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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 ending in a pygostyle and accompanied by aerodynamic fanning rectrices is one of the most remarkable adaptations of early avian evolution. However, no fossils directly capture this transition, and information regarding the structural morphology and the early evolution of the pygostyle in Mesozoic birds and their integuments is relatively limited. Here we provide a review of the pygostyle morphology of Early Cretaceous birds with comparison 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. There further exist distinct differences in pygostyle morphology between Sapeornithiformes, Confuciusornithiformes, Enantiornithes, and Ornithuromorpha. The morphology of the pygostyle and rectrices in early ornithuromorphs appear 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-

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avian and avian) (Xu et al., 2014). To be concise, we will 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). Together, 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, there still exist significant gaps in our understanding of the structural transformation of birds from the theropod condition. One such evolutionary transformation is the reduction of the long boney 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 is in the 130.7 Ma *Protopteryx*-horizon of the Huajiying Formation, the earliest stage of the Jehol Biota, with the first appearance of three pygostylian 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: Therizinosauroidea, 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 consisting of 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 imbedded 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 paleognathus 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 (Pennycuick, 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 is poorly understood. Several short discussions have been published regarding specific taxa: *Jeholornis* (O'Connor et al., 2012, 2013), *Eopengornis* (Wang X et al., 2014), *Shanweiniao* (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.

Measurement abbreviations MLH, the mid-length height of the pygostyle; MLW, the mid-length width of the pygostyle; TLF, the total length of femurs; TLH, the total length of the humerus; TLP, the total length of the pygostyle.

2 Materials and methods

This study mainly 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 (Zhou et al., 2013; Heers et al., 2014), 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, 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 etc.) preventing the use of geometric morphometric analysis methods (Zelditch et al., 2012). Thus, three simple but reliable measurements were chosen: TLP, MLW (for dorsally/ventrally preserved specimens), and MLH (for laterally preserved specimens). In order to reduce the effects of body size, we normalized the TLP using TLH and TLF, 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 Description and analysis

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 the 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 (Fig. 1) 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).

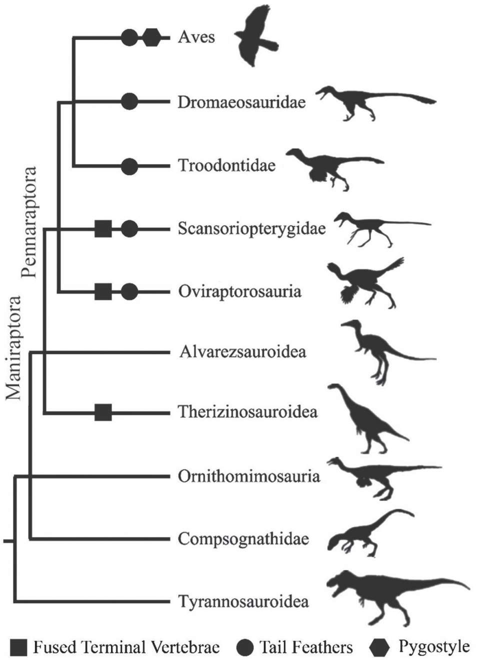

Fig. 1 Phylogeny of Maniraptora and related Theropoda dinosaurs
Modified from Brusatte et al., 2014

Some members of the Oviraptorosauria (basal most 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 distal most 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 these 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 (Fig. 2).

One member of the Scansoriopterygidae, *Epidexipteryx*, 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.

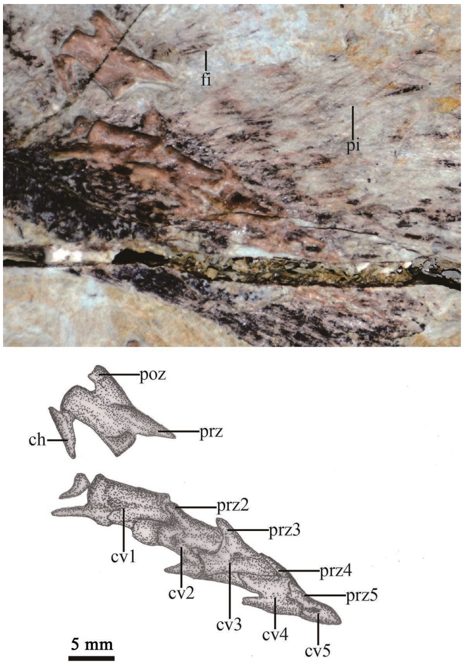

Fig. 2 Photographs and camera lucida drawings of distal caudal vertebrae of *Caudipteryx* sp. (IVPP V 22606)
Abbreviations: ch. chevron 人字骨; cv. caudal vertebra 尾椎; fi. filaments 丝状羽毛; pi. pinnules 羽枝; poz. postzygopophysis 后关节突; prz. prezygopophysis 前关节突

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 discriminate rectricial pterylae (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* (Gao et al., 2012; Pu et al., 2013). 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 (Fig. 3). 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

