Large Mammalian Carnivores as a Taphonomic Factor in the Bone Accumulation at Zhoukoudian

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Abstract

The entire fossil assemblage of *Homo erectus* excavated from Zhoukoudian Locality 1 has been studied from casts and available originals to assess taphonomic damage and determine the agent(s) of damage. Body part representation, the micromorphology of breakage, and the close similarity of Zhoukoudian *Homo erectus* damage to that documented in modern African hyaenid-modified bone assemblages lead us to conclude that the Pleistocene hyaenid, *Pachycrocuta brevirostris*, was responsible for most of the taphonomic bone modification. We reconstruct a pattern of hyaenid bone gnawing that accounts for the observed pattern of damage to the *Homo erectus* crania, including the lack of faces and enlarged foramina magna, previously postulated as evidence of cannibalism. *Homo erectus* postcrania reveal extensive evidence of puncture bite marks and fracturing in a pattern characteristic of modern hyaenid damage, and one specimen (Femur V) shows clear signs of stomach acid etching and regurgitation by hyaenids. Our findings suggest that *Homo erectus* remains were transported into the cave by hyaenids, and that Zhoukoudian was primarily a bone assemblage accumulated by hyaenid activity.

Key words: Zhoukoudian; *Homo erectus*; Hyaenidae; Taphonomy; Cannibalism; *Pachycrocuta brevirostris*

Since the mid-19th century, discovery of the physical remains and archaeological artifacts of early hominids (or hominins) has been of paramount interest to paleoanthropologists. But as paleoanthropology develops greater sophistication, it is increasingly clear that attention must be paid to the interpretative context of the fossil and archaeological documents of our evolutionary past. Without question, the cave site of Zhoukoudian is one of the most important anthropological sites for understanding the context of human evolution. It is widely accepted as evidence of the earliest controlled use of fire by humans, and with somewhat less support, has long been touted as proof of early human interpersonal violence and cannibalism. The cave's faunal and floral remains constitute some of anthropology's most significant data on *Homo erectus* diet. Moreover, due to extensive earth science investigations of the cave sediments, Zhoukoudian is one of the best dated and most well known paleoenvironmental contexts of *Homo erectus*. Based on this evidence, along with the documented presence there of over forty individuals—still the largest single near contemporaneous early hominid population in the fossil record —many scholars have argued for a *Homo erectus* "cave home." Our research informs many of these contextual aspects of *Homo erectus* at Zhoukoudian.

Despite the tragic loss of the original fossils during World War II, casts were made that are of significant scientific value. Yet, a prevailing sense of loss over the originals seems to have led paleoanthropologists to ignore important new discoveries of Zhoukoudian *Homo erectus* by Chinese excavators. This is especially true with respect to Skull V (PA 109), which is now housed in the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing. Our methodology involved a thorough re-assessment of the Zhoukoudian *Homo erectus* fossil remains and their taphonomic damage through both gross and microscopic examinations of the casts and remaining original fossils. We then compared our results with well-documented cases of human and non-human bone

modification, as well as damage caused by geological processes, in order to determine the primary causal factors in the Zhoukoudian hominid fossil assemblage.

1   Taphonomic History of the *Homo erectus* Fossil Remains

Table 1 and Figure 1 summarize body part representation of the *Homo erectus* assemblage from Locality 1 of Zhoukoudian [1-3]. The *Homo erectus* bone assemblage shows a preponderance of isolated teeth, skull parts, and mandibles, a low incidence of proximal limb elements, and a virtual absence of distal limb elements, hands or feet. This is the taphonomic signature of large carnivore-modified bone assemblages, insofar as it bears a close resemblance to Brain's [4] experimental results with leopard feedings of baboon carcasses, observations from modern African hyena dens[5-6], and analyses of fossil assemblages accumulated by hyaenids [7]. The large size of the skeletal elements and the nature of the damage necessarily precludes avian predator accumulation [8]. Furthermore, we did not observe unambiguous rodent gnaw marks on any of the hominid remains. The sediments in which the remains were found were not water-lain, and thus, the pattern of postcrania damage is inconsistent with sediment abrasion caused by stream or river transport.

