

Morphological coevolution of the pygostyle and tail feathers in Early Cretaceous birds (Postprint)

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Full Text

Preamble

Morphological Coevolution of the Pygostyle and Tail Feathers in Early Cretaceous Birds

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Abstract

The transformation from a long reptilian tail to a shortened tail terminating in a pygostyle and accompanied by aerodynamic fanning rectrices represents one of the most remarkable adaptations of early avian evolution. However, no fossils directly capture this transition, and information regarding the structural morphology and early evolution of the pygostyle in Mesozoic birds and their integuments remains relatively limited. Here we provide a review of pygostyle morphology in Early Cretaceous birds with comparisons to the structure in living birds. This study emphasizes the convergent evolution of distally co-ossified caudal vertebrae in non-avian maniraptorans and early birds. Distinct differences further exist in pygostyle morphology among Sapeornithiformes, Confuciusornithiformes, Enantiornithes, and Ornithuromorpha.

The morphology of the pygostyle and rectrices in early ornithuromorphs appears similar to that of extant birds, whereas the pygostyle in more primitive birds does not appear morphologically capable of supporting the rectricial bulbs and musculature necessary to control an aerodynamic fan-shaped tail. The rectricial bulbs and rectricial fan appear to have coevolved with the plough-shaped pygostyle early in the evolution of the Ornithuromorpha. This study also shows that the confuciusornithiform pygostyle was more similar to that of enantiornithines than previously recognized, consistent with the presence of nearly identical ornamental tail feathers in both groups.

Key words Jehol Biota, Aves, rectricial bulb, rectrices

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1 Introduction

Avian origins have been studied for over a century, but the hypothesis that “birds are maniraptoran theropod dinosaurs” only became universally accepted in the past two decades following the discovery of abundant feathered maniraptorans in northeastern China (both non-avian and avian) (Xu et al., 2014). For conciseness, we hereinafter use “theropod” to refer to non-avian theropod dinosaurs and “maniraptoran” for non-avian maniraptoran theropods. To date, hundreds of specimens of derived maniraptorans and birds have been collected from the Late Jurassic Tiaojishan Formation and the Early Cretaceous Jehol Group (Zhou, 2004, 2014; Wang et al., 2015). The Jehol Group, consisting of the 125 Ma Yixian Formation and the 120 Ma Jiufotang Formation, has also produced thousands of early bird specimens representing half the known Mesozoic

taxonomic diversity. Together with the Protopteryx-horizon of the Huajiying Formation, the fossils from the Jehol Group form the spectacularly diverse Jehol Biota (Pan et al., 2013). These faunas preserve a wealth of paleobiological evidence (such as stomach contents, soft tissue structures, and behavior) that greatly elucidate the dinosaur-bird transition and the early evolution of birds (Xu et al., 2014).

Despite this wealth of new data, significant gaps remain in our understanding of the structural transformation of birds from the theropod condition. One such evolutionary transformation is the reduction of the long bony tail (present in theropods and the basalmost birds Archaeopteryx and Jeholornis) into an abbreviated tail ending in a pygostyle, a compound element formed through fusion of the distalmost caudal vertebrae. All birds with a pygostyle form a monophyletic clade, the Pygostylia (Chiappe, 2002), which excludes only the long bony-tailed birds, Archaeopteryx and the Jeholornithiformes (Jeholornis and kin).

The earliest record of the pygostyle occurs in the 130.7 Ma Protopteryx-horizon of the Huajiying Formation, the earliest stage of the Jehol Biota, with the first appearance of three pygostylia lineages: the Confuciusornithiformes, Enantiornithes, and Ornithuromorpha (Zhang and Zhou, 2000; Zhang et al., 2008a; Wang et al., 2015). Unfortunately, no intermediate morphotypes are known. The only specimen that may potentially elucidate this important transition is the holotype of *Zhongornis haoae* from the Jiufotang Formation (Gao et al., 2008). Although initially described as having an intermediate tail morphology, the only known specimen of this taxon is a juvenile and poor preservation obscures interpretations. Descriptions of the tail vary from 14 to 20 vertebrae (Gao et al., 2008; O'Connor and Sullivan, 2014), and thus the transmutation of the tail during early avian evolution remains poorly understood. Historically, the pygostyle has been considered a uniquely avian feature (Haeckel, 1883). However, more recently pygostyle-like structures have been discovered in three clades of maniraptorans: Therizinosauroidae, Oviraptorosauria, and Scansoriopterygidae (Xu et al., 2003; Barsbold et al., 2000a, b; Zhang et al., 2008b).

In Neornithes (the clade that includes all living birds), the tail complex consists of two parts: the tail feathers and the uropygium, the latter comprising the caudal vertebrae and associated soft tissue (Fisher, 1959; Baumel, 1988; Baumel et al., 1990; Gatesy and Dial, 1993, 1996a, b; Balmford et al., 1993; Thomas, 1997). The aerodynamic tail feathers, called rectrices, are stiff and asymmetrical and overlapped dorsally and ventrally by rows of short tail coverts (called tectrices or deck feathers). There are usually 5–6 free caudal vertebrae with expanded transverse processes followed by a small mediolaterally compressed pygostyle (Baumel and Witmer, 1993). The blade-like dorsal portion, the pygostyle lamina (lamina pygostyli), is inferred to form through the fusion of the neural spines and arches. The cone-shaped pygostyle base (basis pygostyli) is formed through the fusion of the vertebral bodies (centra) (Baumel et al., 1990; Baumel and Witmer, 1993). The pygostyle base has ventral processes that are

weakly excavated for muscle attachment. Paired fibroadipose tissue structures called rectricial bulbs lie on both sides of the pygostyle and predominantly attach to the pygostyle lamina; the calami of the rectrices are embedded in this tissue, except for the medial pair which attach directly onto the dorsodistal end of the pygostyle (Baumel, 1988). Spiraling around the surface of each bulb is a striated muscle, the rectricial bulb muscle (*m. bulbi rectricium*), primarily responsible for controlling the spread of the tail feathers (Baumel, 1988; Baumel and Witmer, 1993; Gatesy and Dial, 1996a, b). In some birds (e.g., in Piciformes and Coliiformes), the ventral processes are laterally expanded forming the ventrally concave pygostyle disc (*discus pygostyli*) that provides an expanded area for the attachment of the well-developed caudal depressor muscle (*m. depressor caudae*) present in these species; the disc is inferred to be derived from rudimentary transverse processes (Baumel, 1988; Baumel and Witmer, 1993).

