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Mapping and taphonomic analysis of the *Homo erectus* loci at Locality 1 Zhoukoudian, China

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Abstract

From a detailed analysis of published and unpublished sources, we constructed a digitized three-dimensional, stratigraphically-controlled excavation grid of Zhoukoudian Locality 1 in order to assess the spatial relationships of the excavated materials. All 15 fossil Homo erectus loci were mapped on the grid. Meter cubes were used in excavation starting in 1934, and Loci H through O, established between 1934 and 1937, were mapped to within 1 m³ vertical and horizontal provenience. Loci A through G, established between 1921 and 1933, were excavated in the northernmost part of Locality 1 by unmapped quarrying, but their stratigraphic levels were recorded. We could localize Loci A through G on the grid system by utilizing locations of remaining walls, stratigraphic sections, excavation reports, excavation maps, and photographs. Loci contained skeletal elements of Homo erectus individuals scattered over areas of the cave floor of up to 9 m in diameter. Scoring of taphonomic damage on the Homo erectus sample, as observed on casts and originals, demonstrates that 67% of the hominid sample shows bite marks or other modifications ascribed to large mammalian carnivores, particularly the large Pleistocene cave hyena, Pachycrocuta brevirostris. Virtually all of the remaining Homo erectus skeletal assemblage shows breakage consistent with this taphonomic pattern of fragmentation. Bioturbation by digging carnivores is the most likely explanation for a fragment of Homo erectus Skull XI discovered 1 m below its other conjoined portions in Locus L. Carbon on all the Homo erectus fossils from Locus G, a circumscribed area of 1-meter diameter, earlier taken to indicate burning, cooking, and cannibalism, is here interpreted as detrital carbon deposited under water, perhaps the result of hyaenid caching behavior. Locus G records the close stratigraphic and horizontal association of stone artifacts with Homo erectus and other vertebrate skeletal elements, an association that is seen at other loci as well. Layer 4 of the excavation contains equid cranial bone previously interpreted to have been burned while fresh. We here document that Locus B Homo erectus, including Skull I, is stratigraphically associated with this evidence, but at some 10-12 m distance. Even though the presence of wood-stoked fires and hearths is not supported by geochemical results, evidence of fire at Locality 1 in the form of burned bone is confirmed. Contextual relationships of fossil skeletal elements, relationships of carnivore damage and stone tool cutmarks on bone, and evidence of the burning of fresh bone associated with Homo erectus and stone tools support a model of transient

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hominid scavenging aided by the use of fire at the large hyenid den that became Zhoukoudian Locality 1. Although the original excavation catalogue from Locality 1, as well as a significant number of fossils and stone artifacts, were lost during World War II, catalogue numbers on the many surviving specimens can be used to locate fossils and artifacts within the three-dimensional grid provided in this paper.

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Introduction

The fossiliferous potential of the Zhoukoudian area, northern China, was first investigated by geologist J. Gunnar Andersson in 1919 (Andersson, 1919) at the site of Chi Ku Shan ("Chicken Bone Hill" in Chinese and now termed Zhoukoudian Locality 6). It was later studied by Zhongjian Yang (C.C. Young) and hypothesized by him to have been an infilled deposit preserving a middle Pleistocene canid lair (Young, 1930:18). The main cave infilling near the village of Zhoukoudian (translating as "shop on the Zhoukou"), some 5 km to the northwest and rising some 50 m above the Zhoukou (also Baerhe) River, is a hill of Ordovician limestone (Fig. 1). The hill itself is referred to as "Longgushan" or "Dragon Bone Hill" in Chinese. It was discovered by J. Gunnar Andersson, Otto Zdansky, and Walter Granger in 1921 following a tip from a local villager (Andersson, 1922). Zdansky undertook unmapped paleontological quarrying at Locality 1 in 1921 and 1923. He recovered three isolated hominid teeth during these years, although two were not announced as such until 1926 (Black, 1926; Zdansky, 1927; Weidenreich, 1937) and the third was not recognized and published until 1952 (Zdansky, 1952). All three specimens are housed in the Paleontological Institute of the University of Uppsala, Sweden. A Homo erectus premolar discovered during quarrying at Locality 1 by a team directed by Birger Bohlin in 1927 (Bohlin, 1980) served as the type specimen for the nomen Sinanthropus pekinensis (Black, 1927). From 1928 to 1937-excavation at Locality 1 continued yearly, under the field direction of Zhongjian Yang in the early years, and Wengzhong Pei (W.C. Pei) and Lanpo Jia (L.P. Chia) in the later years. Homo erectus Skull I and a number of mandibular and dental remains were discovered in 1928, and Skulls II and III were discovered in 1929 (Pei, 1930; Black, 1931a; Black et al., 1933). The recovery of the well-preserved Skull III by Pei was a turning point in the investigation of the site and helped to ensure continued funding (Cormack, 2000). Hominid discoveries were made each field season through 1937, but the excavation of Skulls X, XI, and XII during 11 days in November 1936 by Lanpo Jia was particularly noteworthy (Jia, 1999). All fieldwork was suspended at Zhoukoudian from July 1937, until August 1949 when excavation directed by Jia was re-initiated (Jia, 1980: 24–25). All original hominid fossils recovered between 1927 and 1937, many other vertebrate fossils, many stone artifacts, and most written records from Zhoukoudian disappeared during the war years (Lin, 1994: 55-59; Li and Yue, 2000; Qian and Li, 2000; Boaz and Ciochon, 2004). Cranial (portions of Skull V), mandibular (Adult Mandible IX), dental, and postcranial remains tentatively attributable to seven additional individuals were recovered from the site and from laboratory analysis of previously excavated sediments between 1949 and 1981 (Woo and Chia, 1954; Wu and Dong, 1985; Wu and Poirier, 1995: 60-67; Qian and Li, 2000: 24-25). These specimens are housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing.

Geological and dating studies have extended the time frame for the deposit and now bracket the age of the hominids at Locality 1 to between 400– 500,000 yrs BP for the stratigraphically uppermost *Homo erectus* (Skull V, Locus H) and 600–800,000 yrs BP for the lower loci (Shen and Jin, 1991; Grün, et al., 1997; Qian and Li, 2000; Zhou, et al., 2000; Shen et al., 2001). Stratigraphic levels of the



Fig. 1. (A) Dragon Bone Hill ("Longgushan") is located 50 kilometers southwest of Beijing, near the town of Zhoukoudian. (B) The location of ancient dragon bone quarrying was on the eastern slope of Dragon Bone Hill, but when the site was discovered by science (and renamed "Locality 1"), excavation began on the northern slope of the hill. (C) A plan view of Locality 1 with a history of the excavations. The first excavation by Otto Zdansky was in 1921 above what was later named the "Lower Cave" and at the entrance to the site used by modern-day visitors. The last excavations of dragon bone quarriers. (A) and (B) are modified after Andersson (1943): 21); (C) is modified after Goldberg et al. (2001): 485).

Zhoukoudian hominid finds and geological history of Zhoukoudian Locality 1 have been well documented (Li, 1927; Xie et al., 1985; Xu et al., 1997; Goldberg et al., 2001), but the horizontal provenience of fossils and hominid "loci" within the site have been problematic. A sequence of formation of the cave was presented by Ren (1985; see also Lin, 1994: 22-23), extended by Liu (1985), and related to Pleistocene climatic cycles (Liu, 1985; Xu et al., 1997; Zhou et al., 2000). From facies changes in the sediment, Goldberg et al. (2001) deduced that the cave opened to the south during the deposition of Layers 8/9 and to the north during Layer 7. These authors also noted that angular boulders in Layer 6 indicate that roof collapse of the cave occurred at this time, that deposition in Layer 4 was primarily loessal, and that Layer 3 travertine was laid down by a spring or springs. Despite continuing interest in the depositional history of the site (Binford and Ho, 1985; Binford and Stone, 1986; Dong, 1996), significant questions still surround the contexts and taphonomy of the hominid fossils from Zhoukoudian.