Table 1. Zhoukoudian Locality 1 *Homo erectus* Skeletal Elements

Body Parts	Number of Elements
Calvaria & Cranial Fragments	13
Mandibles and Fragments	15
Teeth (Isolated and in bone)	157
Vertebral Column (Atlas)	1
Shoulder Girdle (Clavicle)	1
Humerus	3
Radius	0
Ulna	0
Carpus (Lunate)	1
Pelvic Girdle	2[1]
Femora and Femoral Fragments	7
Tibia (Fragment)	1
Fibula	0
Tarsus	0
TOTAL	201

[1]Although Weidenreich and later Chinese workers have not included in tabulations of hominids from Zhoukoudian these two unassociated iliac fragments, we believe that these iliac epiphyseal specimens were indeed hominid and include them here.

In comparison with modern African hyena-den mammalian faunal assemblages, the Zhoukoudian hominid assemblage shows a lower proportion of distal limb elements. This is to be expected given that the relatively smaller hominid body size in comparison with modern African herbivore prey species would result in relatively greater destruction of more heavily muscled primate forearm, leg and cheiridia. The body part representation of Zhoukoudian *Homo erectus* is

in accordance with frequencies expected in a skeletal assemblage of primates accumulated by large carnivores.

Upon examination of the extant curated fossil and cast inventories in China at Zhoukoudian and at the IVPP and at the American Museum of Natural History, we concluded that this pattern of body part representation is real; that is, it represents what was preserved in the cave sediments, rather than an artifact of collection or excavation bias. This conclusion is predicated on our analysis of published and unpublished records which reveal that all bone was excavated, along with individual teeth and unidentifiable bone fragments, down to 1 cm in length [1-2, 10].

Pei [10-11] was the first to suggest that Zhoukoudian may have been a hyena den rather than a human dwelling site. Zapfe [12] then followed suit, undertaking feeding experiments to support his contention that the Pleistocene cave hyena played a major role in bone modification and accumulation. Zapfe's arguments were later applied to the Zhoukoudian *Homo erectus* remains by Weidenreich [1-2] who, in turn, reevaluated his own position with respect to the presence of carnivore damage on at least some of the remains.
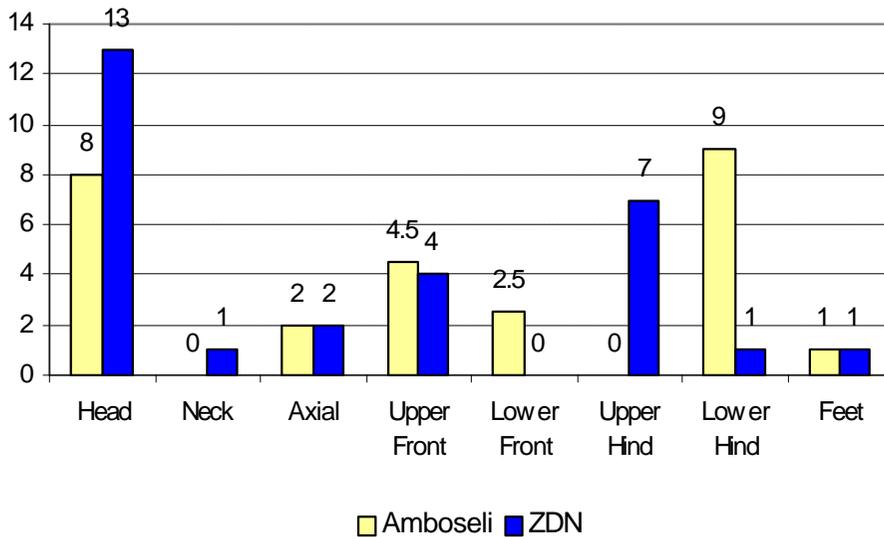

