

Pygostyle-like Structure from *Beipiaosaurus* (Theropoda, Therizinosauroida) from the Lower Cretaceous Yixian Formation of Liaoning, China

XU Xing¹, CHENG Yennien², WANG Xiaolin¹ and CHANG Chunhsiang²

¹ Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; E-mail: xu.xing@ivpp.ac.cn

² Division of Geology, National Museum of Natural Science, Taichung, China

Abstract Pygostyle was previously considered as a unique structure of ornithothoracine birds, used to maneuver tail feathers. A similar structure from an oviraptorosaurian dinosaur was considered functionally associated with the rectrices as in birds. We report a pygostyle-like structure from a therizinosauroid dinosaur. The presence of filamentous integuments, but absence of rectrices, on the tail of this therizinosauroid, combined with other lines of evidence, suggests that the initial function of the pygostyle was not related to the rectrices.

Key words: pygostyle-like structure, Therizinosauroida, Yixian Formation, western Liaoning, China

1 Introduction

A number of important dinosaur taxa were recently found from China (Ji and Ji, 1996, 1997; Chen et al., 1998; Ji et al., 1998, 2001, 2003; Xu et al., 1999a, b, 2000, 2001a, 2002a, b, c; Luo and Wang, 2000; Pang and Cheng, 2000; Wang and Xu, 2001; You and Dong, 2003; You et al., 2003a, b) and advanced significantly the study on the morphology and evolution of dinosaurs. In 1999, we reported filamentous integumentary structures in the basal therizinosauroid *Beipiaosaurus inexpectus* (Xu et al., 1999a) from the Lower Cretaceous Yixian Formation (Xu and Wang, 1998; Swisher et al., 1999) at the famous Sihetun locality of Beipiao, Liaoning, China. The discovery of *Beipiaosaurus* provides fresh evidence indicating that therizinosauroids are a group nested within coelurosaurian dinosaurs. Considering the importance of *Beipiaosaurus*, we re-excavated the quarry where the holotype of *Beipiaosaurus inexpectus* was found, and other material of the holotype was collected, including a nearly complete tail and some elements of the pelvis (IVPP V11559) preserved in one slab (Fig. 1a).

Surprisingly, a pygostyle-like structure was observed on the tail of *Beipiaosaurus*. Pygostyle was previously considered as a unique structure of ornithothoracine birds (Chiappe, 1997), used to maneuver tail feathers. A similar structure has been reported from a recently discovered oviraptorosaurian dinosaur (Barsbold et al., 2000a, b), and *Beipiaosaurus* documents the second non-avian theropod taxon with a pygostyle-like structure. Also interestingly,

there are filamentous integuments preserved on the tail of this therizinosauroid (Fig. 1b). In this paper we will describe briefly the newly collected material and discuss the possible original function of pygostyle or pygostyle-like structure.

2 Description

The specimen (IVPP V11559; Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing) includes a nearly complete ilium, two incomplete ischia, two sacrals, and 30 caudals. The well-articulated distal tail is composed of 11 caudals, with a steady distal reduction in dimensions and no pathological structures. The last few caudals are the most interesting in terms of their morphology and possible function (Fig. 2a). Distal caudals 6 and 7 are completely fused together. The neural arch of distal caudal 7 is completely co-ossified with that of distal caudal 6, and so is the centrum. Laterally, on the border of centra of the distal caudals 6 and 7, there is a well-developed tubercle. The last five caudals are also completely fused into a pygostyle-like bone. The pygostyle-like structure is a relatively straight co-ossified structure, with a slightly concave ventral margin, a slightly convex dorsal margin, and a relatively blunt distal end. The two anterior lines of fusion of the centra are slightly visible, but the two posterior ones are completely obscured. The lines of fusion of neural arches of the five caudals are all obscured. Laterally on the intervertebral articulations of the centra, there are less developed tubercles. The centrum of

