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Osteological evidence for predatory behavior of the giant percrocetid (*Dinocrocuta gigantea*) as an active hunter

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We present osteological evidence that a rhinocerotid skull belonging to a female *Chilotherium wimani* was bitten by a giant percrocetid, *Dinocrocuta gigantea*. Aided by comparative evidence of black rhino (*Diceros bicornis*) predation by extant spotted hyenas *Crocota crocuta*, we interpret the healed wound on the *C. wimani* female as an injury incurred by the late Miocene *D. gigantea*. The hunting paleoecology of the giant percrocetid *D. gigantea* has long been speculated, but thus far no clear evidence has been discovered to point to the predatory habits of this carnivore. The present specimen of *C. wimani* provides evidence to indicate that the giant percrocetid shared similarities in predatory behavior to the modern spotted hyena: it was an active hunter in spite of the specialized bone-cracking craniodental morphology which imparted superb capability for processing bone.

predation, rhinocerotid, chilothere, *Dinocrocuta*, Miocene, China

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Unique fossil preservations give us a glimpse into mammalian predatory activities of the past [1]. Here we report on a rhinoceros skull that possesses a prominent bite mark presumably made by a large predator. The specimen was collected from the red clay of the late Miocene Liushu Formation at the locality Shuanggongbei (LX 0009) in the Linxia Basin of northwestern China. The geologic age of the locality is estimated to be equivalent to the MN 10 (Vallesian age in Europe) or ca. 9.2 Ma (early late Miocene), based on fossil mammal biochronology and paleomagnetic dating [2].

As examples of agonistic interactions in the fossil record, cranial injuries have been reported in dire wolf [3,4],

borophagine canids [5], musk oxen [6], *Mammuthus* and mastodons [3,7], rhinocerotids (*Iberotherium* [1] and *Amphicaenopus* [8]), *Coryphodon* [9], and entelodonts [10]. In extant *Hylobates*, healed fractures were present in 36% of one free-ranging population [11].

The extant hyenas (*Crocota*, *Parahyaena*, and *Hyaena*) exhibit specialized morphological and physiological features which make them highly efficient in utilizing all parts of animal remains. The most outstanding craniodental features of these hyenas are the highly robust, micro-structurally modified third premolars in the upper and lower jaws, which are used in bone cracking. In addition, all extant hyaenids maintain highly functional carnassial shearing teeth (upper fourth premolar and lower first molar) for cutting through hide and meat. These two sets of functionally differentiated teeth are critical in the hyena's ability to rapidly consume animal tissues [12].

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The extant spotted hyenas (*Crocuta crocuta*) are often considered mere scavengers; however, detailed research revealed that they are very efficient predators [12]. In contrast to other members of African large predator guild, spotted hyenas do not preferentially prey on a particular species. Food habits of fossil carnivorans are less well-known, but the Eurasian percrocotid *Dinocrocota gigantea* is among the most charismatic of fossil carnivorans. Many questions remain concerning its predatory behavior: was *Dinocrocota* an active and versatile predator like the spotted hyena, or was it more of a scavenger? A recent study on the cranial biomechanics of *D. gigantea* showed that the skull in the fossil taxon is as adapted to bone-cracking as the spotted hyena [13]. In this paper, the behaviour of the giant percrocotid *Dinocrocota* and aspects of its paleoecology are discussed in the context of a specific example of predatory interaction.

1 Material and description

The *Chilotherium* specimen (HMV 1452) is a complete cranium with associated mandible. The moderate wear on all teeth and small lower second incisors indicate that this skull belonged to an adult female individual of *Chilotherium wimani*. *Chilotherium* was well adapted to steppe environments, and were the dominant rhinocerotid in the late Mio-

cene. Its legs were shorter than those of any other aceratherine, mimicking in some ways those of the teleoceratines [14]. The manus, however, was already tridactyl. *Chilotherium* was a grass-eater in a group of grazing animals (although its diet certainly included a number of non-graminaceous herbs); the shortening of the legs in this genus can be explained on the basis of this grass-based diet. In common with aceratherines, *Chilotherium* was a hornless rhino with a pair of tusk-like lower incisors, which were probably used in intraspecific fighting. In contrast with that of today's grass-eating rhinos, the head of *Chilotherium* maintained a horizontal position, so grazing was possible only after the shortening of the legs to allow the head to dip at a shallow angle to the ground [15].