Methods

Our study, begun in 1999 and conducted in China at Zhoukoudian, the Zhoukoudian Museum, the IVPP, Beijing, and in New York at the American Museum of Natural History (AMNH), has centered on ascertaining contextual data of the hominid assemblage from Zhoukoudian in order to place specimens within a threedimensional grid of the site. We undertook an exhaustive literature search and examined all relevant excavation documents preserved in Beijing and elsewhere, as well as published records. We digitized each excavation plan view, stratigraphic profile, and Homo erectus locus from Locality 1, and placed them in a three-dimensional grid using AutoCAD[®] software. This software allows different perspectives of the excavated site to be generated.

We examined all original hominid fossils preserved at IVPP, and all first generation casts at IVPP, the Zhoukoudian Museum, and at the AMNH in order to determine and score taphonomic damage to Homo erectus remains. Specimens were examined by naked eye and under $10 \times$ magnification. Geltrate or Silastic peels were made on selected originals and casts to examine surface damage by binocular microscope and scanning electron microscope in the laboratory following the methods of Bromage (1984). Specimens were photographed at 1:1 and 2:1 in ambient light and raking light to highlight surface detail and damage. We studied taphonomic damage on a sample of approximately 100 mammalian fossil remains from Zhoukoudian Locality 1 preserved in IVPP for comparison with the hominid cast and fossil sample. Taphonomic damage on bones was scored using categories provided in the Table 1 caption and is consistent with definitions in Lyman (1994) and with references cited in the text.

Plans and a three-dimensional plot of the Zhoukoudian excavation

The vertical and horizontal relationships of the fossils, stone artifacts, and other features of Zhoukoudian Locality 1 have been difficult to appreciate in the absence of a three-dimensionally controlled plot of the excavation. The originals of all records from the excavations were lost or destroyed during World War II, but Jia's (n.d.) transcribed records are available in the IVPP in Beijing in a document entitled "Plans and Sections of Different Levels of Loc. 1 of Choukoutien by L.P. Chia [Lanpo Jia], Vol. 1 (1934-37.)." These data provide plan views of the 1×1 m squares excavated at successive 1-meter levels, a nonexhaustive list of specimen numbers excavated from each level, and stratigraphic sections through the site at nine different planes.

Jia and Huang (1990: 86) state that the excavators removed 2-meter-square blocks of sediment at a time and that this "was twice the size originally conceived, due to the stony earth structure." Photographs of the excavations in progress show the 2×2 m excavation units, but also document that horizontal and vertical gridlines painted on the excavation walls and floor were in 1-meter units. Jia's (n.d.) maps have a scale of 2 m for the horizontal grid, but this is clearly erroneous, a

confusion between the units of measure and the size of sedimentary blocks excavated. We deduce that this error occurred during Jia's surreptitious transcription of the maps in the Cenozoic Research Laboratory at Peking Union Medical College in Beijing under Japanese occupation between 1937 and 1941 (see Boaz and Ciochon, 2004).

"Levels," the depth-controlled excavation units of 1 m, were distinguished from "layers," one of the 17 established stratigraphic units in the deposit (Xie et al., 1985). Stratigraphic levels were mapped and recorded as they were excavated. Jia (n.d.) recorded four stratigraphic sections along north– south rows through the site and five sections along east–west rows. Xie et al. (1985) provided a detailed stratigraphic profile of the western wall of the excavation and Weiner et al. (2000) recorded a photographic mosaic of this same section.

Hominid discoveries and other points of discovery considered important during excavation were mapped on Jia's (n.d.) maps. All hominid specimens recognized as such in the field were individually plotted, but in general individual fossils and artifacts were not mapped by the original excavators. Most numbered specimens were listed by level. For example, on Jia's (n.d.) map of Level 2 only "layer of Celtis seeds" and "upper travertine" are mapped, but specimens numbered "34:64" through "34:87" are listed and therefore can be deduced to have derived from this stratigraphic level and from somewhere within this excavated area. Meter-square numbers were labelled directly on specimens as part of their catalogue numbers. Fossil specimens and stone artifacts from Locality 1 in the IVPP collections still retain their original catalogue numbers, and thus their stratigraphic and horizontal provenience to within 1 m³ can be determined even without the original excavation catalogue, presumably now lost. All hominid specimens recognized during excavation can be pinpointed on the horizontal grid, and localized to within a 1 m vertical level of the site. More fragmentary hominid specimens, which were not recognized during excavation, but were identified during laboratory analysis, can be localized only to the excavated area of a locus, and localized to within a 1 m vertical level of the site.

Catalogue numbers in their full form were written in the format: "Loc.Lev.Yr:#.(Ph).Sq", where Loc=Locus, Lev=Level (sometimes also with Layer noted), Yr=year of recovery, #=catalogue number, Ph=reference photograph, if provided, and Sq=meter square. Hominid fossils were also referred to by a numerical listing by body part: Skulls I through XIII, Adult Mandibles I through IX, Juvenile Mandibles I through VI, Femora I through VII, and Humeri I through III. A shorter "general catalogue" numbering in the form of "PA" (for "Palaeo-Anthropology") numbers was also employed. For example, Skull VII is listed by Weidenreich (1943: 5) as "Locus I, Level 22, 36:81, B -4" and also as "PA 326." The longer designation for this specimen translates to "specimen number 81 from the 1936 field season, discovered at Level 22 [22 m below datum, elsewhere recorded as within Layer 8/9 in Square (B - 4) in Hominid Locus I ['eye']." In addition to these terms of reference, hominid skulls were also referred to as a numbered skull within a locus. For example, Skull VII could also be termed Skull II, Locus I. Table 1 lists all specimen data and associated catalogue numbers for the Locality 1 hominids. Reference photograph numbers, when they are included in a specimen catalogue number, are useful in establishing excavation context. Reference photographs have been widely published (e.g., Jia and Huang, 1990; Jia, 1999) and are conserved at IVPP in Beijing and AMNH in New York. Reference numbers are to be found near the centers of photographs.

In order to map all hominid fossils from Zhoukoudian Locality 1, we digitized all of Jia's (n.d.) maps and stratigraphic sections. The stratigraphic section on the western wall of the site (Xie et al., 1985) was also digitized. We plotted the data onto a three-dimensional grid in AutoCAD[®]. Data were rotated and exported to Adobe Illustrator[®] to produce final three-dimensional plots of the hominid loci (Fig. 2 and Fig. 3). Both figures are views of the site from the northeast. Fig. 2 plots the stratigraphic profile along the east–west section between rows -3 and -4 (Jia, n.d.), intersecting with the western wall profile (Xie et al., 1985). Loci A, B, C, D, E, F, G, and H are plotted on Fig. 2. Fig. 3 plots the east–west Table 1

