



A Lujiatun-like dinosaurian assemblage from the Jehol Biota of Ningcheng, Inner Mongolia, Northeast China

HONGGANG ZHANG, DONGXIANG YU, YUHUI FENG, RUI PEI, and CHANG-FU ZHOU

The Lujiatun Unit of the Yixian Formation yields the only three-dimensionally preserved fossils from the Early Cretaceous Jehol Biota and crops out only in western Liaoning. Here, we report a new fossil site for the Jehol Biota with three-dimensionally preserved fossils from Ningcheng, Inner Mongolia. The fossils that have been discovered at this new site are predominantly dinosaurs and include a *Sinovenator*-like troodontid skeleton, three isolated sauropod teeth, some disarticulated skeletons of neornithischians and ceratopsians, and fragmentary lower jaws from a lizard and a mammal. The faunal composition, as well as the lithological features of the fossil beds, are comparable with those of the Lujiatun Unit of the Yixian Formation at Beipiao, western Liaoning, China. This discovery expands the geographical range of the Lujiatun-like dinosaurian assemblage of the Jehol Biota, and increases the biodiversity of the Jehol Biota in the Ningcheng Basin, China.

Introduction

The Early Cretaceous Jehol Biota that occurs in the Mesozoic basins of the conjoined area of Liaoning, Inner Mongolia, and Hebei in northeastern China yields numerous exquisitely preserved two-dimensional fossils (e.g., Chang et al. 2003; Zhou et al. 2003; Xu and Norell 2006; Xu et al. 2020). As an exception, the Lujiatun Unit of the Yixian Formation of the Jehol Biota, crops out in western Liaoning and yields only three-dimensionally preserved fossils (e.g., Chang et al. 2003; Zhou et al. 2003; Xu and Norell 2006; Xu et al. 2020). It is dominated by dinosaurian fossils, but also has records of lizards and mammals, which can be differentiated from the rest of the Jehol Biota in terms of its faunal composition, paleoecology and taphonomy (e.g., Xu et al. 2002, 2004; Xu and Norell 2004; Hu et al. 2005; Zhou et al. 2006; Evans et al. 2007; Zhao et al. 2007; Ji et al. 2009; Xu et al. 2020). Here, we report a new Lujiatun-like dinosaurian assemblage from the Ningcheng Basin, Inner Mongolia, shedding new light on the paleobiodiversity and paleoenvironment of the Jehol Biota in the Ningcheng Basin.

Institutional abbreviations.— PMOL, Paleontological Museum of Liaoning, Shenyang Normal University, China; SDUST, Vertebrate Palaeontological Collection of College of Earth Science and Engineering, Shandong University of Science and Technology, Qingdao, China.

Geological setting, material, and methods

This new fossil site was discovered at Xidayingzi, Bisiyinzhi, Ningcheng, Inner Mongolia during our field expeditions (Fig. 1). The lithology of this section is a set of volcanic rocks interbedded with sedimentary rocks, with a total thickness of about 80 meters. The volcanic rocks are mainly basaltic andesite, rhyolitic breccia lava and andesitic tuff, and the sedimentary rocks are mainly gravel-bearing tuffaceous siltstone, tuffaceous sandstone and conglomerate with volcanic and igneous fragments. The lithologic assemblage and the sequence of this site are similar to those of the Lujiatun Unit of the Yixian Formation at Beipiao, except that the bottom of the sequence of this new site is a set of acidic volcanic rocks (Jiang et al. 2014; Rogers et al. 2015).

The fossils yielded by this site were three-dimensional and semi-articulated (Fig. 2). They were prepared under a Leica M80/M165c microscope. One sauropod tooth (SDUST-V1064) and the mandibles of a lizard (PMOL-AR00268) and a mammal (PMOL-AM00036) were CT-scanned at Zhejiang University using the High-Resolution X-ray CT scanner (Nikon XT H 320). The scanning process was performed without a filter; PMOL-AR00268 and -AM00036 produced 2500 slices (10 μm in thickness) at 100 kV and 100 μA , respectively; SDUST-V1064 produced 2520 slices (20 μm in thickness) at 120 kV and 180 μA . The 3D reconstruction was processed using VG Studio 3.0 (Volume Graphics).

