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Diverse tooth marks on an adult sauropod bone from the Early Cretaceous, Korea: Implications in feeding behaviour of theropod dinosaurs

In Sung Paik [a,*], Hyun Joo Kim [a], Jong Deock Lim [b], Min Huh [c], Ho Il Lee [a]

[a] Department of Earth Environmental Sciences, Pukyong National University, Busan 608-737, South Korea
[b] Research Division of Natural Heritage, National Research Institute of Cultural Heritage, Daejeon 302-834, South Korea
[c] Faculty of Earth System and Environmental Sciences, Chonnam National University, Gwangju 500-757, South Korea

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Although carnivorous dinosaurs probably engaged in both predation and scavenging, it has been suggested that the tyrannosaurids were uniquely scavengers. The fossil record of bone damage resulting from predation by carnivorous theropod dinosaurs is sparse, and it is often difficult to determine whether tooth-marks were produced through predation or scavenging. In this study unusual tooth-marks on a caudal vertebra of an adult sauropod from the Lower Cretaceous Hasandong Formation, Korea, which are the deepest and longest scores ever documented, are described. In addition to these tooth-marks, small tooth-strike lesions, including shallow gouges and divots, are present on the same bone. These tooth-marks provide insight into the feeding behaviour of dinosaurs that scavenged the bodies of large, adult dinosaurs. The presence of both large and small tooth-marks on a single bone suggests that theropods of different sizes or kinds exploited the same adult sauropod carcass to deflesh it and/or to obtain bone nutrients, in a manner identical to that of modern carnivores.

1. Introduction

Although the idea that tyrannosaurids may have been scavengers is still debated, carnivorous dinosaurs probably engaged in scavenging (Holtz, 2008; Hone et al., 2010). Hone and Rauhut (2010) suggested that theropods rarely hunted and ate adult animals in contrast to the traditional view of large theropods hunting the adults of large or giant dinosaur. However, evidence of theropod's predatory behaviour for adult hadrosaur has been documented (Carpenter, 1998), and cannibalism by theropods has been proposed (Tanke and Currie, 1998; Rogers et al., 2003). It is therefore considered that theropod dinosaurs hunted, attacked, and scavenged both adult and juvenile prey species as modern carnivores.

The predatory behaviour of theropod dinosaurs can be understood through dento- or osteopathy (Rothschild and Tanke, 1992; Hone and Rauhut, 2010), and the tooth-marks left by theropods can contribute to the understanding of predator–prey interactions and carcass use by theropods (Fiorillo, 1991; Hunt et al., 1994; Currie and Jacobsen, 1995; Erickson and Olson, 1996; Chin, 1997; Currie, 1997; Carpenter, 1998; Chure et al., 1998; Tanke and Currie, 1998; Rogers et al., 2003; Buffetaut et al., 2004; Holtz, 2004; Carpenter et al., 2005; Bell and Currie, 2010; Hone et al., 2010). Bone injuries formed by the teeth of carnivorous dinosaurs are classified as punctures, gouges, scores (tooth-drag imprints), parallel shallow furrows formed by the serrated edges of theropod teeth, and embedded teeth (Jacobsen, 1998; Tanke and Currie, 1998). Documented tooth-marks on dinosaur and pterosaur bones are generally less than 1 cm deep and a few centimetres long. Hitherto, there has been no evidence to indicate that bones of a large adult dinosaur carcass may have been used by a succession of theropods of different sizes or types, with diverse feeding strategies, like those of modern carnivores, such as defleshing or obtaining bone nutrients.

This paper describes diverse types of tooth-marks on the caudal vertebra of an adult sauropod (*Pukyongosaurus millenniumi*) (Dong et al., 2001), including the longest and the deepest scores described to date. This evidence provides insight not only into the palaeoecology of Cretaceous theropods but also allows comparison of the feeding ecology of theropods with that of extant carnivores.

2. Occurrences of the bone bed

The tooth-mark-bearing bone (PKNU GS08-05) is from a bone bed in a 70-cm-thick calcareous sandy mudstone deposit of a fluvial floodplain that is now exposed on a small island in a modern tidal flat (Fig. 1). The bone bed underwent calcareous pedogenesis on the distal part of a floodplain under a semi-arid climate with alternating wet and dry periods and was subsequently buried by channel avulsion. The bones are generally encrusted with calcite, which facilitated their preservation.