The upper margin of the right orbit of HMV 1452 is marked by a distinct imprint (length: 61.5 mm; width: 24.7 mm; depth: 8.8 mm), with clear loss of bony matter when compared to the left side (Figure 1). In this area, the bone has been quite deeply perforated and partially stripped-off. The curvature of the healed wound is relatively abrupt, indicating that a curved object was responsible for creating the imprint.

The wound on this rhino had been completely healed, and shows the same features with the healed bony wound of modern mammals. The imprint has a rough and granular healed surface with bony replacement of fibrocartilage.

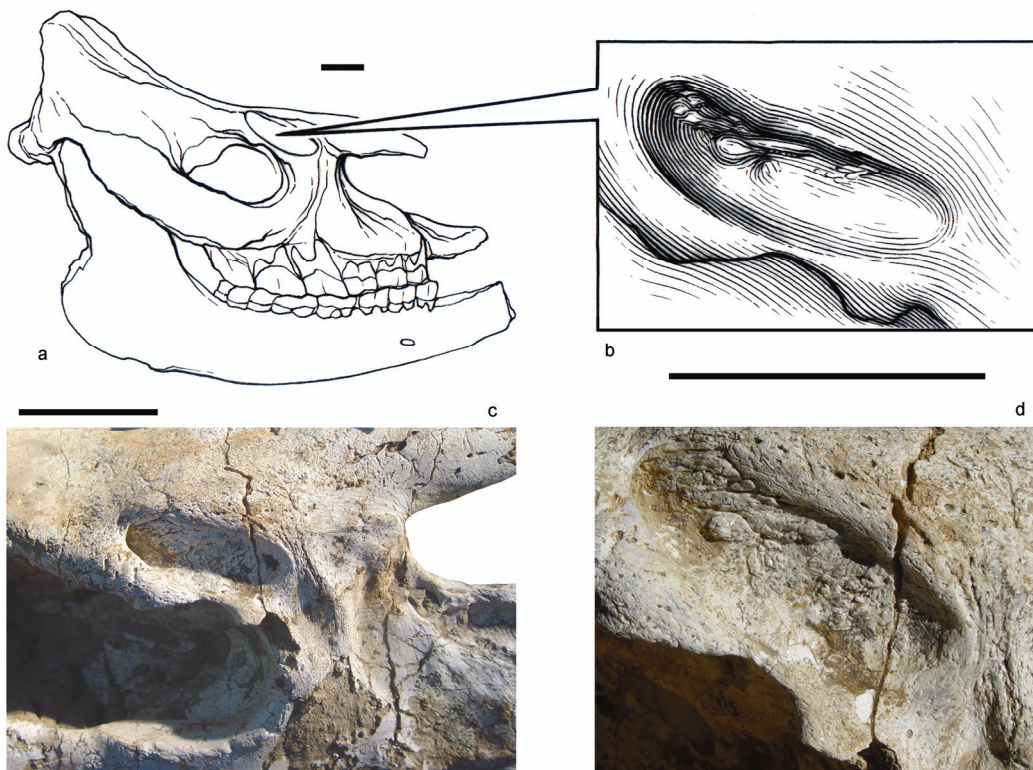


Figure 1 Cranium and mandible (HMV 1452) of *Chilotherium wimani*, showing the imprint on the upper margin of its right orbit. a, Drawing of the cranium and mandible; b, enlarged drawing of the imprint; c, orbital area to show the imprint's position; d, enlarged photo of the imprint made by the predator's right canine. Scale bars = 5 cm.

Thick undulating reactions have been shown to occur with healing rickets [16], and new bone formation at the border of the wound occurs. Both features are observed on HMV 1452. Furthermore, the healed site exhibits evidence of Haversian remodeling [17]. These features indicate that the wound was not immediately fatal to this individual. A similar case of a healed bite wound was observed on a skull of the cat-like predator *Nimravus bumpenis*, which had a wound in the frontal bone exactly fitting the outline of the upper canine of another saber-toothed nimravid, *Eusmilus dakotensis*. The canine of *E. dakotensis* entered the frontal sinus of *N. bumpenis*, but the wound eventually healed [18].

