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## A NEW EARLY CRETACEOUS ENANTIORNITHINE (AVES, ORNITHOTHORACES) FROM NORTHWESTERN CHINA WITH ELABORATE TAIL ORNAMENTATION

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**ABSTRACT**—We provide a detailed description of a well-preserved enantiornithine specimen (GSGM-05-CM-004) from the Lower Cretaceous (Aptian) Xiagou Formation of northwestern Gansu Province, China, for which we erect the new taxon *Feitianius paradisi*, gen. et sp. nov. This specimen has a distinctive pelvic morphology and can be further distinguished from all other Mesozoic birds by a unique caudal plumage formed by multiple rectricial morphotypes. This newly documented tail morphology reveals a previously unrecognized level of complexity in the plumage of basal birds. This complex tail-feather morphology has a parallel in extant sexually dimorphic birds in which the males have the most altered tails; thus, we identify this specimen as male. Ornamental tail morphologies, such as the novel tail plumage described here, dominate Enantiornithes. This reinforces hypotheses that sexual selection was a major driving force in the evolution of basal bird plumage.

<http://zoobank.org/urn:lsid:zoobank.org:pub:8BEF4422-58C5-487B-B76A-51C5855CF87B>

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

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### INTRODUCTION

Initiated in 2002, renewed paleontological explorations of exposures of the Lower Cretaceous (Aptian) Xiagou Formation in the Changma Basin of northwestern Gansu Province, China, have yielded approximately 100 partial to nearly complete fossil avian skeletons, many preserved with soft tissues. Although the majority of these specimens are referable to the ornithuromorph *Gansus yumenensis* Hou and Liu, 1984 (You et al., 2006), three other ornithuromorph species have recently been recognized based on isolated specimens (Wang et al., 2013), and at least 12 other specimens pertain to Enantiornithes (You et al., 2005; Harris et al., 2006; Lamanna et al., 2006, 2009; Ji et al., 2011; Wang et al., 2015), a group that is widely recognized as the dominant clade of Cretaceous landbirds (O'Connor et al., 2011). None of the Changma enantiornithine specimens preserve either cranial material or an association of pectoral and pelvic

elements, frustrating attempts to decipher their taxonomy; nevertheless, the collection appears to be taxonomically diverse, although only two taxa (Ji et al., 2011; Wang et al., 2015) have been erected to date.

Although most of the Changma enantiornithine specimens are fragmentary, a few are more complete and anatomically informative. The most remarkable of these are two articulated partial specimens, GSGM-05-CM-004 and GSGM-07-CM-001, which each include the caudal half of the axial skeleton, the pelvic girdle, the hind limbs, and extraordinarily preserved soft tissue structures (Lamanna et al., 2009). Both specimens preserve numerous feathers of multiple morphologies; however, the tail feathers have only been described in GSGM-07-CM-001 (O'Connor et al., 2012). This specimen preserves a pair of elongate, rachis-dominated 'racket plumes,' the most common rectricial morphology observed among Early Cretaceous birds, present in confuciusornithiforms and numerous enantiornithines (e.g., *Bohaiornis guoi* Hu et al., 2011, *Dapingfangornis sentisornis* Li et al., 2006, *Paraprotopteryx gracilis* Zheng et al., 2007, *Protopteryx fengningensis* Zhang and Zhou, 2000). Here we describe the second specimen, GSGM-05-CM-004, which preserves a rectricial morphology that has not been observed in any

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other Mesozoic bird but that is reminiscent of the elaborate tails of some extant sexually dimorphic birds. We erect a new taxon based on this specimen and discuss the implications of its unique caudal plumage for our understanding of tail evolution among basal birds.

**Institutional Abbreviations**—**DNHM**, Dalian Natural History Museum, Dalian, Liaoning Province, China; **GSGM**, Gansu Geological Museum, Lanzhou, Gansu Province, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **LPM**, Liaoning Paleontological Museum, Shenyang, Liaoning Province, China.

## SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

ORNITHOTHORACES Chiappe, 1995a

ENANTIORNITHES Walker, 1981

*FEITIANIUS PARADISI*, gen. et sp. nov.

**Holotype**—GSGM-05-CM-004, an incomplete but articulated specimen preserving the caudal half of the skeleton (mostly in left lateral view) on a single slab, including carbonized vestiges of the caudal body coverts, rectrices, and keratinous pedal ungual sheaths.

**Diagnosis**—A small enantiornithine bird with the unique combination of the following features: shallow pneumatic excavations on the lateral surfaces of the thoracic vertebrae; ilium with a very small cuppedicus fossa; robust, curved, weakly retroverted pubis with a dorsally tapered pubic boot; ischium weakly sigmoid with a delicate ridge inferred for muscle attachment on the cranial half of the lateral surface; medial plantar crest well developed on the tarsometatarsus, but lateral plantar crest minimally developed; penultimate pedal phalanges the longest in each digit; non-ungual phalanges of digit II are dorsoplantarly compressed and mediolaterally wide; and pedal unguals large and relatively weakly recurved with long horny sheaths. The species can further be distinguished by its unique tail plumage, which is composed of several different rectricial morphotypes (all other known enantiornithines preserve only a single rectricial morphotype).

**Etymology**—*Feitianius paradisi*, meaning Paradise's feitian (飞天), referring to the hundreds of paintings of feitian, or 'flying apsara,' in the Mogao caves that are not far from the type locality. Like the new species, the feitian were beautiful flying creatures. 'Paradisi' (Latin, genitive 'from paradise') refers to the similarity in tail morphology between the new fossil and the highly sexually dimorphic plumages of extant birds of paradise. For fun, we decided to masculinize the genus name because the holotype specimen appears to be a male.

**Measurements**—See Table 1.

**Locality and Horizon**—Lower Cretaceous (lower-middle Aptian) (124–120 Ma; (Suarez et al., 2013) Xiagou Formation, near Changma Village, Yumen City, Gansu Province, northwestern China.

**Taxonomic Remarks**—The specimen can be referred to Enantiornithes based on its possession of the following characters: excavated thoracic vertebrae with centrally located parapophyses; distinctive, large pygostyle with craniodorsal fork, ventrolateral processes, and distal constriction; ischium with strap-like proximodorsal process; and reduced metatarsal IV. Specimen GSGM-05-CM-004 can be differentiated from *Qiliania graffini* Ji et al., 2011, another enantiornithine from the same formation, by several features. First, *Feitianius paradisi* bears a medial plantar crest on metatarsal II (absent in *Q. graffini*). Although the proportions of the pubis and ischium are similar between the two taxa, the dorsal (caudal) margin of the pubis and ventral (cranial) margin of the ischium are concave in *F. paradisi*, whereas both of these surfaces are relatively straight in *Q. graffini*. Furthermore, the proportions of the pedal digits are

quite different: the combined length of digit III compared with that of metatarsal III is 1.05 in the new species compared with 0.92 in *Q. graffini*; the same ratio for digit II is 0.77 in *F. paradisi* and 0.70 in *Q. graffini*. In addition, in *F. paradisi*, the hallucal claw is comparatively more recurved and the penultimate phalanx of digit III is subequal in length to the proximal phalanx (the proximal phalanx is longest in *Q. graffini*). The pubis of the indeterminate Xiagou Formation enantiornithine GSGM-04-CM-007 is rod-like, and its distal end is curved 90° to the proximal shaft (Lamanna et al., 2006), whereas in *Feitianius* the pubis is dorsoventrally compressed and ends in a pubic boot. Unfortunately, there are no overlapping skeletal elements to compare with *Dunhuangia lii* Wang et al., 2015, a newly described enantiornithine from Changma (Wang et al., 2015). Compared with other enantiornithines, the pygostyle is proportionally shorter than in species of the Longipterygidae, the tarsometatarsus is considerably more gracile than in all species within the Bohaiornithidae or Avisauridae, and the metatarsal and digit I are shorter than in species of the Pengornithidae. *Feitianius paradisi* is most similar to Jehol 'cathayornithiforms' such as species of *Cathayornis*, *Eoenantiornis*, *Protopteryx*, and *Sinornis* but differs from these taxa in the detailed anatomy of the pelvic girdle.

