



# Insights into the evolution of rachis dominated tail feathers from a new basal enantiornithine (Aves: Ornithothoraces)

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Received 14 February 2014; revised 28 March 2014; accepted for publication 28 March 2014; published 17 October 2014

We report on a new enantiornithine *Eopengornis martini* gen. et sp. nov. from the lowest horizon of the Jehol Biota in Hebei, China; dated at 130.7 Mya, this is the second oldest avian bearing fossil deposit in the world, recording the First Appearance Datum of Enantiornithes. The new specimen, only the second enantiornithine and third bird reported from this horizon, preserves numerous synapomorphies with the largest Lower Cretaceous enantiornithine *Pengornis houi* from the Jiufotang Formation dated at 120 Mya. Together, they form a new avian lineage that lasted over 10 Myr, which is longer than any known clade of Lower Cretaceous enantiornithine. *Eopengornis* reveals new information about basal enantiornithine morphology such as the presence of a metatarsal V, helping to clarify the early evolution of these dominant Cretaceous avians. Furthermore, *Eopengornis* preserves a previously unrecognized tail morphology: a pair of elongate fully pennaceous rachis dominated feathers. This discovery confirms hypotheses proposing that the rachis dominated racket-plumes in basal birds represent modified pennaceous feathers. We suggest that the ornamental racket-plumes in enantiornithines and *Confuciusornis* evolved independently from the basal pygostylian condition, which we infer was a tail formed of normal flight feathers. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 805–819.

ADDITIONAL KEYWORDS: Cretaceous – Huajiyang – Jehol – *Pengornis* – Pengornithidae – rectrix.

## INTRODUCTION

More information about the early evolution of birds and feathers is known from the Lower Cretaceous Jehol Group than any other deposit in the world, preserving the greatest taxonomic diversity of any Mesozoic avifauna, as well as providing a unique taphonomic window into the biology of early birds through the common preservation of feathers and soft tissue, such as skin impressions and ovarian follicles (Zheng *et al.*, 2013a; Zhou, Barrett & Hilton, 2003). This lithologic unit contains three formations: the lower Huajiyang Formation (formerly the Dabeigou), the middle Yixian Formation, and the upper Jiufotang Formation, and spans 120–130.7 Mya (Zhou, 2006; Jin

*et al.*, 2008; Pan *et al.*, 2013). The lower Huajiyang Formation, containing the 'Protopteryx-horizon', is the oldest geological unit to preserve fossil birds belonging to the Jehol Biota. Currently, only two taxa are known, *Protopteryx fengningensis* (Zhang & Zhou, 2000), the oldest known member of Enantiornithes (the most diverse clade of birds in the Mesozoic), and *Eoconfuciusornis zhengi* (Zhang, Zhou & Benton, 2008a), the earliest basal pygostylian and beaked bird, both collected from near Fengning in northern Hebei Province. By the deposition of the Yixian Formation, enantiornithines are trophically specialized, diverse, and speciose; confuciusornithiforms are present in great numbers; and jeholornithiforms, sapeornithiforms, and ornithuromorphs join the avifauna (Gao *et al.*, 2012; Ji *et al.*, 2002; Zhou & Zhang, 2006a). Diversity is highest in the Jiufotang Formation: sapeornithiforms and jeholornithiforms are present

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ZooBank registration: urn:lsid:zoobank.org:pub:033E8FB0-4781-4BF7-ACF1-2B33D982B23A

in greater numbers and ornithuromorphs and enantiornithines are even more abundant (Zhou & Zhang, 2006a); the largest Lower Cretaceous enantiornithine, *Pengornis houi* (Zhou, Clarke & Zhang, 2008), is from this formation.

Most specimens from the Jehol Biota are exceptional: almost complete, articulated, and preserving feathers, revealing a wealth of biological data (Zhou *et al.*, 2003). Tail feather morphologies are known in every clade of Jehol birds, recording an incredible diversity particularly among the enantiornithines (O'Connor *et al.*, 2012); first reported in *Confuciusornis sanctus* (Hou *et al.*, 1995), the most common morphology is a pair of rachis dominated 'racket-plumes' (Chiappe *et al.*, 1999). These feathers represent an extinct morphotype that apparently parallels the racket-plumes of some living birds, yet there still exists controversy regarding the evolutionary origin and function of these unusual feathers (Zhang & Zhou, 2000; O'Connor *et al.*, 2012); this is complicated by the fact that, although feather preservation is common, well preserved specimens are rare and most do not reveal morphological details (Zhang & Zhou, 2000; Hu *et al.*, 2011). In the present study, we report on a second specimen of enantiornithine from the Huajiyang Formation representing a previously unrecognized taxon. The new specimen preserves excellent feather impressions helping to clarify the early evolution of avian tail feathers. Furthermore, the specimen reveals morphologies that align it with the genus *Pengornis*, revealing a previously unrecognized lineage of enantiornithines. New specimens from the Huajiyang Formation are of particular importance for understanding the earliest radiation of avians, as well as the appearance of many morphological and structural innovations unique to birds.

#### INSTITUTIONAL ABBREVIATIONS

GSGM, Gansu Geological Museum, Lanzhou, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; STM, Tianyu Natural History Museum of Shandong, Pingyi, China.

## RESULTS

### SYSTEMATIC PALAEOLOGY

#### AVES LINNAEUS 1758

#### ORNITHOTHORACES CHIAPPE 1995

#### ENANTIORNITHES WALKER 1981

#### PENGORNITHIDAE FAM. NOV.

*Phylogenetic definition:* The most recent common ancestor of *Eopengornis martini* and *P. houi* and all its descendants.

*Type genus:* *Pengornis* IVPP V15336 Zhou, Clarke & Zhang, 2008.

*Included genera:* *Eopengornis* gen. nov. (present study).

*Stratigraphic distribution:* Huajiyang and Jiufotang Formations, 120–130.7 Mya (Zhou, 2006; Jin *et al.*, 2008; Pan *et al.*, 2013).

*Geographical distribution:* Fengning, northern Hebei Province, and Lingyuan and Dapingfang, Chaoyang, north-eastern Liaoning Province, China.