Results

Four dinosaurian groups, one lizard, and one mammal are identified from this fossil assemblage (Fig. 2). Dinosaurian specimens make up to 90% of the total number of fossils, although many of them are isolated or fragmentary bones.

Troodontid.—A single troodontid individual (SDUST-V1062; Fig. 2A) is represented by an articulated postcranial skeleton, possibly representing a species of *Sinovenator*. *Sinovenator* is an early-diverging troodontid that was first reported from the Lujiatun Unit (Xu et al. 2002). SDUST-V1062 shows primitive troodontid features like *Sinovenator*, such as the distal caudal vertebrae that are sulcate along the dorsal midline and missing neural spines, the deltopectoral crest of the humerus relatively short, an asymmetrical subarctometatarsalian foot, and an un-ginglymoid metatarsal II (e.g., Xu

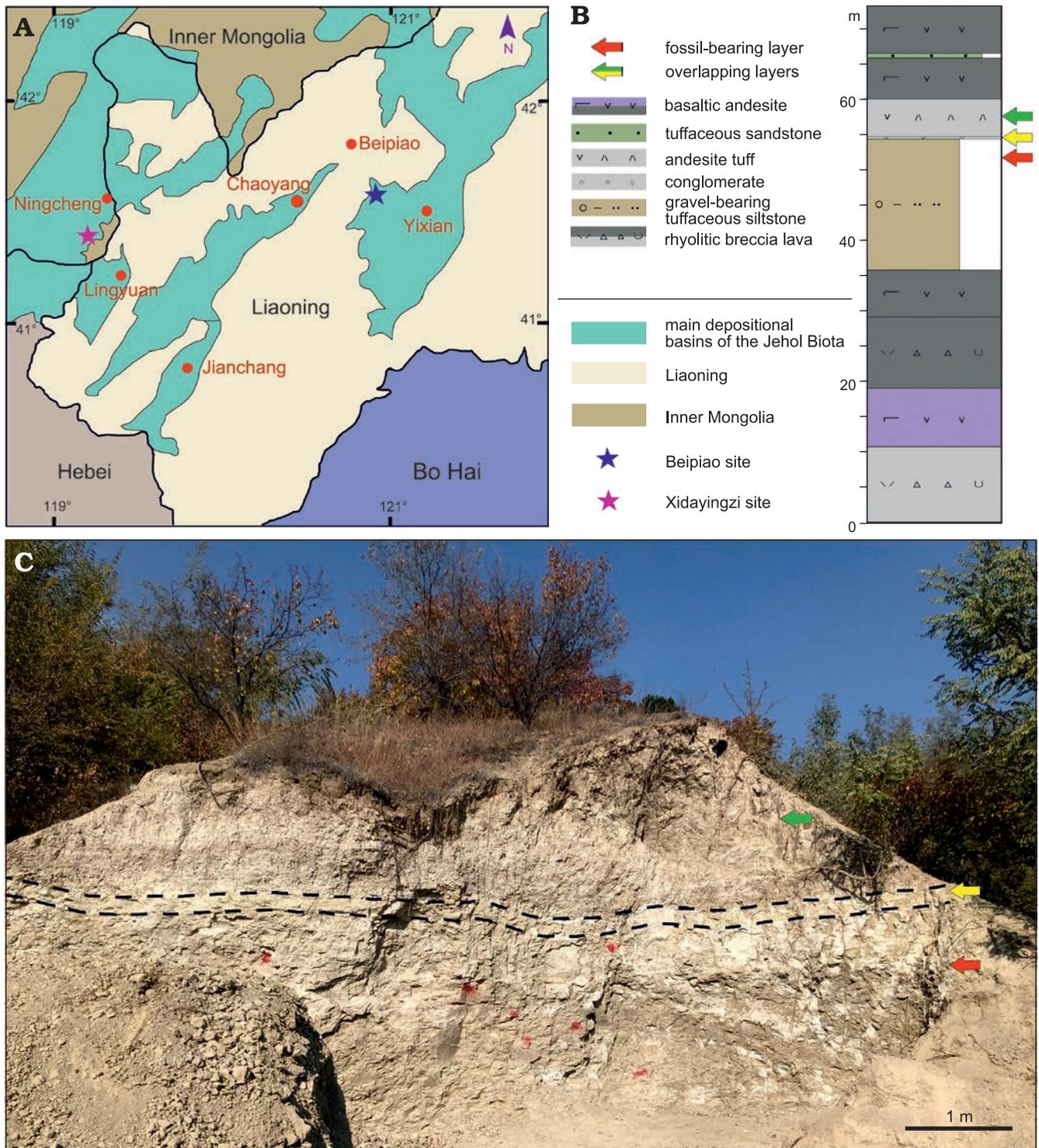


Fig. 1. Map of the Inner Mongolia, Liaoning and Hebei (A) showing location of the Xidayingzi site and the outcrops of the Lujiatun Unit of the Yixian Formation of the Jehol Biota in Beipiao, western Liaoning Province, China. Stratigraphic column (B) and corresponding photographic image (C) of the Early Cretaceous Xidayingzi site.

et al. 2002; Makovicky and Norell 2004; Turner et al. 2012; Xu et al. 2017). This specimen can be differentiated from previously reported specimens of *Sinovenator* in having a round anterior margin of the preacetabular process of the ilium and a moderately developed ambiens process of the pubis (Xu et al. 2002).

Sauropods.—Two of the three isolated sauropod teeth (PMOL-AD00176, SDUST-V1064) are well preserved. They are spatulate, and bulbous basally and lingually, similar to the teeth of *Euhelopus*, a titanosauriform close in age to the Jehol Biota (Barrett and Wang 2007; Wilson and Upchurch 2009). As shown in Fig. 2D, the tooth crown is asymmetrical in medial