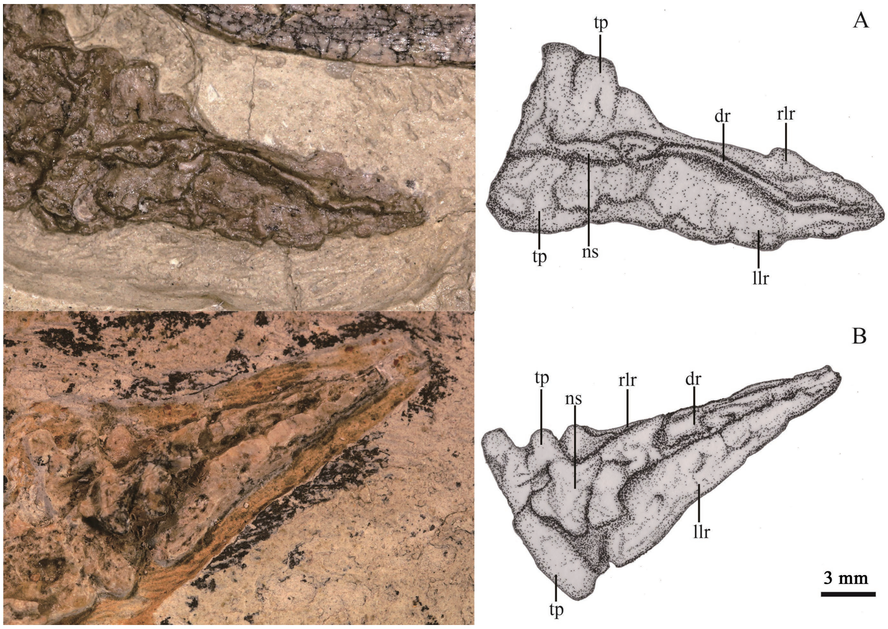

Fig. 3 Photographs and camera lucida drawings of pygostyles of Sapeornithiformes
A. *Sapeornis*, IVPP V 13276, in dorsal view; B. *Sapeornis*, IVPP V 13275, in dorsal-lateral view
Abbreviations: dr. dorsal ridge 背侧脊；llr. left lateral ridge 左侧脊；ns. neural spine 棘突；rlr. right lateral ridge 右侧脊； tp. transverse process 横突

(STM 16-18); this specimen preserves multiple elongate rectrices preserved 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 (Fig. 4A) and another pair of proximoventral processes (Fig. 4B). The proximoventral processes project cranially beyond the proximal articular surface (Fig. 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 that it forms a majority of the pygostyle corpus (Fig. 4B). The caudal margin is rounded and slightly laterally expanded (Fig. 4C). 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 (Fig. 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, accordingly they show a 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 (Fig. 5). The distal end of the pygostyle is tapered, formed by a constriction in the mediolateral width of the dorsal surface and the fact 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

