



A sauropod rib with an embedded theropod tooth: direct evidence for feeding behaviour in the Jehol group, China

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LETHAIA



Xing, L., Bell, P.R., Currie, P.J., Shibata, M., Tseng, K. & Dong, Z. 2012: A sauropod rib with an embedded theropod tooth: direct evidence for feeding behaviour in the Jehol group, China. *Lethaia*, Vol. 45, pp. 500–506.

A fragmentary rib from the Lower Cretaceous (Barremian) Yixian Formation in north-eastern China preserves rare, direct evidence of feeding behaviour by an unidentified theropod. The rib, which comes from the holotype of *Dongbetitan*, preserves an embedded, broken theropod tooth. Comparison of the tooth with all known theropods from the Yixian Formation suggests that it belongs to a new taxon of medium-sized theropod. Given the large size difference between the sauropod and the theropod and the absence of reactive bone growth around the tooth, the bite likely occurred post-mortem during scavenging. Recognition of a new, medium-sized theropod increases the known diversity of taxa from the Yixian Formation and helps fill a gap in the theropod palaeoecology of that formation, which previously consisted of only small (<2 m) forms. □ *China, Cretaceous, feeding behaviour, theropod, titanosauriformes, sauropod.*

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Dinosaur feeding behaviour can be interpreted from tooth gouges, punctures and serration marks on bone (Tanke & Currie 2000). Supplementary anatomical descriptions (including probable gut contents), tooth wear and replacement rates, finite element analysis and mathematical approaches have added significantly to our understanding of dinosaur feeding behaviour (Erickson 1996; Erickson & Olson 1996; Varricchio 2001; Snively & Russell 2007; Bell *et al.* 2009; Tanoue *et al.* 2009; Bell & Currie 2010).

Despite the frequency of bite marks reported from isolated elements, skeletons, and bone beds (Jacobsen 1998, 2001; Ryan *et al.* 2001; Farlow & Holtz 2002; Eberth & Getty 2005), broken teeth embedded in the bone are rarely encountered. Broken teeth embedded in bone (type 5 bite marks of Tanke & Currie 2000) provide direct predatory or scavenging evidence, but require pathological information to identify whether injuries were incurred prior to or following the death of an animal (Buffetaut *et al.* 2004). Such examples of embedded theropod teeth are rare although several occurrences have been described involving pterosaur (Currie & Jacobsen 1995; Buffetaut *et al.* 2004), hadrosaur (Farlow & Holtz 2002), and tyrannosaur (Bell

& Currie 2010) bones. Most of these examples provide clear evidence of predator-prey interaction. A broken tyrannosaurid tooth found embedded in the jaw of another tyrannosaurid may represent a fatal agonistic encounter, scavenging, or both (Bell & Currie 2010).

Herein we describe a theropod tooth embedded in a fragmentary sauropod rib (LDRCv2) from the Early Cretaceous of Liaoning, China. This is the first sauropod bone reported with an embedded theropod tooth and provides new information on the palaeoecology of the Yixian Formation.

Geological setting

LDRCv2 was recovered from the Jianshangou Bed of the Yixian Formation, Jehol Group, Lower Cretaceous (Barremian) near Beipiao City in western Liaoning, China. The Jehol Group consists of shale, sandy conglomerates, tuffaceous sandstones, siltstones and andesites (Chen *et al.* 2005). Together with the underlying Lujiatun Bed, the Jianshangou Bed comprises the lower part of the Yixian Formation and preserves the earliest portion of the Jehol Biota. The

Table 1. Selected measurements of the teeth of Jehol theropods.