No. Locus Individual Part identification Layer Square Level Year Sex Age No. of body parts 1 А 1 RI₂, LI₁, LP₃, LP₄, LM₁, RM^{1a} 5 1921-27/52 F 7 - 81 2 2 Adult Mandible I+RM² 5 1927-28 F Adult 2 А 3 А 3 $M_1 + M_3$ 5 1928 Μ Adult 1 4 В Juvenile Mandible I+7 teeth 1928/35 F 8-9 1 4 1 5 В 2 Skull I, Adult Mandible II, 4 1928/35 Adult Μ 4 Humerus I, Lunate 6 В 3 Juvenile Mandible II 4 1928/35 Μ 8–9 1 Juvenile Mandible III+M₂ 7 В 4 4 1928/35 F 5-6 1 _ 8 В 5 Juvenile Mandible IV 4 1928/35 Μ 11 1 _ 9 С 1 Juvenile Mandible V+LC⁻, P⁻, 8/9 1929 F 8-9 2 _ RP_4 , RM_2 10 С 2 LC^{-}, LM^{1} 8/9 1929 2 Μ Adult 11 С 3 LM₁, RI₂, RM₁, Femur I 8/9 1929/38? Μ 9-10 1 _ 12 С 4 8/9 1929 F Adult C _ 1 D F 13 1 Skull II+6 teeth 10 1929 Adult 1 14 D 2 LI¹, LM¹, LM², RC, RM₂ 10 1929 М Adult 2 E 15 1 Skull III 10 1929 Μ Juvenile _ 1 16 F 1 Juvenile Mandible VIb 10 1930 Μ Juvenile 1 _ 17 F 2 LI^2 , LP^4 , LM^3 , RM_2 10 1930 F 5 2 F 3 LP³, RP⁴, RM³ 10 F Adult 18 1930 1 F LI^1 , RI^2 , RC^- , RP^3 19 4 10 13 - 14_ _ 1930 M 1 20 G 1 Adult Mandible III 7 1931 Μ Adult 1 _ 21 G 2 Skull IV, Clavicle 7 Juv 2 _ 1931 Μ 22 H 1 Adult Mandible IV+ RP₃ 3 A, 7 _ 1934 F Old 1 23 2 3 1934 F Η RP₃ A, 7 _ Adult 1 Skull V+RM3 3 3 1934-36/1966 Old 24 H A, 7 _ Μ 1 Adult Mandible V^c 25 Η 4 3 F Old A, 7 1934/35 1 26 I 1 Skull VI, 4 teeth, atlas^d 8/9 F, 3; L, 2; K, 22 1936 F Adult 2 -2; M, -1;M, -3 27 I 2 Skull VII 8/9 B, -422 1936 Μ Juvenile 1 B, -328 J 1 Skull VIII 8/9 23 1936 Juvenile 1 F 29 J 2 Femur II 8/9 B. -323 1936/38 F Adult 1 30 J 3 Femur III, Humerus II 8/9 B, -323 1936/38 Μ Adult 2 31 J 4 Skull IX 8/9 L, -3 23 1936 6 M 1 32 Κ 1 Adult Mandible VI 8/9 I, O Adult 24 1936 Μ 1 33 Κ 2 RI₂ 8/9 I, O 24 1936 F 7-8 L_1 1 8/9 J_{-3} 25 Adult 34 Skull X+8 upper teeth 1936 Μ 1 L_1 35 2 Skull XI+13 upper teeth 8/9 $J_{.} - 3$ 25 1936 Μ Adult 1 L_2 36 3 Skull XII 8/9 I, 2 25 1936 Μ Adult 1 L_2 37 4 1 upper+3 lower teeth 8/9 I, 2 25 1936 Μ Juvenile 2 Adult Mandible VII+Femur VI F, -1 38 Μ 1 8/9 26 1937/38 Μ Adult 2 F. -1 39 Μ 2 Adult Mandible VIII 8/9 26 1937 F Adult 1 40 Μ 3 Femur VII 8/9 F, -1 Adult 26 1937/38 Μ 1 F, -1 41 Μ 4 Femur IV+V 8/9 26 1937/38 Adult 2 M E, -2 42 Ν 1 Ldp_4+LM^1 8/9 27 1937 F 4–5 2 H, -4 43 0 1 Skull XIII+6 upper teeth 10 29 1937 **M**? Adult 1 44 2 H, -4 1937 0 LM_1 10 29 Adult 1 LI¹, LM₁, LM₂ 45 8/9? 1949 Adult 2 RP³ 8/9? 46 1951 Adult 1

Listing of hominid specimens from Zhoukoudian Locality 1, grouped by individual number, stratigraphic layers, and loci (see end of table for further discussion)

47	Humerus III	8/9?			1937?/1951		Adult	1
48	Tibia	8/9?			1937?/1951		Adult	1
49	RP^4	8/9?			1951		Adult	1
50	Adult Mandible IX with LM ₁	10	R, -1	27	1959	F	Adult	1
51	RP ₃	3			1966		Adult	1
Total								66

Number of body parts is deduced from the fragments present, for example, if lower and upper teeth are present, two body parts (cranium and mandible) are calculated. Attribution of individuals and identifications of age and sex follow Weidenreich (1935, 1937), and Weidenreich (1943) and Wu and Poirier (1995), except where indicated. Stratigraphic information follows Xie et al. (1985) and Jia (1980). Stratigraphic layers are known for all specimens. Horizontal (1×1 m) provenience does not exist for the quarried specimens prior to 1934, although inferred locations are plotted in Fig. 2 and Fig. 3. Loci H through O have been mapped in Figs. 4–11.

^aWeidenreich mistakenly lists an additional isolated tooth, a nonexistent LI², to A1.

^bWeidenreich (1935: 445) notes that the Locus F juvenile mandible "perhaps belongs to E1," i.e., Skull III, but here we follow his attribution of Skull III and Juvenile Mandible VI to two different individuals.

^cWeidenreich (1935: 446) suggests the possibility that Adult Mandible V (Individual H4) "perhaps belongs together" with Skull V, which he designated as Individual H3. We retain his determination of two separate individuals here.

^dThe Locus I atlas is associated with Skull VI spatially, stratigraphically, and morphologically, and is thus considered here a part of the II ("eye-one") individual, not a separate I3 individual.

stratigraphic section between rows 0 and -1, intersecting with the north–south section between rows F and G (Jia, n.d.). Loci H, I, J, K, L, M, N, and O are plotted on Fig. 3. Important parts of the site and individual loci are described below.

The opening and shaft of the original "dragon bone" cave are mapped in Fig. 2. Digging for fossilized vertebrate bones and teeth, used in traditional Chinese medicine, had been undertaken for many years, perhaps centuries, at Dragon Bone Hill. This cave is located on the eastward slope of Locality 1, facing the town of Zhoukoudian, and is known as the "gezitang" (also spelled "kô-tzetang" and "kotzetang", and colloquially termed "Pigeon Hall (or Hole) Cave" (see Fig. 1C). The gezitang is dug into Layer 7 and the upper part of Layer 8/9 and must have yielded innumerable fossils. At its western terminus it is closely associated with Locus G and Quartz Horizon 2 discovered in 1931 (Jia and Huang, 1990: 72). Below the eastern opening of the gezitang, in Layer 10, Adult Mandible IX was discovered in 1966 (Lin, 1994: 14).