Figure 1   Comparison of ungulate body part percentages from a modern African spotted hyena den in Amboseli National Park, Kenya [9] with body part representation of Zhoukoudian *Homo erectus* Locality 1 assemblage. Mandibles and isolated teeth from Zhoukoudian are not associated with crania; they have not been corrected for minimum numbers of individuals, and thus are not included in "Head" category

2   Postcrania

The bones most obviously modified by hyaenid activity are the *Homo erectus* postcranial remains. Figure 2 shows Femurs III, VI and VII [2] with breakage characteristic of hyaenid bone fracturing. While Femur V, shown in Figure 3, displays similar breakage, it also reveals puncture bite marks and acid-etching, which indicates ingestion and regurgitation by a hyaenid. This femoral fragment therefore provides direct evidence of hyaenid consumption, and presumably predation or scavenging of *Homo erectus* by hyaenids at Zhoukoudian.
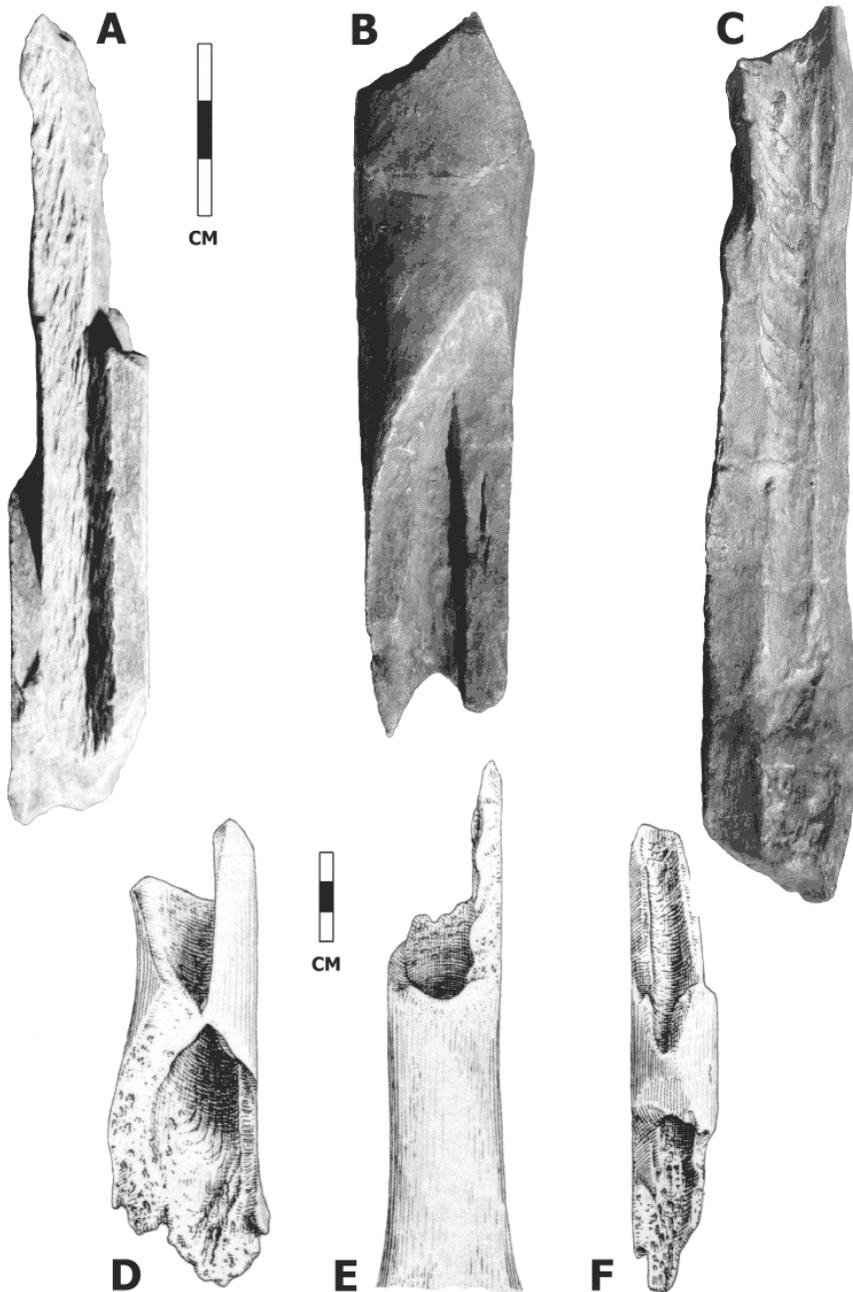
Figure 2   Views of Zhoukoudian *H. erectus* Femurs III, VI and Femur VII (A-C), compared to the pattern of breakage seen in *Bos* long bones (D-F) chewed by hyenas in Zapfe's feeding experiments [12] and figured by Weidenreich (p. 150, Plate XXXIV)[2]
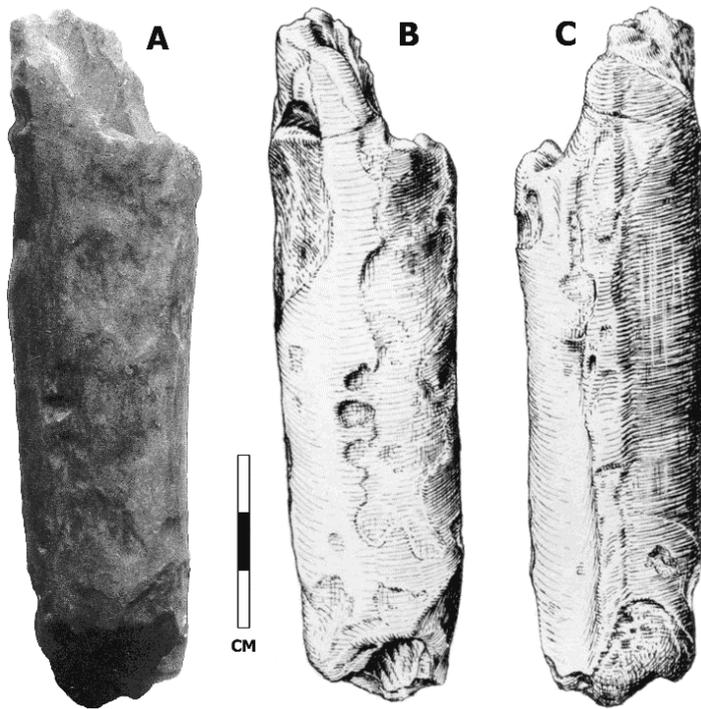
Figure 3   Zhoukoudian *H. erectus* Femur V, a specimen which shows the breakage pattern characteristic of hyenas and also evincing the rounded edges and pitting associated with ingestion, partial digestion, and regurgitation by a hyena. A, photograph of cast, anterior aspect; B, drawing, anterior aspect; C, drawing, posterior aspect. B and C from Weidenreich (p. 96, Plate VII) [2]