* Corresponding author. Tel.: +82 51 6296625; fax: +82 51 6296623.
E-mail address: paikis@pknu.ac.kr (I.S. Paik).

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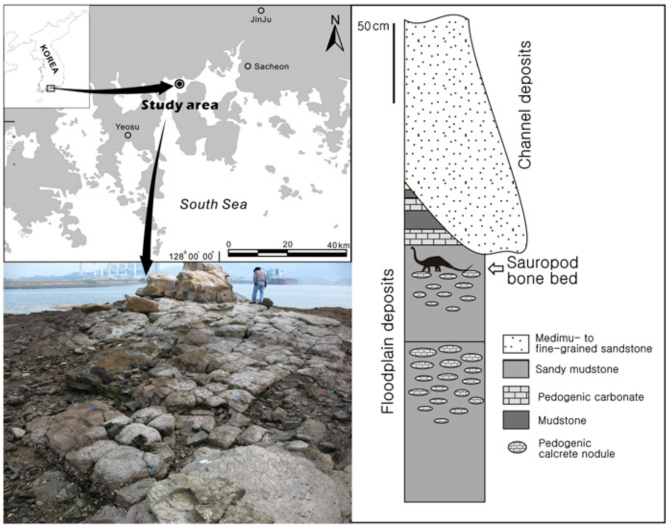

Fig. 1. Location and stratigraphic section of the sauropod bone bed in study area.

Bones and bone fragments of *Pukyongosaurus millenniumi* are dispersed in a NE-trending, sub-linear zone that is about 12 m long and 2 m wide. The bones include seven cervical vertebrae, a nearly complete dorsal centrum, a cervical rib, an incomplete dorsal rib, an incomplete caudal vertebra, a complete chevron, an incomplete chevron, part of a sternum, and a nearly complete tooth. Over 100 bone fragments a few centimetres to approximately 10 cm in length are also present.

The strongly lithified nature of the bed precluded excavation of all bone materials present, but some aspects of bone distribution and bone preservation are nonetheless apparent. In the southwestern part of the bone bed the bones are relatively concentrated, and some cervical vertebrae are partly articulated, whereas in the northeastern area the bones are scattered and consist predominantly of fragments and chips. The cervical vertebrae form a sub-linear array, whereas small bone fragments are scattered. The dorsal centrum and the chevron are associated with the cervical vertebra in the southwestern part of the bed, which is an unusual association. Although most of the bones are disarticulated, incomplete, and fragmented, bone tissue textures are well preserved and the bones exhibit little evidence of weathering before burial. A dorsal rib, a bone that is generally vulnerable to weathering, shows none of the longitudinal cracks that typically develop during subaerial exposure before burial.

A broken, isolated, tooth-marked bone (50 cm long, 25 cm wide, 5–10 cm thick) in the northeastern part of the bone assemblage is slightly compressed. The bone is an incomplete caudal vertebra. Only the left side of the caudal vertebra, in which the ventral part of the centrum is missing, is preserved (Fig. 2). The vertebra has a well-developed neural spine, a postzygapophysis with a pronounced concavity, and a hook-like transverse process; these features indicate that it is one of the proximal caudal vertebrae. The neural spine is low, vertically oriented, robust, straight-edged, and rectangular in lateral view.

Spongy bone textures are partially exposed on the surface of the specimen, in contrast to most of the other bones in the bed, which lack exposure of such cancellous textures. Spongy bone textures are best exposed around the tooth-marks. Most of the bone surface, including the broken margins and tooth-marks, is encrusted with calcite, indicating that bone breakage took place before burial. The smooth surface of the external compact bone is generally encrusted with a calcite film (<3 mm thick), whereas the irregular surface of exposed cancellous bone is encrusted with micro-botryoidal calcite.