Except for the flightless paleognathous birds (the “ratites”), all modern birds share nearly the same tail complex formed by pygostyle, rectricial bulbs, and rectrices. Although in many taxa the rectrices are modified for display, most birds have an aerodynamic fan consisting of 10–12 feathers (Thomas and Balmford, 1995). This sophisticated tail complex plays a significant role in avian flight. The rectricial fan produces lift to supplement the wings, the force of which can be adjusted by controlling the surface area of the rectricial fan by adjusting the spread of the feathers (Thomas and Balmford, 1995; Thomas 1997). This supplemental lift is particularly important during takeoff, landing (for decelerating and braking), and slow flight (Pennycuik, 1968; Spedding et al., 1984; Tucker, 1992; Gatesy and Dial, 1993). Tail fanning is also used when turning, acting as a paddle or rudder (Baumel et al., 1990; Thomas, 1993, 1997), and the presence of a tail helps to maintain stability and balance, and streamline the body (Thomas, 1993). Because the tail complex functions as an integrated whole, the uropygium and integument are morphologically correlated and one can be used to predict the other (Felice and O’ Connor, 2014). Furthermore, pygostyle morphology can be used to predict flight or foraging style in both extinct and extant birds (Felice, 2014). These results support the hypothesis that pygostyle and rectricial morphology co-evolve (Clark et al., 2006).

Despite the large number of specimens uncovered from the Jehol Biota over the past several decades (Zhou, 2004, 2014; Xu et al., 2014), the early evolution of the avian tail complex remains poorly understood. Several short discussions have been published regarding specific taxa: *Jeholornis* (O’ Connor et al., 2012, 2013), *Eopengornis* (Wang X et al., 2014), *Shanweinia* (O’ Connor et al., 2009), *Yixianornis* (Clarke et al., 2006), and *Iteravis* (Zhou et al., 2014). However, the only research focused on the morphological changes that occur in the derived maniraptoran tail during early avian evolution predates most important discoveries (Gatesy and Dial, 1993, 1996a, b). The pygostyle and tail feathers, when preserved, are typically only briefly described (Chiappe et al., 1999; Clarke et al., 2006; O’ Connor et al., 2009; Hu et al., 2015), and very little information is available regarding the soft tissue (rectricial bulbs and muscle), although potential traces are reportedly preserved in the ornithuromorph *Iteravis* (Zhou et al.,

2014) and the enantiornithine *Feitianius* (O' Connor et al., 2015). Extensive interspecific comparison is lacking and the relationship between skeletal features and integument has only been explored in the pengornithid enantiornithines (Hu et al., 2015; O' Connor et al., 2016). Here we describe in detail the morphological characteristics of the pygostyle and tail feathers in Mesozoic birds and closely related theropods. We discuss morphological differences between clades, potential function, and place this information in the context of recent phylogenetic analyses in order to test hypotheses regarding the origin of the extant avian tail fanning complex.

Institutional abbreviations BMNH, Beijing Natural History Museum, Beijing, China; CAGS, Chinese Academy of Geological Sciences, Beijing, China; CNU, Capital Normal University, Beijing, China; DHNM, Dalian Natural History Museum, Dalian, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LPM, Liaoning Paleontology Museum, Shenyang, China; STM, Tianyu Natural History Museum of Shandong, Pingyi, China.

2 Materials and Methods

This study primarily utilized the collections of the IVPP, supplemented by data from the collections of the STM. Only taxonomically identifiable specimens with pygostyle or tail integument preserved were included in this study. Because the morphology of the caudal skeleton is affected by post-hatching development (Heers et al., 2014; Zhou et al., 2013), juvenile specimens (such as the holotype of *Zhongornis haoae*) were excluded from this study.

Anatomical nomenclature primarily follows the “Handbook of Avian Anatomy” using English equivalents for the Latin terminology (Baumel and Witmer, 1993).

Preserved in finely laminated lacustrine sediments, almost all specimens from the Jehol Biota are compressed and preserved nearly two-dimensionally in slabs. This preservation limits the information available from individual elements to a single exposed surface (e.g., dorsal, lateral, ventral, or dorsolateral), preventing the use of geometric morphometric analysis methods (Zelditch et al., 2012). Thus, three simple but reliable measurements were chosen: the total length of the pygostyle (TLP), the mid-length width of the pygostyle (MLW, for dorsally/ventrally preserved specimens), and the mid-length height of the pygostyle (MLH, for laterally preserved specimens). To reduce the effects of body size, we normalized TLP using the total length of the humerus (TLH) and the total length of the femur (TLF), the two most reliable and widely used proxies for body size and mass in most birds (Liu et al., 2012; Hone, 2012).

Most of the data (27 specimens) were collected directly from specimens measured using stainless hardened digital calipers; measurements from four specimens were taken from the literature (*Sapeornis* CAGS-03-07-08 (Yuan, 2005), *Zhouornis* (Zhang et al., 2013), *Sulcavis* (O' Connor et al., 2013), *Shanweiniao* (O' Connor et al., 2009)).