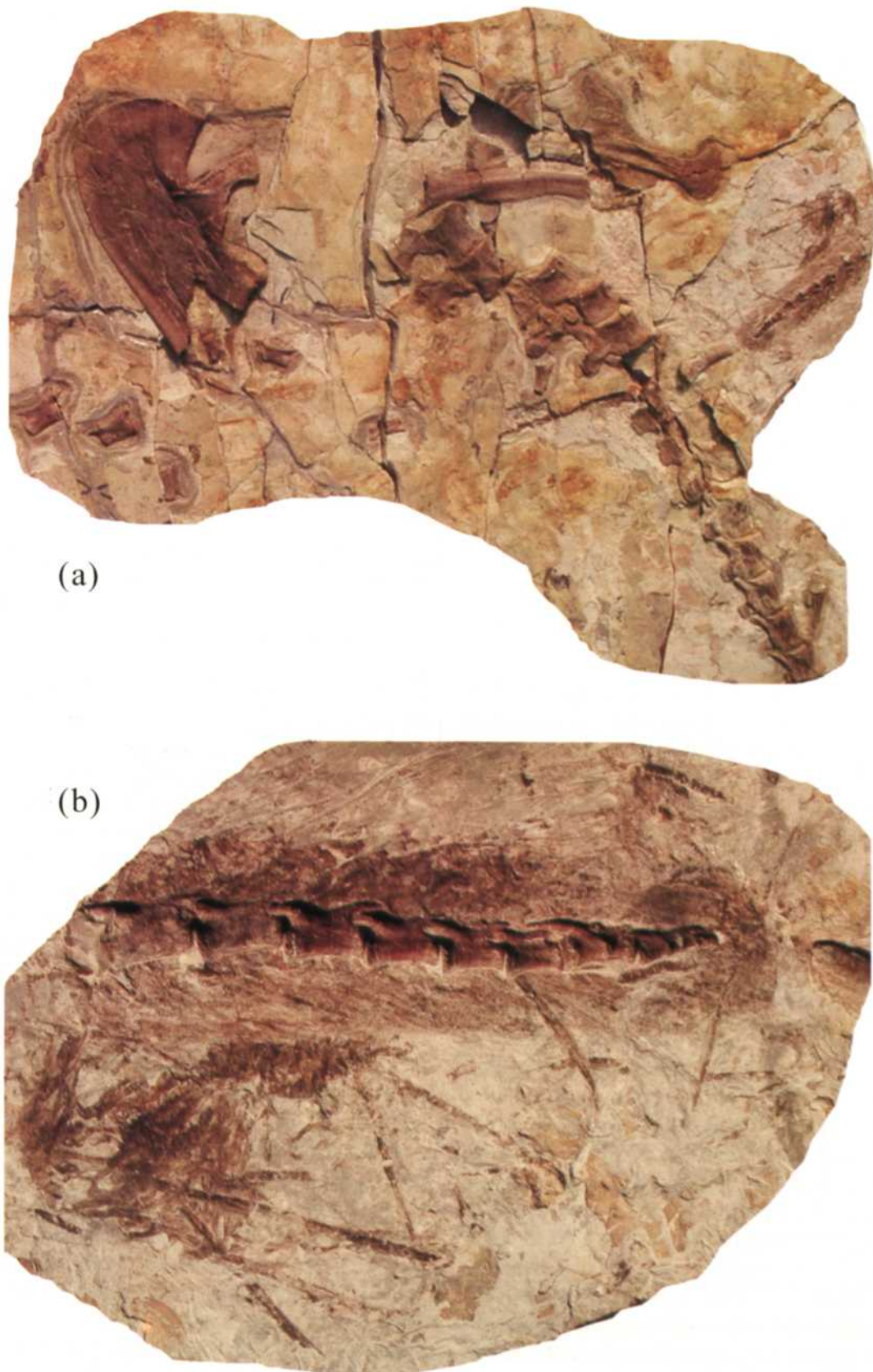


Fig. 1. (a) Newly collected material of the holotype of *Beipiaosaurus inexpectus* (IVPP V11559); (b) close-up of the distal tail and attached integuments.