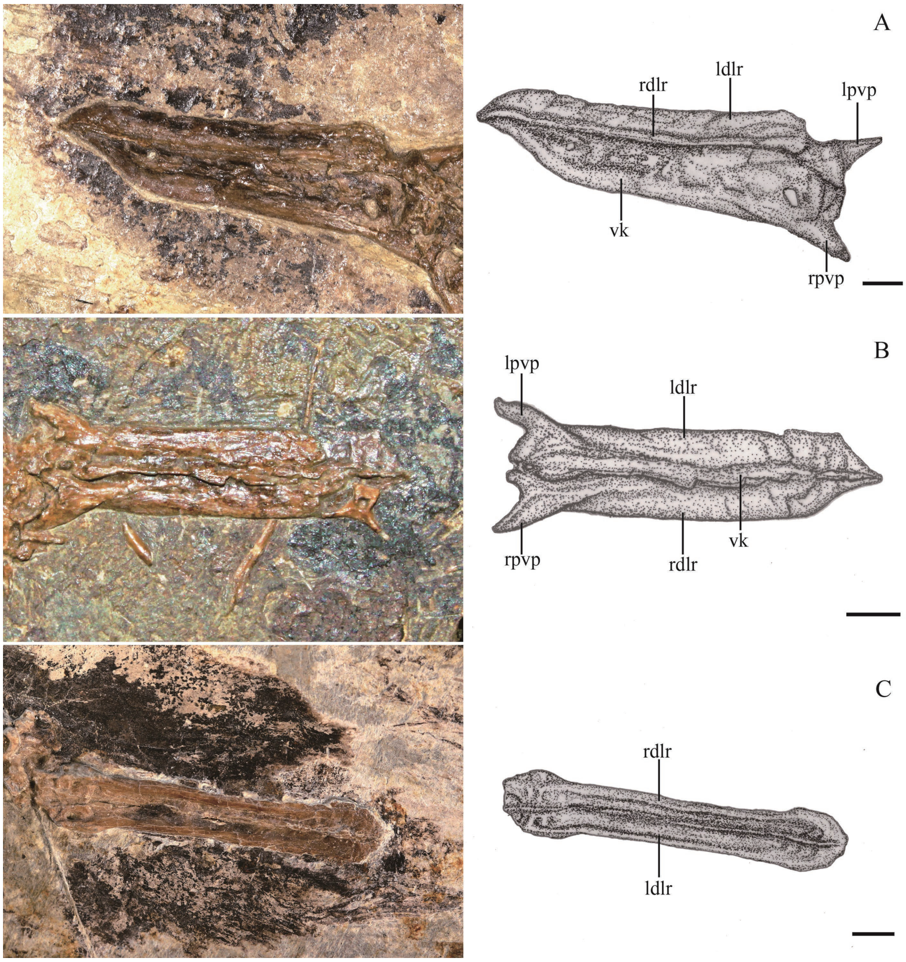

Fig. 4 Photographs and camera lucida drawings of pygostyles of Confuciusornithiformes
A. *Confuciusornis*, IVPP V 11640, in right doesolateral view; B. *Jinzhouornis*, IVPP V 12352, in ventral view; C. *Confuciusornis*, IVPP V 13156, in dorsal view
Abbreviations: ldlr. left dorsolateral ridge 左背侧脊；lpvp. left proximoventral process 左腹侧前突；rdlr. right dorsolateral ridge 右背侧脊；rpvp. right proximoventral process 右腹侧前突；vk. ventral keel 腹侧脊
Scale bars=3 mm

end is untapered: the ventrolateral processes are proximally restricted and the dorsal surface maintains an even width (*Pengornis* IVPP V 15336; Fig. 5A). 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 (Fig. 5B, C) is more slender and the ventrolateral processes taper gently rather than end abruptly as in most enantiornithines (Wang M et al., 2014). The Longipterygidae, the family that includes *Longipteryx*, *Rapaxavis*, and *Shanweiniao*, 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 (Fig. 5D).