3.1 Description of Pygostyles and Tail Feathers

Non-avian Theropoda Non-maniraptoran theropods have typical reptilian tails usually consisting of dozens of free caudal vertebrae, e.g., about 35 in *Tyrannosaurus* (Persons and Currie, 2011a) and 42 in *Carnotaurus* (Persons and Currie, 2011b). The proximal vertebrae have short centra with neural arches and transverse processes present. These processes are completely reduced in the distal vertebrae, which have elongate centra with length more than four times the centra height/width in some taxa (e.g., *Sinosauropteryx*, *Ornitholestes*) (Pittman et al., 2013). The fusion of distal caudal vertebrae is unknown in non-maniraptoran theropods and rare in non-avian maniraptoran theropods. The most primitive known pygostyle-like structure is present in the basal therizinosaur *Beipiaosaurus* (IVPP V 11559) (Xu et al., 2003). The complete tail of *Beipiaosaurus* (V 11559) consists of 30 vertebrae. Preserved in lateral view, the last five caudals are well co-ossified into a rod-like element with a slightly convex dorsal margin formed by the prezygopophyses. The distal sixth and seventh caudal centra are completely fused to each other but not to the other five fused vertebrae. The tail plumage consists of filamentous (without a fused rachis) “proto-feathers” with no proximodistal differentiation (Xu et al., 2003). No composite filaments are observed on the tail of *Beipiaosaurus*, which falls outside Pennaraptora (the derived clade of maniraptorans in which pennaceous feathers are present) (Brusatte et al., 2014).

Some members of the Oviraptorosauria (the basalmost clade in the Pennaraptora) also possess fused terminal caudals. Some members of this bird-like clade have at one time been considered secondarily flightless birds, although most similarities are derived cranial features and probably related to the presence of herbivory (Dyke and Norell, 2005). In one specimen of the primitive taxon *Similicaudipteryx* (IVPP V 12056), the distalmost caudal vertebrae (at least two) are co-ossified into a dagger-like mass (He et al., 2008). This morphology is also observed in derived oviraptorosaurs, such as *Nomingia*, *Citipati*, and *Conchoraptor* (Barsbold et al., 2000a, b; Persons et al., 2013). In the very primitive *Caudipteryx*, the distal five caudal vertebrae articulate tightly through the presence of well-developed prezygopophyses, and the last three of these are ankylosed but remain unfused (IVPP V 22606). These vertebrae lack neural spines and transverse processes, which are present in the proximal caudal vertebrae. Tail feathers are preserved in at least three primitive oviraptorosaurs: *Protarchaeopteryx*, *Caudipteryx*, and *Similicaudipteryx*. The holotype of *Caudipteryx* has an estimated eleven pairs of tail feathers attached to the caudalmost five or six vertebrae, which form the incipient pygostyle. Although the tail feathers in all three taxa are pennaceous (vaned), no specimen preserves evidence of hooklets on the barbules (Ji et al., 1998). In *Caudipteryx* V 22606, two layers of tail feathers are evident: one shorter layer of rachis-less body feathers and another longer layer of pennaceous rectrices [Figure 2: see original paper].

One member of the Scansoriopterygidae, *Epidipteryx*, has a reduced tail consisting of 16 vertebrae ending in a rod-like structure approximately formed by

the distal ten caudal vertebrae which are unfused. The distal ten vertebrae are reduced to simple centra without processes. Two pairs of elongate feathers project from the pygostyle in *Epidexipteryx*; described as “ribbon-like” (Zhang et al., 2008b), these tail feathers resemble the poorly preserved “rachis-dominated” feathers present in some enantiornithines. Pennaceous tail feathers are otherwise unknown in the Scansoriopterygidae.

Basalmost Birds With the exceptions of *Archaeopteryx* and *Jeholornis*, all Mesozoic birds have a pygostyle. *Archaeopteryx* is the basalmost bird with a tail composed of 21–22 articulated caudal vertebrae (Elzanowski, 2002; Foth et al., 2014), suggesting that the plesiomorphic avian tail was composed of no fewer than 20 caudal vertebrae. Pennaceous tail feathers, presumably attached through ligamental connections, line the lateral surfaces of the tail, overlapping to form a frond-like morphology (Gatesy and Dial, 1996b; Mayr et al., 2007).

The 11th specimen of *Archaeopteryx* preserves a notch in the caudal margin of the tail frond. The proximal rectrices are asymmetric and shorter than the symmetrical overlapping distal rectrices (Feduccia and Tordoff, 1979; Foth et al., 2014). The slightly more derived *Jeholornis* has 27 free caudal vertebrae (IVPP V 13350), forming a tail longer than that of *Archaeopteryx* (Zhou and Zhang, 2002a, 2003a). *Jeholornis* possesses a unique tail plumage with two functionally discriminant rectricial pterygiae (O’ Connor et al., 2012, 2013). One consists of a short fan-shaped array of rectrices presumably embedded in the soft tissue dorsal to the short proximal caudal vertebrae, and the second is distally located, consisting of laterally oriented cranially curved rectrices forming a frond-like arrangement without an extensive aerodynamic surface. Vane symmetry is equivocal due to preservation.

Although the lift generated by the tails in these two taxa are insignificant when compared with that of the extant pigeon, the tail complex in *Jeholornis* is relatively more efficient than that of *Archaeopteryx*, producing similar lift while at the same time incurring much less estimated drag (O’ Connor et al., 2013).