Scientific quarrying for fossils at Zhoukoudian was undertaken in 1921 and in 1923 by Otto Zdansky and crew at the north-facing slope of the outcrop at a high stratigraphic horizon in the cave deposit known as Layer 5. Paleontologist Birger Bohlin and crew re-initiated quarrying in 1927 and 1928 at the same place and stratigraphic level as Zdansky's earlier work. These sediments were profiled but not mapped during quarrying. Their relatively limited extent, compared to the later excavations, allow their approximate positioning within the metered grid established for the site in 1935 (Jia, 1999: 95). Locus A is plotted in Fig. 2 with the aid of Jia's (n.d.) stratigraphic section at -3/-4 (made in 1934) that shows the walls of earlier quarrying. Vertical control is provided by the measured stratigraphic section of the western wall at Layer 5. It was from this deposit, later termed "Locus A," that the original individual teeth of Zhoukoudian Homo erectus, including the type specimen of Sinanthropus pekinensis Black 1927, were recovered. In all, 10 hominid fossils assigned to three individuals were recovered from Locus A (Table 1). Black et al. (1933: 20) described Locus A in the following passage:

The original worn upper M3 [type specimen, Individual A2, an adult and probably an M²] recovered by Dr. Zdansky came from a level now known as Layer 5 (i.e. at the base of Cultural sub-zone Ac). It was from this level that the lower M1 [Individual A1, a juvenile] was obtained by Dr. Bohlin in 1927, and from which subsequently in 1928 the fragment of the right side of an adult lower jaw was obtained ["Adult Mandible I," Individual A2, to which



Fig. 2. Three dimensional map of Locality 1 at Zhoukoudian, showing Loci A through H. The stratigraphic profile on the western wall of the site is plotted with the horizontal (X and Y) coordinates (1-meter-squares) and the vertical (Z) coordinates (1-meter-levels) as mapped by Xie et al. (1985). Loci A through G were mapped by matching their excavation walls seen in the -3/-4 section (drawn in 1934; see Jia, n.d.) with their recorded stratigraphic layers extended eastward from the western wall, as discussed in the text. The western wall is oriented north-south (a 5°–185° axis). Stratigraphic layers (and levels after 1934) of each locus and the contained hominid individuals are given in Table 1.



Fig. 3. Three dimensional map of Locality 1 at Zhoukoudian, showing Loci H through O. These loci were established between 1934 and 1937 and were mapped by Jia (n.d.). The western wall section is plotted, as are a north–south stratigraphic section along row F/G and an east–west section along row 0/-1.

the original molar was also assigned]. This region of Layer 5 above the Lower Fissure has accordingly been distinguished from the outset as *Sinanthropus* Locus A.

Pei and Zhang (1985: 260) note that Locus A was in a 2-meter-thick "thin breccia layer of black matrix, resting on the stalagmitic crust formed on the top of Layer 6."

Locus B was established in 1928 at the eastern end of Locus A and at one stratigraphic unit higher, Layer 4. Black (1929: 15) reported that "a new aggregation of Sinanthropus material has been discovered at the north-eastern corner of the main deposit and at a level some ten meters above the stratum in which occurred the type lower molar." Locus B is plotted on Fig. 2 accordingly. Black et al. (1933: 20) described it as "a small pocket rich in Sinanthropus remains." From this locus, the remains of five individuals were recovered, including the first hominid postcranial remains, a partial humerus and lunate from Individual B2, associated with Skull I. Locus B also yielded Juvenile Mandibles I through IV and Adult Mandible II (Table 1). Locus B is stratigraphically associated with burned bone (see below).

Beginning in 1928, Bohlin's crew began excavating directly down into the sediments below Loci A and B. This deposit is known as the "Lower Fissure" and contains Loci C through F. Locus C was established when Pei discovered an in situ hominid upper canine (part of Individual C1) at Layer 8 (now regarded as one stratigraphic unit termed 8/9). Locus D was established in 1929 at Layer 10 (originally designated as Layer 9 by Black et al. [1933: 21]) and yielded Skull II along with dental remains. Locus E is at the same stratigraphic level as Locus D, but is in a lateral extension to the east of the Lower Fissure known as the "Lower Cave" (Fig. 1C, Fig. 2). It was here that Pei and crew discovered the first relatively complete cranium of Homo erectus, Skull III, at the end of the 1929 excavation season (Pei, 1930). Locus F was discovered in 1930 at the same stratigraphic level east of Locus E and yielded a mandible (Juvenile Mandible VI, Individual F1) and teeth ascribed to a young juvenile and two adults (Individuals F2, F3, and F4).

Locus G was established during excavation of Layer 7 in the gezitang in 1931. This important locus was the first mapped association of hominid fossil remains with abundant stone artifacts ("Quartz Horizon 2"), as well as with presumed evidence of fire. Its location was mapped on Fig. 2 by reference to Fig. 7 of Pei and Zhang (1985: 20), where we could match areas of excavation by year, and then interpolation between the area of excavation in 1930 and the mapped area of the gezitang opening by Jia (n.d.). Black et al. (1933: 22) describe Locus G:

In July 1931 while excavating Quartz Horizon 2 in the Kotzetang (Cultural Zone C) Mr. Pei discovered three fragments of an adult Sinanthropus skull [Skull IV, Individual G2], together with two adult jaw fragments (GI, including the complete right lower dental arcade; GII including the whole left posterior jaw region) [both constituting Adult Mandible III, Individual G1]. All the specimens occurred within an area less than one meter in diameter, associated with crude stone artifacts and imbedded in a black charcoal-laden [sic] stratum. Subsequently, from the same horizon but somewhat further removed, there was recovered the greater part of the shaft of a stoutly built left clavicle [assigned to Individual G2]. The region from which all these specimens have been recovered was designated Sinanthropus Locus G.

In the 1932 and 1933 field seasons, "trenching" of the sediments near the eastern wall of the excavation and controlled removal of gridded blocks of sediment of Locality 1 were carried out. Most of the excavation effort was directed toward the Upper Cave (Fig. 1C) and recovery of the *Homo sapiens* remains from this much later time horizon (Jia and Huang, 1990: 81–91). No *Homo erectus* fossils were recovered in these years from Locality 1.

The Zhoukoudian site was excavated in the years 1934 to 1937 using a grid with 1-meter-cubes (Jia and Huang, 1990: 86). The horizontal squares were denominated east-west in alphabetical order from A, starting at the western wall of Locality 1 and extending 18 m to end at square R at the eastern-facing opening of the gezitang (Fig. 2 and



Fig. 4. Map of Locus H in Level 1, Layer 3, the site of discovery of *Homo erectus* Skull V (PA 109). Data for this and Fig. 5 through 12 are from maps recorded by Jia (n.d.). In this and later figures, a line pointing to a square indicates generalized provenience within the square; a dot at the end of a line in a square indicates a point provenience as mapped by Jia (n.d.).

Fig. 3). North-south squares were designated beginning with 1 at the northernmost remnant of sediment of Level 1, where excavation commenced in 1934 (square H1) (Jia and Huang, 1990: 87). The grid was extended 4 m to the south, to row 5, and 6 m to the north (from row 0 to -6) to incorporate later excavations as well as prior excavated sediments. Shen et al. (2001: 681) have recently presented stratigraphic schematic sections of the southern wall and "East Hillside" of the Locality 1 site and extended the grid 13 m to the south to encompass these sections.

Locus H was described by Pei and Zhang (1985: 260) as "the highest spot in the southern fissure [Layer 3] ... where a great number of well trimmed chert (or flint) implements were recovered." Fossils ascribed to four hominid individuals (H1 through H4) were recovered from this locus between 1934 and 1936. Thirty years later, in 1966, frontal and parietal fragments (PA 109) that

articulated with the cast of Skull V (Individual H3) were excavated from this locus (Chiu et al., 1973; Lin, 1994: 10). Weidenreich (1943: 5) record that the left temporal of Skull V was found on June 14, 1934, and because Jia's (n.d.) beginning date for his "Plans and Sections" is June 16, 1934, Skull V is not mapped or recorded. However, Xie et al. (1985) included Locus H on their stratigraphic profile of the western wall and plot it centered on square 7. This location accords with Jia's Level 1 plan (Fig. 4) and we consequently locate Locus H in square A7. Uranium-series dating of flowstone from Locus H by Shen et al. (2001) yielded ages of 400–500,000 yrs BP.

Locus I was excavated in 1936 at stratigraphic Layer 8/9 (Level 22), and yielded Skull VI (an adult, Individual II ["eye-one"]) and Skull VII (a juvenile, Individual I2 ["eye-two"]). Skull VI was found in 4 fragments—a frontal fragment (PA 90) and a right temporal fragment (PA 91) in Square



Fig. 5. Map of Locus I in Level 22, Layer 8/9, the provenience of Skull VI, which we interpret as having been broken, scattered, and gnawed by hyaenids, and Skull VII. After map by Jia (n.d.).