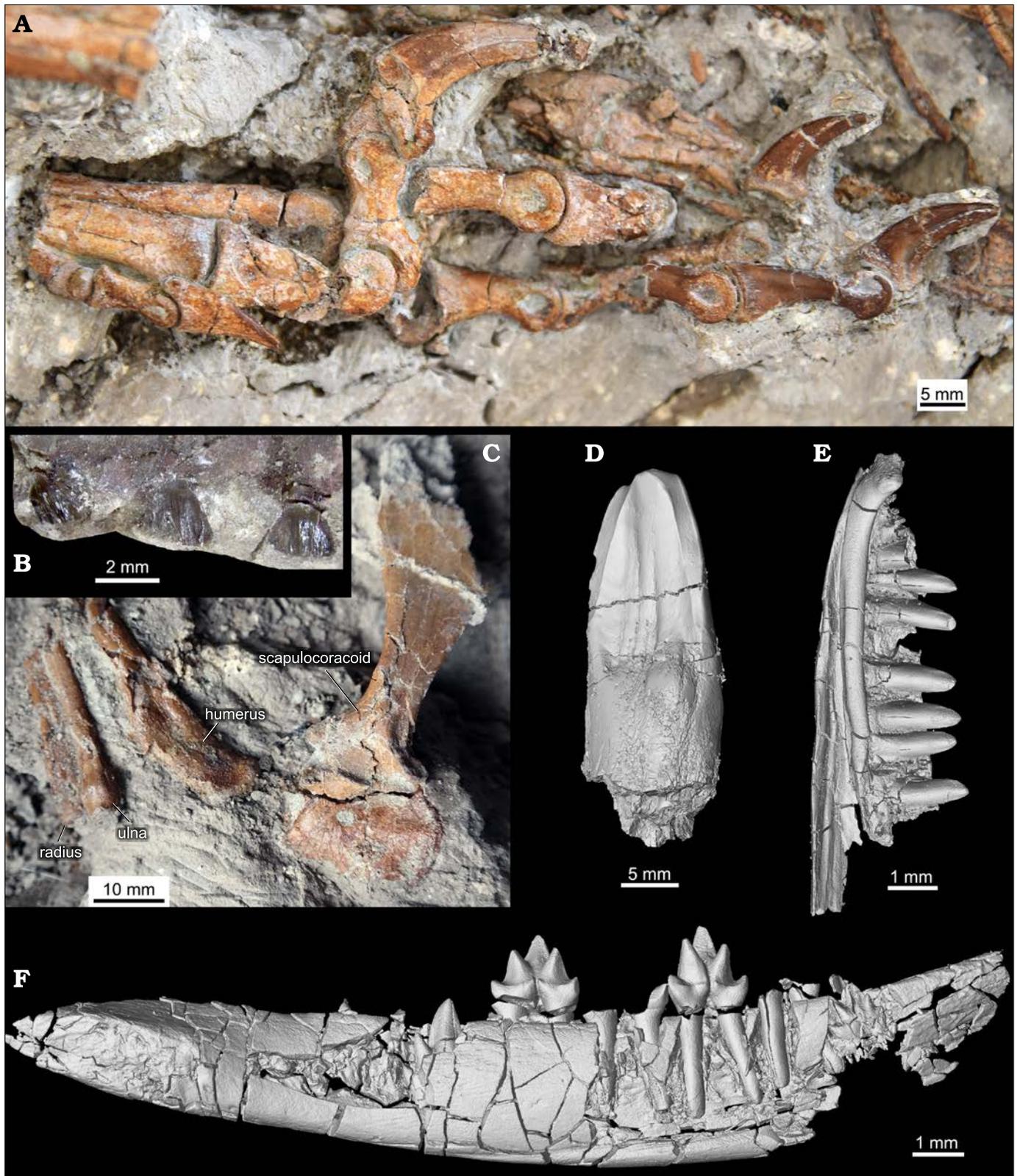


Fig. 2. Fossils found in the Xidayingzi site from the Early Cretaceous Ningcheng Basin, Inner Mongolia. **A.** *Sinovenator*-like troodontid dinosaur (SDUST-V1062), the left pes is exposed in medial view. **B.** Ceratopsian dinosaur *Psittacosaurus* sp. (PMOL-AD00163), the maxillary teeth are loosely arranged and exposed in lateral view. **C.** Neornithischian dinosaur *Jeholosaurus* sp. (SDUST-V1063), the scapulocoracoid, humerus, ulna, and radius in lateral view. **D.** *Euhelopus*-like sauropod (SDUST-V1064), digital image of the tooth crown in medial view. **E.** Indetermined lizard (PMOL-AR00268), digital image of the fragmentary mandible in lingual view. **F.** Symmetrodont-like mammal (PMOL-AM00036), digital image of the mandible in lingual view.

view, convex labially and concave lingually. The lingual concavity is shallow and sculptured by three low and rounded ridges. Below the concavity, the bulbous tubercle is positioned more mesially at the base of the crown, which is typical in *Euhelopus* (Barrett and Wang 2007; Wilson and Upchurch 2009). Two high-angled wear facets are developed along the mesial and distal edges of the crown, merging at the crown apex.

Neornithischian.—Four of eight new neornithischian fossils (PMOL-AD00169 and AD00170; SDUST-V1064 and V1065) have semi-articulated partial postcranial skeletons, but the crania are missing. They show features that are characteristic of *Jeholosaurus*, such as the presence of the scapular spine (Fig. 2C), the presence of two distal tarsals, and a proportionally short pedal phalanx I-1 (e.g., Butler et al. 2011; Han et al. 2012). *Jeholosaurus shangyuanensis* is a small neornithischian only known from the Lujiatun Unit (e.g., Han et al. 2012).