Weidenreich [2] considered the absence of the acromial end of the clavicle, and an associated indentation thought to be a bite mark, as evidence of large carnivore modification. We concur with Weidenreich, while also noting that the missing portion of the clavicle is that which attaches to the deltoid muscle, and is consistent with hyaenid predation. At the same time, Weidenreich [1-2] argued that the large, longitudinally fractured bones at Zhoukoudian were the result of hominid tool modification, since in his view, animals were not capable of splitting such robust bones. Yet, *Pachycrocuta brevirostris*, the largest hyaenid to have lived in the cave, was far greater in size and strength than either *Homo erectus* or modern African hyaenids. The ability of this very large Pleistocene carnivore to process human bone should not be underestimated, and we believe that fragmentary *Homo erectus* postcrania are consistent with hyaenid, rather than hominid, bone modification [13].

3   Crania

Paleoanthropologists have routinely dismissed Weidenreich's [1] statements that most of the skulls show evidence of peri-mortem damage, which he posited may have been caused by rock falls, pressure by enclosing cave sediments (e.g., Skulls X, XI, XII), intentional cutting and blunt-force trauma inflicted by other hominids, and/or gnawing by large carnivores. Indeed, Weidenreich [1] concluded that carnivore bites best explained the damage to several crania, including Skulls IV, V and VI. Nevertheless, in his now infamous words, Weidenreich [1] stated: "My verdict is that the destruction of the base and the blows on the top of the skull are the incidental work of man." Based on comparative data and a detailed reexamination of the evidence, we assert that this position is no longer tenable.
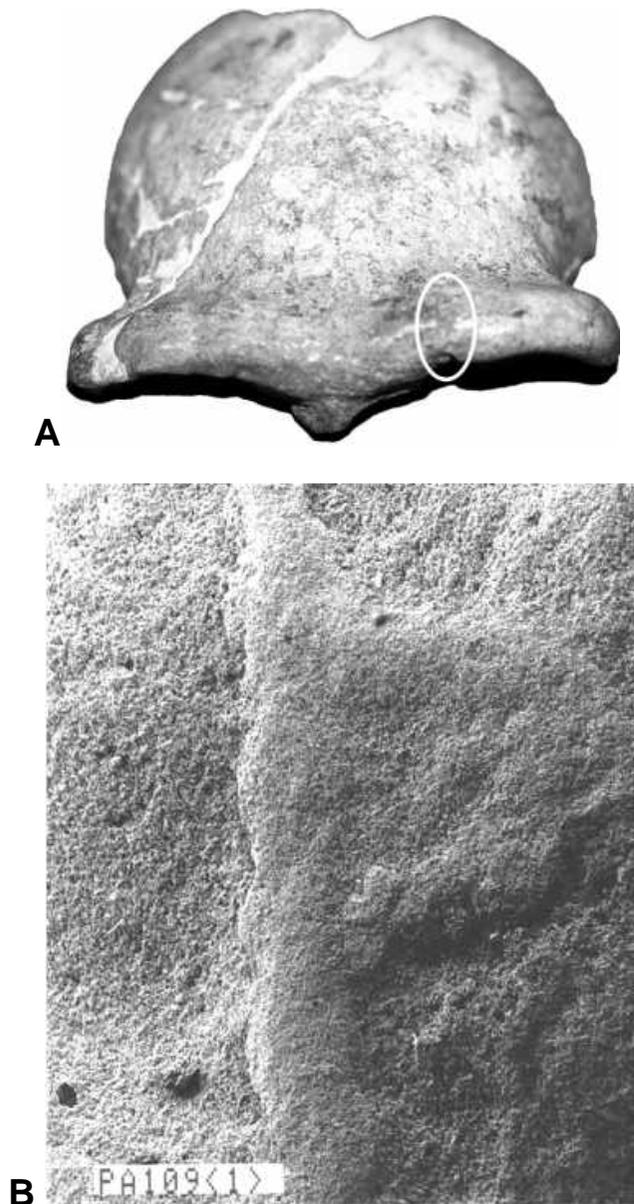
Figure 4   A, Oblique frontal view of *Homo erectus* frontoparietal (Skull V or PA 109) excavated at Zhoukoudian in 1966. Circle on left superior orbital rim indicates probable hyena bite mark. B, SEM photograph of area in circle shows magnified view (17X) of probable hyena bite mark on the original bone surface of Skull V

It is important to note, as did Weidenreich [1], that all *Homo erectus* crania found at Zhoukoudian are, to varying degrees, fragmentary. Of the more complete remains, Skulls IV and V were reconstructed from fragments found widely separated at the site. This disarticulation occurred prior to cave sediment burial and is accompanied by bite marks and breakage patterns characteristic of large carnivores [1].

There is also evidence that compression by cave sediments damaged some crania. The parietal of Skull XII was broken into more than fifty fragments, all of which Weidenreich found to be closely related. In our view, geological damage to the crania is not a major source of taphonomic bias that would account for the differential loss of cranial parts, since bones smashed *in situ* by enclosing breccia were all found in close association and reconstructed by Weidenreich. Given that isolated nasal bones of less than 1 cm in diameter were found some distance from the remainder of Skull XI, we believe that most or all of the cranial fragments were, in fact, collected and subsequently reconstructed [1]. However, the missing cranial base bones were never recovered.