## DESCRIPTION

### Skeletal Anatomy

**Axial Skeleton**—The caudal-most five thoracic vertebrae are preserved in near-complete articulation with each other and the synsacrum (Fig. 1). They are similar to those of other enantiornithines (Chiappe and Walker, 2002), except that the lateral excavations are shallow and notably less groove-like. The first preserved vertebra appears to be slightly craniocaudally shorter than the rest. The parapophyses are centrally located, as in other enantiornithines, just cranioventral to the transverse processes. The neural spines are tall and dorsally expanded both cranially and caudally, such that they are fan-shaped in lateral view, with longer dorsal than ventral ends. The vertebrae are amphiplatyan. The ventral surfaces of the cranial-most three thoracic vertebrae each bear a slight groove—this is absent in the caudal-most two vertebrae, which may indicate that it is a diagenetic artifact. The articular surfaces of the thoracic vertebrae are much larger than the vertebral foramen. The synsacrum is largely obscured by the articulated pelvic girdle; however, the visible portions are fully fused. The cranial articular surface of the synsacrum is flat. The lateral surface is also flat, lacking the pneumatic fossae ('pleurocoels') present in ornithuromorphs (Clarke, 2004). The synsacrum is dorsoventrally taller at the cranial end, gradually decreasing in height caudally. A well-developed spinous crest appears to be present along the entire length of the synsacrum, slightly decreasing in height caudally.

Five to six articulated free caudal vertebrae are preserved in left lateral view, revealing tall neural spines that are more than half the heights of their respective centra. These vertebrae also possess broken, distolaterally oriented transverse processes. The prezygapophyses are reduced, whereas the postzygapophyses are approximately one-third the length of the centrum (Fig. 2B). The combined length of the free caudals slightly exceeds that of the pygostyle, as in some enantiornithines, whereas the pygostyle is longer in many other members of the clade (e.g., *Iberomesornis romerali* Sanz and Bonaparte, 1992, *Longipteryx chaoyangensis* Zhang et al., 2000) and much shorter in others (all species in the Pengornithidae).

The pygostyle is typically enantiornithine in morphology (Chiappe and Walker, 2002; Chiappe et al., 2002): it is fairly large and robust, and bears paired ventrolateral processes that extend the proximal three-fourths of the pygostyle before disappearing distally to form a constriction along the distal one-fourth; the distal tapered portion is poorly preserved and the tip is preserved only as an impression (Fig. 2B). The proximal end of the left ventrolateral process is thick compared with that of

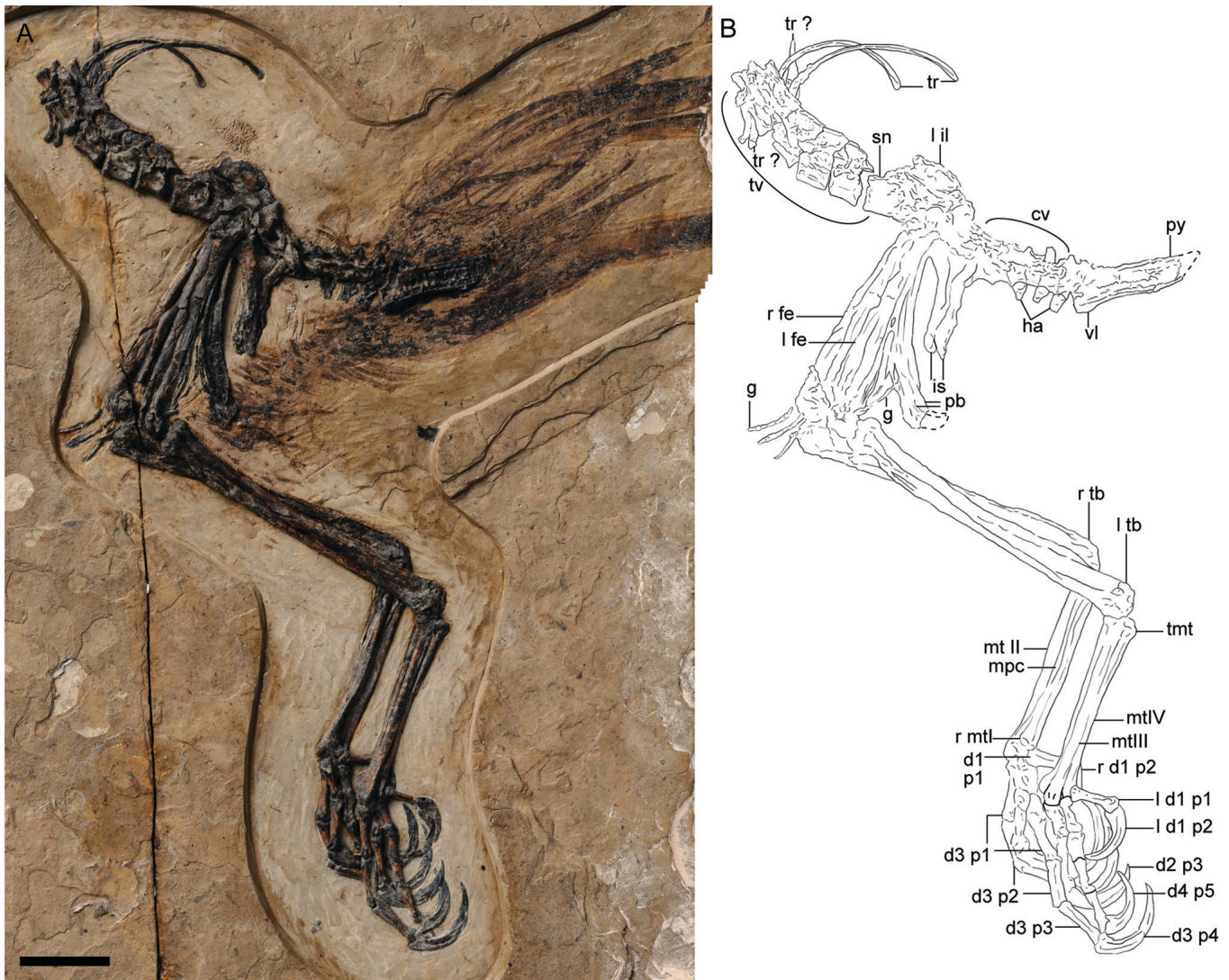


FIGURE 1. **A**, photograph and **B**, line drawing of specimen GSGM-05-CM-004, the holotype of *Feitianius paradisi*, gen. et sp. nov. **Abbreviations:** **cv**, caudal vertebrae; **d**, digit; **fe**, femur; **g**, gastralia; **ha**, hemal arches; **il**, ilium; **is**, ischium; **mpc**, medial plantar crest; **mtI–IV**, metatarsals I–IV; **p**, phalanx; **pb**, pubis; **py**, pygostyle; **sn**, synsacrum; **tb**, tibiotarsus; **tmt**, tarsometatarsus; **tr**, thoracic ribs; **tv**, thoracic vertebrae; **vl**, ventrolateral process; **r** and **l** as prefixes denote right and left, respectively. Scale bar equals 10 mm.

other known enantiornithines, whereas this process is thin and of an even thickness throughout in *Halimornis thompsoni* Chiappe et al., 2002. This process appears more laterally directed than in *H. thompsoni*, such that the pygostyle is dorsolaterally excavated, as in *Sinornis santensis* Sereno and Rao, 1992. This suggests that the ventral surface was not as deeply concave as in *H. thompsoni* but formed a shallow and wide excavation, as in *Rapaxavis pani* Morschhauser et al., 2009. The proximodorsal surface also bears a pair of short, triangular processes (often described as a ‘dorsal fork’), as in most other enantiornithines, but only the left process is visible; it cannot be determined if the proximodorsal fork was continuous with the proximal end of a dorsal concavity as in *Halimornis*. Faint but distinguishable remnants of the processes of the incorporated caudal vertebrae are visible throughout the pygostyle; they are especially clear in the proximal half. These processes are not as obvious as in the holotype of *I. romerali*, which is regarded as ontogenetically immature (Sanz and Bonaparte, 1992). Although any such estimate is inherently tentative, we suggest that nine or 10 vertebrae were incorporated into the pygostyle.