*Diagnosis:* Medium to large enantiornithine birds (minor metacarpal projecting distally farther than major metacarpal; straight scapula; dorsolaterally excavated furcula with rami defining a V; metatarsal IV reduced) with the unique combination of the following characters: upper and lower jaws with numerous small teeth (over ten in the maxilla alone); scapular acromion process hooked; sternum with single pair of trabeculae, intermediate trabeculae absent; xiphial region of sternum defines wide V (xiphoid process absent); short pygostyle with rounded distal margin; cranial surface of proximal humerus flat; ulna 15% longer than the humerus; femur almost as long as the tibiotarsus; fibula almost reaching the proximal tarsals; metatarsal I > 30% the length of metatarsal II; first phalanx of hallux longest pedal phalanx; and pedal claws heterogeneous.

#### *EOPENGORNIS MARTINI* GEN. ET SP. NOV.

(FIGS 1, 2; SEE ALSO SUPPORTING INFORMATION, FIGS S1, S2, S3, S4, S5, S6)

*Holotype:* STM24-1, an almost complete and fully articulated subadult individual preserved in a slab (primarily ventral view; see Supporting Information, Fig. S1) and counterslab (primarily dorsal view; Fig. 1), preserving remiges, rectrices, and contour feathers as an outline of the body.

*Locality and horizon:* Near Luozigou Village, Fengning, Hebei, China. Lower Cretaceous 'Protopteryx horizon' (130.7 Mya), the first sedimentary member of the Huajiyang Formation (previously also called Dabeigou Formation or Dadianzi Formation) (Jin *et al.*, 2008; Pan *et al.*, 2013).

*Etymology:* The genus name refers to the older age of the new specimen relative to known specimens of *Pengornis*; the species name is in honour of the late Larry Martin for his numerous contributions to the field of palaeornithology.



**Figure 1.** *Eopengornis martini* gen. et sp. nov. STM24-1. A, main slab, scale bar = 2 cm. B, close up of the caudal plumage, scale bar = 2 cm. C, close up of the right rectrix, scale bar = 5 mm.

*Diagnosis:* A pengornithid enantiornithine bird with the following unique characters: numerous, small, occlusally tapered and slightly recurved teeth in the upper and lower jaws; accessory foramina piercing nasal absent; fibula ends in a rounded expansion; and elongate hallux with metatarsal I and the proximal phalanx each almost half the length of metatarsal II.

*Differential diagnosis:* The specimen can be referred to Enantiornithes on the basis of the dorsolaterally excavated V-shaped furcula with elongate hypocleidium, straight scapula, and minor metacarpal extending distally farther than the major metacarpal.

The unmodified first phalanx of the major digit and large recurved pedal claws further support this identification. The specimen preserves all diagnostic characters of Pengornithidae. The specimen differs from younger pengornithids in tooth morphology; in STM24-1, the teeth have tapered and slightly recurved apices and are similar to the teeth in bohaiornithids, except they are much smaller (Wang *et al.*, 2014). By contrast to previous reports (Zhou *et al.*, 2008), the teeth in *Pengornis* are similar with tapered apices but they are still more blunt and low-crowned than those of *Eopengornis*. STM24-1 also differs from *Pengornis* in that the tarsometatarsus is



**Figure 2.** Comparative anatomy of Pengornithidae fam. nov. Detailed photographs: sternum in IVPP V18632 (A) and *Eopengornis* (B); scapular acromion process in *Pengornis houi* (C) and *Eopengornis* (D); maxilla in *Pengornis houi* (E) and *Eopengornis* (F); foot of *Pengornis houi* (G) and *Eopengornis* (H). Scale bars = 1 cm in (A), (B), (G), (H); scale bar = 5 mm in (C), (D), (E), (F). Anatomical abbreviations: acr, acromion; bc, bicipital crest; cor, coracoid; l, left; lt, lateral trabecula; max, maxilla; mtI, metatarsal I; mtI 1, first phalanx of hallux; mtI 2, hallucal claw; mtII, metatarsal II; mtII 1, first phalanx of second digit; mtII 2, second phalanx of second digit; mtII 3, claw of second digit; mt III, metatarsal III; mtIII 3, third phalanx of third digit; mtIII 4, claw of third digit; mtIV, metatarsal IV; mtIV 5, claw of fourth digit; mtV, metatarsal V; sca, scapula; stn, sternum; st r, sternal ribs; th r, thoracic ribs; xr, xiphial region.



greater than half the length of the tibiotarsus (less than half in *Pengornis*; see Supporting Information, Table S1). STM24-1 differs from IVPP V18632 in that the furcular rami form a narrower interclavicular angle, as in IVPP V15336, and the lateral trabeculae of the sternum are proportionately shorter and more robust (level with the caudal margin in STM24-1, whereas they extend further distally in *Pengornis* IVPP V18632), although the latter character may potentially be affected by ontogeny. STM24-1 differs from IVPP V15336 in that metatarsal I is proportionately longer, almost half the length of metatarsal II (43% versus 35%), and from IVPP V18632 in that the first phalanx of the hallux is proportionately longer, almost half the length of the tarsometatarsus (30% in IVPP V18632). STM24-1 further differs from the holotype of *P. houi* in size, degree of fusion of compound bones, and geological age; the much larger holotype is from the younger Jiufotang Formation, whereas the smaller STM24-1 comes from the lower member of the Jehol Biota, the first sedimentary member of the Huajiyang Formation, thus the two specimens are separated by an estimated 10.7 Myr.

**Remarks:** Given that histology (see Supporting Information, Fig. S7) indicates the specimen is a subadult and not a juvenile and that tooth morphology in fossil birds shows limited ontogenetic variation (O'Connor & Chiappe, 2011), we justify the creation of a new taxon for this specimen.

**Ontogenetic status of STM24-1:** The new specimen is much smaller than the holotype of *P. houi* IVPP V15336 and shows a lesser degree of skeletal fusion (synsacrum poorly fused, proximal tarsals unfused to the tibia). Bone histology (see Supporting Information, Fig. S7) confirms the specimen is probably not an adult, although the presence of a well ossified periosteum and an inner circumferential layer indicate that the specimen is also not a young juvenile. The sternum is typically the last element to ossify (Zheng *et al.*, 2012); given that this element is fully fused into a single element, we consider STM24-1 to be a subadult and not likely to experience drastic skeletal changes

other than the potential fusion of compound elements as it continued to grow (prolonged growth in Enantiornithes; Chinsamy, Chiappe & Dodson, 1995).