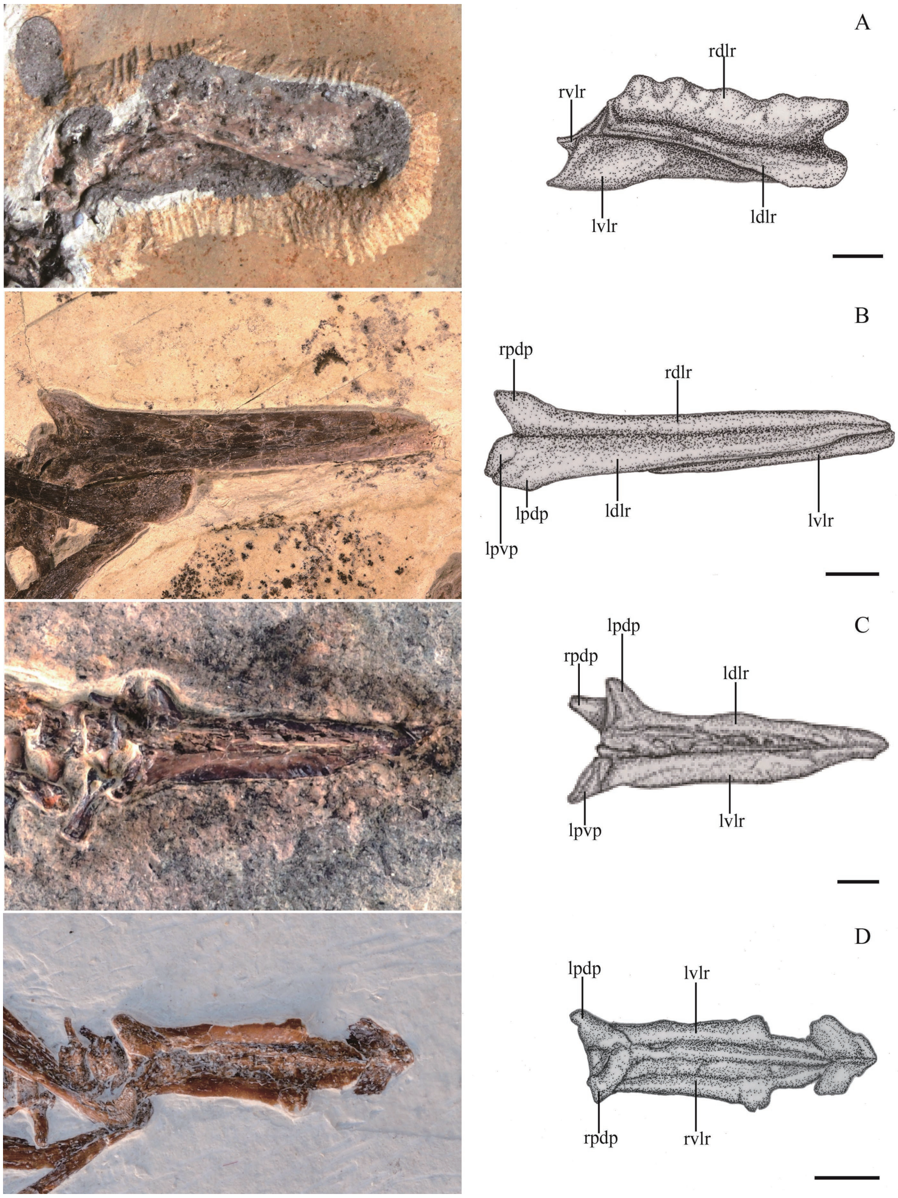

Fig. 5 Photographs and camera lucida drawings of pygostyles of enantiornithines
A. *Pengornis*, IVPP V 15336, in left dorsolateral view; B. *Parabohaiornis*, IVPP V 18690, in left laterodorsal view; C. *Sulcavis*, BMNH-Ph 00805, in left lateral view; D. *Rapaxavis*, DNHM D 2522, in ventral view
Abbreviations: ldlr. left dorsolateral ridge 左背侧脊；lpdp. left proximodorsal process 左背侧前突；lpvp. left proximoventral process 左腹侧前突；lvlr. left ventrolateral ridge 左腹侧脊；rdlr. right dorsolateral ridge 右背侧脊；rpdp. right proximodorsal process 右背侧前突；rvlr. right ventrolateral ridge 右腹侧脊
Scale bars=3 mm

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 rachis-less 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 regards 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; Jetz et al., 2012; O'Connor and Zhou, 2013; Jarvis et al., 2014; Wang et al., 2015). Several Early Cretaceous fossil ornithuromorphs preserve evidences 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 (Fig. 6). 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 (Fig. 6). In lateral view the pygostyle is upturned (Fig. 6) 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 *Schizooura lii* (IVPP V 16861), which preserves a forked tail, considered by aerodynamic models to be the most efficient tail shape (Thomas et al., 1993; Zhou et al., 2012). All other ornithuromorph specimens with caudal integument preserve the impression of an aerodynamic tail fan

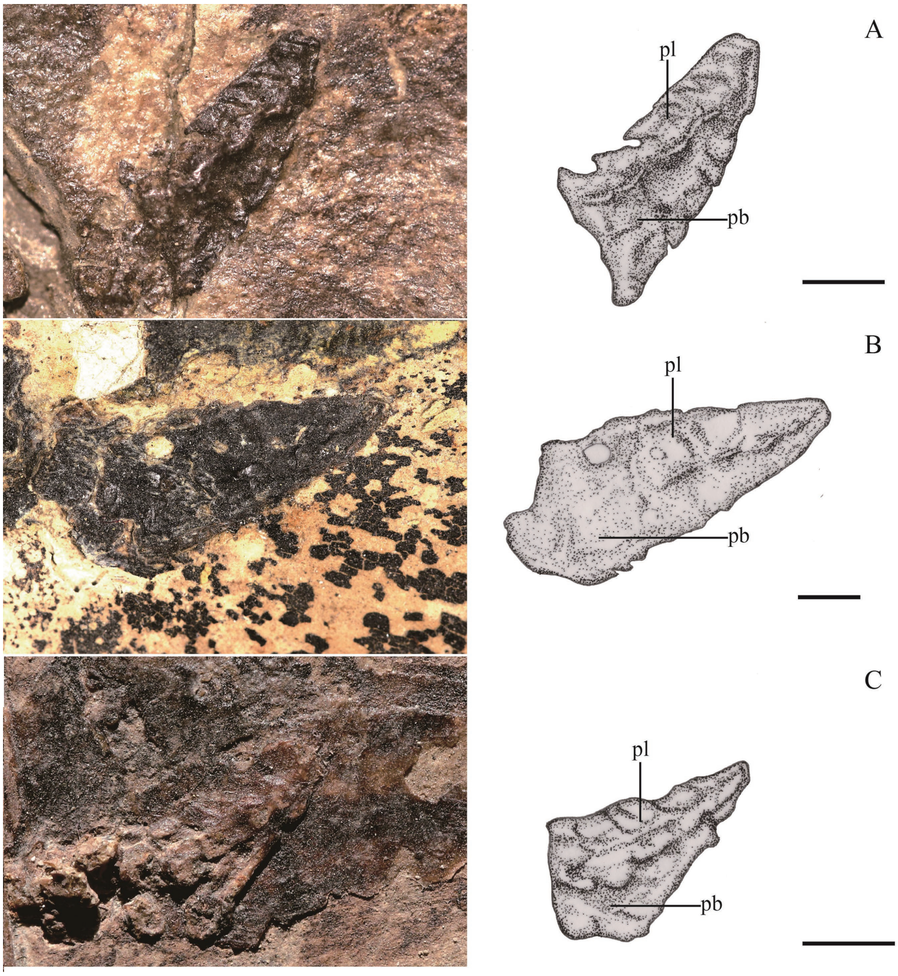

Fig. 6 Photographs and camera lucida drawings of pygostyles of ornithuromorphs in left lateral view
A. *Yixianornis*, IVPP V 12631; B. *Piscivoravis*, IVPP V 17078; C. *Iteravis*, IVPP V 18958
Abbreviations: pb. pygostyle base 尾综骨基部；pl. pygostyle lamina 尾综骨板。 Scale bars=3 mm