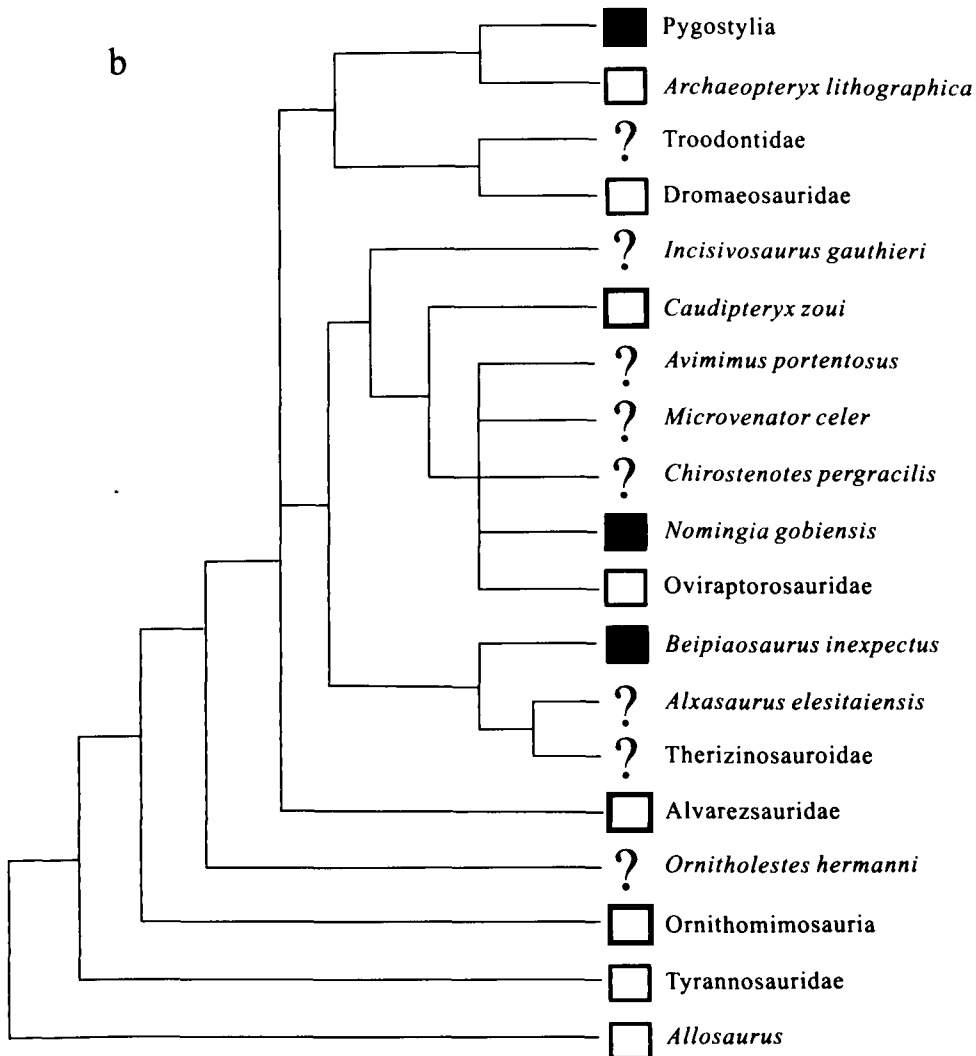
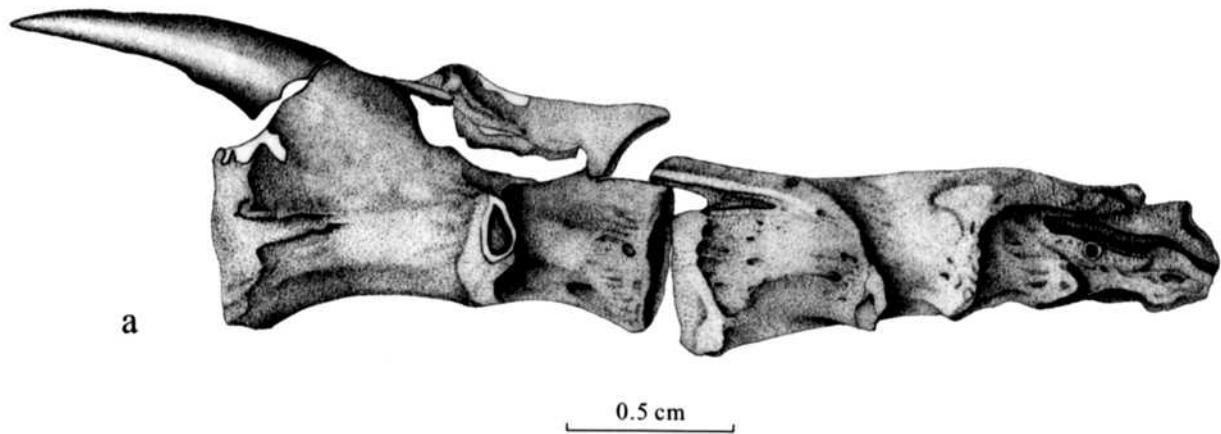