L-2, and two fragments of a left parietal (PA 92 and PA 93) in Square F3 some 7 m away (Weidenreich, 1943: 5) (Fig. 5). Three isolated teeth (RI^2 , LM_1 , RM_3) are associated with Skull VI on the basis of their adult age and same stratigraphic level (Weidenreich, 1937: 8), but as Fig. 5 (from Jia, n.d.) demonstrates, these teeth are located in 3 adjacent squares (K-2, M-1, and M-3) around the Skull VI frontal and temporal fragments, and between 7 and 9 m to the northeast of the Skull VI parietal fragments. Jia (n.d.) did not list or plot Skull VII and we can surmise from its high catalogue number (PA 326, versus PA 90–93 for Skull VI) that it was identified later in the laboratory. Weidenreich (1943: 5) listed Skull VII in Square B-4 and it is plotted accordingly on Fig. 5. Locus I then must include virtually the entire extent of the excavated Level 22 of Layer 8/9. We also attribute the isolated adult atlas from this level to Individual I1, but no data at present are available to locate it within the Locus I grid.

Locus J was established in 1936 over a broad area of Layer 8/9 (Level 23) (Fig. 6). Skull VIII (PA 95; Individual J1) derives from Level 23, square B-3 (Weidenreich, 1943: 5) and Skull IX (PA 315; Individual J4) derives from Level 23, square L-3 (Weidenreich, 1943: 6), some 10 m to



Fig. 6. Map of Locus J in Level 23, Layer 8/9, from which Skull VIII (Individual J1) and Skull IX (Individual J4) derive. Point proveniences mapped by Jia (n.d.) for field-identified ungulate horn or antler fragments have been indicated as possible locations for Femora II and III and Humerus II. Femur II is ascribed to Individual J2, and Femur III and Humerus II are ascribed to Individual J3. Small black dots represent in situ excavated stone artifacts mapped by Jia (n.d.). Both Skull VIII and Skull IX occur in squares in which stone tools are mapped, indicating close stratigraphic and spatial relationships between fossil hominid bone and artifacts, even though bioturbation probably precludes the preservation of a living floor in the cave.

the west. These fragmentary hominids were not listed on Jia's (n.d.) excavation map, indicating that they were recognized as hominid only later in the laboratory. Specimens attributed to two additional individuals (J2 and J3) derive from this locus. Weidenreich (1941: 4) noted that Pei had recognized a hominid femur from Locus J, prompting a re-analysis of the collection that then revealed a femur (Femur I ["one"]) from Locus C that had been identified as an "antler." We suspect that field identifications of the 3 hominid postcrania diaphyseal shafts from Locus J (Femur II, Femur III, and Humerus II) were perhaps also initially catalogued as ungulate horn cores or antlers in Jia (n.d.) (or, like the skull fragments, not catalogued at all). Further research to determine their field catalogue numbers will be required to locate these specimens more precisely on the excavation map for Locus J.

Locus K was established in 1936 with the discovery of *Homo erectus* Adult Mandible VI (Individual K1) at Level 24, square I0 ["eye-zero"]



Fig. 7. Map of Locus K in Level 24, Layer 8/9, from which Adult Mandible VI derived. Locus K is surrounded by abundant in situ stone artifacts as mapped by Jia (n.d.).

(Fig. 7). A second individual at this locus is represented by a right I_2 (Weidenreich, 1937: 7) but its exact provenience is unrecorded. Jia (n.d.) recorded numerous stone tools at this level surrounding Locus K, plotted as points in Fig. 7.

Locus L was established in 1936 and is subdivided into L_1 , located in square J-3, from which Skulls X (PA 98; Individual L1) and XI (PA 99; Individual L2) derive, and L_2 , located in square I2 ("eye-two"), from which Skull XII (PA 100; Individual L3) and 4 associated teeth (Individual L4) derive. Because these two squares are approximately 5 m apart from each other, Locus L is outlined as an oblong area trending north to south on Fig. 8.

Locus M was established in 1937, the last season of excavation at Zhoukoudian before the outbreak of World War II, in Layer 8/9, level 26. In Jia's (n.d.) excavation map Locus M is plotted at square F-2 but locations of Adult Mandible VII (Individual M1, square E-2) and Adult Mandible VIII (Individual M2, square D-3) are in fact in adjacent squares. Exact locations of Femur VII (Individual M3) and Femur IV+V (Individual M4) were not recorded, but are placed within mapped Locus M. Square J-3 of Level 26 yielded a hominid supraorbital fragment that fit Skull XI, in the same



Fig. 8. Map of Locus L in Level 25, Layer 8/9. During a period of 11 days in November of 1935, Lanpo Jia and his team discovered Skulls X, XI, and XII here. The northern portion of Locus L is referred to as L_1 and is the provenience of Skulls X and XI (the latter discovered in two fragments), all mapped within square (J-3) by Jia (n.d.). The southern portion of Locus L is referred to as L_2 and is the provenience of Skull XII, mapped by Jia (n.d.) in square 12 ("eye-two"), as well as four unmapped isolated teeth from the same square referred to Individual L4. Also mapped in this figure is the location in square (R - 1) of Adult Mandible IX (PA 86), discovered during excavation of the floor of Pigeon Hall Cave (Level 27, Layer 10) in 1958 (Woo and Chao, 1959).

square but 1 m higher, in Level 25 (Jia and Huang, 1990: 144) (Fig. 9). The fact that this fragment articulated with Skull XI from Locus L, but was found 1 m below its level is evidence for disturbance of the cave floor and lends support to the suggestion by Goldberg et al. (2001) that significant bioturbation by digging carnivores played a part in the deposition of the site.

Locus N was established in 1937 in Layer 8/9, Level 27 at the recovery site of two *Homo erectus* teeth (a left dm_2 , and a left M^1 , Individual N1; from Weidenreich, 1937: 12) in square E-2 (Fig. 10). Jia (n.d.) maps two points at which human teeth were discovered in square E-2 during the excavation of Level 27, but he did not label them as Locus N. Weidenreich (1937: 12), however, confirmed the square and stratigraphic provenience of these specimens, which he attributed to a female aged 4 to 5 years, as deriving from Locus N.

Locus O was the site of discovery of Skull XIII (PA 313; Individual O1 ["oh-one"]) (Weidenreich, 1943: 6) and M_1 (Individual O2) (Weidenreich, 1937: 12), in Layer 10, Level 29. The specimens are listed by Jia (n.d.) and plotted in square H-4. However, Jia (n.d.) incorrectly labelled Locus O as "Locus N" on his map of this level. We deduce that this was a transcription error introduced in



Fig. 9. Map of Locus M in Level 26, Layer 8/9, the provenience of mapped Adult Mandibles VII (square E-2) and VIII (square D-3) as mapped by Jia (n.d.). Adult Mandible VII and Femur VI have been referred to the same individual, Individual M1 (Weidenreich, 1941; Wu and Poirier, 1995) and were found in adjacent squares (Femur VI unmapped). Femur VI was discovered in two fragments that articulated at hyaenid puncture bite marks (see Fig. 151) and reported by Weidenreich (1943: 100–104) as having been found 1 m apart, presumably at opposite sides of square (F-2). Found also in square (F-2) were Femur VII, assigned to Individual M3, and Femora IV and V, assigned to Individual M4. These specimens showed evidence of isolated puncture bite marks or gnawing by hyaenids, and Femur V showed acid etching interpreted as indicative of hyaenid ingestion and regurgitation (see Fig. 15H). A fragment of the Skull XI frontal bone, the supraorbital, was found at Level 26, 1 m below the Locus L provenience of the rest of the specimen. This association indicates some vertical mixing of the levels in Locality 1, ascribed here to bioturbation by digging carnivores or rodents.