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) (Zhou et al., 2013; Chiappe et al., 2014; Zheng et al., 2014; 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 (Table 1). Almost all ornithuromorph pygostyles are preserved laterally and do not provide data on the MLW. The width was measured from the holotype of *Schizooura 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 the phylogeny. We choose TLH and TLF, which are commonly used, both as the appropriate proxies of avian body size (Liu et al., 2012; Hone, 2012). The result (Table 1) 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 of enantiornithines (0.34–0.66, exclude those of Pengornithidae). The result can be visible in Fig. 7A: scatter points belonging to sapeornithiforms and ornithuromorphs are more closed to TLH-axis, while those of confuciusornithiforms and enantiornithines are near TLP-axis. In the enantiornithines, low TLP/TLH values can also be found in the Pengornithidae (0.18–0.30). Consistent result also can be confirmed when the proxy is changed into TLF (see TLP/TLF in Table. 1; Fig. 7B). The two aspects of results both suggest proportionally shorter pygostyles relative to body size in sapeornithiforms and ornithuromorphs, especially in the latter.

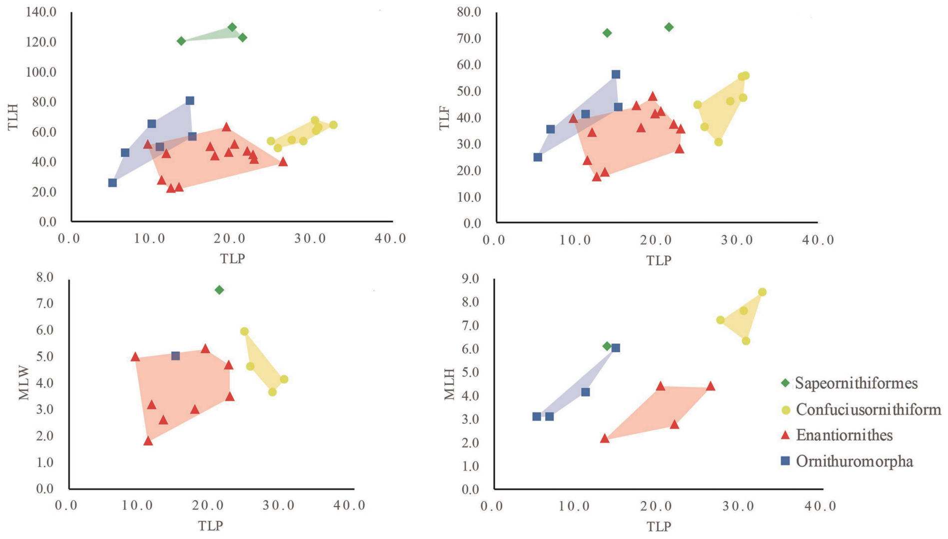

Fig. 7 Scatter diagram of metrical data (Table 1) of fossil pygostyles
In accord with the phylogenetic result, all the data can also be separated into four parts by each parameter-couple in rectangular plane coordinate systems

Table 1 Measurements of pygostyles, humeri and femurs of Mesozoic avian fossils (mm)

	Genera	Specimen	TLP	MLW	MLH	TLH	TLF	TLP/ TLH	TLP/ TLF	MLW/ TLP	MLH/ TLP
Sapeornithidae (the only family of Sapeornithiformes)	*Sapeornis*	IVPP V 13275	21.3	7.5		122.9	74.1	0.17	0.29	0.35	
		IVPP V 13276	13.7		6.1	120.4	72.1	0.11	0.19		0.45
		CAGS-03-07-08	20.0			130.0		0.15			
Confuciusornithidae (the only family of Confuciusornithi- -formes)	*Confuciusornis*	IVPP V 13175	30.4		7.6	67.2	55.3	0.45	0.55		0.25
		IVPP V 16066	27.5		7.2	54.0	44.5	0.51	0.62		0.26
		IVPP V 10932A	25.7	4.6		48.7	36.3	0.53	0.71	0.18	
		IVPP V 13172	28.9	3.6		53.1	45.8	0.54	0.63	0.12	
		IVPP V 11640	32.6		8.4	64.5		0.51			0.26
		IVPP V 13156	30.5	4.1		60.4	47.1	0.50	0.65	0.13	
		IVPP V 13171	30.7		6.3	62.3	55.5	0.49	0.55		0.21
	Jinzhouornis	IVPP V 12352	14.8	5.9		53.3	30.5	0.47	0.49	0.24	
Protopterygidae	*Protopteryx*	IVPP V 11665	11.2	1.8		28.0	23.7	0.40	0.47	0.16	
Pengornithidae	*Pengornis*	IVPP V 15336	19.3	5.3		63.5	48.1	0.30	0.40	0.27	
		IVPP V 18632	11.7	3.2		45.8	34.6	0.26	0.34	0.27	
	Parapengornis	IVPP V 18687	9.4	5.0		51.7	39.8	0.18	0.24	0.53	
Bohaiornithidae	*Longusunguis*	IVPP V 17964	22.7	3.5		41.8	35.8	0.54	0.63	0.15	
	Parabohaiornis	IVPP V 18691	17.8	3.0		43.9	36.0	0.41	0.49	0.17	
		IVPP V 18690	21.9		2.8	47.3	37.5	0.46	0.58		
	Bohaiornis	IVPP V 17963	20.2		4.4	51.7	42.6	0.39	0.47		0.22
	Zhouornis	CNUVB-0903	17.3			50.6	44.5	0.34	0.39		
	Sulcavis	BMNH-Ph 00805	19.6			46.5	41.3	0.42	0.47		
Longipterygidae	*Longipteryx*	IVPP V 12325	22.5	4.7		44.6	28.1	0.50	0.80	0.21	
		IVPP V 12552	26.3		4.4	40.1		0.66			0.17
	Longirostravis	IVPP V 11309	13.4	2.6	2.2	23.1	19.5	0.58	0.69	0.19	0.16
	Shanweiniao	DNHM 1878	12.4			22.4	17.6	0.55	0.70		
Hongshanornithidae	*Hongshanornis*	IVPP V 14533	5.2		3.1	25.6	24.9	0.20	0.21		0.60
Songlingornithidae	*Yixianornis*	IVPP V 12631	11.1		4.1	49.4	41.0	0.22	0.27		0.37
	Yanornis	IVPP V 13278	10.0			64.8		0.15			
	Piscivoravis	IVPP V 17078	14.8		6.0	80.6	56.0	0.18	0.26		0.41
(undetermined)	*Iteravis*	IVPP V 18958	6.8		3.1	45.7	35.2	0.15	0.19		0.46
	Schizooura	IVPP V 16861	15.1	5.0		56.8	43.6	0.27	0.35	0.33?	

