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A Possible Long-tailed Bird with a Pygostyle from the Late Mesozoic Yixian Formation, Western Liaoning, China

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Abstract An incomplete caudal vertebral series (IVPP V11309) from the Yixian Formation of late Mesozoic, Jianshangou area of Beipiao, western Liaoning Province, may represent a new bird. The tail is composed of at least 12 free caudal vertebrae and the most distal 5 caudal vertebrae co-ossified into a pygostyle. The pygostyle is plate-like and slightly curved dorsally. The anterior free caudals are amphiplatyan. The anterior caudal surfaces of the last three free caudals are concave, but their posterior articular surfaces are convex. The pygostyle is regarded as the first appeared flight apparatus during the evolutionary process from *Archaeopteryx* to neornithes. The pygostyle appeared in most early fossil birds and almost all the modern birds. Although their morphologies are different, they are basically formed by at least four last caudal vertebrae. The specimen V11309 is regarded as a bird rather than a non-avian theropod dinosaur based on the following characters: short caudal vertebrae, numerous pits present on the surfaces of the centra and, a foramen present between the basal part of the fused neural spines, which is similar to that of *Struthio camelus*. The discoveries of pygostyles from the therizinosauroids and oviraptorosaurs may provide strong evidence for supporting the origin of birds from small theropod dinosaurs. The structure of the pygostyle in specimen V11309 is different from those of *Beipiaosaurus* (Therizinosauroid) and *Nomingia* (oviraptorosaur). The most parsimonious interpretation is that these pygostyle-like structures are independently acquired by *Beipiaosaurus* and *Nomingia* during their evolutionary process.

Key words: western Liaoning, Yixian Formation, late Mesozoic, pygostyle

1 Introduction

Since the naming of the first Mesozoic bird *Cathayornis* from western Liaoning Province (Zhou et al., 1992), many other fossil birds have been found in western Liaoning and its peripheral areas (Hou et al., 1995; 1996, 1999; Hou, 1997; Hou and Chen, 1999; Chiappe et al., 1999; Zhang and Zhou, 2000; Zhou and Zhang, 2001; Zhou and Zhang, 2002). These discoveries have made this region world famous, becoming the most noted region for producing fossils of early birds. The pygostyle, a section of fused caudal vertebrae is an important feature in bird evolution, and it appears in many early birds. In different taxa of fossil birds, the pygostyle shows variation in shape and size. Herein described is an incomplete caudal vertebral series with a pygostyle, which may represent a new bird.

2 Description

A partial tail (IVPP V11309), including at least 12 free caudal vertebrae with the last five caudal vertebrae fused into a pygostyle (Fig. 1, Table 1). The anterior five vertebrae are preserved as impressions. The length and the height of the centra are nearly equal in the anterior four caudal vertebrae. Their anterior and posterior articular ends are flat and their prezygopophyses and postzygopophyses are relatively short.

Among the 12 preserved caudal vertebrae anterior to the pygostyle, they become shorter and narrower posteriorly. The 7th vertebra is the longest, and the posterior five vertebrae increasingly become shorter and slender. Weak ventral keels are present in the 8th and the 9th vertebrae. The surfaces of the preserved free caudal vertebrae are covered by many small holes (Fig. 2a), which may be a unique character of this bird. The anterior articular ends of three caudal vertebrae adjacent to the pygostyle are clearly larger than their posterior articular ends, and their articular surfaces are slightly concave, while their posterior articular surfaces are convex. The lengths of the prezygopophysis of the three vertebrae are relatively longer, occupying the 2/3 length of the anterior centrum. The axis of the pygostyle is slightly curved dorsally in lateral view (Fig. 2b). The sutures between the vertebrae are clear. The pygostyle is composed of five vertebrae, and the neural arches of the anterior three are developed and are fused into a plate, but their sutures are still traceable. There is a foramen between

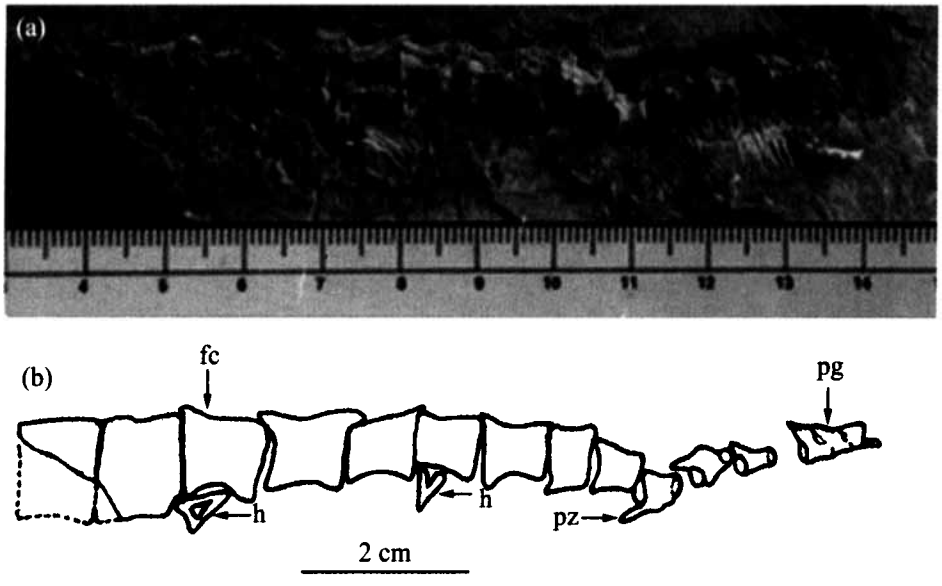

Fig. 1. A possible long-tailed bird (V11309): photograph (a) and line drawings (b).
Abbreviations: fc – free caudals; h – haemal arch; pg – pygostyle; pz – prezygopophysis.