1937–41. Fig. 11 shows the correctly labelled plan view of Locus O.

Fig. 2 and Fig. 3 are composites of the data discussed above and provide a reference for interpreting the many photographs that have survived from the excavations, e.g., as published in Jia and Huang (1990), Jia (1999), and in the archives of the

IVPP and AMNH. During excavation, reference photographs were taken three times a day from fixed angles to the south, east, and west, and overview photographs of the entire site were taken twice a week (Jia and Huang, 1990: 84–85). With Fig. 2 and Fig. 3 it is possible to determine which part of Locality 1 was being excavated in a



Fig. 10. Map of Locus N, Level 27, Layer 8/9 (after Jia, n.d.). Two isolated teeth of a juvenile hominid were discovered in square (E - 2).

photograph and to relate these photographs to mapped hominid loci and artifactual occurrences. Boaz and Ciochon (2004) reproduce several oriented reference photographs of the excavation in progress.

The maps of Locality 1 presented in this paper can be used to help interpret the abundant literature on this site. We used catalogue numbers of five specimens of upper teeth excavated in 1935 (specimens 35-69-N7 [3 pieces], 35-70-O5, and 35-71-O6) and belonging to two *Equus* crania, as

reported by Binford and Stone (1986: 460), to interpret their provenience as squares O5, O6, and N7 in the southeast quadrant of the 1935 excavation, Level 12 of Layer 4 (Fig. 12). Binford and Stone (1986: 460) interpreted the damage on these specimens to indicate burning while fresh and inferred roasting of horse heads by *Homo erectus*. It is now apparent that these remains derive from the same stratigraphic level, Layer 4, as the hominids from Locus B (Individuals B1 through B5), although separated from them by 10 to 12 m to the



Fig. 11. Map of Locus O, Level 29, Layer 10 (after Jia, n.d.). This locus preserves Skull XIII (PA 313, Individual O1) and an isolated lower first molar (Individual O2), deriving from the lowest stratigraphic level from which hominid fossils have been discovered at Locality 1.

southeast. Locus B is outside the area of Fig. 12, but was mapped to an inferred horizontal location of (J-3) as seen in Fig. 2.

A further example utilizing our maps and interpretation of catalogue numbers to review the literature reinforces the association between the Locus B hominids and burned fresh bone at Locality 1. Binford and Stone (1986: 460) discussed another occurrence of burned equid teeth and stated: "Specimens 28-43-4 (a P^2) and 28-55-7 (a P^3) were burned while fresh and were recovered

in 1928 from the excavation located 'east of the 1927 excavation' near Locality 8, Levels 3–4." Reference to Fig. 2 shows that Locus B, not "Locality 8", is located immediately east of the 1927 excavation (Locus A), and that indeed Locus B is located stratigraphically in Layer (not Level) 4. We interpret the catalogue numbers to refer to specimens number 43 and number 58 discovered in 1928 at Layer 4 (the "7" in the latter catalogue number having been misread). These specimens must have been within a meter or two of Locus B



Level 12 35:62-35:75 35:112-35:120

Fig. 12. Map of Level 12, Layer 4 of the 1935 excavation (from Jia, n.d.) showing the squares containing putatively burned equid upper molar specimens 35-69-N7 (3 pieces), 35-70-O5, and 35-71-O6, as noted by Binford and Stone (1986: 460). The level of these specimens is deduced from the catalogue numbers, which record the year and square in which they were excavated. From Jia's (n.d.) maps and catalogue number ranges, specimen numbers 69, 70, and 71, excavated in 1935, derive from Level 12, a level that falls within Layer 4 (see Fig. 2 and Fig. 3, or Xie et al., 1985). Layer 4 is the same stratigraphic level as hominid Locus B.

itself because they were excavated in the same year. Thus, both cases of apparent equid head roasting, not previously associated spatially or stratigraphically, can be said with some degree of confidence to have been distributed in the same stratigraphic level as hominid Locus B, the provenience of *Homo erectus* Skull I, and over an area of some 12 m in diameter within the site.

Hominids, hyaenids, and the bone assemblage at Zhoukoudian

In a previous study (Boaz et al., 2000; Ciochon et al., 2000) we documented evidence of extensive

hyaenid-caused damage to the hominid bone sample from Zhoukoudian. In agreement with Cruz-Uribe's (1991) criteria for characterizing hyena bone accumulations, we note: (1) that Locality 1 has a high proportion of carnivores (Aigner, 1981; Dong, 1996); (2) that there is much evidence of hyena damage on bones (Pei, 1934); (3) that long bones tend to be preserved as diaphyseal shafts; (4) that the larger ungulates are represented by relatively few cranial remains (Pei, 1938); (5) that small, hard bones are rare; and (6) that the age profile of the hominids is attritional, rather than catastrophic in character, as established by Weidenreich (1935).

Table 1 and Table 2 show that there is a markedly skewed representation of body parts in the Zhoukoudian hominid assemblage (see Fig. 13 for breakdown). The Homo erectus bone assemblage shows a preponderance of cranial parts and mandibles, a low incidence of proximal limb elements, and a virtual lack of distal limb elements, hands, or feet. Weidenreich (1941, 1943) considered this pattern of differential body part representation the true composition of the preserved fossil assemblage and not an artifact of collection or excavation methodology. Chinese records (Jia, n.d., 1980, 1999; Jia and Huang, 1990) indicate that all bone was excavated, and individual teeth and unidentifiable bone fragments down to approximately 1 cm in length were collected or recovered in sieves (see photographs documenting sieving operations at Zhoukoudian from 1929 to 1934 in Jia, 1999: 6, 7, 10, 25, and 91). Weidenreich (1941: 29) described the method of excavation in the following manner:

Every bone, bone fragment or tooth, however small, is picked up and put aside in a basket which each technician has ready for this purpose. A group of technicians always works together, so that practically each lump of earth will be scrutinized. Nevertheless, the loose !h, too, is afterwards transported to a special place and passed through a fine sieve.

The Zhoukoudian hominid assemblage overall has a taphonomic signature of large-carnivoremodified bone assemblages (Pei, 1934; Zapfe, 1939; Sutcliffe, 1970; Potts, 1982; Hill, 1985; Binford and Stone, 1986). In comparison with modern African hyena den mammalian faunal assemblages (e.g. Hill, 1985), the Zhoukoudian hominid assemblage only shows a lower proportion of distal limb elements. Artiodactyls dominate the faunal assemblages in the modern hyena dens studied, and we explain this difference on the basis of the more robust skeletal anatomy of distal limb bones in artiodactyls compared to muscleensheathed distal limbs of primates, thus rendering the former less susceptible to destruction (cf. Brain, 1981; Pickering and Carlson, 2002). The body part representation of Zhoukoudian Homo erectus is in concordance with the frequencies expected in a skeletal assemblage of primates accumulated by large carnivores (Brain, 1981; Boaz et al., 2000; Ciochon et al., 2000).