	Maxillary teeth				Dentary teeth			
	mesial carina		distal carina		mesial carina		distal carina	
	Tooth position	denticles/mm	Tooth position	denticles/mm	Tooth position	denticles/mm	Tooth position	denticles/mm
<i>Sinosauropteryx prima</i> ¹	*	*	1	11	*	*	?	10
	*	*	2	12	*	*	*	*
<i>Sinornithosaurus millenii</i> ²	2	0	2	14	2	0	2	14
	3	0	3	10	3	0	3	13
	4	13	4	10	4	0	4	10
	5	11	5	8	5	12–13	5	9–10
	6	9	6	8	?	10	?	7
	8	12	8	9.5	*	*	*	*
<i>Sinornithosaurus haoiana</i> ³	?	7.2–7.5	?	7.2–7.5	?	7–8.5	?	6–7
<i>Huaxiagnathus orientalis</i> ⁴	*	*	?	7	*	*	?	7
<i>Sinocalliopteryx</i> sp. ⁵	2	?	2	3	*	*	*	*
	3	4	3	4	*	*	*	*
	4	?	4	3.5	*	*	*	*
	5	?	5	4	*	*	*	*
	6	?	6	3.5	*	*	*	*
	7	?	7	3.5	*	*	*	*
LDRCv2	?	3	?	3	*	*	*	*

1, Currie & Chen 2001; 2, Xu & Wu 2001; 3, Liu *et al.* 2004; 4, Hwang *et al.* 2004; 5, measurements of this paper, *Sinocalliopteryx* sp. (CAGS-IG-T1).

Jianshangou Bed is interpreted as having been deposited in a predominantly volcanoclastic landscape (Liu *et al.* 2002) punctuated by lakes of varying sizes (Fürsich *et al.* 2007). These lakes received sediments from catastrophic floods and air-fall volcanic ash (Fürsich *et al.* 2007) that were responsible for the remarkable preservation quality of many of the fossils recovered from the lower Yixian Formation. The Jehol Biota consists of a diverse assemblage of primitive mammals and birds, feathered dinosaurs and other reptiles in addition to abundant invertebrates and angiosperms (Chen *et al.* 2005; Fürsich *et al.* 2007) that flourished between 125 and 120 Ma (Swisher *et al.* 1999, 2002; He *et al.* 2004, 2006).

Material

LDRCv2 is an incomplete thoracic rib shaft from the holotype of *Dongbeititan dongi* (D2867; Wang *et al.* 2007). *Dongbeititan* is known from a single, partial, associated skeleton that comprises 16 cervical vertebrae, seven dorsal vertebrae, three proximal caudal vertebrae, one dorsal rib, several pectoral and pelvic girdle elements and a nearly complete left hind limb. Based on the fused neural arches in both the cervical and caudal vertebrae, the individual was relatively mature. Although the rib (LDRCv2) was collected along with the holotype skeleton, it was not described by those authors (Wang *et al.* 2007). *Dongbeititan* is considered a basal titanosauriform and is the only

known sauropod from the Lower Cretaceous Jehol Group (Wang *et al.* 2007). Both the transverse section shape, size and the presence of pneumatic canals (see Description) in LDRCv2 are consistent with the morphology of titanosauriform (including *Dongbeititan*, but excluding *Fusisaurus*; Mo *et al.* 2006) dorsal ribs (Wang *et al.* 2007). Given that no other large herbivorous dinosaurs aside from *Dongbeititan dongi* (Wang *et al.* 2007) were discovered from the holotype quarry, we assign LDRCv2 to *Dongbeititan*.

Institutional abbreviations: CAGS-IG, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; D, Dalian Natural History Museum, Dalian, Liaoning, China; LDRC, Lufeng Dinosaur Research Center, Lufeng, Yunnan, China; P, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada.

Description

LDRCv2 is a partial *Dongbeititan* thoracic rib shaft 11.5 cm long and anteroposteriorly broader than it is mediolaterally wide (Fig. 1). The ends of the rib were fractured transversely presumably during excavation/collection as evidenced by the fresh surfaces and sharp edges. In cross-section, two ovoid pneumatic chambers (Wang *et al.* 2007) can be observed, which extend parallel to each other through the length of the rib (Fig. 1B, C). The external surface is broken, exposing the smooth-walls of these longitudinal canals

(Fig. 1B). The opposing contralateral surface of the rib is intact and shows a fine-grained longitudinal surface texture (Fig. 1A). In places, the bone has suffered from post-depositional compression resulting in disturbed bone texture and fractures as revealed by their jagged and transversely broken edges (Fig. 1A).