3. Tooth-marks

Distinct tooth-strike lesions are present in five parts of the specimen (Fig. 2). The first set of marks is on the anterior surface of the neural spine (Fig. 3A and B). The marks consist of two pairs of longitudinal, V-shaped scores with W-shaped cross-sections on the external compact bone surface, and expose internal spongy bone. One pair of parallel scores is slightly curved and shallows outwards. The space between the pointed grooves of the two scores is 1.8 cm. One of the two scores, the largest of all of the tooth-marks, is 17 cm long, 2 cm wide, and 1.5 cm deep, with a cross-sectional angle of about 80°. The other score (1.6 cm wide and 1.2 cm deep; angle of approximately 60°) is distinct at the ventral end but diffuse at the dorsal end. The second pair of parallel scores is located 10 cm from the ventral end of the first pair, and overlaps one of the first pair of scores at an angle of about 30°. The second pair is 5 cm long, and the space between the pointed troughs of the two scores is 1.1 cm. The inner score of the second pair is similar to the overlapped score in size and shape, and the outer score is 1.3 cm wide and 7 mm deep. The cross-sectional angle of the outer score is about 25°. The external ridge of the outer score is partially fractured.

The second set of tooth-strike marks, 6 cm away from the first one, is situated on the opposite side (posterior surface) of the first one and affects the external compact bone surface. It consists of three parallel longitudinal scores that are sub-parallel to the first pair of scores (Fig. 4). The scores have moderately sharp to obtuse ridges and are smaller than the first pair of scores in both size and depth. The largest score is the inner one (3.5 cm long, 12 mm wide, 15 mm deep), which has a cross-sectional angle of about 40°. The middle score (2 cm long, 3 mm wide, 4 mm deep) and outer score (7 mm long, 3 mm wide, 2 mm deep) have angles of about 30°. The spaces between the pointed grooves of the three scores are 8 mm and 5 mm, and the widths of ridges are 2 to 5 mm.

The third tooth-mark, a flute-like transverse gouge (2 cm long, 5 mm wide, 7 mm deep), is on compact bone of the posterior surface of the prezygapophysis (Fig. 5) and has a cross-sectional angle of about 50°. An irregular divot 1 cm in diameter on spongy bone is present 1 cm from this score.

The fourth tooth-strike lesion is on the anterior margin of the centrum. It is on compact bone and consists of a pair of longitudinal, sub-parallel gouges (3 cm long, 5 mm wide, 5–6 mm deep) (Fig. 6A) with many drag imprints on the gouges and the ridge (Fig. 6B). The spacing between the gouges is about 1.5 cm, and the ridge is 1 to 1.5 cm wide. The angles of the gouges are about 60°. Drag imprints are

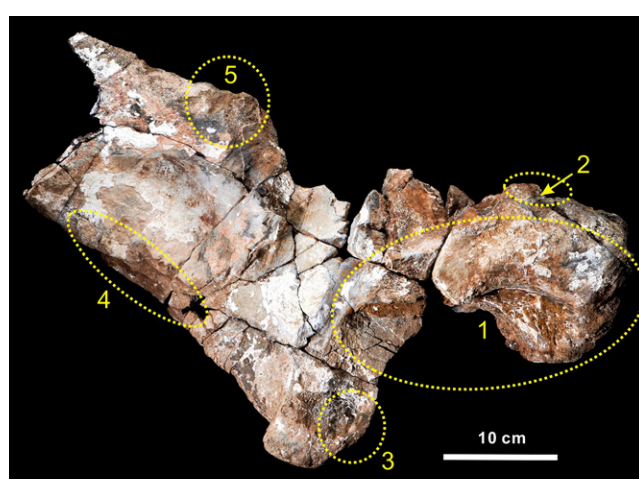

Fig. 2. Tooth-marked caudal vertebra (PKNU GS08-05) of *Pukyongosaurus millenniumi* (right lateral view). The location of tooth-marks is indicated, and close views of each tooth marks are shown in Figs. 3 to 7. The second tooth-marks cannot be seen in this figure.