Specific damage observed on the Zhoukoudian fossils (Table 2) shows that, of the 42 hominid non-dental skeletal elements in the Zhoukoudian collection, 28 (67%) show indirect or direct evidence of bite marks, gnawing, chewing, punctures, regurgitation, or fracture patterns made by a large carnivore, most likely a hyaenid. An additional 14 (33%) are too fragmentary to be diagnostic of a specific taphonomic agent, but they are consistent with damage by a large bone-crushing carnivore such as a hyaenid. Even the sole carpal bone (a lunate), an element of the B2 skeleton (Black, 1932), shows damage consistent with, if not uniquely ascribable to, carnivore damage. Fig. 14 includes a scanning electron micrograph of the right supraorbital torus area of the frontal of PA 109 (an original specimen, discovered in 1966, and part of Skull V, deriving from Layer 3), showing a wide, U-shaped groove that we ascribe to the bite mark of a carnivore, probably hyaenid (see Lyman, 1994). Similar bite marks at the same locations on other crania are to be seen on casts of Skulls I, II (see Fig. 15D), VI, IX, and X. Elongated and puncture bite marks are seen in most of the other fragmented crania (Table 2; Fig. 15A, B, E, and F). These patterns of bite marks suggest initial chewing and destruction of the face by hyaenids, and then subsequent advancement of gnawing onto the frontal, temporals, and parietals in order to crack open the neurocranium to gain access to the brain. All femora (see Fig. 15H and I) show the characteristic fragmentation pattern of hyaenid bone modification, i.e., relatively complete shafts, but lacking the epiphyseal ends (Cruz-Uribe, 1991), and some show multiple puncture marks (gnawing). Femur V (Fig. 15H) shows bite marks characteristic of hyena-gnawed bone, and the rounded and acid-etched damage contours of regurgitated bone. The overall pattern of bone modification is consistent with modern African hyaenid bone-chewing behavior and regurgitation.

Weidenreich (1935: 453) initially believed that "transportation [of the hominid bones] ... 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". But after the publication of Zapfe's (1939) paper, Weidenreich (1941, 1943) attributed damage on several *Homo erectus* fossils to mammalian carnivores, probably hyaenids. He reserved to hominid agency only what we term here the "spalled" fragments, because he believed they were "much too long to have been cleft by an animal" (Weidenreich, 1941: 77). *Pachycrocuta brevirostris*, however, was a hyaenid that stood 1.5 m at the shoulder and was able to fracture bone fragments of this size, as seen in bone damage ascribed to this species at the early Pleistocene site of Venta Micena, Spain (Arribas and Palmqvist, 1998).

In the most widely cited attribution of bonemodifying agency to hominids at Zhoukoudian, Weidenreich (1935, 1941, 1943) maintained that the damage to the bases of the hominid skulls was the result of cannibalistic activity. We find no evidence to support this conclusion. The facial skeletons are missing or fragmented on most skulls and the foramina magna have been enlarged. Breakage patterns on the skull base in fact correspond to contralateral skull vault puncture and bite marks that were made as large carnivores sought to gain purchase in prying open the skull vault to gain access to the lipid-rich brain, a part of the carcass prized by hyenas (Kruuk, 1972). Bone fracturing around the foramen magnum and bite marks seen on the skull base are consistent with large carnivore, probably large hyaenid, bone breakage.

There are an estimated 51 hominid individuals and a total of 66 separate body part elements represented in the collection (Table 1), yielding an average of 1.29 skeletal elements per individual. This value is low and is further support for the observation that hominid remains are quite fragmentary. Our hypothesis explaining this observation is that the remains were transported into the cave by hunting and scavenging activities of large mammalian carnivores, and then subjected to significant pre-depositional modification, probably primarily by hyaenids. Actualistic support for this model is sparse, but Sutcliffe's (1970: 1111) study of human fossil bone collecting by modern spotted hyenas from a cemetery in Kenya shows that such postulated activity is well within the behavioral repertoire of hyaenids.

Consideration of spatial and contextual associations of hominid skeletal remains in Locality 1 also assists interpretation of the taphonomy of the site. Such associations argue persuasively against generalized cave roof collapse and sedimentary crushing to explain fragmentation of fossils (for example, Locus I, Fig. 5). This locus shows a pattern of bone dispersal that fits well with an interpretation of hyaenid scavenging of hominid remains. We suggest that one or more hyaenids broke apart Skull VI in or near square L -2, scattering individual teeth into adjacent squares and leaving two cranial fragments (PA 90 and PA 91) behind. The rest of the skull was carried to the edge of the cave, square F3, where it was gnawed, breaking it into two fragments (PA 92 and PA 93). Skull VI shows elongated, raking bite marks, isolated puncture bite marks, and perimortem breakage consistent with patterns of modern hyaenid bone modification (Table 2). A similar scenario seems to be documented in the disarticulation of Skull XI, fragments of which were broken off and transported (or buried) between Locus L and the level below (Fig. 8 and Fig. 9). Skull XI shows elongated, raking bite marks, and similar perimortem breakage (Table 2).

The selective patterns of bone fragmentation and dispersal apparent here argue strongly against generalized crushing of remains by cave sediments, as might be seen in roof collapse. We would expect spatial contiguity of all conjoining bone fragments in the case of sedimentary crushing, which is not seen, as well as evidence of micro-damage on the remains consistent with such crushing, also not observed. Cases of clear indentation of fossil specimens by matching angularly shaped fragments of breccia seen in some fossils from the South African australopithecine caves of Sterkfontein and Swartkrans (Brain, 1958; pers. obs., NTB) form our basis for comparison. It is also relevant that major roof collapse did not occur until Zhoukoudian Layer 6, substantially later in time than the Layer 8/9 provenience of Loci I and L (Table 1).

Another preservational pattern of the hominid remains—isolated teeth lacking their corresponding mandibular or cranial bone—may be explicable on the basis of hyaenid bone modification as

Specimen	Damage	Anatomical location of damage
Skull I (PA 21 and PA 78)	HBr	Isolated right (?) parietal and left frontal bone fragments from broken skull
Skull II (PA 17) (Fig. 15A, D)	Bi	Left supraorbital torus and right parietal; possibly right temporal
Skull III (PA 16) (Fig. 15E, F)	Bi, HBr	Occipital-midline and left squama; left parietal and right parietal
Skull IV (PA 23)	Bi, HBr	Right parietal
Skull V (PA 74, PA 86, and PA 109) (see Fig. 14)	Bi	Right supraorbital and right temporal
Skull VI (PA 90–93)	Bi, HBr, P	Fragments of right frontal, left parietal, and right temporal with intervening damage
Skull VII (PA 326)	HBr	Right parietal (mastoid angle)
Skull VIII (PA 95)	FBr	Occipital fragment
Skull IX (PA 315)	HBr, Bi	Left fragment of frontal; disconnected vault fragments
Skull X (PA 98)	HBr, Bi, P	Fragmented skull with damage at edges of fragments, especially left supraorbital, right parietal
Skull XI (PA 99)	HBr, Bi	Left parietal, right temporal
Skull XII (PA 100)	HBr, P	Right frontal, right parietal, and occipital
Skull XIII (PA 313)	FBr	Facial skeleton, left maxilla
Adult Mandible I (Fig. 15G)	W, Sp, P	Symphysis, corpus, and ramus
Adult Mandible II	FBr	Condyle
Adult Mandible III	Bi, Sp, P (right); Sp, W (left)	Symphysis and corpus (left); corpus and coronoid process (right)
Adult Mandible IV	Sp, W, G	Symphysis and corpus
Adult Mandible V	Sp, W, G	Corpus, symphysis, ramus
Adult Mandible VI	FBr, W	Symphysis
Adult Mandible VII	FBr	Corpus
Adult Mandible VIII	FBr	Corpus
Adult Mandible IX (PA 86)	FBr, M	Rami
Juvenile Mandible I	W, Sp, P	Symphysis, corpus, ramus

Table 2
Taphonomic damage ascribable to hyaenid bone modification in the Zhoukoudian Homo erectus sample (see end of table for key)

