Paleogeographical significance of carcharodontosaurid teeth from the late Early Cretaceous of Ruyang, Henan Province of central China

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Four carcharodontosaurid teeth from the Cretaceous deposits of Ruyang County, Henan Province of central China are described in detail. The discovery of these large teeth indicates that some of the largest predatory dinosaurs coexisted with the gigantic plant-eating dinosaurs of this fauna, and these predators were likely the top consumers in the food chain. The teeth also further corroborate the biogeographic model by previous researchers that the carcharodontosaurids were broadly distributed rather than restricted to Gondwana, and this report expands the known non-Gondwanan record of the clade. Gigantic sauropod dinosaurs such as *Ruyangosaurus* and *Huanghetitan ruyangensis* were also found in the same area.

Keywords: carcharodontosaurid teeth; late Early Cretaceous; Henan Province; China

1. Introduction

Recently, many dinosaur fossils have been discovered from the early Late Cretaceous Haoling Formation of Liudian Town, Ruyang County, Henan Province (Figure 1). These include the gigantic sauropods Huanghetitan ruyangensis (Lü et al. 2006; Lü, Xu, Zhang, Hu et al. 2007) and Ruyangosaurus giganteus (Lü, Xu, Jia et al. 2009), the medium-sized sauropods Xianshanosaurus shijiagouensis (Lü, Xu, Jiang et al. 2009) and Yunmenglong ruyangensis (Lü et al. 2013), the nodosaurid Zhongyuansaurus luoyangensis (Lü, Xu, Zhang, Ji 2007; Xu et al. 2007), the oviraptorid Luoyanggia liudianensis (Lü, Xu, Jiang et al. 2009), several unnamed ornithomimids (Lü, Xu, Jiang et al. 2009), iguanodontian dinosaurs (Zhang et al. 2013) and other unprepared specimens. This distinct fauna has been referred to as the 'Ruyang Gigantic Sauropod Dinosaur Fauna' (Lü, Xu, Jiang et al. 2009).

Carcharodontosauridae, a major group of large-bodied theropod dinosaurs, was originally named by Stromer (1931), and is defined as *Carcharodontosaurus saharicus* and all taxa share a more recent common ancestor with it than with *Allosaurus fragilis* or *Sinraptor dongi* (Holtz et al. 2004). They are part of the larger allosauroid radiation from the Middle Jurassic to the mid-Cretaceous (Brusatte et al. 2009). All the presently recognised carcharodontosaurids are from the Cretaceous (Stromer 1931; Stovall and Langston 1950; Coria and Salgado 1995; Sereno et al. 1996; Alcober et al. 1998; Harris 1998; Currie and Carpenter 2000; Novas et al. 2005; Coria and Currie

2006; Brusatte and Sereno 2007; Sereno and Brusatte 2008; Brusatte et al. 2010, 2012; Ortega et al. 2010; Cau et al. 2013). However, Rauhut (1995) suggested that some isolated teeth from the Upper Jurassic Tendaguru Group of Tanzania might be representative of the carcharodonto-saurid lineage and teeth of *Megalosaurus(?) ingens* possibly belong to carcharodontosaurid allosauroid (Rauhut 2011).

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Hu (1964) described the first carcharodontosaurid specimens from Asia, although the skeletal remains, which do not include teeth, were not recognised as belonging to this family until recently (Brusatte et al. 2009). Potential carcharodontosaurids from Asia are represented primarily by teeth, and include specimens from Japan (Chure et al. 1999), Korea (Lee 2007) and Thailand (Azuma, personnel comm., 2009). Thus, while the carcharodontosaurids were once thought to be strictly Gondwanan in distribution, a small but growing body of evidence suggests that this clade is more cosmopolitan (Sereno et al. 1996; Brusatte and Sereno 2008; Brusatte et al. 2009; Benson et al. 2010; Eddy and Clarke 2011; Carrano et al. 2012).

Four carcharodontosaurid teeth have previously been mentioned as having been recovered at Ruyang (Lü, Xu, Jiang et al. 2009). Although no large theropod skeletons have been found in the area, the discovery of these teeth indicates that some of the largest predatory dinosaurs coexisted with the gigantic plant-eating dinosaurs of this fauna, and these predators were likely the top consumers in the food chain. In this paper, these four carcharodonto-

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Figure 1. Map of the fossil locality. Solid pentagon represents fossil site.

saurid teeth are described in detail. Discovery of these teeth further corroborates the biogeographic model of Brusatte et al. (2009) that the Carcharodontosauridae were broadly

distributed rather than restricted to Gondwana, and this report expands the known non-Gondwanan record of this major theropod subgroup.