Fig. 2. (a) Drawing of the seven distal caudals, including the pygostyle-like structure; (b) distribution of pygostyle-like structures or pygostyles among coelurosaurians. Black square indicates the presence of the pygostyle-like structure or pygostyle; white square indicates the absence of the pygostyle-like structure or pygostyle.

the last caudal appears somewhat triangular on lateral view, with a dorsoventrally high anterior end and a shallow posterior end. Compared with the Mongolian oviraptorosaur (Barsbold et al., 2000a, b), the pygostyle-like structure of the basal therizinosauroid *Beipiaosaurus* is more bird-like, having better co-ossification and slightly dorsally curved axes.

Surprisingly, the last sacral (we identified it as sacral based on the sacral rib on the lateral surface of its centrum) appears to be preserved separately from other sacrals (Fig. 1a). Unfused sacrum is a good indication for a juvenile stage of the animal, and we thus suggest that the pygostyle-like structure is developed in an early ontogenetic stage in *Beipiaosaurus*.

Along the tail, both dorsal and ventral to the caudals, there are filamentous integumentary structures, forming an angle of about 35 degrees to the long axis of the tail and directed posteriorly (Fig. 1b). The integuments are composite structures containing multiple, nearly parallel filaments, and they vary from about 40 to 70 mm in length, and are about 1.5 mm in width. Whether the parallel filaments converge to a basal point is unknown. Some integumentary structures are rather stiff as indicated by its length and straightness. This may indicate that this type of composite integumentary structures has a central shaft (thickened central filament); however, this explanation needs to be confirmed by better preserved material. We did not observe composite integumentary structures with slender filaments fused serially to a central filament as in basal dromaeosaurid *Sinornithosaurus* (Xu et al., 2001b). However, the latter structure appears to be preserved around the forelimb of *Beipiaosaurus* (Xu et al., 1999a). We have not observed rectrices with prominent rachis along the distal tail.

3 Discussion

Therizinosauroids are a group of enigmatic dinosaurs that are not closely related to birds (Paul, 1984; Gauthier, 1986; Makovicky and Sues, 1998; Sereno, 1999). As in oviraptorosaurs (Barsbold et al., 2000a, b), the pygostyle-like structure of *Beipiaosaurus* is assumed non-homologous to that of birds. However, the distribution of pygostyle-like structure is poorly known among non-avian theropods because most specimens do not preserve complete caudal series (Fig. 2b), and thus this assumption is tentative and the presence of pygostyle-like structure or pygostyle could be a synapomorphy for a more inclusive group. The presence of a pygostyle-like structure in therizinosauroids and oviraptorosaurs could be explained as a synapomorphy for a therizinosauroid-oviraptorosaur clade (Sues, 1997; Makovicky and Sues, 1998; Xu et al., 1999a). However, pygostyle-like structures need to be

documented in other taxa and the phylogenetic implications of this structure need to be determined by cladistic analysis.