The Sapeornithiformes and the Confuciusornithiformes are the basalmost known avian lineages with a pygostyle (Zhou and Zhang, 2002b; Zhang et al., 2008a). Despite published diversity, the Sapeornithiformes is considered a monospecific clade with all taxa referable to *Sapeornis chaoyangensis* (Pu et al., 2013; Gao et al., 2012). The pygostyle is best preserved in two specimens, IVPP V 13275 and V 13276, both preserving this element in left dorsolateral view. In the cranial three vertebrae of the pygostyle, neural spines and transverse processes can be faintly distinguished; the subsequent vertebrae are more completely fused and individual processes cannot be identified. The dorsal surface is interpreted as forming a weak pygostyle lamina [Figure 3: see original paper]. On each lateral surface of the lamina there is a laterally projecting ridge inferred to form through fusion of the transverse processes. More than ten additional specimens of sapeornithiforms preserving the pygostyle were examined at the STM. In roughly a third of these specimens, fusion of the pygostyle is incomplete, suggesting that the pygostyle fully co-ossifies late during ontogeny. Tail feathers are rarely

preserved, present in only one published specimen (STM 16-18); this specimen preserves multiple elongate rectrices in lateral view, interpreted as forming a long, strongly graded tail-fan (Zheng et al., 2013; Wang X et al., 2014; Xu et al., 2014). Two other specimens (STM 15-18, 16-5) preserve this feature in dorsoventral view, revealing a tail consisting of 8-10 narrow, symmetrical, non-overlapping feathers.

Distinct from that of sapeornithiforms, the pygostyle in confuciusornithiforms is more strongly co-ossified, proportionately longer, and more robust (Martin et al., 1998; Chiappe et al., 1999). This detailed study of the confuciusornithiform pygostyle reveals a more complex morphology than previously recognized (Martin et al., 1998; Chiappe et al., 1999). The pygostyle has a pair of dorsolateral ridges [Figure 4A: see original paper] and another pair of proximoventral processes [Figure 4B: see original paper]. The proximoventral processes project cranially beyond the proximal articular surface [FIGURE:4A, B] and are proximally restricted, whereas the dorsolateral processes extend the entire length dorsally, defining a deep concavity. The ventral surface is keeled; the height of the keel is obscured by compression, but it appears to form a majority of the pygostyle corpus [Figure 4B: see original paper]. The caudal margin is rounded and slightly laterally expanded [Figure 4C: see original paper]. In lateral view, foramina are present in some specimens (e.g., IVPP V 16066, STM 13-58). The number and position of these foramina are variable, and we suggest these may represent a subadult feature, subject to ontogenetic change and lost with maturity. Numerous confuciusornithiform specimens preserve a single pair of rectrices that are elongate, rachis-dominated, and only distally pennaceous (racket-plumes). Other specimens preserve only short rachis-less body feathers surrounding the pygostyle [FIGURE:4A, C]. These racket-plumes are interpreted as sexually dimorphic ornaments present only in males, evolved under sexual selection (Chiappe et al., 2008).

Enantiornithes Enantiornithes is the most diverse group of Cretaceous birds. Although their pygostyle and tail feathers do not vary to the extent observed in extant birds, they accordingly show greater morphological diversity than other known Cretaceous clades. The caudal vertebrae are well fused; sutures and individual processes cannot be recognized in adults. The three-dimensionally preserved pygostyle of *Halimornis* (Chiappe et al., 2002) clearly reveals that a typical enantiornithine pygostyle consists of paired dorsolateral ridges demarcating a deeply incised dorsal surface (in the case of *Halimornis*, incised forming a deep V-shaped excavation); ventrally, the body is very narrow, with a pair of ventrolateral processes. The dorsolateral ridges project cranially beyond the proximal articular surface, forming the dorsal fork described by Chiappe et al. (2002). Together with the smaller ventrolateral ridges, the pygostyle appears X-shaped in proximal view [Figure 5: see original paper]. The distal end of the pygostyle is tapered, formed by a constriction in the mediolateral width of the dorsal surface and the fact that the ventrolateral processes do not extend the entire length of the pygostyle.

Although most if not all known enantiornithine taxa share this unique general morphology, appreciable variation within this template is observed. The basal Pengornithidae (Zhou et al., 2008; Wang X et al., 2014; Hu et al., 2015) possess all the characteristic enantiornithine features, but their pygostyle is proportionately shorter and broader, and the distal end is untapered: the ventrolateral processes are proximally restricted, and the dorsal surface maintains an even width (Pengornis IVPP V 15336; [Figure 5A: see original paper]). The dorsal surface is broadly concave, rather than deeply incised as in Halimornis. The caudal margin of the pygostyle has a medial cleft, unique to this family of enantiornithines. Compared to the typical condition, the bohaiornithid pygostyle [FIGURE:5B, C] is more slender, and the ventrolateral processes taper gently rather than ending abruptly as in most enantiornithines (Wang M et al., 2014). The Longipterygidae, the family that includes Longipteryx, Rapaxavis, and Shanweinia, is characterized by a pygostyle that is proportionately larger and more robust than other enantiornithines (O' Connor et al., 2011). In Rapaxavis, the distal end of the pygostyle caudal to the ventrolateral processes forms a spade-like expansion that is distally tapered [Figure 5D: see original paper]. Other simpler morphologies have been reported (e.g., Vescornis) (Zhang et al., 2004), but in the absence of additional evidence, these are interpreted as due to poor or incomplete preservation.

In some enantiornithine specimens (e.g., Eoenantiornis IVPP V 11537, Longipteryx IVPP V 12325), rectrices are distinctly absent, with only rachisless body feathers present, similar to some confuciusornithiform specimens. Many specimens preserve a single pair of elongate rachis-dominated tail feathers (e.g., Protopteryx IVPP V 11665, Dapingfangornis LPM 00039, Bohaiornis LPM B00167, Parapengornis IVPP V 18687) (Zhang and Zhou, 2000; Li et al., 2006; Hu et al., 2011; Hu et al., 2015). Paraprotopteryx (STM V 001) preserves two pairs of feathers (Zheng et al., 2007). These feathers vary with regard to the extent of the pennaceous vane, being fully pennaceous in Parapengornis and Eopengornis and distally restricted in all other specimens in which preservation is clear (Dapingfangornis, GSGM-07-CM-001, Paraprotopteryx STM V 001). The shape of the distally restricted pennaceous portion varies between taxa, being distinctly racket-shaped in Dapingfangornis and Paraprotopteryx, whereas the distal expansion is more gradual in other specimens (GSGM-07-CM-001) (O' Connor et al., 2012).