A single pair of complete thoracic ribs is preserved in association with the cranial-most preserved thoracic vertebra; these are still in articulation with the vertebra but not in situ, having been dorsally displaced, possibly when the cranial half of the skeleton was disarticulated and lost (Fig. 1). Additional thoracic rib fragments are clustered near the first preserved thoracic vertebra. Several disarticulated gastralia are preserved between the pubes and femora. Three additional gastral elements are preserved, apparently in articulation, near the cranial margin of the knee joint. Because they all appear to be from one side of the gastral basket, a minimum of three pairs of gastralia were present in *F. paradisi*, although we suggest that the gastral basket was probably larger (because it ranges from six to 10 pairs of elements in known enantiornithines; O'Connor et al., 2015). The free caudal vertebrae are articulated with large, unfused hemal arches that are plate-like, approximately twice as long as they are wide, and bluntly tapered distally.

**Appendicular Skeleton**—The pelvic girdle elements are unfused. All are represented, but the ilia are incomplete: only a fragment of the preacetabular wing of the left ilium is preserved



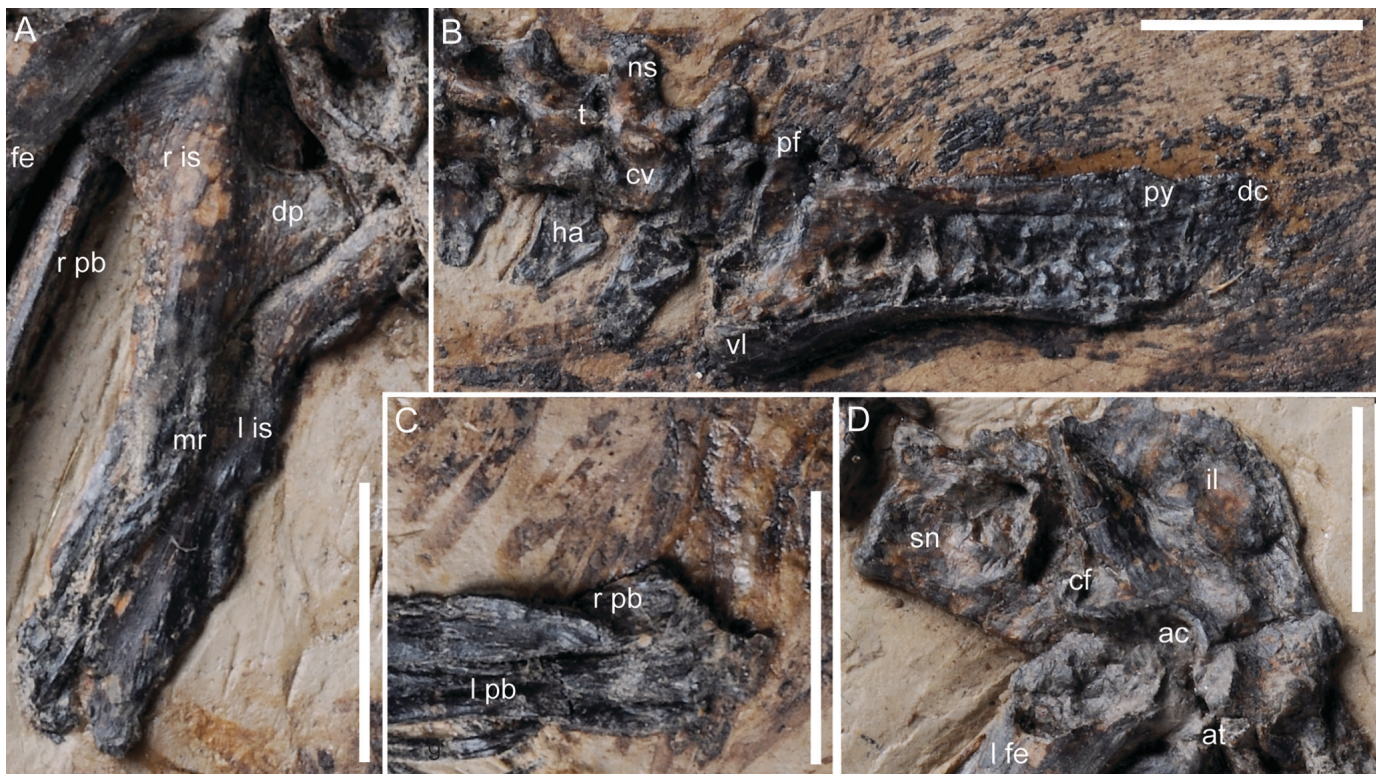


FIGURE 2. Detail photographs of important morphologies preserved in GSGM-05-CM-004. **A**, ischia; **B**, caudal vertebrae including pygostyle; **C**, distal ends of the pubes; **D**, right hip. **Abbreviations:** ac, acetabulum; at, antitrochanter; cf, cuppedicus fossa; dc, distal constriction; dp, dorsal process; mr, muscle ridge; ns, neural spine; pf, proximal fork; t, transverse process; and as in Figure 1. Scale bars equal 5 mm.

(Fig. 2D). This fragment suggests that the preacetabular wing was dorsoventrally broad, as in other enantiornithines. A small cuppedicus appears to excavate the ventral surface cranial to the acetabulum. The preacetabular wing is laterally concave. Compared with the ischiadic peduncle, the pubic peduncle is more robust and projects farther ventrally, as in most other enantiornithines (O'Connor, 2009). The pubic peduncle is not mediolaterally compressed, in contrast to the compressed and hook-like pubic peduncles of *L. chaoyangensis* (Zhang et al., 2001) and *Parabohaiornis martini* Wang et al., 2014a.

The pubes are preserved nearly in perfect articulation with the ilium and ischium; they have been compressed together, such that the left is in dorsolateral view and the right is in medial view. The proximal half of each pubic shaft has a lachrymiform (i.e., teardrop-shaped) cross-section, with the long axis oriented mediolaterally and the tapered side positioned medially. The shaft is dorsoventrally compressed and approximately twice as wide as it is thick, as in *Q. graffini*. The pubes are more rod-like in the indeterminate enantiornithine GSGM-04-CM-007. The pubic shafts become laterally compressed distally, and the distal one-tenth of the right pubis bears a flange for articulation with the left pubis. The pubis ends in a dorsally projecting, tapered boot (Fig. 2C); the extreme dorsal curvature present in the distal pubis of GSGM-04-CM-007 was clearly absent, whereas in *Q. graffini* the distal end of the pubis is bent ventrally as preserved. The pubic shafts of *F. paradisi* are weakly curved, such that their dorsal surfaces are concave, whereas the pubic shafts are straight in *Q. graffini*. The pubes are not strongly retroverted, although we interpret this condition as exaggerated by the disarticulation of the pelvic girdle and synsacrum. Although visually obfuscated by their curvature, the ischia are parallel to the pubes, as in *Q. graffini* (Ji et al., 2011).

Both ischia are preserved, the left overlapping the right, in lateral and medial views, respectively (Fig. 2A). The ischia are slightly less than two-thirds the length of the pubes; each is mediolaterally thin and plate-like, with a distinct, tab-like, craniodorsally directed dorsal process, as in most other enantiornithines (Chiappe and Walker, 2002). As in *Q. graffini* and other enantiornithines, the dorsal process is not fused to the postacetabular wing of the ilium (Ji et al., 2011). The pubic peduncle of the ischium is broad and much larger than the narrower iliac peduncle; the dorsal process of the ischium is slightly smaller than the pubic peduncle. The ventral surface of the ischium is weakly concave, such that it curves toward the pubis, similar to the morphology in *Shenqiornis mengi* Wang et al., 2010, whereas this surface is straighter in *Q. graffini*. The distal end of the ischium of *Feitianius* is slightly deflected dorsally, which gives the bone a weakly sigmoid appearance; the distal tip is also deflected in the generally straighter ischium of *Q. graffini*, but such deflection is absent in *S. mengi*. This deflection is pronounced in *S. santensis*, such that the blade of the ischium is curved dorsally (Serenó et al., 2002). A blunt, longitudinal lateral ridge is present along the proximal half of the ischial corpus; this ridge seems to disappear distally, but its distal half is obscured by breakage. A similar ridge is present in several ornithuromorphs (e.g., *Schizoura lii* Zhou et al., 2012, *Yixianornis grabaui* Zhou and Zhang, 2001) and in the enantiornithines *Q. graffini* and *S. santensis*; in the latter two taxa, this ridge is more strongly developed and has greater lateral projection than in both *Feitianius* and Early Cretaceous ornithuromorphs. This ridge may correspond to the attachment of the m. puboischiofemoralis lateralis (Hutchinson, 2001). The lateral surface of the ischium is convex proximally and flat distally, such that the bone becomes more mediolaterally compressed along its caudal half, similar to the condition in *S.*



*santensis*. The medial surface of the ischium is flat. In *Q. graffini*, the lateral ridge for muscle attachment is reduced distally, such that the caudal half of the ischium has a triangular cross-section, with the apex formed by the muscle ridge. In *Feitianius*, by contrast, the cross-section of this part of the ischium is flat. Due to compression, the two ischia are preserved parallel to one another, as are the pubes; nevertheless, some degree of medial curvature was surely present in the pubes and also cannot be ruled out for the ischia. Medially curved ischia are evident in enantiornithine pelvises exposed in dorsal view (e.g., those of GSGM-07-CM-001 and *Concornis*).