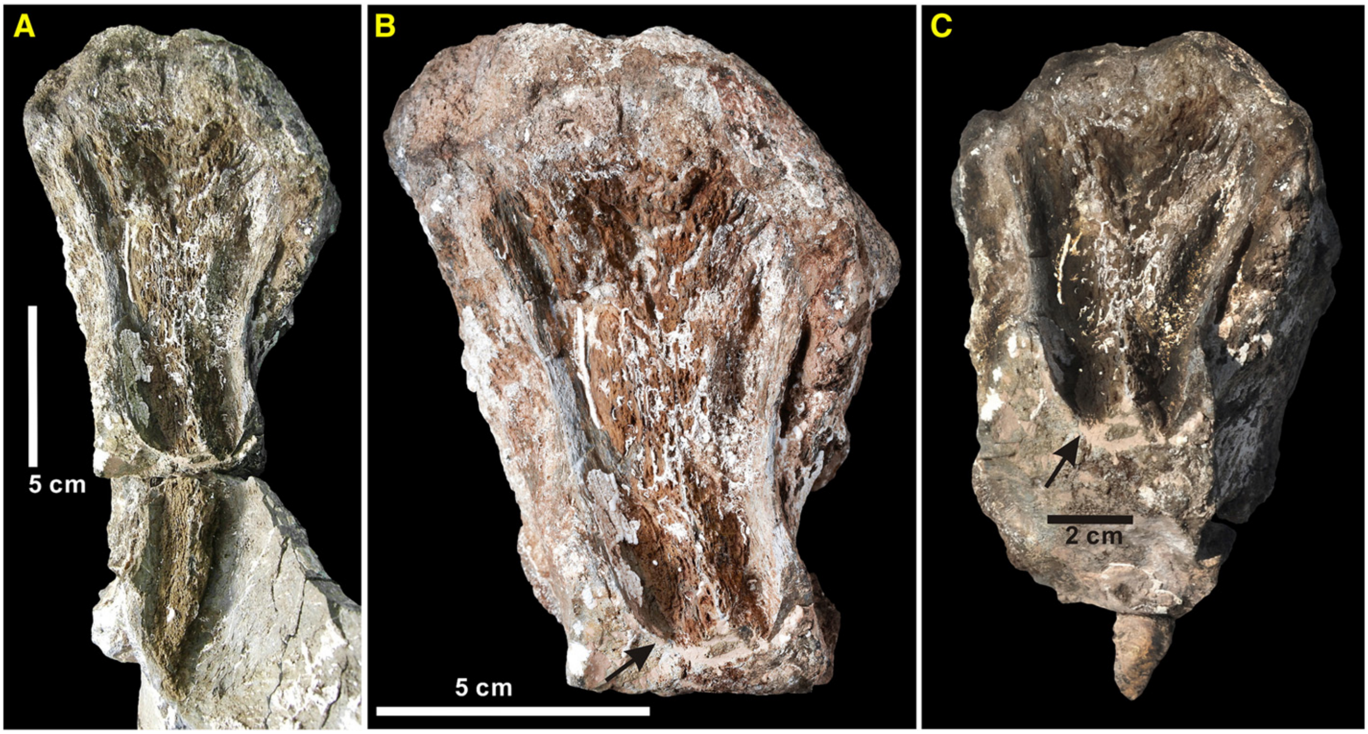

Fig. 3. The first set of tooth-marks (No. 1 in Fig. 2). A. Planar view of the first set on the anterior surface of the neural spine consisting of two pairs of longitudinal, V-shaped scores. B. Oblique sectional view showing W-shaped cross-section (arrow) of scores. C. Image-adjusted sectional view showing distinct W-shaped cross-section (arrow).

generally less than 1 mm wide and deep, approximately 1 cm long, and are predominantly on the ridge. They are sub-parallel to the gouges, and some are obliquely overlapped by others.

The fifth tooth-strike lesion, on exposed spongy bone of the posterior margin of the centrum, is a divot-type lesion caused by low-angle tooth-strike (Fig. 7). It consists of three arcuate divots (each 2.5 cm long, ~1 cm wide, ~3 mm deep). In addition to these tooth-marks, indistinct bone traumas are also locally present.

4. Discussion

During the Early Cretaceous on the Korean Peninsula, herbivorous and carnivorous dinosaurs lived on fluvial plains characterised by dry woodlands and a semi-arid climate (Paik et al., 2001). The semi-arid climate and associated low sedimentation rate may have allowed dinosaur carcasses to be exposed long enough for them to be weathered and scavenged. Bone-borings by dermestid beetles associated with bone-chip-filled burrows in the Hasandong Formation are good examples of scavenging of dried dinosaur carcasses (Paik, 2000).