Figure 2. Measured section of Lower Cretaceous Haoling Formation of Yezuibeigou of Santun Town, Ruyang County-Upper Cretaceous Shangdonggou Formation, showing the fossil position in the section (Modified from Xu et al. 2012).

2. Stratigraphy

The teeth come from what was once called the 'Mangchuan Formation', which was originally regarded as Cenozoic in age, and this rock sequence was regarded as Paleocene by local geologists (Bureau of Geology and Mineral Resources of Henan Province 1989). More recent work has shown that the unit is Mesozoic in age (late Early Cretaceous) (Lü et al. 2006; Xu et al. 2012). The dinosaurbearing strata are divided into three formations in ascending stratigraphical order: the Xiahedong Formation,



Figure 3. (Colour online) Photographs of 41HIII-0093 (A), 41HIII-0094 (B, C), 41HIII-0095 (D) and 41HIII-0096 (E). Scale bars = 10 mm.

Haoling Formation and Shandonggou Formation (Xu et al. 2012).

Dinosaur fossils are found in the massive brownish red muddy siltstones of the Haoling Formation, which are interbedded with grey-greenish sandy shales, near the Santun–Liudian Areas of the Ruyang Basin (Figure 2). The first sauropod specimens found from Liudian Town of Ruyang County established that the dinosaur-bearing deposits were definitively Cretaceous (late Early Cretaceous) (Lü et al. 2006; Xu et al. 2012).

3. Materials and methods

This study describes four carcharodontosaurid teeth (one nearly complete and three with missing tips) with specimen numbers 41HIII-0093, 41HIII-0094, 41HIII-0095 and 41HIII-0096 (Figure 3). They were discovered in the Haoling Formation, Haoling of Shijiagou villages, Liudian Town of Ruyang County, Henan Province (Xu et al. 2012). The specimens are housed at the Henan Geological Museum, Zhengzhou, China. The labial–lingual basal width and the fore-aft base length of teeth were measured in millimetres with a micrometre Mitutoyo # CPM30-25MJ. The bivariate scatter plots were constructed using Microsoft Excel.

4. Description and results

The Ruyang Basin teeth are relatively flat, narrow blades that are similar in general shape and proportions to the teeth of other carcharodontosaurids (Sereno et al. 1996; Novas et al. 1999; Vickers-Rich et al. 1999; Coria and Currie 2006). The fore-aft base length and the labial– lingual basal width of 41HIII-0093 are 38.6 and 15.4 mm, respectively. The tooth is blade-like with 8–9 serrations per 5 mm on the mesial and distal carinae, similar to the larger teeth of *Mapusaurus roseae* (Coria and Currie 2006). Both the anterior and posterior carinae extend to the base of the enamelled crown. The root is not well preserved, but the preserved portion shows that depressions appear near the boundary of the tooth crown and the tooth root and extend longitudinally towards the



Figure 4. (Colour online) Bivariate scatter plots comparing aspects of tooth dimensions with those of various theropods. FABL versus BW of tooth crowns in *Fukuiraptor* (X), dromaeosaurids (diamonds), carcharodontosauridsae (squares), tyrannosaurids (small triangles) and the Henan carcharodontosaurid (large triangle) (data based on Currie and Azuma 2006).

basal end of the root. The fore-aft base length and the labial-lingual basal width of 41HIII-0094 are 37.1 and 14.4 mm, respectively. Teeth 41HIII-0094 and 41HIII-0095 are also blade-like, although their tips are missing. There are 14 serrations per 5 mm on their anterior and posterior carinae. Tooth 41HIII-0095 is slightly different from the other teeth. The posterior carina of the tooth twists towards the midline, which is similar to the anterior dentary teeth of Mapusaurus roseae (Coria and Currie 2006). According to Coria and Currie (2006), the posterior carina of the anterior dentary teeth of Mapusaurus twists labial to the midline, which indicates that 41HIII-0095 is an anterior right dentary tooth. It has a taller but narrower crown than that of Mapusaurus and has an oval cross section near its tip. There are 10 serrations per 5 mm on the anterior and posterior carinae of 41HIII-0095, which is identical to the denticle size of Carcharodontosaurus (Russell 1996; Currie and Carpenter 2000). Except for 41HIII-0095, the teeth have distinct enamel wrinkles in the enamel, which covers part of the tooth and curves towards the posterior carina as in potential carcharodontosaurid dinosaurs (Chure et al. 1999).