An anterior view of Skull II shows a wide, U-shaped groove running across the left superior orbital rim, which Weidenreich (his Fig. 13) [1] figured, but did not label or discuss. Viewed in cross-section, this groove is identical to large carnivore bite marks we observed previously and have therefore identified as such on this specimen. A superior view of Skull II shows a long "artificial sulcus" which Weidenreich (his Fig. 15) [1] labeled as 'sa.' The groove is consistent with canine scoring on the surface of the parietal by a large carnivore, probably hyaenid, as it attempted to gain purchase on the skull with its teeth. The taphonomic damage to Skull II is comparable to that identified on bones recovered from modern African hyena bone assemblages [5-7], and from feeding experiments with large carnivores [4]. We therefore contend that damage to this skull is consistent with the feeding strategy of a large hyaenid at Zhoukoudian Locality 1.

Damage on Skull III, originally described by Black (his Plates XI-XVI) [14] shows long "striations" which he considered, along with Weidenreich (p.188) [1], to be carnivore bite marks.

With reference to Skull V, Weidenreich (p. 189) [1] suggested that an "artificial cut" ('a') on the superior vault was most likely caused by a carnivore bite. This specimen was lost in 1941. The actual fossil bone surface of an adjoining frontoparietal fragment of Skull V, discovered in 1966 and labeled as PA 109, reveals a clear longitudinal bite mark on the right parietal, located 2 cm anterior to the broken margin of the bone and 9 cm posterior to the supraorbital torus. A second bite mark is seen on the left supraorbital torus of Skull V, depicted by an SEM photograph of a peel taken from the original specimen (Figure 4). Not only is the cross-section of this damage U-shaped, unlike a cut-mark made by a stone tool, but the lack of chipping or flaking at the edge of the groove indicates that the bone was fresh when the damage occurred. Furthermore, the absence of surrounding damage, regularity of the groove, and lack of plastic bone deformation are not consistent with damage by enclosing sediments or geological pressure.

According to Weidenreich (p. 189) [1], the damage on Skull VI provides definitive evidence of carnivore gnawing. The skull, fragmented prior to burial into several pieces, shows what both Weidenreich (his Figs. 32 and 35, labeled 'sa' and 'rc') [1] and we consider carnivore bite marks on the margin of fragment II (a left parietal bone) and at the intersection of fragments II and III. In addition, damage to the inferoposterior margin of the frontal bone of this skull (fragment I) also shows a wide-grooved longitudinal depression figured by Weidenreich (his Fig. 34, labeled as 'da')[1] that we consider a likely carnivore bite mark.

In our view, the U-shaped parasagittal groove on Skull X is consistent with the raking anterior tooth mark of a large carnivore, probably a hyaenid.

Weidenreich (p. 186) [1] asserted that basicranial damage to Zhoukoudian *Homo erectus*, seen on Skulls II, II, V, X, XI and XII, is comparable to that identified on Neandertal crania and attributed to human agency. Although Breuil [15] had earlier posited the preponderance of skull parts at Zhoukoudian to be evidence of intentional internment of decapitated heads, this supposition was refuted by data from subsequent excavations [1].

4   Model of Hyaenid Damage of *Homo erectus* Crania

Based on the observable damage to *Homo erectus* crania from Zhoukoudian we propose a generalized sequence of hyaenid biting, chewing and skeletal manipulation. As illustrated in Figure5, the sequence involves the hyaenid's efforts to: (1) strip off the edible temporalis and masseter muscles from the head, damaging the zygomatic arches and mandibular rami in the process;