Table 1 Measurements of caudal vertebrae and the pygostyle of a possible long-tailed bird (V11309) (mm)

	Length	Height
Caudal vertebra 1	6	--
Caudal vertebra 2	10.3	9.3
Caudal vertebra 3	10.3	9.3
Caudal vertebra 4	8.4	5.7
Caudal vertebra 5	6.3	6.3
Caudal vertebra 6	6.3	5.9
Caudal vertebra 7	7.2	5
Caudal vertebra 8	5.1	--
Caudal vertebra 9	5.1	--
Caudal vertebra 10	4.7	--
Caudal vertebra 11	4	--
Caudal vertebra 12	3	--
Caudal vertebra 13 to 18 (pygostyle)	8.6	--

Note: The vertebrae are numbered in the order preserved, not anatomical position.

the bases of the neural arches, similar to that of *Struthio camelus* (Fig. 3), although the function of the foramen is unknown. The neural arches of the last two vertebrae are not clear, and they may be not preserved. The haemal arches are preserved in several anterior caudal vertebrae, however, no fused haemal arches are found associated with the pygostyle.

3 Discussion

Most non-avian theropod dinosaurs have long tails with elongate caudal centra (Barsbold et al., 2000a), and some primitive birds, such as *Archaeopteryx* and *Shenzhouraptor*, also have long tails with elongate caudal centra (Ji et al., 2002, 2003). The free caudal vertebrae of the V11309 show short centra, the pygostyle is composed of five vertebrae and the lateral surfaces of the centra are covered by numerous pits. These suggest that the new specimen is of a bird rather than a non-avian theropod dinosaur. The last three free caudal vertebrae with slightly concave anterior ends and convex posterior ends, and the laminar pygostyle of the new material are similar to those of an Iberomesornithid bird (Sanz and Bonaparte, 1992; Sereno, 2000). However, it is clearly larger than *Iberomesornis* and has fewer fused caudal vertebrae in the pygostyle. The fused spines forming a plate-like structure in the pygostyle is also similar to that of flightless bird *Struthio* (see De Beer, 1956, Fig. 2 of Plate 5; Holmgren, 1955), but it is different from other kinds of birds and the non-avian theropod dinosaurs *Nomingia gobiensis* (Barsbold et al., 2000a) and *Beipiaosaurus expectus* (Xu et al., 2003).

Although birds generally have 18 to 23 caudal vertebrae, most of them are fused into synsacrum and pygostyle (Barsbold et al., 2000a), leaving five to nine free caudal vertebrae (Oort, 1905). More than nine free caudal vertebrae may indicate a primitive condition. The avian pygostyle is composed of centra, neural arches and haemal arches (Parker, 1888). The neural arches and the centra are not highly fused in the specimen V11309, and their sutures are traceable. There is no evidence of the fused haemal arches.

The pygostyle is regarded as one of the first characters acquired during the transformation of the flight apparatus from *Archaeopteryx* to Ornithurae (Sanz and Bonaparte, 1992). The pygostyle in the new specimen is laminar in lateral view. It is different from that of *Confuciusornis*, where the pygostyle ends in a transversally rounded tip (Chiappe et al., 1999) and that of *Liaoxiornis delicates*, which is slender and rod-like (Hou and Chen, 1999).

The total number of vertebrae in the pygostyle varies in different birds. It is at least four in *Sapeornis chaoyangensis* (Zhou and Zhang, 2002), eight and ten in *Confuciusornis sanctus* according to Hou et al. (1996) and Martin et al. (1998) respectively, about 10 to 15 in *Iberomesornis romerali* (Sanz and Bonaparte, 1992;