In birds, the pygostyle is used to maneuver rectrices. A similar function was assumed for the pygostyle-like structure of the oviraptorosaur from Mongolia (Barsbold et al., 2000a, b). However, in the therizinosauroid *Beipiaosaurus*, although there is a similar pygostyle-like structure, no rectrices have been observed and may not be present when *Beipiaosaurus* is alive. The absence of rectrices in *Beipiaosaurus* could also be due to the preservation. However, this explanation is much more speculative than the former one. The filamentous integuments are well preserved along the tail of *Beipiaosaurus*, in a dense manner. This preservation suggests that rectrices are most likely to be absent when the animal is alive. Additionally, to date reported rectrices are always present along with other types of feathers or feather-like structures showing modern feather morphology, such as the semi-plume-like structures in *Protarcharopteryx* and *Caudipteryx* (Ji et al., 1998). However, the preserved integuments of *Beipiaosaurus* show little distinctive features of modern feather, despite that they may have a primitive branching pattern linking them to bird feathers. The absence of feather-like structure with modern features in *Beipiaosaurus* conflicts the presence of rectrices in *Beipiaosaurus*. Interestingly *Caudipteryx* has rectrices but no pygostyle. The combined lines of evidence strongly suggest that the pygostyle-like structure evolved initially for some unknown function(s), other than maneuvering tail feathers. This provides additional evidence that some previously thought salient bird features, e.g., bird-like shoulder girdle (Xu et al., 1999b) and feathers (Ji et al., 1998), have a wide distribution and initial function unrelated to birds and their flight (Feduccia, 1999). Thus, exaptation appears to be common in the evolution of coelurosaurian dinosaurs.

Acknowledgements

We thank James Clark for reading the manuscript and giving constructive comments, Wang Huijun for preparing the specimens, Li Rongshan for making the drawings. Thanks also go to members of the Liaoxi expedition team of the IVPP. This work was supported by grants from the National Natural Science Foundation of China (No. 40125006), the Special Funds for Major State Basic Research Projects of China (No. G2000077700), and the Chinese Academy of Sciences (No. KZCX3-J-03).