Citations: *Sapeornis* CAGS-03-07-08 (Yuan, 2005), *Zhouornis* (Zhang et al., 2013), *Sulcavis* (O'Connor et al., 2013), *Shanweiniao* (O'Connor et al., 2009).

Clades cannot be easily distinguished by MLW/TLP values (Table 1; Fig. 7C). Because the data of sapeornithiforms and ornithuromorphs are too questionable and limited (only one datum of 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 *Schizooura lii*, is not reliable due to deformation. However, we hypothesize that wide spread 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 interpreted from 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; Fig. 7D). This greater dorsoventral depth is produced by the prominent neural spines in sapeornithiforms and the dominant pygostyle lamina in ornithuromorphs, which both 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 four investigated clades. Despite of the ratio values discussed above, cluster distributions of four clades can be more or less separated as their borders with slight overlaps show (Fig. 7). Therefore, four avian clades can be, to some extent, differed according to the absolute sizes.

4 Discussion

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; Gao et al., 2008; Persons and Currie, 2011a, b; Persons et al., 2013). 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 distal most 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 that 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 (Fig. 3) (Zhou and Zhang, 2003b). As a result of the increased caudal fusion, the pygostyle in confuciusornithiforms have comparatively smoother margins. Compared to sapeornithiforms, the pygostyle is proportionately longer in confuciusornithiforms and enantiornithines (only exceptions 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 (Fig. 6). However, in some taxa of living birds (like pheasant and raptors) the transverse processes are inferred to secondarily form the ventral process, and expanded in wood peckers to form the pygostyle disc (Baumel, 1988) (Fig. 8). 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 sapeornithiform pygostyle or the unfused processes on the lateral surface in ornithuromorphs (Fig. 3).

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 regards 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 sapeornithiforms. Tail feathers are not present in all confuciusornithiform specimens, some of which preserve only rachis-less body feathers like those found on the neck and other parts of the body, which are also present in sapeornithiform, enantiornithine and ornithuromorph fossils also preserving 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; Li et al., 2006; Zheng et al., 2007). 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 (Fig. 8). These bulbs root the calami of the rectrices forming the tail fan, 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 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 that in ornithuromorphs. The tail complex can be considered absent in the confuciusornithiforms based on the absence of a fan-shaped tail in all the hundreds of known specimens; this is supported through differences in pygostyle morphology, notably the absence of a pygostyle lamina.