Ceratopsian.—Six new ceratopsian specimens (PMOL-AD00163–AD00168) are fragmentary and not as abundant as the neornithischians, which differs from the Lujiatun Unit of western Liaoning in which the ceratopsians are more abundant (e.g., Chang et al. 2003; Xu and Norell 2006; Xu et al. 2020). These ceratopsian specimens could be identified as species of *Psittacosaurus* based on the presence of the rostral, the edentulous premaxilla, and the shape of the maxillary teeth. *Psittacosaurus* is a small early-diverging ceratopsian used as a index fossil in the Lower Cretaceous of East Asia (Lucas 2006), and is widely distributed in the Jehol Biota (e.g., Zhou et al. 2006; Zhao et al. 2007). The rostral and the premaxilla of the new specimen form a rounded buccal margin ventrally, and rim the external naris dorsally, as is typical in *Psittacosaurus* (e.g., Zhou et al. 2006; Sereno 2010). Interestingly, the maxillary teeth of the new specimen appear to be spaced apart (Fig. 2B), rather than being imbricated as in all other known psittacosaurids.

Non-dinosaurian vertebrates.—Non-dinosaurian vertebrates are rarely recorded in Lujiatun-like fossil beds, but the fragments of a lizard and a mammal were discovered in the Xidayingzi site. A fragmentary lizard mandible (PMOL-AR00268) is preserved with pleurodont, conical, single-cusped, and closely packed teeth, which is a common feature in Mesozoic lizards (e.g., *Yabeinosaurus*, *Dalinghosaurus*; Evans et al. 2007; Zhou et al. 2021). The mammalian mandible (PMOL-AM00036) is preserved with one premolar, five molars, and eight empty alveoli, implying a possible lower dental formula of I2-C1-P4-M5 (I, incisor; C, canine; P, premolar; M, molar). The molars have acutely-triangulated molar cusps like symmetrodonts, which flourished in the Jehol Biota, especially in the Lujiatun Unit of the Yixian Formation, including *Maothierium*, *Anebodon*, and *Origolestes* (e.g., Ji et al. 2009; Bi et al. 2016; Mao et al. 2020). In contrast, the new specimen is distinct from typical Jehol symmetrodonts, in having one more molar and main cusps of the molars that are more acutely arranged than in *Anebodon*, and in lacking the distinct diastema between the premolars that is present in *Origolestes* and *Maothierium*. The lower dental formula of

this new specimen is also different from other Jehol symmetrodonts (e.g., *Zhangheotherium*; *Akidolestes*; Hu et al. 1997; Li and Luo 2006). Therefore, the mandible possibly represents a new symmetrodont in the Jehol Biota.

Many of the identifiable fossils from the Xidayingzi site are commonly found in the Lujiatun Unit of the Yixian Formation near Beipiao. As the lowest part of the Yixian Formation, the Lujiatun Unit mainly crops out in Beipiao, and is distinct from the other fossiliferous units of the Jehol Biota in bearing numerous three-dimensionally preserved fossils (e.g., Chang et al. 2003; Xu and Norell 2006; Xu et al. 2020). Its fossiliferous deposits are dominated by grey siltstone, sandstone, and volcanic debris and ash, which were formed by volcanic debris flows or lahars (e.g., Jiang et al. 2014; Rogers et al. 2015). Similar deposits are also found at this new site, which is possibly equivalent with the Lujiatun Unit.

Conclusions

A new fossil assemblage with three-dimensionally preserved fossils is discovered in the Mesozoic Ningcheng Basin, Inner Mongolia, which is possibly equivalent with the Lujiatun Unit of the Yixian Formation in Beipiao, western Liaoning. The recognized fossils are the first records of the relevant groups in this area, enriching the biodiversity of the Jehol Biota in the Ningcheng Basin.