Both hind limbs are completely preserved. The femur is proportionally longer in the indeterminate enantiornithine GSGM-04-CM-007, but the relative proportions of the hind limb elements of *Feitianius* are similar to those of *Q. graffini*: the femur is approximately 20% longer than the tarsometatarsus (femur to tarsometatarsus length ratio of 1.194 in *Feitianius* vs. 1.197 in *Q. graffini*); the femur to tibiotarsus length ratio is 0.759 (0.755 in *Q. graffini*); and the tarsometatarsus to tibiotarsus length ratio is 0.636 (0.630 in *Q. graffini*). These similar proportions may suggest that the two taxa occupied comparable ecological niches, which would not be surprising given that they were collected from the same locality. Unfortunately, neither of the *Feitianius* femora reveals additional anatomical information due to breakage and their articulation with the pelvic girdle. The tibiotarsus appears to be fully fused. The proximal end of the cranial surface of the right tibiotarsus is exposed, and it appears to have borne a low cnemial crest similar to that of *Soroavisaurus australis* Chiappe, 1993. This crest does not appear to be as pronounced as that of *Q. graffini*. The left tibiotarsus is exposed in caudolateral view. The fibular crest is well developed but short, occupying approximately one-fifth the length of the tibiotarsus and is clearly separated from the proximal end of the bone as in other basal birds. On the proximocaudal surface, the lateral articular facet and popliteus tuberosity (well developed in species of Pengornithidae and Neornithes) do not seem to be developed, nor is a flexor fossa present. The fibula is fairly robust along the proximal one-third of the tibiotarsus; distally, it rapidly becomes reduced to a splint. Although its distal end is not clear, the fibula undoubtedly terminated well proximal to the distal tarsals, as in other ornithothoracines with the exception of pengornithids. We estimate that the fibula was two-thirds the length of the tibiotarsus. Distally, the cartilaginous articular surface of the tibiotarsus extends weakly onto the caudal surface of the bone, as in *Q. graffini* (Ji et al., 2011) and other enantiornithines.

Both pedes are preserved. The left tarsometatarsus is preserved in dorsolateral view, and the right in plantaromedial view (Fig. 3). The tarsometatarsus is fused proximally. Distally, the metatarsals are disarticulated from one another, indicating that they were ankylosed only proximally. As in other enantiornithines, in dorsal view, metatarsal IV is mediolaterally thinner than metatarsals II and III (Chiappe and Walker, 2002). The third metatarsal is the longest, followed by metatarsal IV and then II, although the latter are nearly subequal in length, as is typical of basal birds with the notable exceptions of *Longipteryx chaoyangensis* and *Yungavolucris brevipedalis* Chiappe, 1993 (Chiappe, 1993; Zhang et al., 2001). Metatarsal III is more robust than metatarsal II, as in *Q. graffini* (Ji et al., 2011). The cranial surface of metatarsal III is weakly convex proximally but becomes flatter distally, and is flat along its distal one-fourth. As in *Q. graffini*, a tubercle that is inferred to be the attachment site of the m. tibialis cranialis is located on the dorsal surface of metatarsal II, one-fifth the length from the proximal end. In the left tarsometatarsus, the trochleae of metatarsal II and especially metatarsal IV are preserved plantarly displaced relative to that of metatarsal III. We interpret this as due to disarticulation of the distally unfused metatarsals, because metatarsals II and IV of the right tarsometatarsus do not appear to be plantarly



FIGURE 3. Detail photograph of the pedes of GSGM-05-CM-004. **Abbreviations:** tc, attachment of the m. tibialis cranialis; and as in Figure 1. Scale bar equals 5 mm.

displaced. In *Q. graffini*, the trochlea of metatarsal II is similarly plantarly displaced due to disarticulation. Metatarsal II of *Feitianius* bears a well-developed medial plantar crest along the middle one-third of the shaft, which creates and bounds an excavation on the plantar surface of the tarsometatarsus; whereas only a weak and proximally restricted plantaromedial thickening is present in *Q. graffini*. A very weak lateral plantar crest is present near the midpoint of metatarsal IV. Both medial and plantar crests were reported in the indeterminate enantiornithine

TABLE 1. Pelvic girdle and hind limb measurements (mm) of published enantiornithines from the Xiagou Formation.

Dimension	Specimen			
	<i>Feitianius</i> 05-CM-004	<i>Qiliania</i> 05-CM-006	Lamanna et al., 2006 04-CM-007	07-CM-001
Ilium	16.3*	—	—	16.6‡
Acetabulum	1.9	2.5	1.6	—
Pubis	23.4†	17.5	22.9	—
Ischium	13.7	11.5*	—	14.2
Ischium:pubis	0.585	0.657	—	—
Femur	27.1	24.3	24.0	26.3‡
Femur:pubis	1.158	1.389	1.048	—
Tibiotarsus	35.7	32.2	29.2†	34.4‡
Femur:tibiotarsus	0.759	0.755	0.822	0.765
Fibula	14.9*	—	—	—
Tarsometatarsus	22.7	20.3	20.3	21.6
Tmt:Tbt	0.636	0.630	—	0.628
Femur:Tmt	1.194	1.197	—	1.218
Metatarsal I	4.7	3.2	3.1*	5.4†
Metatarsal II	20.5†	19.2	19.6	20.4
Metatarsal III	22.7	20.3	20.3	21.6
Metatarsal IV	21.3	—	19.1	20.8‡
Pedal phalanx I-1	5.1	4.2	4.3	5.4‡
Pedal phalanx I-2	5.5†	4.4	3.9†	5.2
Pedal phalanx II-1	4.5	3.7	3.6	4.7
Pedal phalanx II-2	6.2	4.8	4.9	5.8‡
Pedal phalanx II-3	5.0†	4.9	4.4	5.9
Pedal phalanx III-1	6.3‡	4.6	4.8	5.9‡
Pedal phalanx III-2	5.5‡	4.0	4.0	5.3
Pedal phalanx III-3	6.2	4.2	5.0	5.9
Pedal phalanx III-4	6.0†	5.8	4.4	5.8‡
Combined digit III:mt III	1.057	0.916	0.897	1.060
Pedal phalanx IV-1	3.2‡	—	2.8	3.4
Pedal phalanx IV-2	2.8‡	2.3	2.0	2.7
Pedal phalanx IV-3	3.1‡	2.4	2.2	3.1
Pedal phalanx IV-4	4.7	2.8	3.7	4.3
Pedal phalanx IV-5	5.5†	4.4	4.7†	5.1†

Measurements are for proximodistal lengths, unless otherwise indicated. Dagger symbol (†) indicates estimated lengths; double-dagger (‡) indicates measurements averaged from the right and left; asterisk (\*) indicates incomplete elements, preserved lengths.

GSGM-04-CM-007 (Lamanna et al., 2009). No proximal vascular foramina are apparent, although it appears that a distal foramen existed between metatarsals III and IV, but has been obscured by the plantar displacement of the latter element; this foramen would clearly have been closed distally by an unfused contact. The trochleae of metatarsals II and III are ginglymous, but that of metatarsal IV is reduced to a single condyle, as in other enantiornithines. Metatarsals II and III have well-developed pits for the collateral ligaments on the medial and lateral surfaces of their trochleae. A shallow dorsal trochlear depression is also present on metatarsal III. The distal margin of metatarsal II appears to be slightly angled, such that the medial trochlear ridge is located slightly proximal to the lateral ridge, which is also comparatively weaker and does not project as strongly in the plantar direction. A similar morphology is observed in GSGM-07-CM-001.