**Description:** Anatomical nomenclature primarily *sensu* Baumel & Witmer (1993), using the English equivalents of the Latin. The premaxillae are small and unfused, with four small teeth that are basally constricted, apically tapered, and slightly recurved, not blunt such as those of *P. houi* (Zhou *et al.*, 2008). The premaxillary corpus is very small; the nasal (frontal) processes are short (see Supporting Information, Fig. S3). The tapering maxillary process appears to have articulated with a lateral groove on the maxilla for most of its length; the rostral margin of the premaxillary process of the maxilla is blunt. The maxilla is delicate with a long ascending (nasal) process. The premaxillary ramus is slightly shorter than the jugal ramus and excavated by a groove for the premaxilla that extends slightly into the base of the nasal process (see Supporting Information, Fig. S3a). Each maxilla has an estimated 11 teeth, comparable to *Pengornis* but double the number typically present in other enantiornithines (O'Connor & Chiappe, 2011); although markedly larger than the teeth in the premaxilla, the maxillary teeth are small (crown height 0.36–0.48 mm) compared to nonpengornithid enantiornithines (although they increase in size distally), strongly constricted at their base, with tapered apices (Fig. 2E, F). The nasals are broad along their caudal three-quarters; the rostral quarter tapers sharply and no maxillary process appears present. The nasals both preserve a shallow fossa excavating the ventral/anterior surface of the distal quarter (see Supporting Information, Fig. S3a). The rostral margin of the fossa is concave and it widens distally, until, at the distal margin, it excavates almost the entire width of the nasal. The accessory nasal foramen is not present, and this feature remains an autapomorphy of *P. houi* (O'Connor & Chiappe, 2011). The jugal is slightly shorter than the maxilla in length and rod-like. The frontals are unfused medially and to the parietals; the interior/ventral surface of each parietal bear two

mediolaterally arranged circular depressions/concavities that are approximately equal in size. The quadrate is bowed and laterally excavated, similar to *P. houi* (O'Connor & Chiappe, 2011). An estimated 12–14 dentary teeth were present, identical to the maxillary teeth in morphology. In medial view, Meckel's groove approaches but does not reach the rostral end of the dentary. The dentary is unforked caudally (see Supporting Information, Fig. S3b).

We estimate the total number of cervical vertebrae to be nine or ten (only six preserved). The cervicals are short, with subequal length and width. The prezygapophyses are elongate, approximately one-third the length of the centrum. The postzygapophyses are shorter but slightly more robust. A short transverse process is preserved on one cervical (see Supporting Information, Fig. S4b). The free cervical ribs are rod-like and as long as the centra. The sacral vertebrae appear incompletely fused; the proximal most sacral is identified based on the absence of an articulating thoracic rib. There appear to be seven free caudals in articulation with the rectangular-shaped pygostyle, which is preserved crushed flat in ventral view, with the lateral margins clearly abraded (see Supporting Information, Fig. S4c); *Pengornis* has a similarly short and broad pygostyle, unlike other enantiornithines.

Three to six sternal ribs articulated with the sternum. Eight to nine pairs of gastralia are preserved in articulation (Fig. 1), which is greater than that reported in any other enantiornithine. Each gastralium is formed by a medial and lateral element; the gastralia decrease in size caudally.

The acromion is hooked ventrally, as in *Pengornis*, and almost as long as the lateroventrally facing glenoid (Fig. 2C, D). The scapular blade is very robust, straight, and shorter than the humerus with a blunt distal margin. The right coracoid is strut-like and expanded along the distal third. The medial and lateral margins are only convex distally forming an expanded sternal margin. The acrocoracoid, scapular cotyla, and glenoid are all almost aligned; an acrocoracoidal tubercle is absent. The furcula is dorsolaterally excavated; the interclavicular angle is approximately 60° (see Supporting Information, Fig. S5). The omal tips are bluntly tapered and slightly angled laterally with respect to the main axis of the clavicular rami. The delicate and sharply tapered hypocleidium is slightly more than 50% the length of the clavicular rami and the ventral surface is keeled.

The sternum is proportionately short, similar to that of *Protopteryx* and *Pengornis* IVPP V18632 (Hu, Zhou & O'Connor, 2014). The lateral margins are straight; the lateral trabeculae angle slightly medially and bear no significant distal expansions, similar

to *Pengornis* IVPP V18632 (Fig. 2A, B). No intermediate trabeculae are present, as in *Protopteryx* and *Pengornis* IVPP V18632. The caudal margin (xiphial region) is V-shaped, defining an angle of approximately 75°, as in *Pengornis* IVPP V18632. The trabeculae end at the same level as the xiphial region (Fig. 2B); they extend distally farther in *Pengornis* IVPP V18632 but do not reach the caudal margin in *Protopteryx*.

The humeral shaft is twisted so that the proximal and distal articular surfaces are in different planes. The proximal margin appears weakly convex, as in *Pengornis*. The proximocaudal margin is convex; a capital incision is present but it is poorly preserved together with the ventral tubercle. The width of the deltopectoral crest is less than that of the shaft; the crest extends for approximately one-third the length of the humerus, tapering distally, similar to *Pengornis* IVPP V18632. As in other pengornithids, the ulna is 115% the length of the humerus (subequal in *Protopteryx*; see Supporting Information, Table S1). The ulna is bowed proximally. The radius is straight and more than 50% the width of the ulna; the ulnare is only slightly larger than the radiale.

The carpometacarpus is entirely unfused (see Supporting Information, Fig. S6a). The semilunate carpal caps the major metacarpal, which is robust and straight. The minor metacarpal is also fairly robust and bowed, demarcating a small intermetacarpal space that does not reach the distal margin of the alular metacarpal. The proximal end extends onto the ventral surface of the major metacarpal, not reaching the proximal margin of the major metacarpal; the distal end extends beyond the distal end of the major metacarpal (enantiornithine autapomorphy). The alular metacarpal is short and rectangular. The alular digit ends approximately level with the distal end of the major metacarpal and the unguis phalanx is larger than that of the major digit as in *Pengornis* IVPP V18632.

