21</sup> the fully pennaceous central plumes of *Yuanchuavis* and other pengornithids have a larger surface area and, accordingly, have induced greater skin friction during flight.<sup>14,29</sup> The expanded pennaceous vane also suggests these fPRDFs are more energetically costly to produce relative to the racket-plume morphology. The line of evidence suggests that the central plumes of *Yuanchuavis* represent an honest signal of quality that probably arose from

the handicap process, possibly multiple times during pennaraptoran evolution.<sup>35</sup>

The Enantiornithes and Ornithuromorpha, as the two dominant groups of Mesozoic birds with their almost worldwide distributions, provide a rare opportunity to study the 65 Ma of parallel diversification of these two sister clades within the context of phylogeny.<sup>3,4,40</sup> Paleontologists traditionally focus on their skeletal morphologies that exhibit clade-specific evolutionary versatility.<sup>3</sup> However, differences in plumage between enantiornithines and ornithuromorphs are emerging in light of the recent exceptional discoveries.<sup>6,14,18,20,26</sup> Specifically, an investigation of approximately 450 Early Cretaceous enantiornithines reveals a ratio close to 1:1 between specimens that have and do not have the central paired elongate rectrices (Table S3), speaking to the wide distribution of this sexual signaling trait across the Enantiornithes. In contrast, among Jehol ornithuromorphs, only a single specimen out of ~90, *Archaeorhynchus* (STM 7-11), preserves traces of elongate, ornamental feathers. *Yuanchuavis* contributes to the apparent dichotomy between Cretaceous enantiornithines, which preserve predominantly ornamental tail morphologies, compared to the dominance of aerodynamic tails observed in ornithuromorphs, nearly all of which preserve a tail fan with no unambiguous ornaments with the exception of the pintail in *Archaeorhynchus*.<sup>10,20,26</sup> The lack of elongate tail ornaments in most early ornithuromorphs cannot be exclusively ascribed to preservational or taphonomic bias, because the ornithuromorphs preserving tail plumages come from the same localities or nearby those that have produced feathered enantiornithines and Confuciusornithiformes (e.g., the Jehol Biota).<sup>15,20,40</sup>

Here, we explore possible explanations for the contrasting patterns of tail plumage observed between enantiornithines and early ornithuromorphs. However, with so many variables and such limited information, it is impossible to fully interpret the available data at this time. The absence of ornamental tail feathers could result from the fact that early ornithuromorphs acquired different strategies for sexual display, such as variations in feather coloration, vocalization, nest buildings, and other more complex behaviors that are common in modern birds but rarely fossilized.<sup>25,36</sup> Alternatively, the role of sexual selection may have been limited by other biological pressures in early evolution of ornithuromorphs, for example, nesting environment and male participation in parental care (Methods S1).<sup>25,41</sup> Differences in relative ornamentation may also simply reflect ecological differences between the two ornithothoracine clades during the Early Cretaceous. All known enantiornithines are interpreted as arboreal,<sup>1,2</sup> whereas early ornithuromorphs were terrestrial and predominantly occupied semi-aquatic niches.<sup>1,42</sup> Different habitats exert different selective pressures and thus shape plumage differently; for example, darker plumages are associated with birds in more heavily vegetated environments.<sup>24</sup> The dense forest and vegetations like those existing in Jehol Biota<sup>19</sup> may have exerted great pressure for enantiornithines to attract potential mates, and elongate tail plumes with morphological modifications could possibly circumvent those barriers and increase mating success, echoing the extravagant tail plumes seen in tropical forest (see Methods S1 for other factors, e.g., mating system).<sup>25,43</sup> In extant birds, aquatic and semi-aquatic taxa tend to exhibit low degrees of ornamentation. The more open

littoral and lacustrine environments occupied by early ornithomorphs may have exerted greater pressure to maximize flight ability, making the long tail plumes more costly to its bearers. The contrasting tail plumage between Early Cretaceous Jehol enantiornithines and ornithomorphs represents a manifestation of the complexity of interplay between sexual and natural selective pressures and ecological opportunities. Regardless of the precise mechanisms that have produced this striking difference, the selective pressures shaping the tail plumage were clearly different in these two sister clades.

### STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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### SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.08.044>.