The pedal phalangeal formula is 2-3-4-5-x, as in other Mesozoic birds. The penultimate phalanges are the longest in each digit, which in living birds is indicative of arboreality (Hopson, 2001), and among Early Cretaceous enantiornithines has only been previously documented in *R. pani* (Morschhauser et al., 2009). Compared with the indeterminate enantiornithine GSGM-04-CM-007, the pedal phalanges of *Feitianius* are more robust and distally elongate, and the ungual phalanges are more recurved. Pedal digits II and III are proportionally longer than in *Q. graffini*, which, in turn, has proportionally longer digits than GSGM-04-CM-007.

Metatarsal I articulates on the caudomedial surface of metatarsal II, but its trochlea angles laterally, such that digit I is fully reversed as in *Q. graffini* and other enantiornithines.

Metatarsal I is 'P'-shaped, with its proximal and distal articular surfaces nearly perpendicular to each other. Its shaft is short and its trochlea is relatively long, such that the former is only slightly longer than the latter (shaft typically longer). The ungual phalanx is more robust and recurved than that of the other digits, although it is slightly shorter than the unguals of digits II and III. The keratinous ungual sheath is long and relatively straight.

In pedal digit II of *Feitianius* the penultimate phalanx is nearly 40% longer than the first phalanx (Table 1). The ungual is long but weakly recurved in order to accommodate the long horny sheath, which increases the length of the claw by two-thirds. The non-ungual phalanges of digit II are dorsoplantarly compressed and mediolaterally wide, such that the proximal articular surface is more than twice as wide as tall; this morphology is absent in *Q. graffini*. The third digit is the most robust in lateral view and is composed of three phalanges of subequal length; of these, the second phalanx is marginally the shortest and the penultimate phalanx is longest. The claw is approximately as long as that of the second digit. The first phalanx of the fourth digit is the shortest but also the most robust; the second and third phalanges are subequal in length. The penultimate phalanx is the longest, as in the other digits.

#### Soft Tissues

In addition to the keratinous sheaths of the pedal unguals described above, specimen GSGM-05-CM-004 preserves an array of soft tissues in the vicinity of the ventral pelvic elements, free caudal series, and pygostyle, including a caudal

plumage that was previously unknown among Mesozoic birds (Fig. 4). Although the specimen only preserves feathers from the caudal and caudoventral regions of the body, several distinct morphologies are evident in these areas. Unfortunately, the overall preservation of the feathers of *Feitianius* is poor, and although multiple varieties of differing sizes can be identified, the morphological details of each are difficult to ascertain. Attempts to interpret these preserved soft tissues are further complicated by the frequent overlap of the feathers with each other and with other tissues. Short body covert feathers are preserved ventrally, between the pubes and hind limbs, sometimes overlapping with band-like soft tissue structures that are clearly preserved only within the soft tissue outline of the body. We tentatively interpret the latter structures as internal soft tissues, possibly bands of collagen, but this identification is equivocal. Similar bands are present in a referred specimen of the confuciusornithiform *Eoconfuciusornis zhengi* Zhang et al., 2008 (STM7-144; J.K.O'C., pers. observ.). As in the referred specimen of *E. zhengi*, the bands in *Feitianius* are of equal length (7–8 mm) and thickness (approximately 0.5 mm) and are oriented largely parallel to each other and roughly perpendicular to the body outline (Fig. 4). A dark organic residue that gradually decreases in dorsoventral thickness distally extends from the last caudal vertebrae past the distal margin of the pygostyle (Fig. 4); the dorsal margin of this mass is straighter and much thinner over the pygostyle than the ventral margin. We interpret this as the carbonized remnant of the 'pope's nose,' the soft tissue that surrounds the pygostyle, including the rectricial bulb muscles and oil glands (Gill, 2007).

Down-like covert feathers delineate the caudal and caudoventral margins of the body, extending caudally from the vicinity of the distal end of the pubis, but not reaching the level of the distal margin of the pygostyle; beyond this point, the coverts are either pressed against the body or not preserved. They are approximately 7 mm in length in the pelvic region, increasing to roughly 12 mm along the dorsal surface. These coverts extend caudally along the dorsal margin of the caudal skeleton, but in this region their details are obscured by overlap with more elongate feathers of varying morphologies that project caudally and caudodorsally from the pygostyle. One ventral-most covert, preserved level with the distal half of the pygostyle and not obscured by overlap, appears to be pennaceous; short barbs are preserved angled towards a narrow rachis (Fig. 4C).

The tail plumage itself is composed of a large number of rectrices of varying lengths and morphologies (Fig. 4A, B). We estimate that a minimum of 12 rectrices were present; however, their suboptimal preservation, substantial overlap, and considerable morphological variation preclude a definitive assessment in this regard. Two distinct morphotypes may be differentiated most readily by length, whereas a third type is most easily distinguished by its morphology. Although distally incomplete, the longer of the former two rectricial morphotypes (here termed 'morphotype A' for ease of description) are at least 40–45 mm in length, whereas the shorter feathers ('morphotype B') are approximately 18 mm long. Although a rachis is not evident in any of these feathers, we interpret this as a taphonomic artifact; vanes are clearly preserved in some, and as such, we consider all of these feathers to be pennaceous. Whereas most of these rectrices appear to project from the dorsal margin of the distal-most free caudals and pygostyle, one or two others seem to originate directly from the distal margin of the latter element.

Approximately five to seven feathers of 'morphotype A' are present. We interpret these as being exposed primarily in lateral view, with only the rachis and lateral vane visible. Thus, we cannot determine if these feathers were asymmetrical. The darker color of the upper margins of these feathers as preserved is thought to be a consequence of overlap with the medial vane.

Barbs only appear to be present along the distal 55% of each of these rectrices. These barbs meet the rachis at an angle of approximately 15° and become more elongate distally. The 'morphotype A' feathers are curved, such that their dorsal margins are convex.

At least five of the shorter, smaller 'morphotype B' feathers are unquestionably preserved, with more almost certainly present but obscured by overlap with other feathers. 'Morphotype B' feathers are approximately one-half the length and distal width of their 'morphotype A' counterparts, at least as the latter are preserved; however, because most of these longer feathers are distally incomplete, they likely were considerably more than twice the length of the 'morphotype B' feathers in life. All 'morphotype B' feathers taper distally. They do not present clear evidence for either a rachis or barbs; several of them, however, preserve a dark longitudinal line that we interpret as the rachis. The presence of this structure, coupled with the lengths of these feathers, strongly suggests that they are pennaceous. The appearance of the several 'morphotype B' feathers preserved in lateral view suggests that they are curved, such that their dorsal surfaces are convex, although to a lesser degree than in 'morphotype A.' In 'morphotype B,' the vane appears to maintain an even thickness and to extend along most of the length of the feather rather than being restricted to its distal preserved half as in 'morphotype A.'

Rachis-dominated feathers similar to those preserved in the holotypic specimen of *P. fengningensis* are also present in GSGM-05-CM-004 ('morphotype C'). Similar to the conditions in the holotypes of *P. fengningensis* and *B. guoi*, only the proximal portions of the 'morphotype C' feathers are preserved in *Feitianius*, so their total lengths and the morphologies of their distal ends cannot be determined. In GSGM-05-CM-004, the rachis-dominant feather(s) is preserved as a single straight swath of organic carbon projecting directly distally from the pygostyle. The feather lacks any evidence of barbs, but the wide rachis is longitudinally 'striped' and bears a narrow strip of undifferentiated vane visible on the dorsally preserved margin, as in the rachis-dominated 'racket-plume' rectrices (i.e., 'elongate ribbon-like tail feathers' of Zhang et al., 2006) of other enantiornithines (e.g., the holotype specimens of *B. guoi*, *D. sentisorninus*, *P. gracilis*, *P. fengningensis*), and confuciusornithiforms (O'Connor et al., 2012). A wide, dark carbonized trace of equal thickness is present ventrally. This structure preserves no discernible features such as barbs, rendering it difficult to interpret. It may represent the lateral or medial vane, multiple overlapping feathers, or both. However, the even thickness of this carbonized structure suggests that it might correspond to a wide medial vane. Similar rachis-dominated feathers are preserved in the holotype of *Eopengornis martini* Wang et al., 2014b, in which the tail is formed by a pair of elongate, fully pennaceous feathers with a wide medial vane (the width of which is greater than the width of the trailing edge vane in the remiges) and a narrow lateral vane, both of which maintain a fairly even thickness throughout the full proximodistal length of the feather (Wang et al., 2014b).