Bivariate scatter plots comparing tooth dimensions with those of various theropods show that the Henan teeth (41HIII-0093, 41HIII-0094, 41HIII-0095 and 41HIII-0096) fall within the expected range of carcharodontosaurid teeth (Figure 4). The tooth from Japan is slightly narrower than the ones recovered from the Ruyang Basin.

5. Discussion

Enamel wrinkles on the external surface of the crown were once used as a 'key character' of carcharodontosaurid dinosaurs. However, such wrinkles are present in several theropod clades and are not confined to the Carcharodontosauridae (Brusatte et al. 2007). Nevertheless, the presence of carcharodontosaurids in Asia (Brusatte et al. 2009, 2010), and the size and shape of the teeth clearly suggest that the four described specimens are carcharodontosaurid in origin. The crown height around 7 cm teeth (41HIII-0093 and 41HIII-0094) is comparable to the largest maxillary tooth in *Carcharodontosaurus* (Stromer, 1931) and implies an animal of similar size. *Shaochilong*, which comes from the Turonian (Early Late Cretaceous) of Inner Mongolia, China, was described as the first carcharodontosaurid found from China (Brusatte et al. 2009, 2010). However, there are no teeth preserved with the type (and only known) specimen of *Shaochilong*. Therefore, the carcharodontosaurid material (teeth) from Ruyang Basin cannot be compared with *Shaochilong*. The four carcharodontosaurid teeth from the late Early Cretaceous deposits of the Ruyang Basin are therefore the first well-preserved, nearly complete carcharodontosaurid teeth found from China (Lü, Xu, Jiang et al. 2009). The large sizes of the teeth indicate that they belong to a large-bodied theropod.

There are two other large Asian theropods from late Early to early Late Cretaceous, which are closely related to carcharodontosaurids. They are *Fukuiraptor* (Azuma and Currie 2000; Currie and Azuma 2006) and *Siamotyrannus* (Buffetaut et al. 1996). Both belong to Allosauroidea, the diverse basal tetanuran clade that includes carcharodontosaurids (Rauhut 2003; Holtz et al. 2004; Benson et al. 2010; Brusatte et al. 2010; Carrano et al. 2012). The recently discovered carcharodontosaurid specimens from the Lower Cretaceous Khok Kruat Formation in Northeastern Thailand further confirms the existence of carcharodontosaurids in Asia during this time (Azuma et al. 2011).

6. Conclusions

Carcharodontosauridae was once thought to be restricted to Gondwana, but the discovery of carcharodontosaurid teeth from the Ruyang Basin further confirms recent phylogenetic and biogeographic work that this clade was cosmopolitan in the Early to Mid-Cretaceous. The contemporary large, even gigantic sauropod dinosaurs such as Huanghetitan ruyanensis (Lü, Xu, Zhang, Hu et al. 2007) and Ruyangosaurus giganteus (Lü, Xu, Jia et al. 2009), and an unnamed iguanodontid found from the same deposits, may have been the main food sources of these large-sized theropods. Large-sized sauropods, Fukuititan (Azuma and Shibata 2010) and *Phuwiangosaurus* (Martin et al. 1994), are also known from Fukui and Thailand, respectively, where other putative carcharodontosaurids were discovered. No large-sized sauropod dinosaurs have yet been found in the same deposits as Shaochilong in Inner Mongolia of China, but this may be the result of sampling bias.