The pubis has an oval cross-section with the long axis oriented approximately dorsolateral–ventromedially. The shaft becomes mediolaterally compressed just proximal to the expanded distal end. The distal ends are unfused but expanded into a boot (see Supporting Information, Figs S1, S2).

The femur is almost straight and approximately 90% the length of the tibia, as in other pengornithids (see Supporting Information, Table S1). The fibular crest is short and weakly developed. In caudal view, two tubercles are present on the proximocaudal margin of the tibia also visible in the holotype of *Pengornis houi*. In STM24-1, the lateral tubercle is more robust and may represent a primitive lateral articular face (*facies articularis lateralis*), whereas the medial tubercle is more proximodistally elongate

and may represent a primitive popliteal tuberosity (see Supporting Information, Fig. S6b). These tubercles appear to demarcate a weak flexor fossa. The fibula almost reaches the distal end of the tibia, as in other pengornithids (reduced in other ornithothoracines). The distal end of the fibula bears a small rounded expansion. The proximal tarsals are unfused to the tibia; the astragalus has a long tapered ascending process.

No free distal tarsals are preserved. The metatarsals are entirely unfused to each other (Fig. 2H). A small splint of bone preserved underlying the left metatarsal IV is interpreted as the fifth metatarsal (also preserved on the left); although present in the basal ornithothoracine *Vorona brevirotrensis* Forster *et al.*, 1996, this feature has not been previously described in any enantiornithine. Metatarsal IV is reduced in width relative to metatarsals II and III, as in all other enantiornithines. Metatarsal III is the longest, followed by metatarsal IV, which is only slightly shorter (see Supporting Information, Fig. S6c). Metatarsal II is the shortest, almost reaching the proximal margin of the metatarsal IV trochlea. Metatarsal II bears a medial plantar crest, which extends the middle third of the bone. Metatarsal I is long, similar to other pengornithids but proportionately longer, almost half the length of metatarsal II (43%; see Supporting Information, Table S1); the proximal end (metatarsal shaft) is mediolaterally compressed, delicate, and tapered. The body of the metatarsal expands until it reaches the dorsal surface of metatarsal II (dorsoplantarly widest point of the shaft) where it becomes caudally deflected so that the hallux was almost fully reversed (Fig. 2H). Metatarsals II and III are ginglymous; metatarsal IV is reduced to a single condyle, as in other enantiornithines.

The hallux is long; the proximal phalanx is the longest in the foot (Fig. 2H). The second digit is slightly more robust than the others. The ungual of digit I is subequal in size to that of digit II but bears a larger flexor process. Both are larger than that of digit III, which in turn is larger than that of digit IV. All the unguals preserve deep medial and lateral grooves; below the groove, the unguals bear lateral ridges. The ungual in pedal digit I has the largest flexor process.

*Tail feathers:* Two elongate rectrices are visible in both slabs (Fig. 1; see Supporting Information, Fig. S1). The preserved length of the feathers measures approximately 90 mm; the proximal quarter of each rectrix is not preserved but the path determined by the preserved length of each feather suggests they would have attached to the caudal margin of pygostyle, similar to the two medial rectrices in

neornithines. Based on this reconstruction, we estimate their full length to be 122–125 mm. On either side of the pygostyle, the tail bears short, rachis-less contour feathers, similar to those that cover most of the body in basal birds (O'Connor, 2009). The tail feathers strongly resemble the rachis dominated 'racket-plumes' present in confuciusornithiforms and enantiornithines from the Yixian and Jiufotang formations: both are paired, elongate, and possess an unusually wide rachis (1.8 mm, 20% the mediolateral width of the feather in STM24-1; in the range 1.3–2.4 mm along proximally narrow portion in *Confuciusornis sanctus* IVPP V13156; Fig. 3C) that extends the length of the feather with a longitudinal medial stripe of uncertain significance. However, unlike the 'racket-plumes' of taxa from younger deposits, in which the pennaceous portion is restricted to the distal part of the feather, the feathers in STM24-1 are fully pennaceous along their preserved length. Although the proximal quarter of both feathers is not preserved, and thus it is possible the feathers had undifferentiated vanes along their proximal quarter, at the proximal preserved end of the feather, the barbs are fully developed. This would limit any undifferentiated vane to only the proximal-most 10% of the feather just before the calamus. In all published well preserved enantiornithine rachis dominated 'racket-plumes' ( $N = 4$ ), the pennaceous portion is limited to the distal 15–30% of the feather, with narrow, undifferentiated vane along the proximal 70–85% of the feather (O'Connor, 2009; O'Connor *et al.*, 2012). Proximally, in both feathers, the medial barbs form a larger angle (17° versus 10°) with the rachis so that the width of the medial vane is much wider than that of the lateral vane (1.3 mm versus 3.7 mm). Distally, where the rachis begins to taper 15% from the distal margin, the angle between the lateral barbs and the rachis increases and the barbs elongate so that the medial and lateral vanes are subequal distally. The distal margin of the feathers are bluntly tapered; the barbs reduce in length along the distal 5% and the tapered rachis extends distally farther than the vane as in confuciusornithiforms and GSGM-07-CM-001 (Fig. 3) (does not reach in some enantiornithines, e.g. *Dapingfangornis*) (O'Connor *et al.*, 2012).