Ornithuromorpha The Ornithuromorpha contains all living birds (Neornithes) and extinct taxa more closely related to living birds than to the Enantiornithes (Chiappe, 2002; O' Connor and Zhou, 2013; Jetz et al., 2012; Jarvis et al., 2014; Wang et al., 2015). Several Early Cretaceous fossil ornithuromorphs preserve evidence of an advanced tail complex.

The pygostyle is most commonly preserved in lateral view (e.g., holotype of Yixianornis grabaui IVPP V 12631 (Zhou and Zhang, 2001), holotype of Piscivoravis lii IVPP V 17078 (Zhou et al., 2013), holotype of Iteravis huchzermeyeri IVPP V 18958 (Zhou et al., 2014), and Gansus yumenensis CAGS-IG-04-CM-002 (You

et al., 2006)), revealing a ploughshare shape approximately like that observed in extant birds and proportionately smaller than in other Early Cretaceous avian taxa [Figure 6: see original paper]. The ratio of dorsoventral MLH compared to TLP in Jehol ornithuromorphs is larger (varies from 0.37 in *Yixianornis* to 0.60 in *Hongshanornis*) than in other Cretaceous clades (*Confuciusornis* 0.25, enantiornithine *Longipteryx* 0.17) with the exception of *Sapeornis* (0.45). Because all available Early Cretaceous basal ornithuromorph specimens preserve the pygostyle in lateral view, their width cannot be successfully measured. We suggest the predominance of lateral preservation implies that the pygostyle is mediolaterally thin, as in neornithines. Generally, the pygostyle in Early Cretaceous ornithuromorphs consists of a pygostyle lamina and a narrow pygostyle base, with the transverse processes forming uneven low ridges on the lateral surface [Figure 6: see original paper]. In lateral view, the pygostyle is upturned [Figure 6: see original paper] so that it is angled relative to the distal free caudals; this morphology is also observed in doves, falcons, and many other living birds (Baumel et al., 1988). Although somewhat similar to sapeornithiforms in overall shape, the ornithuromorph pygostyle is mediolaterally thinner and proportionately shorter than in this taxon and significantly differs from the robust morphology in other Mesozoic avian lineages. Non-feather dark traces preserved surrounding the pygostyle in *Yixianornis* V 12631 and *Iteravis* V 18958 have been interpreted as the carbonaceous remains of the rectricial bulbs (Clarke et al., 2006; Zhou et al., 2014).

The basalmost ornithuromorph preserving tail feathers is the holotype of *Schizoura lii* (IVPP V 16861), which preserves a forked tail, considered by aerodynamic models to be the most efficient tail shape (Zhou et al., 2012; Thomas et al., 1993). All other ornithuromorph specimens with caudal integument preserve the impression of an aerodynamic tail fan formed by multiple (at least 6-10) rectrices. Fan-shaped arrays of rectrices are present in *Hongshanornithidae* (*Hongshanornis* V 14533, DNHM D2945/6; *Tianyuornis* STM 7-53; *Archaeornithura* STM 7-145), *Songlingornithidae* (*Yixianornis*: V 12631; *Yanornis*: STM 9-51), and *Piscivoravis* (V 17078) (Chiappe et al., 2014; Zheng et al., 2014; Zhou et al., 2013; Wang et al., 2015). The rachis and individual barbs are discernible in the rectrices of some exquisitely preserved specimens (e.g., *Yixianornis*: V 12631, *Piscivoravis*: V 17078). At least eight rectrices are preserved in the holotype specimen of *Yixianornis grabaui* (Clarke et al., 2006); a minimum of six feathers were reported in the holotype specimen of *Piscivoravis lii* (Zhou et al., 2013); and more than ten are present in a referred specimen of *Hongshanornis* DNHM D2945 (Chiappe et al., 2014). The caudal margins of these tail fans are weakly graduated. Although the exact number of rectrices cannot be determined in any specimen, more than two rectrices are present in all known basal ornithuromorphs with the possible exception of the poorly preserved tail in the holotype of *Iteravis huchzermeyeri* (Zhou et al., 2014).

3.2 Data Analysis

Pygostyle data was collected from 31 specimens belonging to 20 genera and representing at least 8 families. Almost all ornithuromorph pygostyles are preserved laterally and do not provide data on MLW. The width was measured from the holotype of *Schizoura lii*, but lateral compression of the pygostyle in this specimen and specimens of *Sapeornis* (IVPP V 13275 and V 13276) prevents accurate measurements. Selected linear pygostyle measurements were compared to determine if clades can be differentiated on the basis of pygostyle absolute sizes and relative proportions.

The Mesozoic birds from Jehol can be divided into four groups—Sapeornithiformes, Confuciusornithiformes, Enantiornithes, and Ornithuromorpha—based on phylogeny. We chose TLH and TLF, which are commonly used, as appropriate proxies of avian body size (Liu et al., 2012; Hone, 2012). The result indicates that TLP/TLH values in sapeornithiforms (0.11–0.17) and ornithuromorphs (0.15–0.27) are distinctly lower than those of confuciusornithiforms (0.45–0.54) and most enantiornithines (0.34–0.66, excluding those of Pengornithidae). The result is visible in [Figure 7A: see original paper]: scatter points belonging to sapeornithiforms and ornithuromorphs are closer to the TLH-axis, while those of confuciusornithiforms and enantiornithines are near the TLP-axis. In the enantiornithines, low TLP/TLH values can also be found in the Pengornithidae (0.18–0.30). Consistent results are also confirmed when the proxy is changed to TLF (see TLP/TLF in Table 1; [Figure 7B: see original paper]). Both aspects of results suggest proportionally shorter pygostyles relative to body size in sapeornithiforms and ornithuromorphs, especially in the latter.