2 Comparison and discussion

Among the largest carnivorans in the contemporaneous fauna, *Dinocrocuta* is the only common taxon known from the Linxia Basin. Only one species ascribed to the genus has been recorded from the early late Miocene (Vallesian, MN 9-10) in this basin, i.e. *Dinocrocuta gigantea* [19,20]. We measured the size of the upper canines of the predator based on the corresponding trace (Figure 1), and found that the upper canines (length: 26.5 mm, width: 22.5 mm, height: 45.3 mm) of *Dinocrocuta gigantea* from Shuanggongbei (HMV 1279, 1280) fit almost perfectly into the bite site on the *Chilotherium* specimen. In particular, the 22.5 mm width measured for these canines is striking as they are rather compatible with the canine trace under study. This indicates that the injury may be caused by the large-sized *D. gigantea*. The straight leading edge of the caniniform lower incisors of *C. wimani* would not be able to create such curved wounds; furthermore, the contact surface between the incisor and bone is where the tooth is worn to the dentine, a soft material that cannot scratch bone. These considerations led us to discount the possibility of conspecific competition among *C. wimani* individuals as the cause of the wound. The morphological features and fractured orientation of the carved imprint on the rhino's skull indicate that the attack of *Dinocrocuta* was run from the front left of *Chilotherium*, and the imprint was caused by the right upper canine of the attacker. According to the measurement to the distance between canines of *Dinocrocuta* and the reconstruction to the thickness of muscles on the *Chilotherium* skull, the corresponding bite marks of the left upper canine and two lower canines of *Dinocrocuta* were situated on the facial muscles of *Chilotherium*, so there were no wounded imprints of these teeth on the skull or mandible of this rhino. More than one bite marks on bones of a prey are frequent when the prey is killed and eaten finally by a predator [1], but a single bite mark often appears when a prey escapes and survives [9,18]. Although hyenas have stabbing canines instead of slicing canines so that they can produce round bite marks, but the resist and struggle of a prey can make predator's canines glide to form oval bite marks. The

specimen shows that this *Chilotherium* individual was not fatal in the attack. As a result, it is reasonable to leave a long wounded imprint because of the resist and struggle of this rhino.

The saber-toothed cat, *Machairodus palanderi*, is the second largest carnivoran found in the *Hipparion* fauna of the Linxia Basin. *M. palanderi* was common in this basin, as several skulls have been collected. However, the carved imprint on the upper margin of the rhino's orbit is much wider than the width (15.0 mm) of the canine of *M. palanderi*. This measurement is obviously too narrow for the size of the orbit imprint and thus *Machairodus* could not have been the attacker. In addition, *M. palanderi* was much smaller than *Dinocrocuta* in body size. The estimated body size of *M. palanderi* is about 130 kg, similar to extant African lions. Furthermore, the long and slender upper canines (length: 43.5 mm, width: 15.0 mm, height: 114.8 mm) of *M. palanderi* could not have withstood unpredictable forces from a struggling or moving *Chilotherium*.

In the same lithological horizon at Shuanggongbei, the hyaenids *Hyaenictitherium wongii* and *H. hyaenoides* were both too small in body size to have been the attacker [21]. The former has an estimated body mass of 30 kg, and the latter 50 kg. Even though these taxa are more abundant as fossils from the fossil localities in the Linxia Basin than *D. gigantea*, their canines are too narrow to fit the size of the rhino's imprint.

Hyaenids in general were widespread across much of the Old World in Neogene and Quaternary times, and appeared to have been an important and diverse group of predators [22]. *Dinocrocuta* paralleled true hyaenids to a remarkable degree in both dental and cranial morphology. The cranium was very robust, with powerful zygomatic arches, a strongly domed forehead, and proportionally enormous cheek dentition [20]. *Dinocrocuta* belongs to the family Percrocutidae, which persisted into the early Vallesian from the middle Miocene. *Dinocrocuta* was larger than the middle Miocene *Percrocuta* and displayed more extreme dental adaptations to bone-cracking. *Dinocrocuta* is known from fragmentary remains in Europe [15], but from the late Miocene in China complete skulls have been found, especially from the Linxia Basin in northwestern China.

Dinocrocuta was one of the largest known fissiped carnivorans in the fossil record. Its body mass has been estimated at more than 380 kg in weight, assuming it had a hyaenid-like proportion. The robust *Dinocrocuta* dentition is unambiguously hyena-like, indicating excellent bone-cracking capability. Predation and/or scavenging on a rhinoceros might be expected for such a large carnivoran, as seems to be the case in the highly opportunistic spotted hyenas. Furthermore, the large body size by itself could have enabled *Dinocrocuta* to prey on relatively large mammals, including giraffoids, rhinocerotids and occasionally, proboscideans [23]. This interpretation follows logically from the observation that carnivorans weighing 21.5

kg or less feed mostly on prey that are 45% or less of their own body mass, whereas carnivorans above this threshold feed mostly on prey that are greater than their own mass, a result of simple energetic constraint [24].