Acknowledgements.—We would like to thank Ke-Qin Gao (Peking University, Beijing, China), Lijun Zhang (Shenyang Institute of Geology, China) and Baoyu Jiang (Nanjing University, China) for their helpful discussions about the stratigraphy. We thank Yu Peng (Zhejiang University, Hangzhou, China) for his help with CT scanning of these fossils, Qiang Yang, Shurui Yang, Shuai Shao, Peng Yu, and Yuguo Yang (all Paleontological Museum of Liaoning, Shenyang, China) for their help in field excavations and fossil preparation. We thank Paul M. Barrett (Natural History Museum, London, UK) and Qi Zhao (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China) for their helpful reviews on the manuscript. This study was funded by Taishan Scholar Program of Shandong Province (Grant No. tsqn201812070), Shandong Provincial Natural Science Foundation (Grant No. ZR2017MD031), Program for Innovative Research Team of Excellent Talents in University of Shandong Province (Grant No. 2019KJH004) and the National Natural Science Foundation of China (Grant No. 41972025, 41688103, 42161134003).

References

- Barrett, P.M. and Wang, X.-L. 2007. Basal titanosauriform (Dinosauria, Sauropoda) teeth from the Lower Cretaceous Yixian Formation of Liaoning Province, China. *Palaeoworld* 16: 265–271.
- Bi, S., Zheng, X., Meng, J., Wang, X., Robinson, N., and Davis, B. 2016. A new symmetrodont mammal (Trechnotheria: Zhangheotheriidae) from the Early Cretaceous of China and trechnotherian character evolution. *Scientific Report* 6: 26668.
- Butler, R.J., Jin, L.Y., Chen, J., and Godefroit, P. 2011. The postcranial osteology and phylogenetic position of the small ornithischian dinosaur *Changchunsaurus parvus* from the Quantou Formation (Cretaceous: Aptian–Cenomanian) of Jilin Province, North-eastern China. *Palaeontology* 54: 667–683.
- Chang, M.-M., Chen, P.-J., Wang, Y.-Q., Wang, Y., and Miao, D.-S. 2003. *The Jehol Biota: The Emergence of Feathered Dinosaurs, Beaked*