Clades cannot be easily distinguished by MLW/TLP values (Table 1; [Figure 7C: see original paper]). Because the data for sapeornithiforms and ornithuromorphs are too questionable and limited (only one datum each) to be considered, and the ratio of MLW/TLP present in confuciusornithiforms (0.12–0.24) and enantiornithines (0.15–0.53) are indistinguishable. The single datum point representing the ornithuromorphs, taken from the holotype of *Schizoura lii*, is not reliable due to deformation. However, we hypothesize that the wide spread of lateral preservation in this clade precisely reflects their very low width values. The presence of robust ventrolateral and/or dorsolateral processes may contribute to the width in confuciusornithiforms and enantiornithines (Figs. 4, 5). Higher MLH/TLP values are observed in sapeornithiforms (0.45) and ornithuromorphs (0.37–0.60), indicating proportionately taller and shorter pygostyles compared to confuciusornithiforms (MLH/TLP value is 0.21–0.26) and enantiornithines (MLH/TLP value is 0.16–0.22) (Table 1; [Figure 7D: see original paper]). This greater dorsoventral depth is produced by the prominent neural spines in sapeornithiforms and the dominant pygostyle lamina in ornithuromorphs, both of which are dorsally projecting (Figs. 3, 6).

Four groups (TLP-TLH, TLP-TLF, TLP-MLW, and TLP-MLH) of visibly separated clusters of data represent the pygostyle measurements of the four inves-

tigated clades. Despite the ratio values discussed above, cluster distributions of the four clades can be more or less separated as their borders with slight overlaps show [Figure 7: see original paper]. Therefore, the four avian clades can, to some extent, be differentiated according to absolute sizes.

4.1 Convergent Evolution of the “Pygostyle”

Fusion or partial fusion of the terminal caudal vertebrae in maniraptorans is observed in the Therizinosauroidea, Oviraptorosauria, and potentially also the Scansoriopterygidae (Xu et al., 2003; Persons and Currie, 2011a, b; Persons et al., 2013; Gao et al., 2008). However, morphological differences between these phylogenetically separated taxa indicate these co-ossified structures cannot be considered equivalent to the avian pygostyle. Outside the Ornithuromorpha, no group preserves evidence of a tail complex. The rod-like fused caudals in the primitive *Beipiaosaurus* completely lack rectrices. Although pennaceous tail feathers are present in oviraptorosaurs, the absence of a pygostyle lamina or a similar dorsal ridge makes the development of rectricial bulbs or equivalent structures in this clade unlikely. Co-ossification, when present, only occurs between the centra and prezygopophyses; other processes, such as the transverse processes inferred to fuse into the pygostyle base in ornithuromorphs, are absent in the distal caudal vertebrae of oviraptorosaurs. In the Oviraptorosauria, the presence of extremely deep hemal arches (chevrons) suggests a massive caudofemoralis muscle (Persons et al., 2013). Hemal arches are remarkably shortened in almost all primitive pygostylians and even lost in most living birds (Baumel and Witmer, 1993). Anatomical differences between the tightly associated caudal vertebrae in oviraptorosaurs and the pygostyle in birds suggest the decrease and fusion of caudal vertebrae in maniraptorans occurred through different genetic pathways, indicating fusion of the distalmost caudals evolved independently in different maniraptoran lineages (Rashid et al., 2014). To avoid confusion (Lü and Hou, 2005), fusion in the distalmost caudals of non-avian theropods should be described as pygostyle-like, and a true pygostyle should be regarded as a synapomorphy of the Pygostylia (Aves).

4.2 Evolution of the Tail Complex

In the last major study of the evolutionary transition of the avian tail, researchers considered the pygostyle in the basal bird *Confuciusornis* to be roughly equivalent to that of modern birds (Gatesy and Dial, 1996a, b). However, in light of the numerous specimens uncovered over the past two decades, representing a diverse aviary and a wealth of morphological data, significant differences are now clearly observable between the pygostyle and associated tail feathers of modern birds and those of basal clades (Sapeornithiformes, *Confuciusornithiformes*, *Enantiornithes*, and *Ornithuromorpha*).

The sapeornithiform pygostyle is relatively smaller and poorly co-ossified compared to most other Early Cretaceous pygostylians. Although forming a single

element, individual processes can still be observed in the cranial half of the pygostyle in most specimens; the adult condition is exemplified in the adult or near-adult specimens IVPP V 13275 and V 13276 [Figure 3: see original paper] (Zhou and Zhang, 2003b). As a result of increased caudal fusion, the pygostyle in confuciusornithiforms has comparatively smoother margins. Compared to saepeornithiforms, the pygostyle is proportionately longer in confuciusornithiforms and enantiornithines (with the exception of the Pengornithidae discussed later). Notably, the bilateral dorsolateral ridges present in confuciusornithiforms and enantiornithines define an excavated dorsal platform, whereas in ornithuromorphs (including extant birds) the neural spines are fused, forming the blade-like pygostyle lamina so that the surface area of the dorsal margin is negligible. In the blade-like ornithuromorph pygostyle, the centra fuse, forming the narrow pygostyle base, which is obscured in other pygostylians by the presence of lateral ridges and ventrolateral processes. The transverse processes are highly reduced in primitive ornithuromorphs, forming only a series of uneven low ridges on the lateral surface [Figure 6: see original paper]. However, in some taxa of living birds (like pheasants and raptors), the transverse processes are inferred to secondarily form the ventral process, and expanded in woodpeckers to form the pygostyle disc (Baumel, 1988) [Figure 8: see original paper]. These specialized transverse processes are restricted to the cranioventral end of the pygostyle where present in living birds, differing strongly from the fused transverse processes observed forming a ridge on the lateral surfaces of the saepeornithiform pygostyle or the unfused processes on the lateral surface in ornithuromorphs [Figure 3: see original paper].