(2) crack the mandible near the symphysis (the "wish-bone effect") in order to reach the tongue; (3) crush the mandibular corpus and the facial skeleton overlying the maxillary sinus to obtain marrow, soft tissue and/or edible spongy bone; and (4) break open the skull vault, thereby exposing the brain —a lipid-rich organ highly prized by modern African hyenas [16].
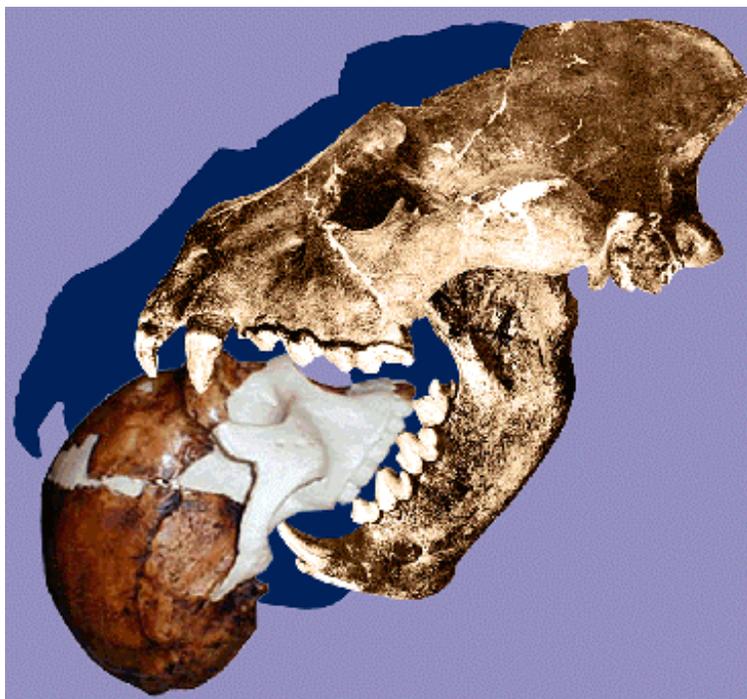

Figure 5   Generalized sequence of hyaenid biting, chewing, and manipulation of *Homo erectus* crania, postulated on the basis of the pattern of hyaenid modification observed. This model shows two steps or bites. Step 1 in the postulated sequence begins with the use of the jaws to grasp the head and crush the face. In order to gain access to the skull base, the supraorbital tori is used as a fulcrum for the upper anterior dentition. Step 2, as presented in shadow, involves using the now damaged basicranium as a fulcrum for lower anterior dentition in order to advance the upper dentition toward the front and sides of the cranial vault. At the conclusion of Step 2, the cranium is cracked open yielding the lipid-rich brain

Step 1 involves the use of the jaws to grasp the head and crush the splanchnocranium. Specifically, the skull base is accessed using the supraorbital tori as a fulcrum for upper anterior dentition. This is documented by the following: (1) observed bite marks on the supraorbitals of Skulls II and V; (2) the absence of facial bones, except fragments of attached nasals, in the Zhoukoudian crania sample; (3) destruction of all basicranium; and (4) comparative behavioral observations indicating that modern hyaenids have a predilection for first biting the face when scavenging the head.

In Step 2, the now damaged basicranium is employed as a fulcrum for the lower anterior dentition to advance the upper dentition toward the front and side of the cranial vault. This is documented by: (1) longitudinal bite marks located parasagittally on the frontal and parietal bones of several skulls; (2) bite marks on the temporal bones of Skull II; and (3) cracked and concave skull vault bones with puncture marks, observed most clearly on the *in situ* cast of Skull III made by Black in 1930.

This model of carnivorous *Homo erectus* skull scavenging is consistent with observations made of hyaenid gnawing sequences involving the skulls of non-human species [5-6, 13].

5   Summary and Conclusion

In a widely overlooked passage, Weidenreich (p. 184) [1] posed the following two questions:

"(1) Why, so far, have only broken crania or fragments of the bones (of *Homo erectus*) come to light in the Choukoutien deposit?" and "(2) Why has the material found been restricted mainly to cranial bones?" Although he noted that "crushing" might account for the damage on some crania, he also writes that: "Surprising, and calling for special explanation, is the incontestable fact that the *Sinanthropus* skulls were already defective and the isolated bones partly broken into small pieces before the earth came in and covered them" [1].   Our findings lead to a single answer: large carnivores, most likely the cave hyena *Pachycrocuta brevirostris,* was responsible for this type of Zhoukoudian hominid skeletal deformation (Figure 6). The dearth of articulated or semi-articulated skeletal remains of any mammalian fossils except *Pachycrocuta brevirostris*, suggests Zhoukoudian could not have been a natural trap for animals living at or near the cave (ie. autochthonous species). Although there is sedimentological evidence of flowing water —that is, sand and gravel in portions of the Zhoukoudian sequence t here is no taphonomic evidence for water transport and/or fossil sorting.