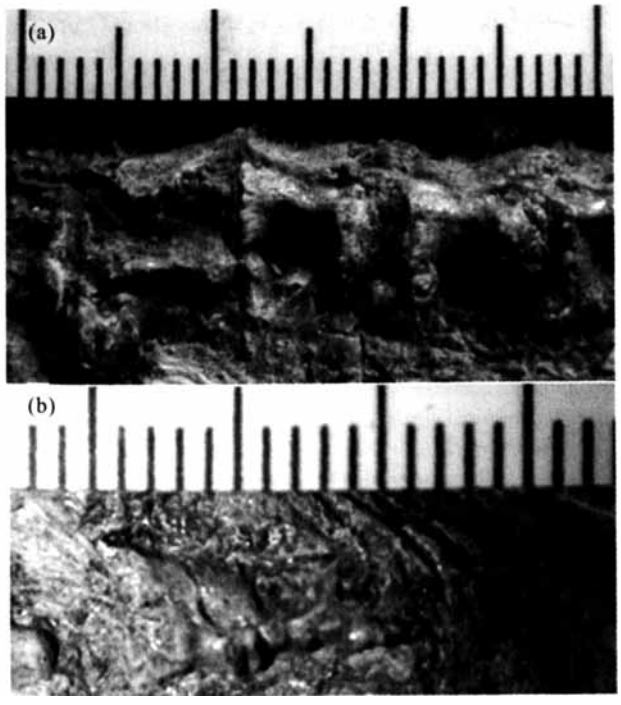

Fig. 2. A possible long-tailed bird (V11309).
a. Free caduals showing plenty of small holes on the lateral surfaces of the centra; b. The pygostyle in lateral view. Scale: mm.

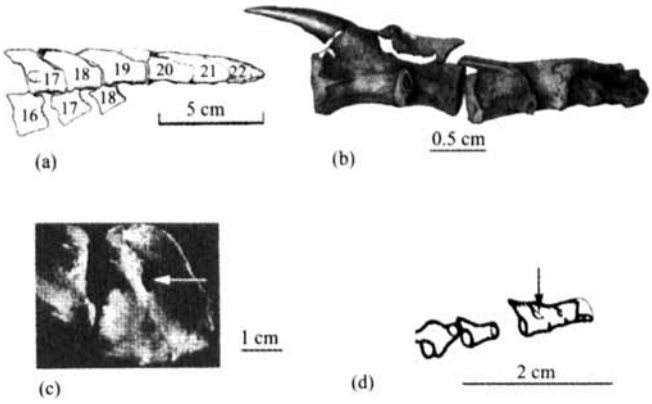

Fig. 3. The pygostyles of *Nomingia gobiensis* (a), *Beipiaosaurus inexpectus* (b), *Struthio camelus* (reversed) (c) and a possible long-tailed bird (V11309) (d).
a is from Barsbold et al., 2000a; b is from Xu et al., 2003; and c is from De Beer, 1956.

Sereno, 2000). The number of free caudal vertebrae is also different in birds. There are at least four in *Liaoxiornis delicates* (Hou and Chen, 1999), five in *Yixianornis grabaui* (Zhou and Zhang, 2001), seven in *Confuciusornis sanctus* (Chiappe et al., 1999), eight in *Iberomesornis romerali*, eight in *Sinornis santensis* (Sereno and Rao, 1992), but at least 12 in the new specimen.

The ornithurae are characterized by the absence of zygapophyses in the caudal vertebrae (Gauthier, 1986). The presence of zygapophyses in *Confuciusornis sanctus* (Chiappe et al., 1999), *Iberomesornis romerali* (Sanz and Bonaparte, 1992) and the new specimen V11309 indicate that they are primitive. Based on its relatively short pygostyle, the ratio of the length of pygostyle to the whole length of the free caudal vertebrae in the specimen V11309 is expected to be much smaller than those of *Confuciusornis* and *Iberomesornis*.

Besides fossil and living birds, a pygostyle is also found in an oviraptorosaur *Nomingia gobiensis* (Barsbold et al., 2000a, b) and a basal therizinosaur *Beipiaosaurus inexpectus* (Xu, 2002; Xu et al., 2003). Oviraptorosaurs are generally regarded as special small non-avian theropod dinosaurs (Gauthier, 1986; Barsbold et al., 1990, 2000a; Barsbold, 1997; Sereno, 1999); however, some recent phylogenetic analyses suggest that oviraptorosaurs fall within Aves, and should be regarded as a group of secondarily flightless birds (Lü et al., 2002; Maryanska et al., 2002), but this is not substantiated by other phylogenetic analyses of Theropoda. The most parsimonious interpretation is that *Nomingia gobiensis* and *Beipiaosaurus inexpectus* independently acquired this character. The pygostyle of the specimen V11309 is different from that of *Nomingia gobiensis* in its small size and well developed neural arches forming a plate-like pygostyle (Fig. 3). The pygostyle of the specimen V11309 shows some similarities with that of ratites in that neural arches fused into a plate-like structure and a foramen is present between the bases of the neural arches (Fig. 3). Except for the structure of the pygostyle, the tail of the specimen V11309 differs also from that of *Beipiaosaurus inexpectus* in having relatively short centra, short prezygopophyses and in having the lateral surfaces of the free caudal centra sculptured with many pits and the neural spines are poorly developed in *Beipiaosaurus inexpectus* (Xu et al., 2003).

4 Conclusion

Pygostyle appears in most early birds, and it usually consists of at least four caudal vertebrae. This may be a useful diagnostic feature of earlier birds, regardless of the number of their free caudal vertebrae. The specimen V11309 is considered to be a bird rather than a non-avian theropod dinosaur based on the following characters: short caudal vertebrae, numerous pits present on the surfaces of the centra and a foramen present between the basal part of the fused neural spines. However, confirmation of this assignment must await the discovery of complete material.

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