## DISCUSSION

Preliminary cladistic analysis of Jehol enantiornithines supports a close relationship between *E. martini* and species of *Pengornis* and the existence of a new clade, Pengornithidae fam. nov. (Fig. 4; see also Supporting Information, Fig. S8). *Pengornis houi* from the Jiufotang Formation is the largest Lower Cretaceous enantiornithine, yet several morphologi-

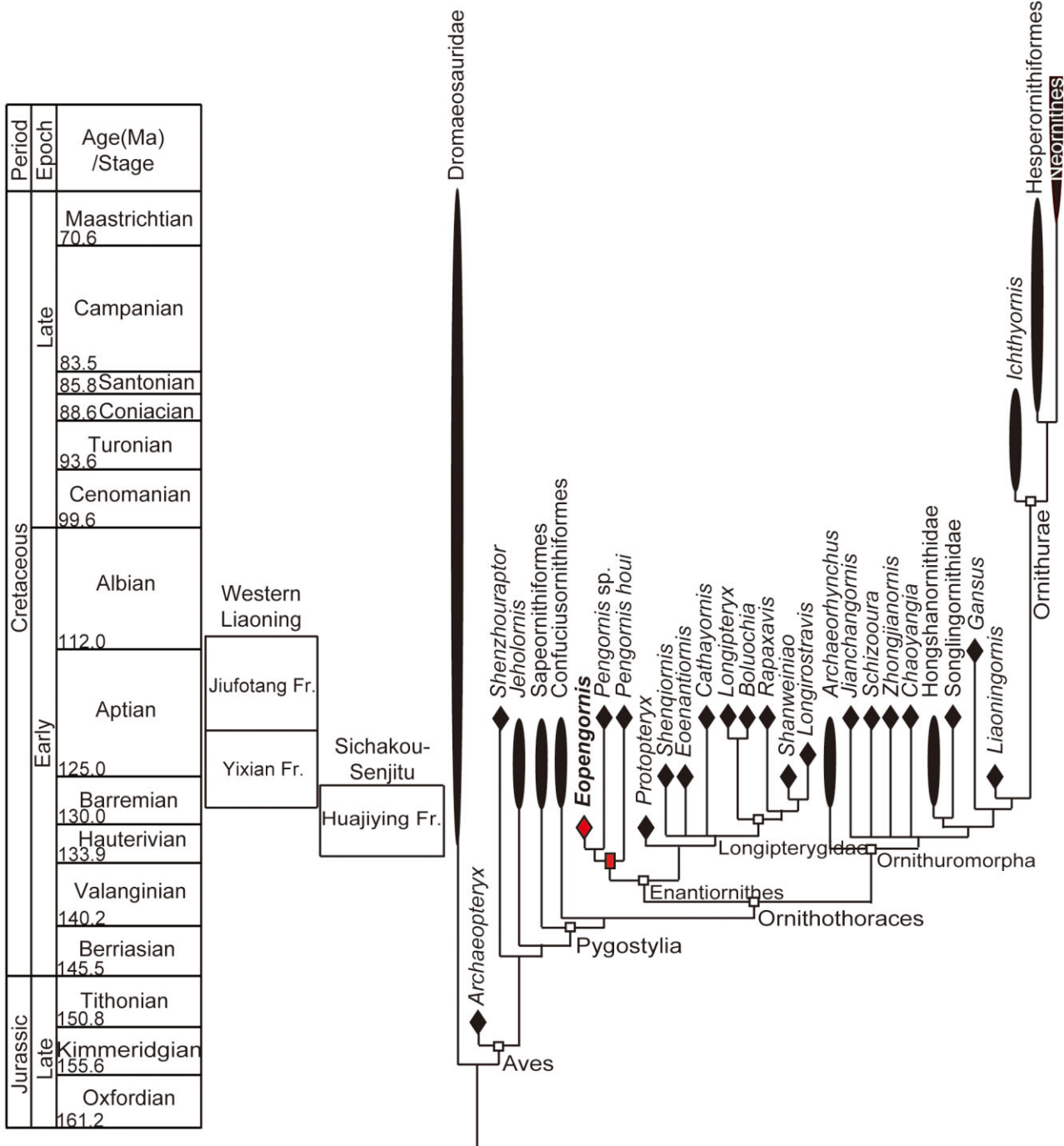


**Figure 3.** Details of basal bird feathers. A, B, details of the remiges in STM24-1, scale bars = 5 mm. C, rachis-dominated racket-plumes in *Confuciusornis* IVPP V13156, scale bar = 2 cm. D, close up of the distally pennaceous portion of one of the rachis-dominated racket-plumes preserved in Xiagou Formation *Enantiornithes* indet. GSGM-07-CM-001, scale bar = 1 cm. E, rachis-dominated racket-plumes in juvenile *Enantiornithes* indet. STM34-7, scale bar = 5 mm. Abbreviations: ms, medial stripe; pv, pennaceous vane; rs, rachis; uv, undifferentiated vane.

cal similarities to basal ornithuromorphs (e.g. convex proximal margin and flat cranial surface of humerus, short hypocleidium) suggested that the taxon was primitive within the clade, a hypothesis supported through several cladistic analyses (Zhou *et al.*, 2008; O'Connor, 2009). More recently, a smaller referred specimen of *Pengornis* sp. (IVPP V18632) was

described, also from the Jiufotang Formation (Hu *et al.*, 2014). The sternum preserved in the referred specimen revealed several previously unrecognized features shared only with *Protopteryx* from the Huajiyang Formation, which is widely considered the most basal enantiornithine (Zhang & Zhou, 2000; Zhou *et al.*, 2008). The basal ornithuromorph





**Figure 4.** Simplified time calibrated cladogram of the strict consensus tree of the 19 most parsimonious trees. Tree length = 668 steps. Consistency index equals 0.462; retention index equals 0.691. Pengornithidae fam. nov. (red node) is supported by five unambiguous synapomorphies: character 1, premaxillae unfused; 100, hooked scapular acromion; 220, fibula almost reaching distal tarsals (amended character); 227, a reduced metatarsal IV; and 232, a J-shaped metatarsal I. Diamonds indicate taxa known from single specimens or localities; ovals represent known ranges.

*Archaeorhynchus spathula* Zhou & Zhang, 2006b preserves a comparable sternal morphology, suggesting that a similar morphotype was plesiomorphic to Ornithothoraces (Zheng *et al.*, 2012; Hu *et al.*, 2014).

The discovery of *E. martini* in the Huajiyang Formation dated 130.7 Mya supports morphological and phylogenetic hypotheses that the Pengornithidae lineage is basal among Jehol enantiornithines, as

resolved in the present study (Fig. 4). Morphological similarities with Jiufotang pengornithids indicate that the sternum was conservative and plesiomorphic features were retained during the documented 10-Myr evolutionary history of the Pengornithidae. Similarly, the fibula remains long in *Pengornis*, whereas it is relatively more reduced in all other enantiornithines. Not all features were static; the cervical vertebrae are considerably more derived in pengornithids from younger deposits with fully heterocoelous articulations and keeled ventral margins, suggesting that heterocoely evolved multiple times within Enantiornithes alone (in Pengornithidae, as well as at least one more time among more derived enantiornithines) (Chiappe & Walker, 2002). All pengornithids have numerous small teeth relative to other birds, although the teeth show additional specialization in *P. houi*, being relatively more blunt and low crowned (O'Connor & Chiappe, 2011).