The bone bed with tooth-marked bone exhibits a nearly linear distribution and partially articulated preservation of cervical vertebrae, and smooth bone surfaces lacking longitudinal cracks or fissures, all of which indicate that these bones were preserved near the site of death, experienced minimal weathering, and were buried rapidly (Behrensmeyer, 1978, 1991; Smith, 1993; Paik et al., 2001). The unsorted distribution of bones and the presence of large bones in hydraulically incompatible muddy sediment indicate that the bones were not hydraulically transported, but are in situ remains. The scattered and broken nature of the bones in part of the bone bed, the absence of appendicular bones, and the presence of tooth-marks on bone suggest that biophysical activity contributed to the disintegration

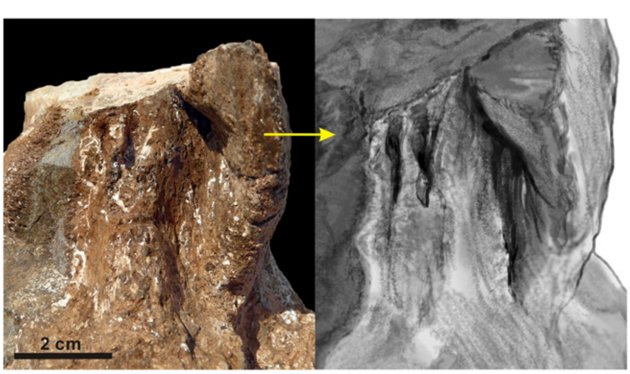

Fig. 4. The second set of tooth-marks (No. 2 in Fig. 2) situated on the opposite side (posterior surface) of the first one consisting three parallel longitudinal scores.

Fig. 5. The third tooth-mark (No. 3 in Fig. 2) on the margin of the centrum. It is flute-like transverse gouge (arrow) on the posterior surface of the prezygapophysis.

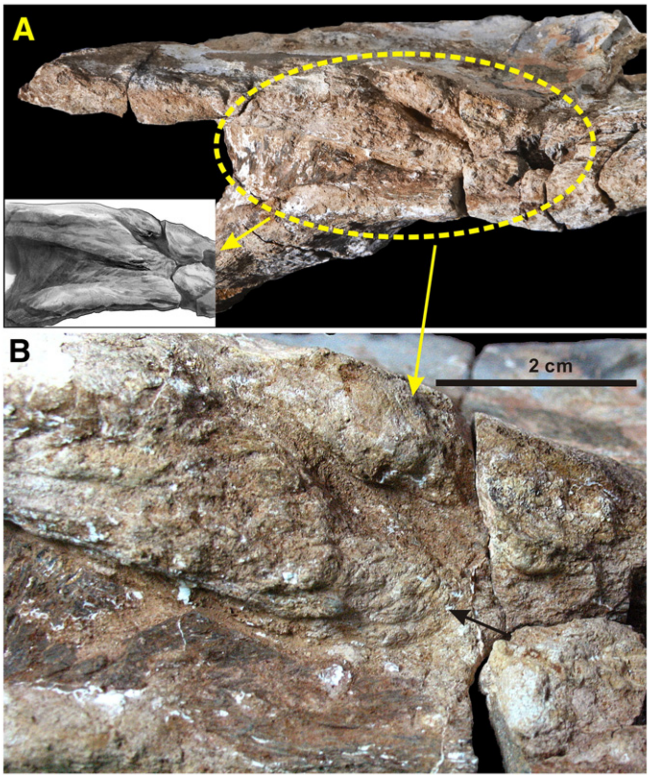

Fig. 6. The fourth set of tooth-marks (No. 4 in Fig. 2) on the anterior margin of the centrum consisting of a pair of longitudinal, sub-parallel gouges (A) with many drag imprints (arrow in B).

and scattering of the bones. These characteristics probably reflect scavenging of the sauropod carcass by carnivores.

