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

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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 saurapod 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.

Geological setting, material, and methods

This new fossil site was discovered at Xidayingzi, Bisiyinzhong, 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 saurapod 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 sutured along the dorsal midline and missing neural spines, the deltopectoral crest of the humerus relatively short, an asymmetrical subarcutmetsartor-salanal foot, and an un-ginglymoid metatarsal II (e.g., Xu 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. Indeterminated 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 AD000170; 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-I (e.g., Butler et al. 2011; Han et al. 2012). Jeholosaurus shangyuanensis is a small neornithischian only known from the Lijiutuan 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 Lijiutuan 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 an 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 Lijiutuan-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, Dalinglehosaurus; 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 Lijiutuan Unit of the Yixian Formation, including Maotherium, Anebodon, and Akidolestes (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 Akidolestes and Maotherium. 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 Lijiutuan Unit of the Yixian Formation near Beipiao. As the lowest part of the Yixian Formation, the Lijiutuan 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 Lijiutuan 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 Lijiutuan 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.

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