A broken theropod tooth is embedded within the intact contralateral surface of LDRCv2, perpendicular

to the long axis of the rib. To more clearly observe the tooth, a small section of the rib enclosing the tooth was removed using an air scribe (Fig. 2A, B). Where the tooth penetrates the bone, the rib is split longitudinally and the resulting crack is filled with light grey and tan siltstone. The exposed portion of the crown is 11 mm in maximum height and an X-ray of the specimen shows an additional 3–7 mm is embedded in the

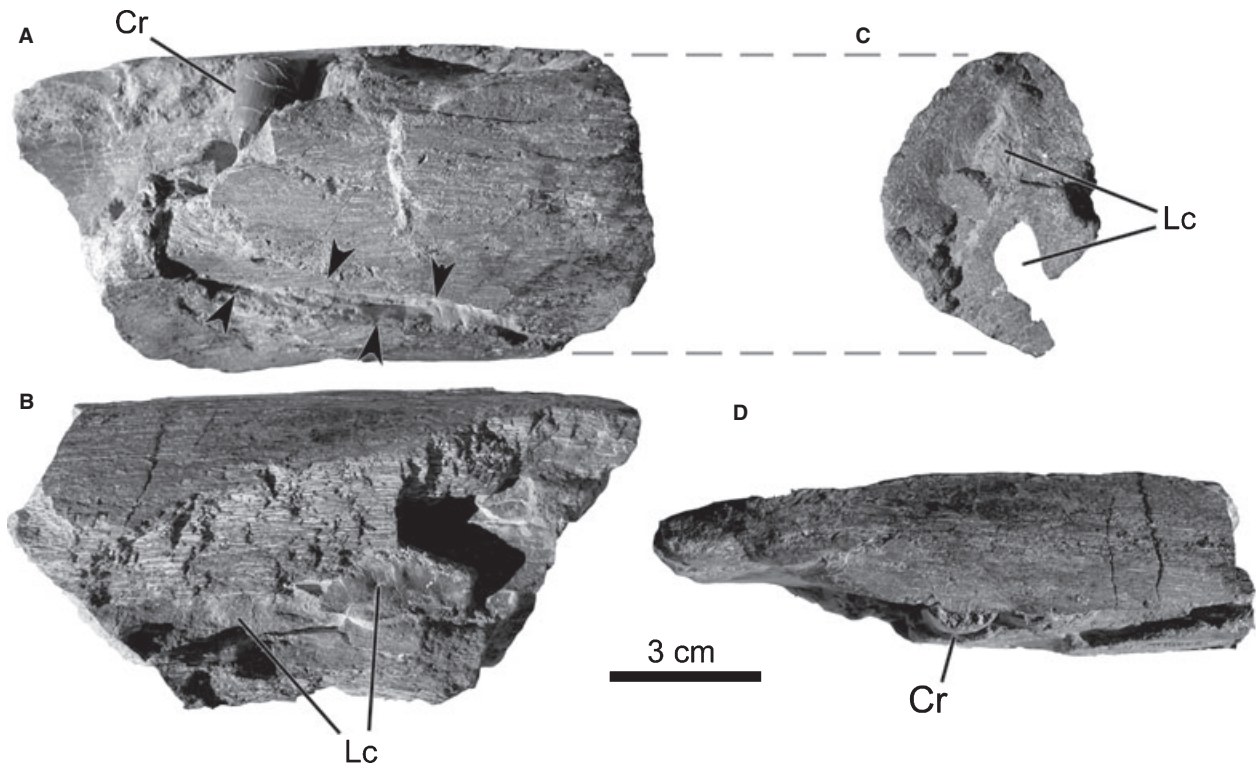


Fig. 1. Partial *Dongbetitan* rib (LDRCv2) with embedded *Sinocalliopteryx* tooth. A, B, contralateral; C, cross-sectional; and D, anteroposterior views. Post-depositional compression fractures are denoted with arrowheads. Cr, tooth crown; Lc, longitudinal canal.