As one of two of the oldest known enantiornithines, *E. martini* also helps to clarify poorly known early stages in the skeletal evolution of enantiornithines. STM24-1 clearly preserves a metatarsal V, which is documented in basal pygostylians (Chiappe *et al.*, 1999) and one basal ornithuromorph, *Vorona* (Forster *et al.*, 1996). This indicates that this metatarsal was independently lost early in the evolution of Ornithuromorpha and Enantiornithes.

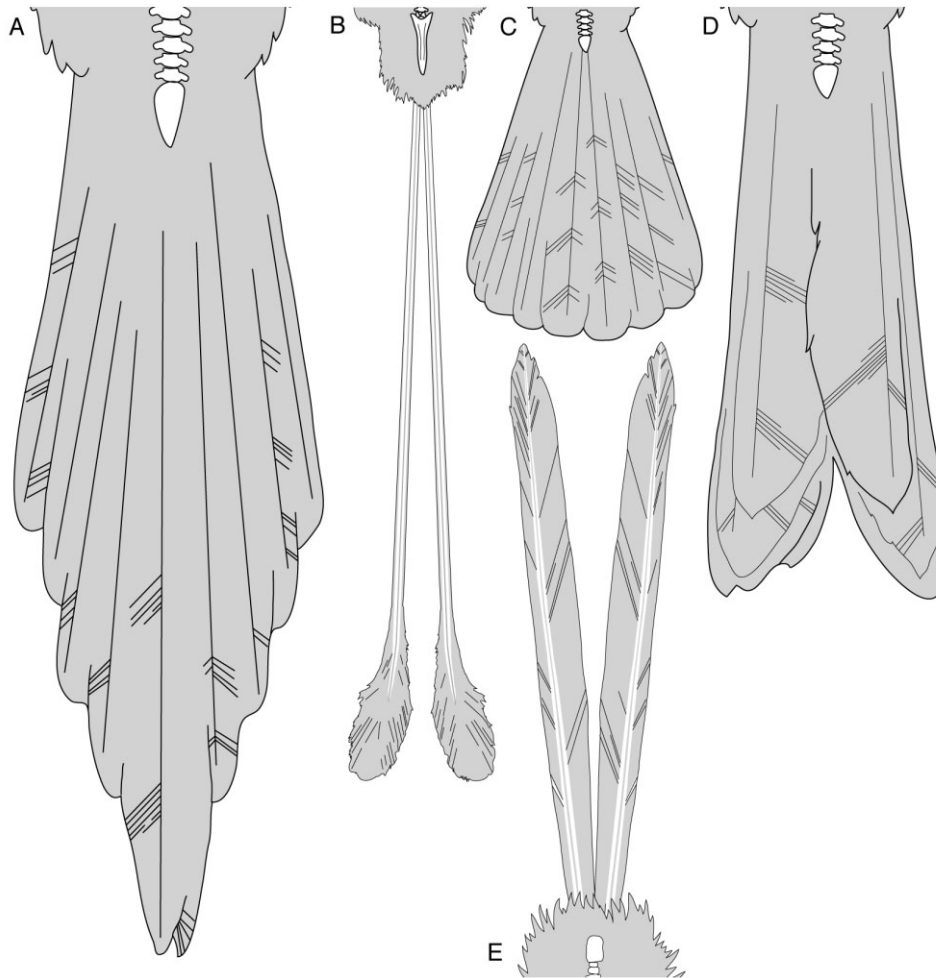
#### TAIL FEATHER EVOLUTION IN ENANTIORNITHES

The tail feathers preserved in STM24-1 are the most complete rectrices known from the Huajiyang Formation and are unique among basal birds (Fig. 1). The holotype of *Protopteryx* also possesses a pair of elongate rectrices; however, they are poorly preserved as an impression of the proximal portion of the rachis (O'Connor, 2009). It has been inferred that these feathers would have been similar to those of well preserved younger Jehol enantiornithines such as *Dapingfangornis fengningensis* Li, Duan, Hu, Wang, Cheng, & Hou, 2006 (and one enantiornithine from the Xiagou Formation) and confuciusornithiforms: distally pennaceous with a narrow strip of proximally undifferentiated vane along the proximal length of a wide rachis (O'Connor *et al.*, 2012). The holotype of *E. martini* preserves a new rectrix morphology in which the rachis dominated feather is fully (or almost fully) pennaceous along its length (Figs 1, 5). Although STM24-1 is a sub-adult, we do not consider this unique feather morphology to be juvenile or subadult plumage. Although ontogenetic changes in plumage have been documented in fossil theropods (Xu, Zheng & You, 2010), STM24-1 is not a young juvenile and is largely adult in morphology; further-

more, 'racket-plumes' are documented in a juvenile enantiornithine (STM34-7; Fig. 3E) indicating that these rectrices can appear early in ontogeny (Zheng *et al.*, 2012).

As in other enantiornithines and confuciusornithiforms, the paired rectrices are 'rachis dominated'. These feathers were originally interpreted as evidence that the feathers evolved from modified scales (Zhang & Zhou, 2000). However, as more complete specimens were discovered, these feathers were reinterpreted as modified pennaceous feathers (Yu *et al.*, 2002; Zhang, Zhou & Dyke, 2006; O'Connor *et al.*, 2012). The discovery of STM24-1, with fully pennaceous rachis dominated feathers, supports this interpretation and parallels the evolution of ornamental neornithine rectrices, which are also modified pennaceous feathers (Bleiweiss, 1987). O'Connor *et al.* (2012) proposed a series of modifications to the molecular morphogenesis of modern pennaceous feathers that could produce a rachis dominated morphotype similar to that observed in basal birds. These hypotheses infer the basal condition of fully pennaceous rachis dominated tail feathers, which we have confirmed with the discovery of STM24-1.