Differences in pygostyle morphology between these four groups correspond to consistent differences in tail plumage. Sapeornis has been interpreted as having a strongly graded fan consisting of approximately eight pennaceous feathers (Zheng et al., 2013; Wang X et al., 2014; Xu et al., 2014), but this taxon has not been studied directly with regard to its rectricial morphology, and only one published specimen preserves this feature in lateral view. Additional specimens preserved in dorsal or ventral view confirm that a fan-shaped array of rectrices is present, but they also suggest that the rectrices did not overlap and thus would not have formed an aerodynamic surface (O' Connor et al., 2016). However, until these specimens can be further studied, tail function remains inconclusive in saepeornithiforms. Tail feathers are not present in all confuciusornithiform specimens; some preserve only rachis-less body feathers like those found on the neck and other parts of the body, which are also present in saepeornithiform, enantiornithine, and ornithuromorph fossils that also preserve rectrices. Other confuciusornithiform specimens additionally preserve a pair of elongate rachis-dominated rectrices interpreted as male-specific ornaments (Chiappe et al., 2008). Consistent with similarities in pygostyle morphology, similar ornamental rachis-dominated rectrices are also present in some enantiornithines (e.g., Protopteryx, Paraprotopteryx, Dapingfangornis) (Zhang and Zhou, 2000; Zheng et al., 2007; Li et al., 2006). The only exception is the pengornithid Chiappeavis (STM 29-11), which has recently been described with a “tail fan”

consisting of approximately eight overlapping rectrices (O' Connor et al., 2016). This fan is proportionately shorter than that observed in Jehol ornithuromorphs. Rectricial fans in early ornithuromorphs apparently consisted of eight to more than ten overlapping rectrices, comparable to living birds.

Differences in the pygostyle between clades of Early Cretaceous birds, supported by differences in rectricial morphology, suggest that the complete modern tail complex only evolved in the ornithuromorph lineage. In neornithines, the rectricial bulbs rest on sockets on either side of the pygostyle, separated medially by the pygostyle lamina [Figure 8: see original paper]. These bulbs root the calami of the rectrices, forming the tail fan and allowing their position to be precisely controlled by the rectricial bulb muscle (Baumel, 1988; Gatesy and Dial, 1996b). The nearly modern morphology of the pygostyle in all Early Cretaceous ornithuromorphs and the common preservation of a rectricial fan strongly suggest the complete tail complex evolved very early in this lineage. A few specimens even preserve carbonized imprints surrounding the pygostyle interpreted as soft tissue traces of the rectricial bulbs (Zhou et al., 2014), supporting inferences that this feature was present. The presence of a fan-shaped array of rectrices and a possible low pygostyle lamina in sapeornithiforms might suggest the presence of rudimentary rectricial bulbs in this lineage as well. However, the proportionately greater length (and width) of the pygostyle indicates that the rectricial bulbs, if present, would have differed from those in ornithuromorphs.

The tail complex can be considered absent in confuciusornithiforms based on the absence of a fan-shaped tail in all the hundreds of known specimens; this is supported by differences in pygostyle morphology, notably the absence of a pygostyle lamina. A pygostyle lamina is also totally absent in enantiornithines. We consider short body feathers (apparently rachis-less) to have been present on the tail in all enantiornithine groups regardless of rectricial morphology. A majority of enantiornithine specimens preserve a pair of rachis-dominated ornamental long rectrices, resembling those in confuciusornithiforms. The “fan tail” from which longipterygid *Shanweinia* gets its name (O' Connor et al., 2009) has been reinterpreted as non-aerodynamic, consisting of at least two pairs of rachis-dominated feathers, similar to the tail in *Paraprotopteryx* (O' Connor et al., 2016). This argument is partially based on pygostyle morphology, which agrees with the detailed observations from this study. The tail fan in pengornithid *Chiappeavis* (STM 29-11) greatly differs from the rectricial morphology in other pengornithids, all other members of which possess a pair of rachis-dominated streamer rectrices (*Parapengornis*, *Eopengornis*). However, the pygostyle of *Chiappeavis* is typical of pengornithids, although it is proportionately shorter and broader than in *Parapengornis*. Given the observed coevolution between pygostyle and tail feathers, similar pygostyle morphologies are expected to share similar rectrices both within Cretaceous primitive birds and living taxa (Clarke et al., 2006; Felice and O' Connor, 2014; Felice, 2014), making the two apparently functionally disparate tail morphologies observed in the Pengornithidae difficult to interpret.

Even if *Chiappeavis* possessed some structural equivalent to rectricial bulbs, their morphology would be expected to differ greatly from that of modern birds given the different shape of the pygostyle in pengornithids. As a result, there may also exist differences in tail function and ability between the two groups. Disparity in the tail plumage of *Chiappeavis* compared to other pengornithids, and differences in pygostyle morphology between *Chiappeavis* and ornithuromorphs, suggests that if a tail complex was present in *Chiappeavis*, it evolved independently in parallel to ornithuromorphs. We suggest that this tail fan may even have been capable of generating lift but did not have the muscular control of the fan shape associated with the ornithuromorph tail complex. The tail complex consisting of a blade-like pygostyle, rectricial bulbs, and aerodynamic rectrices appears to be unique to the Ornithuromorpha, as originally hypothesized by Clarke et al. (2006).