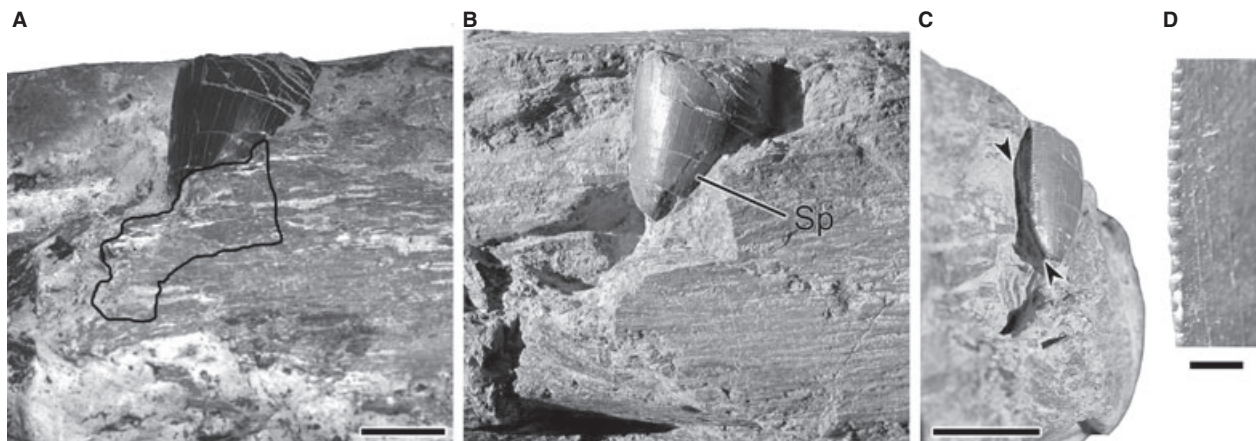


Fig. 2. Close up of embedded theropod tooth before (A) and after (B) preparation. Outline in A indicates the area of bone removed in B. (C) View of mesial carina (viewed from the left in B) showing spalled edge (arrowheads). Discrepancy in the upper border of the rib between A and B is due to slightly different camera angle. (D) Close up of denticles. Sp, spalled surface. Scale bar: A, C = 1 cm, D = 1 mm.

rib. The mesiodistal plane of the tooth is parallel with the long axis of the rib and has a minimal fore-aft basal length of 13 mm. The exposed mesial carina is weakly convex with three chisel-shaped denticles per millimetre (Fig. 2D). There are narrow grooves (blood grooves of Fanti & Therrien 2007) between the bases of denticles. Three incompletely exposed denticles are observable on the distal carina. The denticles do not appear to differ significantly in size or morphology between the mesial and distal carinae.

Following preparation of the specimen and removal of part of the enclosing bone (Fig. 2A, B), it was revealed that both labial and lingual surfaces of the tooth were spalled (Fig. 2B, C). Because the tooth is incomplete and partly obscured by bone, identification of true labial versus lingual siding cannot be established; however, it is clear that the apical tip of the tooth is missing as a result of spalling. It cannot be ascertained whether the tooth was spalled as a direct result of this bite or had already been damaged prior to emplacement. The complete tooth is inferred to have been elliptical in cross-section. The sheared base of the tooth lies flush with the external surface of the rib and there is no sign of perilesional reactive bone growth. Additional bite marks were not observed on the rib.