#### PHYLOGENETIC ANALYSIS

We conducted a phylogenetic analysis to elucidate the relationships of *Feitianius* to other enantiornithine birds. We modified the data matrix of O'Connor and Zhou (2013) to include *Feitianius* as well as all other published enantiornithine taxa (except the recently described *Dunhuangia lii*) and specimens from the Xiagou Formation of the Changma locality (a total of six additional operational taxonomic units; *Qiliania*, GSGM-02-0901, GSGM-04-CM-007, GSGM-04-CM-023, and GSGM-07-CM-001) (You et al., 2005; Harris et al., 2006;



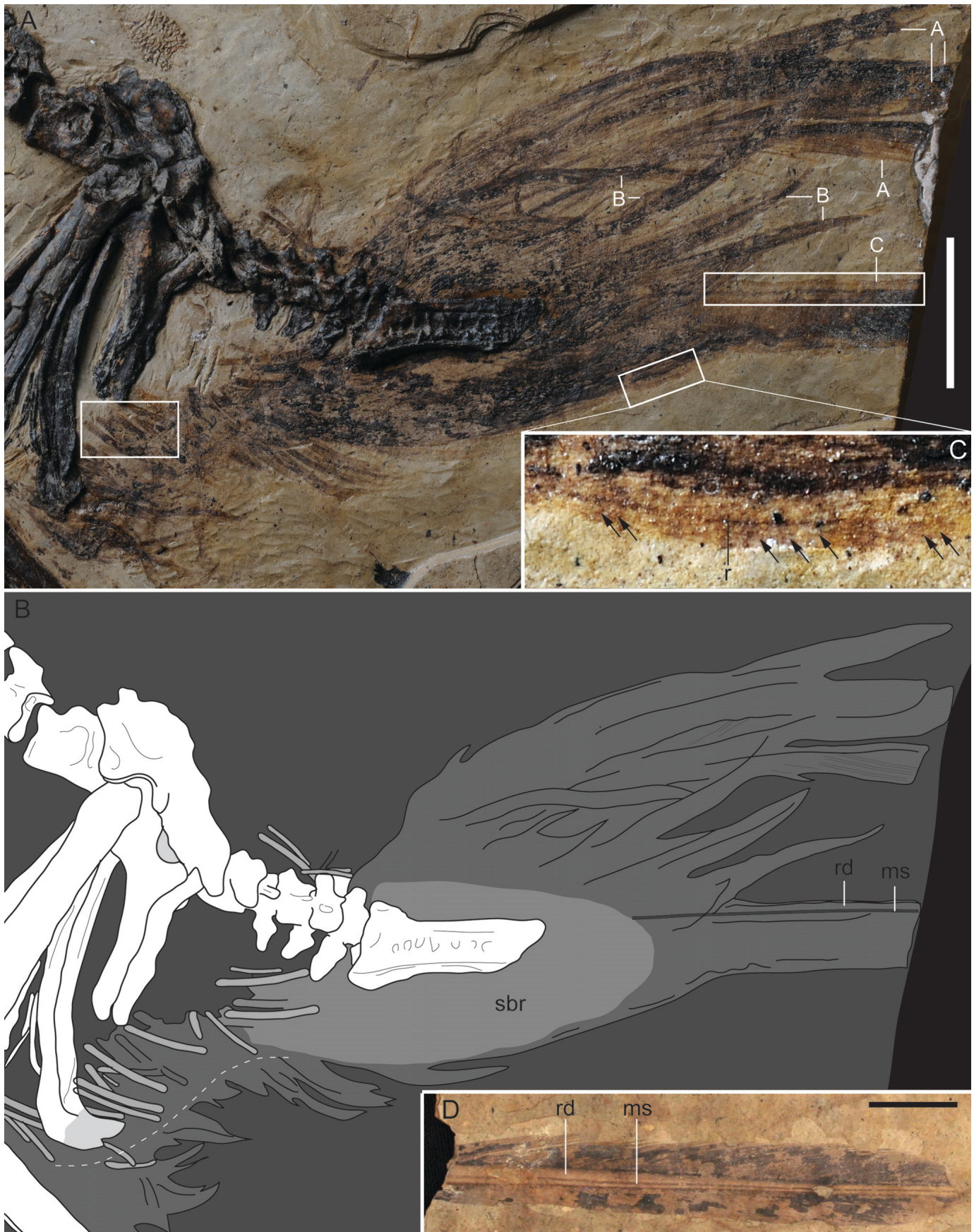


FIGURE 4. Detail images of the caudal plumage of GSGM-05-CM-004. **A**, photograph; **B**, interpretive drawing; **C**, detail of the pennaceous covert; **D**, photograph of one of the 'racket plumes' preserved in GSGM-07-CM-001. **Abbreviations:** **A**, morphotype 'A'; **B**, morphotype 'B'; **C**, morphotype 'C'; **ms**, medial stripe; **rd**, rachis in 'rachis-dominated' feathers; **sbr**, soft body residue. Scale bar equals 10 mm.

Lamanna et al., 2006; Ji et al., 2011; O'Connor et al., 2012). We also removed *Zhongornis haoae* Gao et al., 2008, from the analysis because we consider this taxon to be a non-avian theropod (specifically, a scansoriopterygid) rather than a bird (O'Connor and Sullivan, 2014; You, 2014). The updated data set consists of 64 taxa scored for 245 morphological characters (see Supplemental Data). We analyzed the data set using TNT (Goloboff et al., 2008). We first conducted a traditional (heuristic) search using the tree-bisection reconnection (TBR) swapping algorithm, retaining the single shortest tree of 1000 trees. This produced a well-resolved topology with a length of 834 steps. A second round of TBR yielded 312 most parsimonious trees (MPTs), also of 834 steps, the strict consensus of which places all Changma enantiornithines within a basal polytomy that also includes *Elsornis keni* Chiappe et al., 2006, and *Protopteryx fengningensis*, taxa that are consistently recovered at the base of Enantiornithes. This polytomy also includes the 'longipterygid' enantiornithines *Boluochia zhengi* Zhou, 1995, *Longipteryx chaoyangensis*, and *Rapaxavis pani*, the bohaiornithid *Shenqiornis mengi*, and the probable ornithuromorph *Chaoyangia beishanensis* Hou and Zhang, 1993 (O'Connor and Zhou, 2013). Like most of the Changma enantiornithines, *C. beishanensis* is known only from a single partial skeleton, and probably as a consequence, the hypothesized phylogenetic position of this taxon has varied widely in the literature (Zhou, 1999; Clarke and Norell, 2002). Although *C. beishanensis* has recently been shown to be a basal ornithuromorph (O'Connor and Zhou, 2013), this conclusion is only weakly supported by cladistic analysis. When its phylogenetic relationships have been analyzed, the taxon has commonly fluctuated between the two ornithothoracine clades (Enantiornithes and Ornithuromorpha); indeed, some recent analyses have removed *C. beishanensis* to generate a reduced strict consensus tree (O'Connor and Zhou, 2013).

The equal-length MPTs generated by the present analysis vary considerably in the positions of taxa within the basal enantiornithine polytomy of the strict consensus tree. For example, the isolated pectoral limb GSGM-04-CM-023 (Harris et al., 2006) is resolved both in a basal-most position (as in the results from the first round of TBR) as well as in the most derived position. This lack of topological stability indicates that these relationships are not supported by character data (i.e., they are zero-length nodes).

One noteworthy aspect of our phylogenetic results is that all enantiornithines from the Xiagou Formation are resolved in a polytomy with the most basal known members of this clade. By contrast, *Gansus yumenensis*—the numerically dominant Xiagou bird—is considered a fairly advanced ornithuromorph, typically resolved in a position more derived than any taxon from the penecontemporaneous Jehol Biota of northeastern China (You et al., 2006; O'Connor et al., 2010; O'Connor and Zhou, 2013; Wang et al., 2014a). The other known Xiagou ornithuromorph taxa—*Changmaornis houi* Wang et al., 2013, *Yumenornis huangi* Wang et al., 2013, and *Jiuquanornis niui* Wang et al., 2013—appear to occupy less derived positions in the clade; in particular, the latter taxon shares an archaic sternal morphology with the very basal ornithuromorph *Archaeorhynchus spatula* Zhou and Zhang, 2006, suggesting a close relationship (You et al., 2010; Wang et al., 2013). Therefore, although not strictly revealed as such in the cladogram, it appears that the Xiagou ornithuromorphs may have occupied a much broader phylogenetic spectrum than did the enantiornithines from this formation.