Figure 6   The lion-sized *Pachycrocuta brevirostris*, the largest hyaenid that ever lived, was a formidable predator. This final illustration objectifies this by comparing, at same scale, the prey species *Homo erectus* (left image) with the predator *Pachycrocuta* (right image – actual fossil skull superimposed over life-like reconstruction that is adapted from [23]). Direct fossil evidence, such as skeletons of complete individuals and thousands of isolated elements, and related fossil evidence, including numerous bite, crush, and puncture marks, as well as an abundance of coprolites, make it clear that *Pachycrocuta brevirostris* was an autochthonous member of the Zhoukoudian fossil assemblage. This hyaenid was very likely responsible for the accumulation of the *Homo erectus* fossils at Zhoukoudian

Our findings are consistent with observations made by Pei [10-11], Lin [17], Binford and Ho [18], Binford and Stone [19], and Dong [20], of fossil bone fragmentation and taphonomic damage by carnivores at Zhoukoudian. We therefore conclude that the *Homo erectus* remains probably represent the food refuse of large mammalian carnivores, especially *Pachycrocura brevirostris*.

With respect to Weidenreich's [1-2] scholarship, our main point of contention concerns the breakage of *Homo erectus* cranial bases. Whereas he considered this damage and the absence of bone fragments to be the result of cannibalistic activity, we find no evidence to support this contention. Rather, the skull damage is strikingly consistent with that of other mammalian fossils subjected to modification by hyaenids and other large carnivores. The facial skeleton and nasals are missing on most skulls, while the foramen magnum was enlarged in order for the predator to access the lipid-rich brain. Indeed, breakage patterns on the skull base match puncture, bite and gnaw marks on the more superior parts of the neurocranium which we believe were made as large carnivores endeavored to pry open the skull vault. In our view, the lack of basioccipital and basisphenoid fragments in the bone assemblage are most likely due to ingestion by hyaenids.

However, we should point out that we observed some rare bone damage in this collection that cannot be explained in terms of large carnivore modification. These specimens are still under investigation.

In sum, we examined all hominid fossil bones, either casts or originals, collected from Zhoukoudian, in order to identify and determine the cause of peri-mortem and pre-fossilization damage. Of the 49 non-dental hominid skeletal elements in this collection, virtually all show direct or indirect evidence of bite marks, gnawing, chewing, punctures and/or fragmentation by large carnivores. Our findings contrast rather sharply with those of Weidenreich (p. 453) [21], who wrote that, "transportation ..by beasts of prey is impossible. In the latter case traces of biting and gnawing ought to have been visible on the human bones, which is not the case." He subsequently adopted a more empirical and less rigid position [1-2]. Together with his observations and casts, and our analyses, we conclude that hyaenid bone modification is the most plausible explanation for taphonomic damage to the hominid skeletal assemblage at Zhoukoudian.

Given that the autochthonous member of the Zhoukoudian fauna was *Pachycrocuta brevirostris*, and direct evidence of hyaenid bone modification indicating that this species, rather than *Homo erectus*, accumulated the bulk of recovered faunal remains, our conclusions ultimately call into question the Zhoukoudian *Homo erectus* "cave home scenario." Extensive taphonomic analyses of the remaining, non-hominid Zhoukoudian faunal sample are still needed to verify this hypothesis. However, the cave home scenario has been challenged by Weiner, *et al*. [22], whose findings suggest that ash levels at Zhoukoudian are not indicative of human-made hearth remains. Although evidence of stone tools, cutmarks on bone and fire, even if ephemeral, all point toward the presence of *Homo erectus* in the cave, further research is needed to determine the nature and scope of that presence.

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