4.3 Coevolution of Tail Feathers and the Pygostyle

Modern birds exhibit a huge diversity of tail feather morphologies. To a lesser extent, the shape of the pygostyle also shows considerable variation. Bird tails can have both significant motor and/or display functions. The diversity of tail morphologies in extant birds is hypothesized to be a product of natural and/or sexual selection (Balmford et al., 1993; Thomas, 1997; Hedenström, 2002). Recent work has documented the coevolution of tail feathers with the pygostyle in living birds (Felice and O' Connor, 2014; Felice, 2014), indicating that rectrices with specialized functions require structurally modified pygostyles.

In addition to the rectricial bulbs and their muscle, the caudal depressor and caudal levator (*m. levator caudae*) muscles also form connections with the pygostyle (Baumel, 1988). The fleshy part of the *pars profunda* of the caudal depressor muscle adheres to the ventrolateral portion of the pygostyle base, and the tendon of this muscle attaches along the anterior-ventral margin of the pygostyle. The tendon of the distal part of the caudal levator muscle (*pars distalis*) attaches on the craniodorsal portion of the lateral surface of the pygostyle (Baumel, 1988). In certain extant raptor clades, the birds descend on their prey from great height at great speeds. Such taxa must be capable of generating large braking forces after seizing prey near the ground. This maneuvering requires a robust caudal depressor muscle. To provide an expanded area for the attachment of this expanded muscle, falconids possess an expanded tubercle, or in some cases paired accessory sesamoid flakelets (Richardson, 1972), on or near the cranioventral margin of the pygostyle [Figure 8D: see original paper]. Even greater ventral expansions, in the form of the pygostyle disc (Baumel and Witmer, 1993), are developed in woodpeckers and some piciforms. Woodpeckers have evolved stiffened feathers to support their bodies against gravity as an adaptation for vertical climbing (Manegold and Töpfer, 2013). This posture also requires a strong caudal depressor muscle, as the expanded pygostyle disc suggests. The enantiornithine *Parapengornis* has been described as possessing a pygostyle that is homomorphic to that of woodpeckers, indicating a similar

vertical climbing behavior in some Mesozoic enantiornithines (Hu et al., 2015). However, in the holotype of *Parapengornis eurycaudatus* (IVPP V 18687), the pygostyle is preserved in dorsal view, preventing observation of any expanded ventral surface (also preserved in dorsal view in the referred specimen IVPP V 18632). Instead, V 18687 displays a broad, concave dorsal platform defined by lateral ridges generally similar to those of other pengornithids. The dorsal expansion present in the pygostyle of *Parapengornis* and other pengornithids (Hu et al., 2015; Wang X et al., 2014) is in fact opposite the condition observed in the woodpecker pygostyle, in which it is the ventral surface that is expanded. The dorsal platform present in pengornithids and other enantiornithines is more consistent with the presence of an expanded caudal levator muscle, which attaches dorsally in living birds, rather than an expanded caudal depressor muscle as in woodpeckers and falconids [Figure 9: see original paper]. Furthermore, in woodpeckers, the specialized stiffened rectrices of the tail are not especially elongated and are additionally supported by a layer of tectrices. The tail feathers are proportionately longer in *Parapengornis*, and pennaceous tectrices appear to be absent. Together, it seems unlikely that these rachis-dominated rectrices could serve as a prop.

In extant phasianids with ornamental tails, the craniodorsal margin of the pygostyle is laterally expanded to provide additional surface for the attachment of the enlarged caudal levator muscle, which acts to elevate the elongated ornamental deck feathers (Gatesy and Dial, 1993). This craniodorsal expansion is obviously more strongly developed in males, though it is present in both sexes [Figure 8B: see original paper]. This dorsal platform is reminiscent of that in confuciusornithiforms and enantiornithines (Figs. 4, 5). The pygostyle of the male peafowl (*Pavo*) represents an extreme case: to lift its huge tail (coverts and rectrices), the narrow body of the pygostyle separates enlarged dorsal and ventral surfaces abnormally expanded for muscular attachments (“ Γ ” -shaped in cranial view) [Figure 9: see original paper]. Male birds living in wooded environments, like that inferred for the Jehol (Zhou, 2006), often have extravagant ornaments; the high degree of clutter and reduced visibility in wooded environments allows the evolution of such features under sexual selection (Endler and Thery, 1996). Paired elongate tail feathers are common in enantiornithines and have typically been regarded as ornamental and sexually dimorphic, as in *Confuciusornis*. The tail morphology in *Parapengornis* and other enantiornithine species is reminiscent of those found in male individuals of many extant arboreal birds, such as paradise-flycatchers (*Terpsiphone*). One Early Cretaceous enantiornithine, the holotype of *Feitianius paradisi*, preserves a robust pygostyle of typical enantiornithine morphology and a tail morphology consisting of at least three distinct feather morphologies that strongly resembles tail displays present in living sexually dimorphic birds (O’ Connor et al., 2016). This level of extravagance is only observed in extant polygamous birds. This study suggests that in addition to possessing such sexually specific ornaments [Figure 10: see original paper], some Cretaceous birds also engaged in display behaviors common in extant polygamous birds, including birds of paradise. Soft tissue surrounding

the pygostyle in the holotype of *Feitianius paradisi* was previously identified as including rectricial bulbs (O' Connor et al., 2016), but we consider that this may not be correct—instead, this may include expanded levator musculature, as hypothesized here [Figure 9: see original paper]. We conclude that the dorsal platform present in confuciusornithiforms and enantiornithine pygostyles may have accommodated a fortified caudal levator muscle, like that in phasianids. This strongly suggests these basal birds raised the paired long rachis-dominated deck feathers in some form of display, although whether to attract females or fend off competitors is unknown.

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