Discussion

The Jianshangou Bed is famous for its diverse and characteristically feathered theropod fauna. Non-avian theropods from the Jianshangou Bed include basal avialans *Protarchaeopteryx robusta* (Ji & Ji 1997), *Caudipteryx dongi* (Zhou & Wang 2000), and *Caudipteryx zoui* (Ji *et al.* 1998); several compsognathids, including *Huaxiagnathus orientalis* (Hwang *et al.* 2004), *Sinornithosaurus millenii* (Xu *et al.* 1999a; Xu & Wu 2001), *Sinornithosaurus haoiana* (Liu *et al.* 2004), *Sinosauropteryx prima* (Ji & Ji 1996; Currie & Chen 2001) and *Sinocalliopteryx gigas* (Ji *et al.* 2007); the therizinosaur, *Beipiaosaurus inexpectus* (Xu *et al.* 1999b); a basal tyrannosauroid, *Dilong paradoxus* (Xu *et al.* 2004); and *Grallator* track makers (Xing *et al.* 2009).

Comparisons with the teeth of all known Jianshangou theropods make it possible to identify the animal responsible for the embedded tooth in LDRCv2. The diminutive size (both absolute size of the animal and tooth size) of many Jianshangou theropods precludes them as potential suspects for the embedded tooth. Furthermore, inconsistent morphologies, such as the bulbous teeth of *Protarchaeopteryx* (Ji *et al.* 1998) or the absence of denticles (*Caudipteryx*, Ji *et al.* 1998) dismiss others. Relatively large theropods within the Yixian Formation are rare compared to their smaller

counterparts, and include therizinosauroids (*Beipiaosaurus*), tyrannosaurids (*Dilong*), and compsognathids (*Huaxiagnathus*, *Sinocalliopteryx*). Despite its size (2.2 m; Xu *et al.* 1999b), *Beipiaosaurus* possesses short, bulbous teeth distinctive of therizinosauroids (Xu *et al.* 1999b) and unlike the blade-like teeth in LDRCv2. *Dilong* possesses chisel-shaped denticles similar to *Sinocalliopteryx* the embedded tooth; however, its smaller body size (approximately 1.6 m; Xu *et al.* 2004) and strongly recurved teeth argues against its assignment to LDRCv2.

At 2.37 m in length, *Sinocalliopteryx* is the largest theropod known from the Yixian Formation (Ji *et al.* 2007). Compsognathid teeth (including *Huaxiagnathus*, *Sinocalliopteryx*, and *Sinosauropteryx*) have a unique morphology among theropods: the apical third of the tooth crown is 'kinked' posteriorly; the mid-crown is relatively straight and perpendicular to the long axis of the jaw; and the base is expanded about the circumference (Peyer 2006). It has also been suggested that this particular tooth shape could be common to juvenile theropods in general (Makovicky *in* Peyer 2006). The maxillary tooth shape in *Sinocalliopteryx* is similar to other Chinese compsognathids, in that the longitudinal axis of the tooth is inclined anteriorly. However, with the exception of the anterior maxillary teeth, all teeth of *Sinocalliopteryx* possess serrated mesial and distal carinae (Ji *et al.* 2007), which differ from other typical compsognathids, such as *Sinosauropteryx* (Currie & Chen 2001), *Huaxiagnathus* (Hwang *et al.* 2004), and *Compsognathus* (Ostrom 1978) where only the maxillary and distal dentary teeth have fine serrations on their distal carinae. The largest maxillary tooth in *Sinocalliopteryx* has a fore-aft basal length (FABL) of 9 mm. In both *Sinocalliopteryx* (six denticles/mm; CAGS-IG-T1) and *Huaxiagnathus*, denticle density (seven denticles/mm; Hwang *et al.* 2004), denticle density is more than twice that of LDRCv2. Although *Sinosauropteryx* is the most common theropod in the Yixian Formation, it is dismissed also on account of its small size; the largest specimen of *Sinosauropteryx* measures 1.07 m in length (Therrien & Henderson 2007), inconsistent with the relatively large size of the tooth embedded in LDRCv2.