- Birds and Flowering Plants*. 205 pp. Shanghai Scientific & Technical Publishers, Shanghai.
- Evans, S.E., Wang, Y., and Jones, M.E.H. 2007. An aggregation of lizard skeletons from the Lower Cretaceous of China. *Senckenbergiana Lethaea* 87: 109–118.
- Han, F.-L., Barrett, P.M., Butler, R.J., and Xu, X. 2012. Postcranial anatomy of *Jeholosaurus shangyuanensis* (Dinosauria, Ornithischia) from the Lower Cretaceous Yixian Formation of China. *Journal of Vertebrate Paleontology* 32: 1370–1395.
- Hu, Y.-M., Meng, J., Wang, Y.-Q., and Li, C.-K. 2005. Large Mesozoic mammals fed on young dinosaurs. *Nature* 433: 149–152.
- Hu, Y.-M., Wang, Y.-Q., Luo Z.-X., and Li, C.-K. 1997. A new symmetrodont mammal from China and its implications for mammalian evolution. *Nature* 390: 137–142.
- Ji, Q., Luo, Z.-X., Zhang, X.L., Yuan, C.X., and Xu, L. 2009. Evolutionary development of the middle ear in Mesozoic therian mammals. *Science* 326: 278–281.
- Jiang, B.Y., Harlow, G.E., Wohletz, K., Zhou, Z., and Meng, J. 2014. New evidence suggests pyroclastic flows are responsible for the remarkable preservation of the Jehol biota. *Nature Communication* 5: 3151.
- Li, G. and Luo, Z.-X. 2006. A Cretaceous symmetrodont therian with some monotreme-like postcranial features. *Nature* 439: 195–200.
- Lucas, S.G. 2006. The *Psittacosaurus* biochron, Early Cretaceous of Asia. *Cretaceous Research* 27: 189–198.
- Makovicky, P.J. and Norell, M.A. 2004. Troodontidae. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 184–195. University of California Press, Berkeley.
- Mao, F., Hu, Y., Li, C., Wang, Y., Chase, M.H., Smith, A.K., and Meng, J. 2020. Integrated hearing and chewing modules decoupled in a Cretaceous stem therian mammal. *Science* 367: 305–308.
- Rogers, C.S., Hone, D.W.E., McNamara, M.E., Zhao, Q., Orr, P.J., Kearns, S.L., and Benton, M.J. 2015. The Chinese Pompeii? Death and destruction of dinosaurs in the Early Cretaceous of Lujiatun, NE China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 427: 89–99.
- Sereno, P.C. 2010. Taxonomy, cranial morphology, and relationships of parrot-beaked dinosaurs (Ceratopsia: *Psittacosaurus*). In: M.J. Ryan, B.J. Chinnery-Allgeier, and D.A. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, 21–58. Indiana University Press, Bloomington.
- Turner, A.H., Makovicky, P.J., and Norell, M.A. 2012. A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History* 371: 1–206.
- Wilson, J.A. and Upchurch, P. 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Paleontology* 7: 199–239.
- Xu, X. and Norell, M.A. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* 431: 838–841.