Within Aves, the racket-plume has evolved several times through different mechanisms and Mesozoic birds contribute to this diversity. Motmots (Aves: Momotidae) physically remove the proximal barbs to create the bare rachis, although the racket plumes in some species of parrots and hummingbirds evolved independently through modification of the molecular pathway of the feather (Bleiweiss, 1987), as also inferred for enantiornithine 'racket-plumes' (O'Connor *et al.*, 2012). Morphological differences between extant racket-plumes and the Mesozoic morphotype indicate that basal birds utilized a unique molecular pathway to achieve this morphology, unlike that observed in any living form. In living birds, the 'wire' like proximal portion of the feather (lacking vane) under high magnification is not bare but possesses minuscule barbs and barbules along the entire length, indicating that barb growth was suppressed but not absent (Bleiweiss, 1987). Apparently in racket plumes, barbs are always present; in Mesozoic birds, they are also present along the entire length (although not as reduced as in living taxa and visible to the naked eye) but, rather than forming individual barbs, the vane is undifferentiated. O'Connor *et al.* (2012) hypothesized that along the proximal portion of the rachis cell fate was affected and the marginal plate cells that normally suffer apoptosis (Shh positive zones), creating the separation of individual barbs, survive, resulting in undifferentiated vane. Thus in the 'racket-plumes' of Jehol birds barbs are present (as in extant racket-plumes)



**Figure 5.** Reconstructions of the known tail morphologies in Jehol pygostylians. A, graded fan of pennaceous feathers in *Sapeornis* (based on STM16-18). B, paired rachis-dominated 'racket-plumes' in enantiornithine *Dapingfangornis* (morphologically similar to the tail feathers of *Confuciusornis*). C, fan-shaped tail of pennaceous feathers in ornithuromorph *Hongshanornis*. D, forked tail (presumably formed by asymmetrical pennaceous feathers) in ornithuromorph *Schizoura*. E, paired fully pennaceous rachis dominated feathers in *Eopengornis*. Not drawn to exact scale.

but have not completed their development to become individualized. This is supported by the discovery of pengornithid STM24-1, which confirms the presence of a basal state of fully pennaceous rachis dominated tail feathers.

The holotype of *E. zhengi*, the oldest and basal-most confuciusornithiform (also from the *Protopteryx*-horizon), also preserves paired rectrices (Zhang *et al.*, 2008a). Unfortunately, this specimen does not clarify the early evolution of confuciusornithiform 'racket-plumes'. though the plumage is almost complete, morphological details of the feathers are not preserved. The tail plumage of *E. martini* suggests that previous assumptions that *Protopteryx* also possessed 'racket-plumes' (O'Connor, 2009) may be incorrect; potentially, *Protopteryx* possessed a morphology similar to that present in STM24-1.

#### TAIL EVOLUTION IN PYGOSTYLIA

To understand patterns in pygostylian rectricial evolution, we must explore the plesiomorphic tail condition. Rachis-dominated tail feathers are absent in all known sapeornithiforms and ornithuromorphs, both of which preserve 'modern' fan-shaped tails and more derived morphologies (Fig. 5) (Clarke, Zhou & Zhang, 2006; Zhou, Zhou & O'Connor, 2012; Zheng *et al.*, 2013b; Chiappe *et al.*, 2014). The feathers in *Eopengornis* STM24-1 display slightly greater aerodynamic qualities relative to those of more derived enantiornithines (e.g. *Dapingfangornis*, Fig. 5B; GSGM 07-CM-001, Fig. 3D); the vanes are asymmetrical with the leading vane more narrow than the trailing edge, as in flight feathers, suggesting that these tail feathers evolved from ones that originally

had aerodynamic function. Normal rectrices are present along almost the entire length of the tail in *Archaeopteryx* (Gatesy & Dial, 1996); these are distally restricted in *Jeholornis*, which additionally preserves a fan-shaped pteryla of flight feathers at the dorsal base of the tail, comparable to that observed in some living birds (O'Connor *et al.*, 2013). However, although not previously described, some basal bird remiges also possess a fairly robust rachis preserving a medial stripe (e.g. *Confuciusornis*; J. O'Connor, pers. observ.), similar to that observed in rachis-dominated rectrices; this feature is clearly visible in STM24-1 (Fig. 3A, B). The rachis is proportionately narrower in the tail feathers of *Confuciusornis* (Fig. 3C), and thus the disparity in width between the remiges and rectrices is lesser in this taxon (J. O'Connor, pers. observ.). Thus, although lacking the width of that of the tail feathers, the rachis-dominated rectrices are more comparable to the remiges than previously recognized, suggesting that they represent modified flight feathers. We suggest that the plesiomorphic pygostylian tail plumage consisted of an unknown number of normal flight feathers and that the rachis of the tail feathers was hypertrophied in Enantiornithes and Confuciusornithiformes. In turn, this would indicate that there is some developmental mechanism that facilitated the evolution of this feather morphotype (similar feathers additionally present in the scansoriopterygid *Epidexipteryx*) (Zhang *et al.*, 2008b), or that these rachis-dominated feathers had some functional significance; potentially, the feathers resulted from a combination of these two factors. The full pennaceous feather morphology in the basal enantiornithine *Eopengornis* suggests that the racket-plume morphology evolved in parallel within Enantiornithes and Confuciusornithiformes; alternatively, the tail feathers in *Eopengornis* could also represent a reversal to the basal condition.