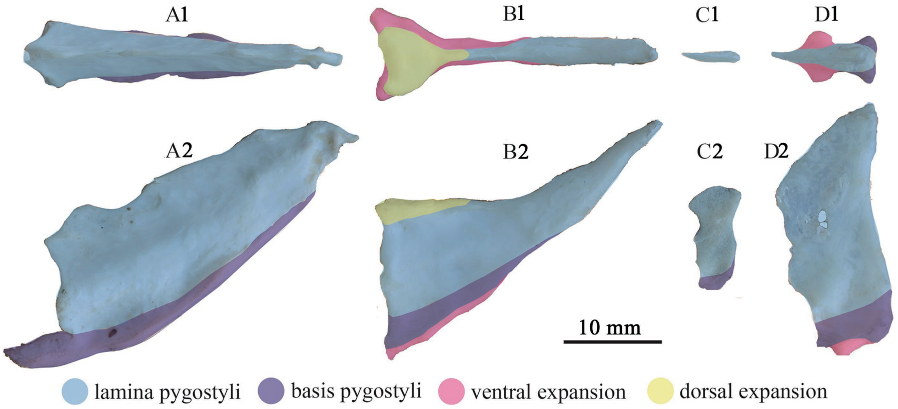

Fig. 8 Illustration of extant avian pygostyles in dorsal (A1, B1, C1, D1) and left-lateral (A2, B2, C2, D2) views
A. *Cynus cynus*, IVPP OV 1721; B. *Lophura nycthemera*, OV 1863;
C. *Streptopelia orientalis*, OV 1883; D. *Buteo buteo*, OV 1888
Light blue: pygostyle lamina, its lateral surfaces are the major attachments for rectricial bulbs and rectricial bulb muscle, anteriorly up-lateral and dorsal surfaces are attachments for caudal levator muscle;
purple: pygostyle base, its anteriorly low-lateral and ventral surfaces are attachments for caudal depressor muscle; peach: ventral expansion of pygostyle base for well-developed caudal depressor muscle;
light yellow: dorsal expansion of pygostyle lamina for well-developed caudal levator muscle

A pygostyle lamina is also totally absent in enantiornithines. We consider short body feathers (apparently rachis-less) were 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 longiptergyid *Shanweiniao* 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, 2014; Felice and O'Connor, 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 even may 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 quite a bit of variation. Bird tails can have both significant motor and/or display functions. The diversity of tail morphologies in extant birds are hypothesized to be a product of natural and/or sexual selection (Balmfold et al., 1993; Thomas, 1997; Hedenström, 2002). Recent work has documented the coevolution of the tail feathers with the pygostyle in living birds (Felice, 2014; Felice and O'Connor, 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). Fleshy part of the pars profunda of the caudal depressor muscle adhere 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. In order 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 probably (Fig. 8D). 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 in order 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 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 (Wang X et al., 2014; Hu et al., 2015) 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 (Fig. 9). 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 presents in both genders (Fig. 8B). 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 ("工"-shaped in cranial view) (Fig. 9). 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