## DISCUSSION

Represented by specimen GSGM-05-CM-004, the new taxon *Feitianius paradisi*, gen. et sp. nov., greatly increases the diversity of recognized tail morphologies within Enantiornithes. Even

prior to this discovery, enantiornithines preserved a greater diversity of caudal plumages than any other Cretaceous avian clade. Several specimens (e.g., *Dapingfangornis sentisorhinus* LPM B00027, GSGM-07-CM-001) possess elongate, paired, rachis-dominated 'racket plumes' that vary substantially in morphology and length between taxa (O'Connor et al., 2012). Unfortunately, these feathers are distally incomplete in the majority of the specimens in which they are preserved, e.g., *Bohaiornis guoi* LPM B00167, *Protopteryx fengningensis* IVPP V11665, DNHM D2884 1/2 (Zhang et al., 2000; Hu et al., 2011), and some specimens (e.g., *Eopengornis martini* STM24-1) possesses rachis-dominated 'streamers' (Wang et al., 2014b). Other specimens (e.g., *Eoenantiornis buhleri* Hou et al., 1999, IVPP V11537, STM29-8) possess no rectrices, only morphologically simple body coverts surrounding the pygostyle (O'Connor, 2009; O'Connor et al., 2012). One taxon, (*Paraprotopteryx gracilis* STMV001, (Zheng et al., 2007) reportedly possesses four rachis-dominated 'racket-plumes,' and the holotype of *Shanweinia cooperorum* O'Connor et al., 2009 (DNHM D1878 1/2), preserves impressions of portions of at least four closely arranged tail feathers that may potentially have formed an aerodynamic surface (O'Connor et al., 2009). In contrast, several Jehol ornithuromorphs (e.g., *Hongshanornis longicresta* Zhou and Zhang, 2005, *Piscivoravis lii* Zhou et al., 2013, *Yanornis martini* Zhou and Zhang, 2001, *Yixianornis grabaui*; Zhou and Zhang, 2005; Clarke et al., 2006; Zhou et al., 2013) preserve large, round tails formed by a fan of 6–10 rectrices, and one taxon (*Schizoura lii*) has a forked tail (Zhou et al., 2012), all considered aerodynamic morphologies. The only exception is the holotype of the recently discovered ornithuromorph *Iteravis huchzermeyeri* Zhou et al., 2014, which preserves what appears to be a pair of short, ornamental rectrices (Zhou et al., 2014). With the possible exception of those preserved in the holotype specimen of *Shanweinia cooperorum*, all preserved enantiornithine rectricial morphologies are interpreted as having ornamental functions, strongly suggesting that sexual selection was a major driving force in shaping tail morphologies within the clade (Wang et al., 2014b).

Unlike the feathers that comprise the wing, those of the tail are not essential for flight in extant birds (Thomas, 1993). Although most extant birds have aerodynamic caudal morphologies, the tail is the most commonly modified part of the plumage and modifications of the tail feathers are most frequently related to ornamentation (Stettenheim, 2000). Exaggerated feather shapes and lengths may be readily identified as sexually driven traits in living birds (Andersson, 1982; Balmford et al., 1993; Fitzpatrick, 1998). The elongate 'streamers' of *Eopengornis martini* and the 'racket plumes' in species of the Confuciusornithiformes, GSGM-07-CM-001, and other enantiornithines are thus interpreted as ornaments (O'Connor et al., 2013; Wang et al., 2014b). The ornamental feathers of these Early Cretaceous birds are unusual in that they are rachis-dominated, which is an extinct morphotype (Zhang and Zhou, 2000; O'Connor et al., 2012). The preserved carbonized residue of what appears to be a wide, medially striped rachis directed toward the pygostyle strongly suggests that GSGM-05-CM-004 possessed a similar pair of elongate ornamental rectrices (Fig. 4). Paired, elongate tail feathers are present in many modern birds, both sexually dimorphic and non-dimorphic species, and are typically associated with a short, aerodynamic rectricial fan (e.g., species in the Momotidae—both genders; *Dicrurus paradiseus*, the greater racket-tailed drongo—both genders; *Trochilus polytmus*, the red-billed streamer-tail—males only; *Ocreatus underwoodii*, the booted racket-tail—males only). Avian plumage is under multiple selective pressures; therefore, such a tail morphology serves both aerodynamic and ornamental functions (Thomas, 1997).

Despite the diversity of recognized caudal plumages, the overwhelming majority of previously described Mesozoic birds have a tail composed of only one rectricial morphotype. The sole



exception in this regard is the long-bony-tailed bird *Jeholornis*, species of which have an autapomorphic ‘two-tailed’ morphology, in which the rectrices in the proximal fan and the distal frond differ from one another in size and morphology, and collectively serve both aerodynamic and ornamental functions (O'Connor et al., 2013). By contrast, no Early Cretaceous bird with paired ornamental feathers (e.g., *Confuciusornis*, enantiornithines) also possesses an aerodynamic tail fan. Specimen GSGM-05-CM-004 is the first Mesozoic bird to preserve rachis-dominated feathers along with additional types of rectrices. Nevertheless, these shorter rectrices (designated ‘morphotype A’ and ‘morphotype B’) appear to have different orientations from the body relative to one another, suggesting that they did not form a cohesive, lift-forming surface. Their degree of dorsal curvature further indicates that these feathers probably did not serve an aerodynamic purpose. The three rectricial morphotypes preserved in the holotype of *Feitianius*, none of which appears to be aerodynamic, suggest that the tail plumage of this bird may be interpreted as entirely ornamental and driven by sexual selection, with minimal visible effects of natural selection on its morphology (Balmford et al., 1993). The considerable differences in morphology between these morphotypes suggest a very elaborate caudal plumage in the new Xigou enantiornithine.

Among extant birds, extreme ornaments consisting of multiple rectricial types are usually limited to males of sexually dimorphic species because of the associated ‘costs’ of such feathers: these ornaments often decrease aerodynamic efficiency and increase conspicuity, and also require energy to grow and maintain (Thomas, 1993; Fitzpatrick, 1999). Limited by their energetic investment in reproduction, female birds—even those of species with mutual ornamentation or reverse sexual dimorphism—never reach the extremes of ornamentation observed in polygamous males with little to no parental responsibility (Wink and Lemon, 1994; Cuervo and Møller, 2000). Among living birds, elaborate tail plumages formed by several types of non-aerodynamic rectrices that vary in length and morphology (and also color) are primarily associated with males of sexually dimorphic species. The prime example here is birds of paradise (Passeriformes: Paradisidae) such as the greater bird-of-paradise (*Paradisaea apoda*) and Princess Stephanie's astrapia (*Astrapia stephaniae*), but other examples include male chickens (cocks) and pheasants (Galliformes: Phasianidae), the lyrebird *Menura* spp. (Passeriformes), and some species of ducks (Anseriformes: Anatidae). These ornaments are used primarily to attract mates, serving as an indicator of fitness because of the difficulty in maintaining such structures (Thomas, 1997; Cuervo and Møller, 2000). Ornamental rectrices are additionally used to signal between competing males. In Neornithes, reverse sexual dimorphism is most often expressed in size (e.g., raptorial birds) and is usually related to resource acquisition (Tobias et al., 2012). In the rare cases where the female of the species has the more attractive plumage (e.g., the paradise shelduck *Tadorna variegata*), this does not approach the degree of elaboration present in male dimorphic plumages and is more commonly associated with sexual dichromatism.