#### RACHIS-DOMINATED FEATHERS: FUNCTION

The unusual width of the rachis, greater than that observed in the remiges, suggests the rachis-dominated tail feathers would have been strong and stiff, more so than the remiges; the lack of deformation in the tail feathers of all observed specimens supports this interpretation (J. O'Connor, pers. observ.). If the feathers were stiff, this would suggest that these feathers would have been an energetically costly feature for the body to produce, which further indicates some function beyond display. This is also supported by the presence of these feathers in juvenile specimens (Fig. 3E) (Zheng *et al.*, 2012). Stiff tail feathers are found in the scansorial woodpeckers, which prop their tails against the tree for support

(Stettenheim, 2000); however, the extreme length, distally tapered rachis (Fig. 3E), and the diversity of morphologies of the distally pennaceous portion of these tail feathers in enantiornithines (the latter feature not present in confuciusornithiforms) are more consistent with an ornamental function (O'Connor *et al.*, 2012) (Fig. 3). Feathers are more commonly modified for display than any other function (Stettenheim, 2000). Elongated tail feathers are the most common form of ornamentation within Neornithes (Fitzpatrick, 1998). Ornamental feathers are considered to be an indicator of 'fitness', with the quality of the feathers being indicative of the health and fitness of the individual; elongation of feathers makes them more prone to damage. The extreme length of the paired tail feathers in primitive birds might have only been achievable by basal birds through a sturdy, wide rachis. Although the feathers are described as rachis-dominated, these feathers are poorly known and it may be incorrect to assume the rachis was an energetically costly feature; it could have been ribbon-like and thus not require an unnecessarily large investment of keratin.

Recent studies on avian tail ornaments indicate that because the tail lies in the wake of the body, even large ornaments have only minimal detrimental effect during low and normal flight speeds (Clark & Dudley, 2009). Given that basal birds were likely poor fliers and Jehol birds lived in a dense forested environment, high-speed flight was probably not an important part of the lifestyle of confuciusornithiforms and Jehol enantiornithines and their large ornaments might have come at minimal cost. The morphology of the racket-plumes in confuciusornithiforms and other enantiornithines relative to those of *Eopengornis* STM24-1 reveal an evolutionary trend in tail ornaments parallel to observations of living birds; in modern taxa, elongate ornamental feathers tend to have narrow proximal widths, which reduces drag (and cost), whereas the distal portion of the feather is typically less asymmetrical, indicating that there is minimal aerodynamic effect from the distal end of the tail (Møller & Hedenström, 1999). Therefore the racket-plumes in Mesozoic birds, which are proximally narrow with symmetrical distal pennaceous portion, would have less of an aerodynamic cost relative to the feathers in *Eopengornis*. As in living birds, the detrimental effects of these ornaments were likely mitigated by the evolution of 'cost-reducing' features such as these. The repeated evolution of the racket-plume morphology within Aves is likely a result of the compromise between maximizing ornamental function and minimizing aerodynamic cost. Hypertrophy (J. O'Connor, pers. observ.) and the evolution of additional pairs of racket-plumes (Zheng, Zhang & Hou, 2007) further supports interpretation of

these feathers as ornaments and suggests that increased ornamental function evolved in some enantiornithines.

#### ACKNOWLEDGEMENTS

We thank Y. Li (IVPP) for preparing the specimen, S. Zhang (IVPP) for assistance with the histology, X-M. Zhang (STM) for assistance, and J. Zhang (IVPP) for photographing the specimen. This research was supported by the National Basic Research Program of China (973 Program, 2012CB821906), the National Natural Science Foundation of China (41172020, 41372014), and the Chinese Academy of Sciences. Data accessibility: the specimen STM24-1 is deposited in the collections of the Shandong Tianyu Museum of Nature, Pingyi, China.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Main slab of STM24-1.

**Figure S2.** Interpretative composite line drawing of the slab and counterslab of STM24-1. Anatomical abbreviations: al, alular metacarpal; al1, first phalanx alular digit; al2, second phalanx alular digit; cav, caudal vertebrae; cev, cervical vertebrae; cor, coracoid; fe, femur; fib, fibula; fur, furcula; gas, gastralia; hum, humerus; hyp, hypocleidium; jug, jugal; lt, lateral trabecula; ma, major metacarpal; ma1, first phalanx major digit; ma2, second phalanx major digit; ma3, third phalanx major digit; mi, minor metacarpal; mi1, first phalanx minor digit; pmx, premaxilla; mtI, metatarsal I; mtI 1, first phalanx of first pedal digit; mtI 2, second phalanx of first pedal digit; mtII, metatarsal II; mtIII, metatarsal III; mtIV, metatarsal IV; pub, pubis; pyg, pygostyle; r, radiale; rad, radius; sca, scapula; sl, semilunate carpal; stn, sternum; str, sternal ribs; sur, surangular; tb, tibia; thv, thoracic vertebrae; u, ulnare; uln, ulna; xr, xiphial region.

**Figure S3.** Close up of the skull in the slab (a) and counterslab (b) of STM24-1. Scale bars = 10 mm. Anatomical abbreviations (not listed in Fig. S2): den, dentary; en, external nares; fr, frontal; l, left; nas, nasal; nf, nasal fossa; max, maxilla; pr, parietal; pr e, parietal embayment; qd, quadrate; r (as prefix), right; th, teeth.

**Figure S4.** Details of axial skeleton in *Eopengornis* STM24-1. (a) Cervical vertebrae, scale bar = 2 mm; (b) cervical vertebra preserving transverse process, scale bar = 2 mm; (c), caudal vertebrae and pygostyle, scale bar = 5 mm. Anatomical abbreviations (not listed in Fig. S2): cp, costal process; poz, postzygapophyses; prz, prezygapophyses; tp, transverse process.

**Figure S5.** Details of the pectoral girdle in Pengornithidae. (a) Close up the main slab of STM24-1; (b) close up of the cranial surface of the humerus in *Pengornis houi* IVPP V15336. Scale bars = 5 mm. Anatomical abbreviations (not listed in Fig. S2): acr, acromion; bc, bicipital crest.

**Figure S6.** Detail of compound bones in *Eopengornis* STM24-1. (a), right carpometacarpus; (b), proximal left tibiotarsus and fibula, caudal view; (c), right distal tarsometatarsus, dorsal view, scale bars = 5 mm. Anatomical abbreviations (not listed in Fig. 2): laf, lateral articular face; pt, popliteal tuberosity.

**Figure S7.** Histology of STM24-1: composite image of entire section of the humerus (A) ulna (B), and femur (C); close up of the LAG in the humerus (D); close up of the ICL and OCL in the femur (E). Note that the humeral (A) and femoral (C) sections are more vascularized in the upper half of the section.

**Figure S8.** Cladogram depicting the consensus of the 19 most parsimonious trees.

**Table S1.** Select comparative measurements of Pengornithidae.