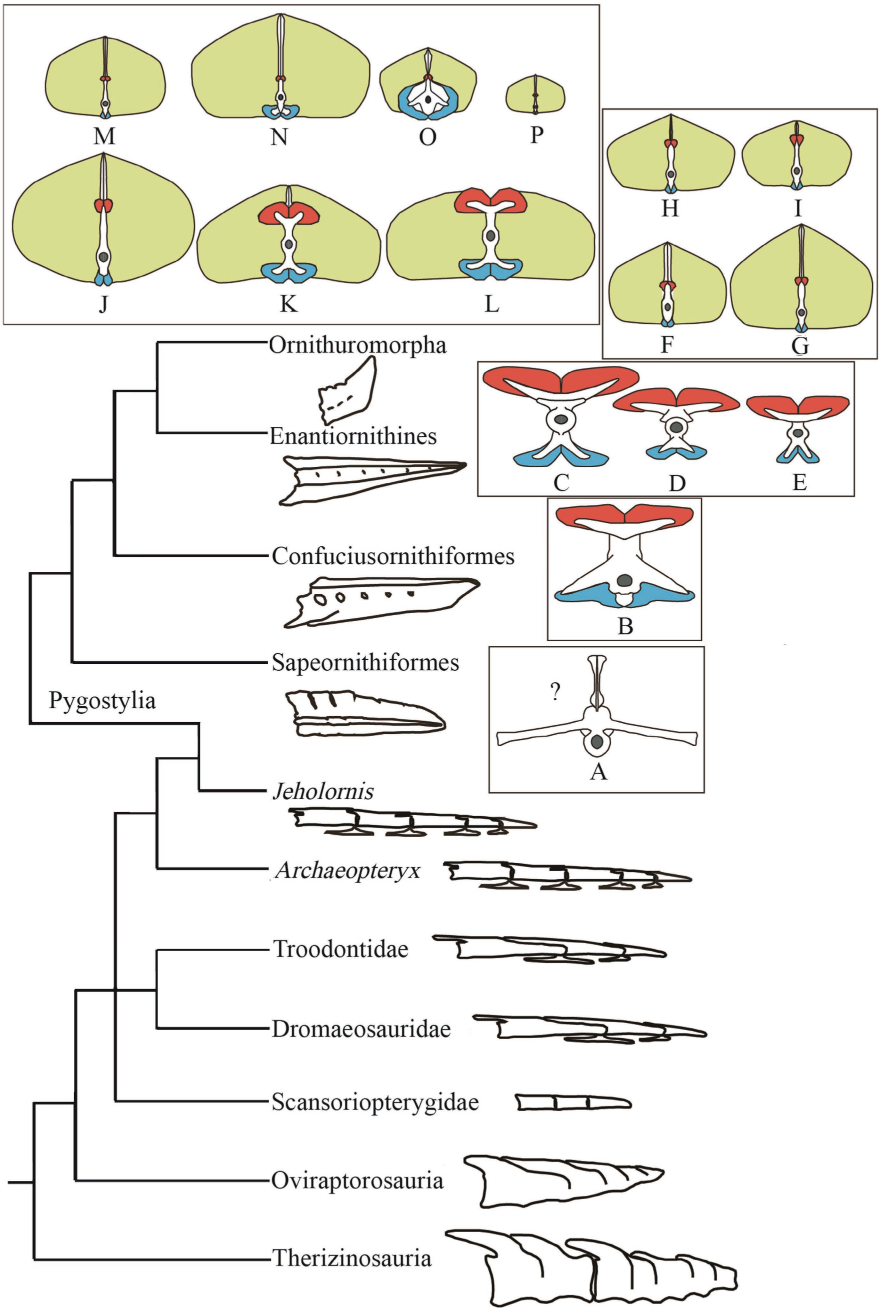

Fig. 9 Reconstruction of caudal fusion/pygostyle from maniraptorans to birds

Line drawing near the group name shows left lateral view of distalest caudal vertebrae of each clade. Line drawing in the box shows proximal/cranial view of pygostyle and soft tissue attachments: bone in white, articular surface is gray dot, caudal levator muscle in red, caudal depressor muscle in blue, rectricial bulb in yellow

A. Sapeornithiformes; B. Confuciusornithiformes; C. *Pengornis*; D. *Parabohaiornis*; E. *Rapaxavis*; F. *Yixianornis*; G. *Piscivoravis*; H. *Iteravis*; I. *Gansus*; J. *Cynus cynus*; K. *Lophura nycthemera*; L. *Pavo cristatus*; M. *Streptopelia orientalis*; N. *Buteo buteo*; O. *Dendrocopos major*; P. *Passer montanus* (not scaled) 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 the 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 (Fig. 10), some Cretaceous birds also engaged in display behaviors as common in extant polygamous birds, including the 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 (Fig. 9). We conclude that the dorsal platform present in the confuciusornithiforms and enantiornithine pygostyle 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 of competitors is unknown.

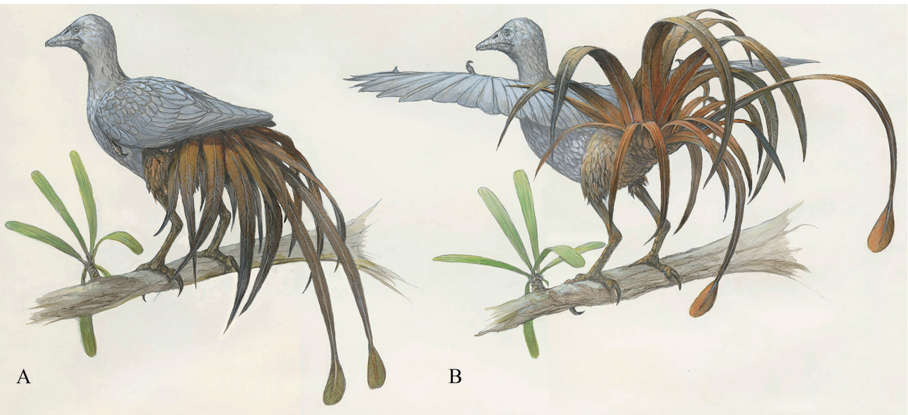

Fig. 10 Reconstruction of *Feinianius paradisi* by Michael Rothman showing the tail relaxed and with the levator musculature flexed, engaged in a display
A. perched and non-displaying; B. perched and displaying

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早白垩世鸟类尾综骨与尾羽之间的形态协同演化

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摘要：从兽脚类恐龙中爬行类的骨质长尾，到以尾综骨为终端，并附着具有空气动力学功能的扇状尾羽的短巧尾部，是早期鸟类演化中最显著的适应性转变之一。但能直接反映这一转变的化石记录匮乏，而且对中生代鸟类尾部形态结构，以及尾综骨和尾羽早期演化的认知也相对不足。在此对早白垩世鸟类的尾综骨形态予以概述并将其与现生鸟类尾部结构类比。本研究强调了非鸟手盗龙类中尾椎的联合骨化与早期鸟类的尾综骨实属趋同演化。本研究表明，会鸟形类、孔子鸟形类、反鸟类和今鸟型类的尾综骨结构存在明显差异。今鸟型类尾综骨和尾羽(舵羽)与现代鸟类的相似，而相对更原始的鸟类的尾综骨，从形态来看，并不能支持舵羽球状膨大和必要的肌肉附着来操控具有空气动力学功能的扇状尾羽。由此可见，舵羽球状膨大、舵羽扇面与犁铧状的尾综骨是在今鸟型类演化早期相伴相生的。相对于从前的认知，本研究还发现孔子鸟类的尾综骨与反鸟类的有更多相似之处，与二者都具有的几乎相同的装饰性尾羽相符合。

关键词：热河生物群，鸟类，舵羽球状膨大，舵羽

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