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References

- Alcober O, Sereno PC, Larsson HCE, Martinez R, Varricchio DJ. 1998. A Late Cretaceous carcharodontosaurid (Theropoda: Allosauroidea) from Argentina. J Vert Paleontol. 18(suppl):23A.
- Azuma Y, Currie PJA. 2000. new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. Can J Earth Sci. 37:1735–1753.
- Azuma Y, Jintasakul P, Shibata M, Hanta R, Thasod Y. 2011. New carcharodontosaurian theropod materials from the Lower Cretaceous Khok Kruat Formation in Northeastern Thailand. Program and abstracts of the world conference on paleontology and stratigraphy 5A; November 28 to December 2 2011.
- Azuma Y, Shibata M. 2010. Fukuititan nipponensis, a new titanosauriform Sauropoda from the Early Cretaceous Tetori Group of Fukui Prefecture, Japan. Acta Geologica Sinica (English edition). 84(3): 454–462.
- Benson RBJ, Carrano MT, Brusatte SL. 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. Naturwissenschaften. 97:71–78.
- Brusatte SL, Benson RBJ, Carr TD, Williamson TE, Sereno PC. 2007. The systematic utility of theropod enamel wrinkles. J Vert Paleontol. 27(4):1052–1056.
- Brusatte SL, Benson RBJ, Chure DJ, Xu X, Sullivan C, Hone DEW. 2009. The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. Naturwissenschaften. 96:1051–1058.
- Brusatte SL, Benson RBJ, Xu X. 2012. A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China. Acta Palaeontol Pol. 57(1):65–72.
- Brusatte SL, Chure DJ, Benson RBJ, Xu X. 2010. The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the late Cretaceous of Asia. Zootaxa. 2334:1–46.
- Brusatte SL, Sereno PC. 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. J Vert Paleontol. 24:902–916.
- Brusatte SL, Sereno PC. 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. J Syst Palaeontol. 6:155–182. doi:10.1017/S1477201907002404.
- Buffetaut E, Suteethorn V, Tong H. 1996. The earliest known tyrannosaur from the Lower Cretaceous of Thailand. Nature. 381:689–691.
- Bureau of Geology and Mineral Resources of Henan Province. 1989. Regional geology of Henan Province. Beijing: Geological Publishing House; p. 1–772.
- Carrano MT, Benson RBJ, Sampson SD. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). J Syst Palaeontol. 10(2):211-300.
- Cau A, Dalla Vecchia FM, Fabbri M. 2013. A thick-skulled theropod (Dinosauria, Saurischia) from the Upper Cretaceous of Morocco with implications for carcharodontosaurid cranial evolution. Cretaceous Res. 40:251–260.
- Chure DJ, Manabe M, Tanimoto M, Tomida Y. 1999. An unusual theropod tooth from the Mifune Group (late Cenomanian to early Turonian), Kumamoto, Japan. In: Tomida Y, Rich TH, Vickers-Rich P, editors. Proceedings of the second Gondwana dinosaur symposium. Monograph 15. Tokyo: National Science Museum; p. 291–296.
- Coria RA, Currie P. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas. 28(1):71–118.
- Coria RA, Salgado L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. Nature. 377:224–226.
- Currie PJ, Azuma Y. 2006. New specimens, including a growth series, of Fukuiraptor (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. J Paleontol Soc Kor. 22:173–193.
- Currie PJ, Carpenter K. 2000. A new specimen of Acrocanthosaurus atokensis (Theropoda, Dinosauria) from the Lower Cretaceous

Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. Geodiversitas. 22(2):207–246.

- Eddy DR, Clarke JA. 2011. New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroidea (Dinosauria: Theropoda). PLoS One. 6(3):e17932. doi:10.1371/journal.pone.0017932.
- Harris JD. 1998. A reanalysis of Acrocanthosaurzu atokensis, its phylogenetic status, and paleobiogeographic implications, based ona new specimen from Texas. New Mexico Mus Nat Hist Sci Bull. 13:1–75.
- Holtz TR, Molnar RE, Currie PJ. 2004. Basal Tetanurae. In: Weishampel DB, Dodson P, Osmólska H, editors. The Dinosauria. 2nd edn. Berkeley: University of California Press. p. 71–110.
- Hu SY. 1964. Carnosaurian remains from Alashan, Inner Mongolia. Vertebr PalAsiatica. 8:42–63.
- Lee YN. 2007. New theropod teeth from the Juli Island (Hasandong Formation), Daedo-ri, Hadong County, South Gyeongsan Province. J Geol Soc Kor. 43(2):151–166.
- Lü JC, Xu L, Jia SH, Zhang XL, Ji Q. 2006. Discovery of a gigantic sauropod femur in Ruyang, Henan, China and its stratigraphic significance. Geol Bull China. 25(11):1299–1302.
- Lü JC, Xu L, Jia SH, Zhang XL, Zhang JM, Yang LL, You HL, Ji Q. 2009. A new gigantic sauropod dinosaur from the Cretaceous of Ruyang, Henan Province, China. Geol Bull China. 28(1):1–10.
- Lü JC, Xu L, Jiang XJ, Jia SH, Li M, Yuan CX, Zhang XL, Ji Q. 2009. A preliminary report on the new dinosaurian fauna from the Cretaceous of the Ruyang Basin, Henan Province of central China. J Paleontol Soc Kor. 25(1):43–56.
- Lü JC, Xu L, Pu H, Zhang XL, Zhang YY, Jia SH, Chang HL, Zhang JM, et al. 2013. A new sauropod dinosaur (Dinosauria, Sauropoda) from the late Early Cretaceous of the Ruyang Basin (central China). Cretaceous Res. 44:202–213.
- Lü JC, Xu L, Zhang XL, Hu WY, Wu YH, Jia SH, Ji Q. 2007. A new gigantic sauropod dinosaur with the deepest known body cavity from the Cretaceous of Asia. Acta Geol Sin. 81(2):167–176.
- Lü JC, Xu L, Zhang XL, Ji Q. 2007. New nodosaurid dinosaur from the Cretaceous of Henan Province, China. J Vertebr Paleontol. 3(Supp):107A.
- Martin V, Buffetaut E, Suteethorn V. 1994. A new genus of sauropod dinosaur from the Sao Khua formation (Late Jurassic or early Cretaceous) of northeastern Thailand. Comptes Rendus de l' Academie des Science de Paris. 319(2):1085–1092.
- Novas FE, de Valais S, Vickers-Rich P, Rich T. 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. Naturwissenschaften. 92:226–230.