The skull of *Dinocrocota gigantea* is exceptionally robust, and shows a series of characters different from contemporaneous hyaenid forms. The most remarkable among them are: the generally short and high proportion of the skull, the sharp doming of the skull roof, the thick and much widened nasal bones, and the exceptionally long meatus acusticus. In this regard, the features of the skull roof in *D. gigantea* resemble more of the borophagine canids *Epicyon* and *Borophagus* than its close relatives in the Hyaenidae. The huge size of *D. gigantea* may not be exclusive evidence for hunting large prey, however. Exceedingly large individuals might be constrained in their abilities to run and turn abruptly [25]; the large size of *Dinocrocota* may have allowed them to displace other predators from their kill, thereby feed via stealing prey [26].

Extant spotted hyenas mostly prefer prey within a body mass range of 56–182 kg, with a mean of 102 kg [27]. In the range of available prey sizes, they appear to take the medium-sized ungulates (wildebeest, zebra) more often than the larger (buffalo) or smaller ones (Thomson's gazelle). Even so, spotted hyenas occasionally take much larger species such as giraffe (*Giraffa camelopardalis*). On a number of occasions hyenas were even observed killing elephant [28] and hippo calves [29]. Hyenas have also been found to hunt black rhinos [30]. Among ungulate prey species such as wildebeest, adult females run the highest predation risk (and adult males the lowest) during calving time. This can be explained by the female's reduced mobility during the weeks immediately before and during birth. A female rhino accompanied by a calf was easily attacked by hyenas in one observed instance [12]. The modern Indian rhino (*Rhinoceros unicornis*) is usually solitary except for females with young. *Chilotherium* might have had the same habit, and the female *Chilotherium* might have had to protect her calf by herself. We speculate that the imprint on the skull of the female *Chilotherium* might have been incurred when the *Chilotherium* female was at her most vulnerable time, around the calving season.

A healthy adult *Chilotherium* would have been a formidable prey even for a large percrocotid. However, during a drought event an animal that was dying, in poor physical condition, or just seeking a watering hole is particularly vulnerable to ambush by predators [1]. Thus it is possible that a weak female *Chilotherium wimani* was attacked during a drought [31]. From the healed wound on HMV 1452, *D. gigantea*'s attack failed to kill the rhinoceros. On the other hand, the imprint on the rhinocerotid skull indicates that the large-sized *Dinocrocota* could and did attack rather large prey, in addition to being able to feed opportunistically by bone-cracking. There were no other contemporaneous carnivorans whose morphological adaptations sug-

gest equivalents of large predatory felids such as extant African lions. Therefore, during early late Miocene times and in the area studied, attacks on large herbivores would have been carried out mostly by the largest and most robust carnivoran at the time, *Dinocrocota gigantea*. Under most circumstances a healthy adult rhinoceros is not an easy prey; this leaves to question whether the attack on HMV 1452 and/or other individuals might have been carried out by multiple predator individuals. These possibilities need to be further assessed, and a study of the postcranial skeleton of *Dinocrocota gigantea* is currently underway to reveal the locomotory modes of this extinct species.

The preceding case does not prevent us from regarding *Dinocrocota gigantea* as the top predator of those times, at the top of the trophic pyramid and occupying an ecological niche that was taken later by large felids. Of course, this certainly does not contradict their capability for scavenging. The evidence of attack on large prey, in combination with the bone-cracking craniodental morphology and very large size, suggest that *Dinocrocota gigantea* was perhaps a highly versatile top predator unrivaled to a larger degree in the late Miocene of Linxia Basin than the spotted hyenas on the African savanna today.

3 Conclusions

A rhinocerotid cranium with associated mandible ascribed to *Chilotherium wimani* from the early late Miocene Liushu Formation from the Linxia Basin exhibits evidence of a large, healed wound on the dorsal cranium near the dorsal margin of the right orbit. We eliminated *Machairodus palanderi* as the attacker; exceedingly rare, *M. palanderi* was most likely not a serious competitor to *Dinocrocota gigantea*, the predator that is inferred as responsible.

The attack might have occurred to an individual in poor physical condition and/or under circumstances making it highly vulnerable to ambush (e.g. at a watering hole). The *Chilotherium* specimen under study shows bone healing and regrowth around the wound area, indicating that the injured individual survived for some time after this encounter. Along with previous functional interpretations, the osteological evidence presented here suggests that *Dinocrocota gigantea* may have been large and versatile carnivorans capable of attacking large prey but also fed opportunistically on carrion with their robust bone-cracking premolars.

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