The paired ‘racket plumes’ originally described in *Confuciusornis* have been suggested to represent a sexually dimorphic feature (Feduccia, 1996). Although similar feathers are present in extant species of both non-dimorphic and sexually dimorphic birds, the paired rachis-dominated ‘racket plumes’ are clearly absent in some confuciusornithiform specimens, despite their excellent feather preservation (Hou et al., 1996; Chiappe et al., 1999, 2008). Alternatively, specimens that clearly lack elongate feathers could conceivably represent molting individuals. Although there are not yet enough known specimens of any one taxon to definitively evaluate this hypothesis, these feathers are similarly interpreted as sexually dimorphic in the enantiornithine species in which they occur (Zheng et al., 2007). In the single

*Confuciusornis* specimen and in the one indeterminate enantiornithine in which the gender can be confidently identified as female (due to the preservation of medullary bone and ovarian follicles, respectively), elongate rectrices are clearly absent, supporting the hypothesis that these feathers are only present in males of these species (Chinsamy et al., 2013; O'Connor et al., 2014).

The tail morphology of *Feitianius* strongly resembles that of males in modern sexually dimorphic species with hyperexaggerated ornamental rectricial displays (e.g., the greater bird-of-paradise *Paradisaea apoda*). Together, the three caudal feather morphotypes of the new Xigou enantiornithine would have formed a visually impressive but energetically costly display, presumably intended for intraspecific signaling. Multiple specimens are typically required to establish the existence of sexual dimorphism in a species. However, based on observations of extant birds (Thomas, 1997), and the exaggerated nature of the rectricial morphology of the holotype of *Feitianius paradisi* versus that of all other enantiornithines, we suggest that this species had sexually dimorphic plumage and that the holotype pertains to an adult male, despite the fact that the taxon is currently known from only this specimen.

The grade of complexity of the ornamental tail feathers provides indirect evidence of behavior in *Feitianius*. The degree of elaboration may indicate that this enantiornithine was socially polygamous, given that these types of birds tend to have a greater degree of caudal dimorphism than monogamous birds (Björklund, 1990) and hypertrophied ornaments are most commonly observed in polygamous neornithines. It also suggests limited paternal care of offspring in *Feitianius* (Wink and Lemon, 1994; Cuervo and Møller, 2000). The level of elaboration of the caudal plumage further suggests that *Feitianius* did not fly often, at great speeds, and/or for long distances, suggesting that it inhabited a densely forested environment (similar to the habitats of extant quetzals, *Pharomachrus* and *Euptiolotis* spp.) (Thomas, 1997); this is consistent with the arboreal ecologies inferred for enantiornithines based on their pedal morphology (Morschhauser et al., 2009; O'Connor, 2009) and is also consistent with the abundance of fossil coniferous trees collected at Changma (M.L., pers. observ.). Among modern birds, the most elaborate tail morphologies are phylogenetically derived (Gluckman, 2014); however, *Feitianius* falls within the large polytomy of basal enantiornithines (Fig. 5), which may suggest that this clade began to experiment with different plumages fairly early in its diversification. As in many modern taxa, there is a strong possibility that the different feather morphotypes varied in color as well: elaborate tail displays are often associated with bright colors, iridescence, and/or visual patterns such as stripes. Regrettably, a varnish applied after preparation makes it impossible to evaluate the feathers of GSGM-05-CM-004 for preserved melanosomes.

The unique tail plumage of *Feitianius* reveals an even greater level of complexity in this part of the integument than was previously recognized and indicates that enantiornithines evolved complex, non-aerodynamic caudal morphologies formed by multiple rectrix types, presumably to form elaborate displays, in parallel to those documented in Neornithes. The diversification of Enantiornithes during the Cretaceous is considered the first major avian radiation (Chiappe, 1995b). Although currently enantiornithines do not approach the skeletal diversity encompassed within Neornithes (O'Connor and Chiappe, 2011), the new specimen suggests that the caudal plumages of these archaic birds may have reached levels of complexity comparable to those of extant taxa. This is unsurprising considering a recent study that suggested that plumage is highly evolutionarily labile, as inferred from the number of times that exaggerated features have independently evolved among closely related modern birds (Gluckman, 2014). The

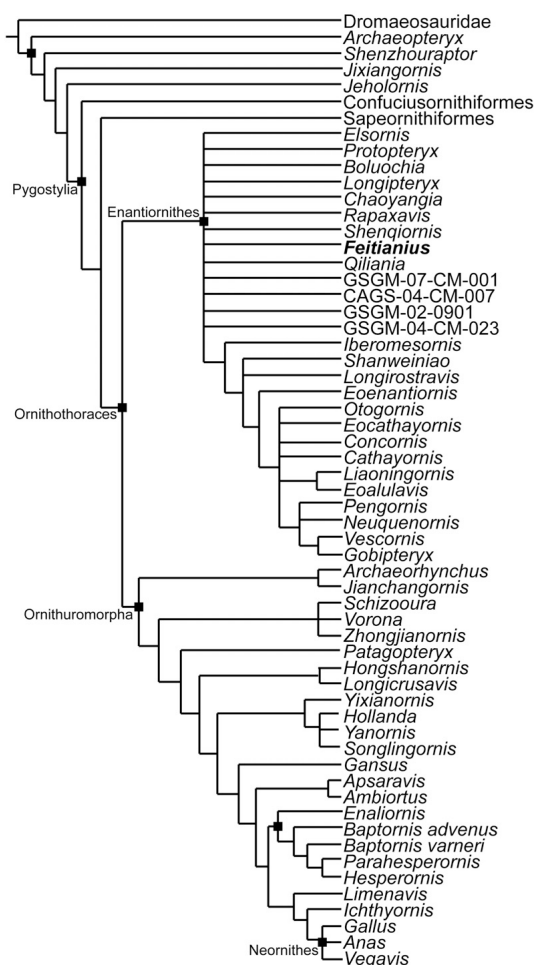


FIGURE 5. Hypothesized phylogenetic relationship of *Feitianius paradiisi*, gen. et sp. nov., relative to a large sample of other Mesozoic birds (Cenozoic neornithines utilized as the ingroup).

diversity of ornamental tail morphologies within Enantiornithes, which more closely approaches modern complexity and diversity than does the morphology of the skeleton, strongly suggests that sexual selection was a major driver of the diversification of feather and plumage morphologies during the early evolution of Aves.

### Body Coverts in Basal Birds

Notably, the holotype of *Feitianius* preserves evidence of pennaceous coverts, which are not observed in Jehol Biota enantiornithine taxa despite the fact that a large number of specimens of these birds preserve feathers (O'Connor, 2009; O'Connor et al., 2012). In Jehol enantiornithines such as the holotype specimens of *Longipteryx chaoyangensis* and *Propteryx fengningensis*, the body feathers appear to be non-shafted (as defined by Zhang et al., 2006). Although these feathers are inferred to have functioned as body contour feathers, they superficially resemble the down feathers of modern birds; they differ in that they do not radiate from a short rachis, but rather seem to consist of proximally undifferentiated vanes that fray into individual barbs distally, a now-extinct feather morphotype (Zhang et al., 2006; O'Connor et al., 2012). By contrast, at least one small covert feather of GSGM-05-CM-004 clearly preserves a herringbone structure and a rachis (Fig. 4C). Pennaceous covert feathers

have also been reported in *Archaeopteryx* (Foth et al., 2014). The absence of pennaceous feathers in enantiornithines and other basal birds (e.g., *Confuciusornis*, *Jeholornis*) from the Jehol Group is seemingly at odds with their phylogenetic placement as more derived than *Archaeopteryx* (Fig. 5). However, the vast number of specimens of these birds challenges any purely taphonomic explanation for this difference in observed feather morphology, and some well-preserved feathers of Jehol avians were clearly non-shafted (Zhang et al., 2006; O'Connor, 2009; O'Connor et al., 2012).

Most feathers of the *Feitianius* holotype GSGM-05-CM-004 do not preserve clear evidence that they were vaned, but instead appear wispy, similar to those of Jehol birds. Nevertheless, vanes may be observed in some regions of the large 'morphotype A' feathers and in a single ventral covert. This suggests that all feather morphotypes of this enantiornithine were pennaceous, but that this has subsequently been obscured by taphonomic processes. No clearly non-shafted feathers are visible in GSGM-05-CM-004. These non-shafted body coverts have so far been documented only in birds from the Jehol ecosystem, for which evidence indicates a fairly cold climate (Amiot et al., 2011). Plumaceous down feathers are considered derived within Neornithes (Stettenheim, 2000); as such, we hypothesize that the non-shafted morphology may also be derived and that basal Jehol birds evolved morphologically comparable non-shafted coverts for insulation from their cold environment.

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