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### AUTHOR CONTRIBUTIONS

M.W. and Z.Z. conceived the study. M.W. performed the phylogenetic analysis. M.W., Z.Z., X.Z., and X.W. collected the tail morphology data of specimens housed in Shandong Tianyu Museum of Nature. T.Z., Y.P., and M.W. conducted the scanning electron microscopy study. M.W., J.K.O., and Z.Z. wrote the manuscript with comments from other authors.

### DECLARATION OF INTERESTS

The authors declare no competing interests.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
<i>Yuanchuavis kompsosoura</i> (IVPP V27883)	This paper	This paper
Software and algorithms		
TNT V.1.5	Goloboff and Catalano <sup>44</sup>	<a href="https://cladistics.org/tnt/">https://cladistics.org/tnt/</a>
Mesquite V. 3.61	Maddison and Maddison <sup>45</sup>	<a href="https://www.mesquiteproject.org/home.html">https://www.mesquiteproject.org/home.html</a>
Avizo V. 9.2.0	Thermo Fisher Scientific	N/A

### RESOURCE AVAILABILITY

#### Lead contact

Further information and request for resource should be directed to and will be fulfilled by the Lead Contact, Min WANG ([wangmin@ivpp.ac.cn](mailto:wangmin@ivpp.ac.cn)).

#### Materials availability

The holotype specimen of *Yuanchuavis kompsosoura* (IVPP V27883) is housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, and are available on request from the institute.

#### Data and code availability

All data including the morphological data, character matrix, and raw measurements are provided in the [supplemental information and Methods S2](#).

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

The study subject is a fossilized holotype specimen of the Cretaceous bird *Yuanchuavis kompsosoura* (IVPP V27883). The specimen was collected in deposits of the Lower Cretaceous Jiufotang Formation (120 Ma) near the Xiaoyaogou site in Jianchang Country, near Huludao City, Liaoning Province, China, and is housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing, China.

### METHOD DETAILS

#### Phylogenetic analysis

In order to investigate the relationship of IVPP V27883 with respect to other Mesozoic birds, we performed a comprehensive phylogenetic analysis using the latest version of the dataset from the Mesozoic Avian Phylogeny (MAP) project, which is actively being maintained by the Institute of Vertebrate Paleontology and Paleoanthropology.<sup>3</sup> The dataset was modified with the addition of the IVPP V27883 and minor revisions of character coding for a few taxa ([Methods S2](#)). The revised dataset consists of 280 characters and 81 taxa that encompass nearly all well-recognized Mesozoic birds (n = 78). Phylogenetic analysis was conducted using TNT v.1.5 under the maximum parsimony algorithm.<sup>44</sup> The most parsimonious trees (MPTs) were searched using the New Technology search method with sectorial, drift and tree fusion with following settings: all characters were equally weighted; 1000 random additional sequences were performed with an initial level of 100, and the minimum length tree were searched for 100 replicates. The resulting 59 MPTs were subjected to a second round of branch-swapping using the traditional tree-bisection-reconnection method to explore treespace more extensively, which produced 1792 MPTs with a length of 1401 (Consistence index = 0.227; Retention index = 0.664). Bootstrap and Bremer analyses were performed to calculate the support indices. The absolute bootstrap values were calculated via 1000 replicates using the same settings as the primary search. The strict consensus tree is consistent with most recent studies in the systematic relationships of major clades ([Figure S4](#)).<sup>3,6,7,46</sup> Following previous study,<sup>47</sup> the Ornithuromorpha refers to the first ancestor of Neornithes that is not an ancestor of Enantiornithes, and all of its descendants. The new topology recovers *Yuanchuavis* as sister taxon to the clade comprising *Chiappeavis* and *Parapengornis*, which are all nested within the Pengornithidae. The Pengornithidae is supported by four synapomorphies: the premaxillae are unfused (character 1:0); the pygostyle is shorter than

the combined length of the free caudal vertebrae (character 75:1); the articular facet for tarsometatarsus of tibiotarsus is restricted to distalmost edge of the caudal surface of the tibiotarsus (character 213:0); and the fibula contacts the proximal tarsals (character 220:0). The clade uniting *Yuanchuavis*, *Chiappeavis* and *Parapengornis* is supported by a single synapomorphy: eight sacral vertebrae are fused into the synsacrum (character 64:2).