Manuscript received Dec. 24, 2002

Accepted Apr. 3, 2003

edited by Wang Si'en and Xie Guanglian

References

- Barsbold, R., Currie, P. J., Myhrvold, N. P., Osmólska, H., Tsogtbaatar, K., and Watabe, M., 2000. A pygostyle from a non-avian theropod. *Nature*, 403: 155–156.
- Barsbold, R., Osmólska, H., Watabe, M., Currie, P. C., and Tsogtbaatar, K., 2000. A new oviraptorosaur (Dinosauria, Theropoda) from Mongolia: the first dinosaur with a pygostyle. *Acta Palaeontologica Polonica*, 45(2): 97–106.
- Chen, P.-J., Dong, Z.-M., and Zhen, S.-N., 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature*, 391: 147–152.
- Chiappe, L. M., 1997. Aves. In: Currie, P. J., and Padian, K. (eds.), *The Encyclopedia of Dinosaurs*. San Diego: Academic Press, 32–38.
- Feduccia, A., 1999. *The Origin and Evolution of Birds*, 2nd ed. New Haven: Yale University Press, 466.
- Gauthier, J. A., 1986. Origin of birds. *Memoirs of the California Academy of Sciences*, 8: 1–55.
- Ji Qiang, Ji Shu'an, You Hailu, Zhang Jianping, Zhang Hongbin, Zhang Nanjun, Yuan Chongxi and Ji Xinxin, 2003. An Early Cretaceous Avialian bird, *Shenzhouraptor sinensis*, from western Liaoning, China. *Acta Geologica Sinica* (English edition), 77(1): 21–27.
- Ji Qiang and Ji Shu'an, 1996. On discovery of the earliest bird fossil in China and the origin of birds. *Chinese Geology*, 233: 30–33 (in Chinese).
- Ji Qiang and Ji Shu'an, 1997. Protarchaeopterygid bird (*Protarchaeopteryx* gen. nov.)-fossil remains of archaeopterygids from China. *Chinese Geology*, 238: 38–41.
- Ji, Q., Currie, P. J., Norell, M. A., and Ji, S. A., 1998. Two feathered dinosaurs from northeastern China. *Nature*, 393: 753–761.
- Ji, Q., Norell, M. A., Gao, K.-Q., Ji, S.-A. and Ren, D., 2001. The distribution of integumentary structures in a feathered dinosaur. *Nature*, 410: 1084–1088.
- Luo Yaonan and Wang Changsheng, 2000. A new sauropod, *Gongxianosaurus*, from the Lower Jurassic of Sichuan, China. *Acta Geologica Sinica* (English edition), 74(2): 132–136.
- Makovicky, P., and Sues, H.-D., 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *American Museum Novitates*, 3240: 1–27.
- Pang Qiqing and Cheng Zhengwu, 2000. A new Family of sauropod dinosaur from the Upper Cretaceous of Tianzhen, Shanxi Province, China. *Acta Geologica Sinica* (English edition), 74(2): 117–125.
- Paul, G. S., 1984. The segnosaurian dinosaurs: relics of the prosauropod-ornithischian transition. *Journal of Vertebrate Paleontology*, 4: 507–515.
- Sereno, P. C. 1999. The evolution of dinosaurs. *Science*, 284: 2137–2147.
- Sues, H.-D., 1997. On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from western North America. *Journal of Vertebrate Paleontology*, 17(4): 698–716.
- Swisher, C. C., Wang Y.-Q., Wang X.-L., Xu, X., and Wang Y., 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature*, 400: 58–61.
- Wang Xiaolin and Xu Xing, 2001. A new iguanodontid (*Jinzhouosaurus yangi* gen. et sp. nov.) from the Yixian Formation of western Liaoning, China. *Chinese Science Bulletin*, 46(5): 419–423.
- Xu, X., and Wang, X.-L., 1998. New psittacosaur (Ornithischia, Ceratopsia) occurrence from the Yixian Formation of Liaoning, China and its stratigraphical significance. *Vertebrata Palasiatica*, 36(2): 147–158.
- Xu, X., Cheng, Y.-N., Wang, X.-L., and Chang, C.-H., 2002a. An unusual oviraptorosaurian dinosaur from China. *Nature*, 419: 291–293.
- Xu, X., Makovicky, P. J., Wang, X.-L., Norell, M. A., and You, H.-L., 2002b. A new ceratopsian dinosaur from China: implications for the early evolution of Ceratopsia. *Nature*, 416: 314–317.
- Xu, X., Norell, M. A., Wang, X.-L., Makovicky, P. J., and Wu, X.-C., 2002c. A basal troodontid from the Early Cretaceous of China. *Nature*, 415: 780–784.
- Xu, X., Tang, Z.-L., and Wang, X.-L., 1999a. A new therizinosaurid dinosaur with integumentary structures from China. *Nature*, 399: 450–454.
- Xu, X., Wang, X.-L., and Wu, X.-C., 1999b. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature*, 401: 262–266.
- Xu, X., Wang, X.-L., and You, H.-L., 2000. A primitive ornithomimid from the Early Cretaceous Yixian Formation of Liaoning. *Vertebrata Palasiatica* 38(4): 318–325.
- Xu, X., Wang, X.-L., and You, H.-L., 2001a. A juvenile ankylosaur from China. *Naturwissenschaften*, 88: 297–300.
- Xu, X., Zhou, Z.-H., and Prum, R., 2001b. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature*, 410: 200–204.
- You Hailu and Dong Zhiming, 2003. A new protoceratopsid (Dinosauria: Neoceratopsia) from the Late Cretaceous of Inner Mongolia, China. *Acta Geologica Sinica* (English edition), 77 (3): 299–303.
- You Hailu, Ji Qiang, Li Jinglu, and Li Yinxian, 2003a. A new hadrosauroid dinosaur from the Mid-Cretaceous of Liaoning, China. *Acta Geologica Sinica* (English edition), 77(2): 148–154.
- You Hailu, Xu Xing, and Wang Xiaolin, 2003b. A new genus of Psittacosauridae (Dinosauria: Ornithopoda) and the origin and early evolution of marginocephalian dinosaurs. *Acta Geologica Sinica* (English edition), 77(1): 15–20.