- Xu, X. and Norell, M.A. 2006. Non-avian dinosaur fossils from the Lower Cretaceous Jehol Group of western Liaoning, China. *Geological Journal* 41: 419–437.
- Xu, X., Currie, P., Pittman, M., Xing, L.D., Meng, Q.J., Lu, J.C., Hu, D.Y., and Yu, C.Y. 2017. Mosaic evolution in an asymmetrically feathered troodontid dinosaur with transitional features. *Nature Communications* 8: 14972.
- Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q., and Jia, C. 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* 431: 680–684.
- Xu, X., Norell, M.A., Wang, X.-L., Makovicky, P.J., and Wu, X.-C. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* 415: 780–784.
- Xu, X., Zhou, Z.H., Wang, Y., and Wang, M. 2020. Study on the Jehol Biota: Recent advances and future prospects. *Science China Earth Sciences* 63: 757–773.
- Zhao, Q., Barrett, P.M., and Eberth, D.A. 2007. Social behaviour and mass mortality in the basal ceratopsian dinosaur *Psittacosaurus* (Early Cretaceous, People's Republic of China). *Palaeontology* 50: 1023–1029.
- Zhou, C.-F., Gao, K.-Q., Fox, R.C., and Chen, S.-H. 2006. A new species of *Psittacosaurus* (Dinosauria: Ceratopsia) from the Early Cretaceous Yixian Formation, Liaoning, China. *Palaeoworld* 15: 100–114.
- Zhou, C.-F., Wang, C.F., and Chang, M.J. 2021. New material of *Yabeinosaurus* from the Early Cretaceous Jiufotang Formation of Jianchang, western Liaoning, China [in Chinese, with English abstract]. *Journal of Shandong University of Science and Technology (Natural Science)* 40: 1–7.
- Zhou, Z.H., Barrett, P.M., and Hilton, J. 2003. An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421: 807–814.

Honggang Zhang [13700017969@126.com], College of Earth Science and Engineering, Shandong University of Science & Technology, Qingdao 266590, China; Paleontological Institute, Shenyang Normal University, Shenyang 110034, China; Paleontological Museum of Liaoning, Shenyang 110034, China. Dongxiang Yu [yudongxiang121@126.com] and Chang-Fu Zhou [zhoucf528@sdust.edu.cn], College of Earth Science and Engineering, Shandong University of Science & Technology, Qingdao 266590, China.

Yuhui Feng [here2009feng@126.com], Paleontological Institute, Shenyang Normal University, Shenyang 110034, China; Paleontological Museum of Liaoning, Shenyang 110034, China.

Rui Pei [peirui@ivpp.ac.cn], Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; CAS Center for Excellence in Life and Palaeoenvironment, Beijing 100044, China.

Received 18 January 2022, accepted 24 February 2022, available online 20 June 2022.

Copyright © 2022 H. Zhang et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see <http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.