### Reconstructions of tail feather evolutions

We formulated two binary characters to describe the tail feather morphology: the presence/absence of rectricial fan, and the presence/absence of elongate central paired plumes (Methods S2). The ancestral states of these two rectricial characters were reconstructed across the strict consensus tree recovered in present study using squared-change parsimony in Mesquite v. 3.61.<sup>47</sup>

### Computed tomography (CT) imaging

The skull of IVPP V27883 has been extracted from the slab and scanned at the Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology. The experiment was conducted using the industrial CT scanner Phoenix v-tome-x with beam energy of 140 kV and a flux of 150  $\mu$ A at a resolution of 11.68  $\mu$ m per pixel. The resulting scanned data were imported into Avizo (version 9.2.0) for rendering. Segmentation and 3D reconstruction of the skull will be present in a future study.

### Scanning electron microscopy of feather samples

Eight samples from different regions of the central paired and the lateral pennaceous rectrices were analyzed using scanning electron microscopy, respectively (Figure 3A). The feather samples were mounted on stubs with carbon tape without gold coating. Observation and photographing were performed using a Sigma 500 Field Emission Scanning Electron Microscope (FE-SEM) at the State Key Laboratory for Mineral Deposits Research of Nanjing University. Impressions of rod-like microbodies were observed in samples from both the lateral and central rectrices (Figures 3C–3E and S3), which were interpreted as the impression of eumelanosomes in following with recent analyses.<sup>16,17</sup> The eumelanosomes of the lateral rectrices are generally larger and have a larger aspect ratio (long axis/short axis) than these of the central paired plumes (average aspect ratio: 3.37 versus 3.04; Table S2), suggesting different colors in life. A two-tailed t test show that the aspect ratios are statistically different between the melanosomes preserved in the central paired and lateral rectrices ( $p < 0.01$ ; Table S2). In order to quantitatively estimate the color variations of tail feathers in *Yuanchuavis*, a biplot of the length and width of melanosomes was constructed by adding the measurements of the eumelanosomes in *Yuanchuavis* into a large dataset of modern feathers.<sup>17</sup> The result shows that the eumelanosomes of the central rectrices fall within the morphospace of the lateral rectrices; more specifically, the eumelanosomes of the central paired rectrices almost fall within the dark feathers, and these of lateral rectrices mainly fall within the morphospace of the gray feathers or feathers showing non-iridescent structural color (Figure S3G).

### Distribution of long tail plumes within the Enantiornithes

In order to have a quantitative understanding about the proportion of specimens that have the elongate central paired plumes, we performed an investigation of all the enantiornithine specimens ( $n = 450$ ) housed in the Shandong Tianyu Museum of Nature (STM), Pingyi. We chose this museum because it has the largest collection of Mesozoic birds in the world, and most of the specimens were collected from the Early Cretaceous Jehol Biota, which conceivably mitigates the impacts caused by taphonomy to some degree. In order to exclude preservational or taphonomic bias as much as possible, we only counted specimens that preserve both the pygostyle and tail feathers completely that enable us to confidently determine whether the absence of long tail plumes is a genius feature for a given specimen. We found 89 enantiornithines that preserve the elongate paired central plumes, and 85 enantiornithines that show no sign of elongate plumes (Table S3). In contrast, we found no Jehol ornithuromorphs housed in STM ( $n = 90$ ), except the single *Archaeorhynchus* (STM 7-11), preserving traces of elongate central plumes, indicating that such sexual display-related tail plumes were rare among early ornithuromorphs.

### Laser stimulated fluorescence photographing

LSF photographs were taken using a 500 milliwatt 450 nanometer blue laser (MDL-III-450-1W, Changchun New Industries Optoelectronics Tech. co., Ltd), a LP-500-62 light yellow longpass filter, and a Nikon D850.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Assessing melanosome geometry

We performed a two-tailed t test to explore whether the melanosomes preserved in the central paired and lateral rectrices are statistically different in aspect ratio (long axis/short axis). The long and short axes of melanosomes preserved in the central paired rectrices ( $n = 12$ ) and the lateral rectrices ( $n = 26$ ) were measured using Sigma 500 Field Emission Scanning Electron Microscope (FE-SEM), respectively. The significant level was set as 0.01.