Carnivores documented from the Hasandong Formation include theropod dinosaurs and crocodiles. Four different theropod dinosaur types, allosauroid (Park et al., 2000), megalosaurid (Lim et al., 2002), carcharodontosaurid (Lee, 2007), and tyrannosauroid (Yun et al., 2007; Lee, 2008), have been identified in the Hasandong Formation on the basis of their teeth. These teeth are about 3 to 8 cm long and about 1 to 2 cm in diameter, with an apical angle of about 30 to 60°. The crocodilian fossils found in the Hasandong Formation are proto-

Fig. 7. The fifth set of tooth-marks (No. 5 in Fig. 2). They are divot-type (arrows) lesion on the posterior margin of the centrum consisting of arcuate divots.

suchian (Archosauria: Crocodyliformes) skull (Lee and Lee, 2005) and mesosuchian teeth (Yun et al., 2007). The skull is about 50 mm long and 25 mm high, and the teeth are about 5 to 6 mm in diameter. It is plausible that theropod dinosaurs inhabiting the Korean Peninsula during the Early Cretaceous could have produced tooth-marks of the size and the shape described above. The first set of scores, which are the largest of all of the tooth-marks, could have been made by a tyrannosaurid theropod considering the size and cross-sectional shape and angle of the scores. The makers of the other tooth-marks are deemed to have been smaller carnivores, but their taxa are uncertain. Considering the size of the Hasandong crocodilians it is improbable that they could have made the tooth-marks described above.

According to the classification of tooth-marks on dinosaur bone (Jacobsen, 1998; Tanke and Currie, 1998), the tooth-marks described above belong to type 2 (gouge or score and divot), which is the most common form of large theropod tooth-marks and is also characteristic of bone that has been bitten by extant carnivores (Blumenschine et al., 1996). Whether these tooth-marks were formed during hunting, predation, scavenging, or gnawing on or chewing the bone after decomposition of all of the flesh can be determined by the characteristics of the tooth-marks.

Bone regrowth in tooth-marks on articulated bone can indicate hunting or aggressive behaviour of carnivorous dinosaurs (Carpenter, 1998). However, broken occurrence of the tooth-marked bone, the absence of bone regrowth in tooth-marks, and the presence of deep, long scores suggest that the tooth-marks documented in this study were not generated during hunting or attack when the prey was alive. The distinct preservation of long, deep scores with little physical damage around the trauma of the first group of tooth-marks indicates that they were generated when the bone was wet and covered with some flesh.

Multiple parallel grooves on prey bone have been interpreted as the result of nipping and scraping behaviour of predatory dinosaurs (Chure et al., 1998). The parallel scores preserved on the caudal bone of *Pukyongosaurus* indicate that more than one premaxillary tooth contacted the bone during nipping. The scoring pattern of the first and the second tooth-marks and their opposing positions on the bone suggest that these tooth-marks resulted from the same bite by premaxillary teeth during nipping and scraping, parallel to the axis of the neural spine. The first set of scores, which is the deepest and the longest, probably represents the teeth of the upper jaw, and the second set of scores the teeth of the lower jaw.

The third and fifth tooth-marks, which are isolated, not parallel to other marks, and lack matching tooth-marks on the opposite side, are not the marks of a bite, but rather those from single strikes of the premaxillary tooth of the upper jaw. The divot-type lesions in the fifth tooth-marks record random tooth-strikes at a low angle to the bone. The fourth group of tooth-marks may have resulted from the repeated dragging of premaxillary teeth across the same bone surface.

The difference between the tooth-marks in shape, size, and pattern indicates that carnivores of different sizes including theropods used the same bone with different feeding strategies. A large theropod defleshed the carcass to produce the first and second marks, and produced the fourth set of marks as it sought bone nutrients. The third and fifth sets of tooth-marks were probably formed by a smaller carnivore that was procuring bone nutrients. The absence of tooth-marks, including punctures or bite-marks, on other *Pukyongosaurus* bones in the same bone bed suggests that the first and second set of tooth-marks resulted from scavenging rather than predation. Although it is uncertain whether the carnivores that exploited the bone were of the same species, it is probable that a sequence of scavenging existed among the Cretaceous carnivores including theropods, just as occurs among living mammalian carnivores. In conclusion the specimen with tooth-marks of diverse type, size, and origin indicates that scavenging was at least occasionally a part of theropod feeding ecology.

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