The maximum fore-aft basal length (FABL = 13 mm) of the embedded tooth is greater than any other described theropod from the Yixian Formation. Based on its large size, serration density and morphology, the embedded tooth likely represents a new taxon of medium-sized theropod. The Yixian Formation contrasts with most other Early Cretaceous faunas around the world (Weishampel *et al.* 2004) in that it is dominated by small-bodied (<2.5 m long) taxa, including a variety of coelurosaurian theropods, basal ceratopsians, ornithomids and

the ankylosaur *Liaoningosaurus* (Barrett et al. 2009). *Dongbetitan* and the iguanodontoid *Jinzhousaurus* are the only known large (>3 m) taxa currently recognized from the Yixian Formation. Zhao & Xu (2008) provided a preliminary report on the partial post cranium of a theropod with possible carnosaurian affinities from the Yixian Formation at Lujiatun (Zhao & Xu 2008). That specimen, however, lacks teeth so it is impossible at this stage to compare it with the theropod tooth in LDRCv2. Regardless of whether or not they represent the same taxon, these discoveries document the presence of medium-to-large theropods in the lower Jehol Group, which have heretofore been absent from the known fauna. Furthermore, LDRCv2 contributes to the mounting evidence that taphonomic, rather than ecological biases are responsible for the current paucity of known large-bodied taxa from the Yixian Formation (Wang et al. 2007; Zhao & Xu 2008; Barrett et al. 2009).

LDRCv2 represents an extremely rare snapshot of dinosaur feeding behaviour and is the first to involve a theropod tooth embedded in sauropod bone. Based on the alignment of the carinae in LDRCv2, the jaws were oriented parallel to the long axis of the rib when the tooth was emplaced. Given the absence of regenerative tissue, it is assumed the bite took place peri- or post-mortem. Tissue repair after bone fracture or damage (including penetrative lesions) occurs almost immediately; however, the osseous response to trauma is not apparent until the third to ninth week (Lovell 1997). Remodelling is identifiable as a callus or compact bone hyperplasia, although no distinct pathological changes were observed in LDRCv2. Similarly, given the relatively small size of the theropod compared to *Dongbetitan* (14 m in length; H.L. You, personal communication, 2011), it is unlikely that the tooth embedded in LDRCv2 was the result of predation, but rather, scavenging (Currie & Jacobsen 1995; Bell & Currie 2010). Predator-prey relationships between theropods and sauropods have been interpreted from shed teeth associated with sauropod remains (Smith et al. 2001; Jennings & Hasiotis 2006) and bite-marked bones (Harris 2007; Bader et al. 2009). LDRCv2 provides the best evidence of feeding interactions between these two groups.

To estimate the bite force required to embed the tooth in LDRCv2, we used the equation, $y = 1008e^{0.1738x}$ generated for *Deinonychus* based indentation experiments (Gignac et al. 2010), where e is constant (2.72), x is the thickness of cortical bone penetrated in millimetres, and y is the bite force in Newtons. This equation is appropriate because of the general similarity between the tooth in LDRCv2 and *Deinonychus* teeth (relatively small size, laterally compressed). Because the tooth in LDRCv2 is embedded