- Novas FE, Martínez RD, De Valais S, Ambrosio A. 1999. Nuevos registros de carcharodontosauridae (Dinosauria, Theropoda) en el Cretácico de Patagonia. Ameghiniana. 36:17R.
- Ortega F, Escaso F, Sanz JL. 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. Nature. 467:203–206.
- Rauhut OWM. 1995. Zur systematischen Stellung der afrikanischen Theropoden Carcharodontosaurus Stromer 1931 und Bahariasaurus Stromer, 1934. Berliner geowissenschaften Abhandlungen. 16:357–375.
- Rauhut OWM. 2003. The interrelationships and evolution of basal theropod dinosaurs. Spec Papers Palaeontol. 69:1–213.
- Rauhut OWM. 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). Spec Papers Palaeontol. 86:195–239.
- Russell DA. 1996. Isolated dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. Bulletin du Muséum national d'Histoire naturelle, série 4. C 18(2–3):349–402.
- Sereno PC, Brusatte SL. 2008. Basal abelisaurid and carcharodontosaurid theropods from the Elrhaz Formation (Aptian-Albian) of Niger. Acta Palaeontol Pol. 53:15–46.
- Sereno PC, Dutheil DB, Iarochene SM, Larsson HCE, Lyon GH, Magwene PM, Sidor CA, Varricchio DJ, Wilson JA. 1996. Late Cretaceous dinosaurs from the Sahara. Science. 272:986–991.
- Stovall JW, Langston W, Jr. 1950. Acrocanthosaurus atokensis, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. Am Midl Nat. 43:696–728.
- Stromer E. 1931. Wirbeltier-reste der Baharije-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung. Neue Folge. 9:1–23.
- Vickers-Rich P, Rich TH, Lanus DR, Rich LSV, Vacca R. 1999. Big Tooth from the Early Cretaceous of Chubut Province, Patagonia: a possible carcharodontosaurid. In: Tomida Y, Rich TH, Vickers-Rich P, editors. Proceedings of the second Gondwana dinosaur symposium. Monograph 15. Tokyo: National Science Museum. p. 85–88.
- Xu L, Lü JC, Zhang XL, Jia SH, Hu WJ, Zhang JM, Wu YH, Ji Q. 2007. New nodosaurid ankylosaur from the Cretaceous of Ruyang, Henan Province. Acta Geol Sin (Chinese edition). 81(4):433–438.
- Xu L, Pan ZC, Wang LH, Zhang XL, Jia SH, Lü JC, Jiang BL. 2012. Discovery and significance of the Cretaceous system in Ruyang Basin, Henan Province. Geol Rev. 58(4):601–613.
- Zhang YY, Lü JC, Pu HY, Xu L, Shang YH, Jia SH, Zhang JM. 2013. The discovery of iguanodontid dinosaur from the late Early Cretaceous strata of Ruyang Basin, Henan and its stratigraphic significance. Geol Bull China. 32(9):1344–1348.