at variable depths (i.e. the surrounding bone is not flush with the broken base of the tooth at all points around its circumference) we used the conservative measurement of 6 mm (the average depth of the embedded tooth as shown by the X-ray; (Fig. 3). Total cortical thickness of the rib in the vicinity of the embedded tooth was 10 mm as determined by gross observation (non-histological) under a Boreal WW57701M00 dissecting microscope. This equation yielded a force of 2861 N required to produce the equivalent bite in *Deinonychus antirrhopus*. However, because this equation is derived from measurements for *D. antirrhopus*, and because of the difference in tooth size between *Deinonychus* and the embedded tooth, we multiplied the *Deinonychus* force (2861 N) by the ratio of the surface areas of the embedded tooth and the apical 6 mm of an equivalent *Deinonychus* maxillary tooth (force of tooth penetration is proportional to its surface area in contact with the surrounding bone; Erickson & Olsen 1996) following the method of Bell & Currie (2010). Surface areas of the teeth were calculated using the equation for an elliptical cone: $\pi([a + b]/2) \times \sqrt{[ab] + h^2}$, where a is the radius of the long axis of the ellipse, b is the radius of the short axis of the ellipse and h is height of the cone. This yielded a value of 8880 N required to embed the tooth in LDRCv2, at which point it broke. It must be stressed, however, that this value should be regarded as approximate due to the differences in anatomy, biomechanics and scaling between *Deinonychus* and Theropoda indet. It also does not take into account the fact that the tooth was embedded at an angle not normal to the bone surface. Further refinement of bite force estimates based on tooth-marked bone and indentation experiments will be necessary to better

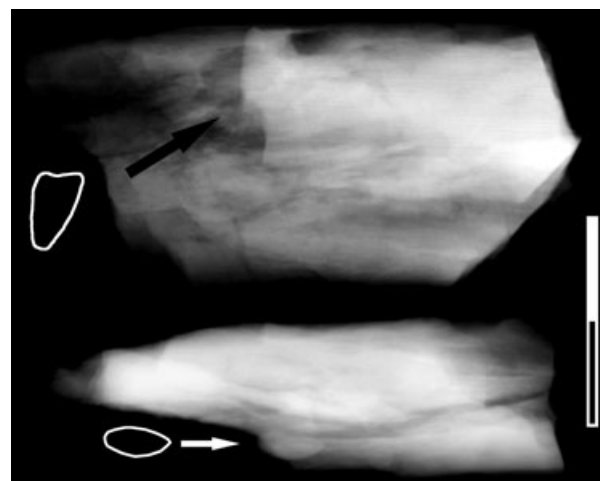


Fig. 3. X-ray scan of LDRCv2 showing outline of the embedded theropod tooth (arrows), contralateral (top) and anteroposterior (bottom) views. Scale = 5 cm.

gauge the bite strength in Theropoda indet. Nevertheless, the estimated bite force of the unidentified Yixian theropod is similar to upper bite force estimates for *Deinonychus antirrhopus* (8200 N), which lends some support to the methodology applied herein. It is also similar to cf. *Gorgosaurus* (6053 N; Bell & Currie 2010) but significantly lower than upper bite force estimates for *T. rex* (13,400 N) and *Alligator mississippiensis* (13,300 N; Erickson *et al.* 1996).

Conclusions

LDRcV2 is the first sauropod bone to preserve an embedded theropod tooth and provides the best evidence for feeding interaction between these two groups. Comparison of the tooth with all known theropods from the Jianshangou Bed suggests that it belongs to a new taxon of medium-sized theropod. The new theropod adds to the faunal diversity of the Yixian Formation and also contributes substantially to the palaeoecology of theropods from that formation, which is dominated by small-bodied (< 2 m) coelurosaurs. The absence of healing and size disparity between the theropod and *Dongbetitan* indicate the bite took place during scavenging. A preliminary assessment of the bite force required to embed the tooth gives a value of 8,880 N, similar to upper bite force estimates for *Deinonychus*.

Acknowledgements. – Thanks to Wang Tao (World Dinosaur Valley Park, Yunnan, China) and Kiko (Paleowonders Fossil and Mineral Museum, Taiwan, China) for providing the fossil for this study. Paul Gignac provided helpful discussion on bite force estimation. Thanks to Hailu You (Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China) for his critical comments and suggestions on an earlier version of the manuscript. We also thank Peter Doyle (editor), Brooks Britt (associate editor), and two anonymous reviewers for helpful comments that greatly improved the final version.

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