Juvenile Mandible II	W	Corpus, ramus
Juvenile Mandible III	FBr	Corpus
Juvenile Mandible IV	FBr, W	Symphysis, corpus
Juvenile Mandible V	FBr	Ramus
Juvenile Mandible VI	FBr	Corpus
Atlas (Fig. 15C)	FBr, P	Right transverse process
Clavicle (Fig. 15J)	A, M, FBr	Medial and lateral ends
Humerus I	Sp	Spalled fragment
Humerus II	A, P	Ends and medial shaft
Humerus III	FBr	Shaft fragment
Lunate	Р	Proximal portion of dorsum
Femur I (Fig. 15B)	A, P, FBr, Bi	Proximal and distal ends, and inferior to greater trochanter
Femur II	FBr, P	Proximal and distal ends
Femur III	Sp, P	Spalled fragment
Femur IV	A, P, G, FBr	Ends and throughout shaft
Femur V (Fig. 15H)	G,V	Most of shaft
Femur VI (Fig. 15I)	P, Sp, V	Proximal and distal ends
Femur VII	Sp, P	Spalled fragment of shaft
Tibia	FBr, F	Proximal and distal ends

Key to abbreviations: A—articular or epiphyseal ends broken irregularly; Bi—elongated, raking bite marks (shallow, U-shaped, with round-shouldered margins); FBr—breakage resulting in very fragmentary remains, consistent with, but not necessarily ascribable to, hyaenid modification; HBr—peri-mortem breakage of bone consistent with patterns of modern hyena bone modification; G—gnawing (multiple and overlapping puncture bite marks); M—muscular attachment area(s) missing; P—isolated punctured bite marks (round outline, with clear circumferential stepped fractures of bone); Sp—spalling or longitudinal cracking of mandibular corpus or longbone; V—surface erosion of bone characteristic of modern hyena-vomited bone; W—parasymphyseal mandibular "wishbone" breakage. Specimen listing follows Wu and Poirier (1995).



Fig. 13. Percentages of individuals (N=51) represented by the indicated body parts at Locality 1, Zhoukoudian. Individuals represented by teeth unassociated with cranial or mandibular remains make up one third of the assemblage (N=17). The skeletal assemblage is dominated by unassociated crania and mandibles (45%, N=23) and shows low percentages of limb elements, especially distal limb elements (total 10%, N=5). Both patterns of preservation are consistent with bone modification primarily by hyaenids. Six individuals (12%) are represented by associations of skeletal elements. Individual B2 from Locus B comprises the only cranial (Skull I) and mandibular (Adult Mandible II) remains from a single individual associated with postcrania (Humerus I and a lunate). Skulls IV and VI are also associated with postcrania. One mandible (Adult Mandible VII) is associated with postcrania (Femur VI) at Locus M, and isolated mandibular teeth from individual C3 are associated with Femur I at Locus C. Individual J3 is the only individual from Loculity 1 represented by an association at Locus J of upper limb (Humerus II) and lower limb (Femur III) postcrania.

well. The initially discovered isolated teeth, including Zdansky's three discoveries reported in 1927 and 1952 and Davidson Black's 1927 molar that served as the type for Sinanthropus pekinensis, are referrable to only three individuals, but none are in situ in alveolar bone. These were identified first by Weidenreich as individual A1, a juvenile aged 7 to 8 years, which he considered likely female based on the small size of the teeth; A2, Adult Mandible I associated with an isolated M², estimated to be an adult female; and A3, a presumed adult male represented by M_1 and M_2 . The same pattern of preservation of individual teeth ascribed to a single individual with no associated or adherent bone is seen in Loci C (individuals C2, C3, and C4), D (individual D2), F (individuals F2, F3, and F4), L2 (individual L4), and N (individual N1). Overall 17

of the 51 individuals (33%) from Zhoukoudian are represented only by dental remains (Fig. 13). In another two cases (A2 and C1) where the mandibles are present, only maxillary teeth are associated.

Many hominid fossil sites preserve isolated teeth, of course. Sedimentary fluviatile abrasion explains the large number of isolated teeth in the Omo Shungura Formation, for example (see Boaz, 1977). A high-energy fluviatile environment is only seen at the base of the Zhoukoudian Formation, in Layer 17 (Xie et al., 1985). Chemical dissolution of bone in acidic soil environments can also lead to the preservation of isolated teeth in fossil deposits (Lyman, 1994). The carbonate-rich, basic cave sedimentary environment at Zhoukoudian (Goldberg et al., 2001) makes this hypothesis



unlikely. A third, more probable explanation for this pattern of fossil deposition is rodent gnawing, evidence of which we and others (e.g. Pei, 1938) have observed on non-hominid fossil bone from Zhoukoudian. Hystricids (Hystrix cf. subcristata) and castorids (Trogonotherium cuvieri and possibly *Castor* sp.), both families known as relatively large and powerful gnawers of bone (e.g., Breuil, 1939: 2), are present at the site (Xu et al., 1997). However, we have not recognized clear rodent gnaw marks on the hominid bones. A fourth possibility is fragmentation by hominid tool-using activity. Noe-Nygaard (1977) and Klein and Cruz-Uribe (1984), among others, have noted the highly fragmented nature of hominid-accumulated bone assemblages, formed from bone fragments resulting from breaking of bones for marrow. One specimen, a femoral diaphysis (Femur VI) with conjoined fragments, classified by us as showing two hyaenid bite marks, could also be argued (less probably in our opinion) to represent two hammer impact points by stone tools (Fig. 15I). We prefer our fifth hypothesis, that of the destruction of enclosing alveolar bone by intensive hyaenid gnawing. Because of the abundant evidence of hyaenid modification of bone that we have demonstrated (Table 2) and actualistic studies that show a high degree of gnawing and thus of fragmentation in hyena den sites (Sutcliffe, 1970; Cruz-Uribe, 1991), we believe this hypothesis the most likely to explain the pattern of isolated teeth in the hominid assemblage. We observed no cases of erosion or etching of enamel or dentine in the published descriptions of teeth (Weidenreich, 1937) or on the casts, so we do not postulate ingestion and regurgitation of teeth by hyaenids. Rather, we suggest that as maxillary and mandibular bone was broken by hyaenids in the process of

Fig. 14. (A) *Homo erectus* frontoparietal (PA 109 or Skull V), in oblique frontal view, excavated at Zhoukoudian in 1966. Location of a probable hyaenid bite mark is indicated by the oval. (B) Close-up of the area of the interest on the right supraorbital torus, showing the indentation from a probable bite mark. (C) Scanning electron micrograph at $17 \times$ of a positive impression of the area within the oval showing a broad, shallow, artificial groove characteristic of a large carnivore bite mark. Paired arrows define the path of the groove.



eating muscle, organ, and marrow, teeth fell out of their enclosing alveoli. Because of their hardness, teeth were preserved, and because of their distinctive morphology, they were likely recovered and identified more readily than small alveolar bone fragments.

Stone tools and fire at Zhoukoudian

Pei and Zhang (1985) reported on 17,091 in situ stone artifacts excavated from Locality 1 (all layers above Layer 11; see Fig. 2 and Fig. 3). Artifacts mapped by Jia (n.d.) are plotted on Fig. 6 and Fig. 7, which show Loci J and K, but the artifacts also occur outside the boundaries of these loci. Stone artifacts are the clearest evidence of hominid presence in or near the cave, but peri- and postdepositional factors, particularly bioturbation, may have disturbed their depositional contexts. Available references (Jia, n.d.; Pei and Zhang, 1985) seem to show, with very few exceptions, a low density and a near random scatter of artifactual distributions, a point that will need to be more fully analyzed by future investigation. Furthermore, Goldberg et al.'s (2001) research demonstrates that there was clearly significant bioturbation in the cave sediments, such as that which may have been caused by digging carnivores and rodents, probably obviating any evidence of a living floor in Locality 1. Pei and Zhang (1985) did note an apparent clustering of artifacts on the eastern edge of the "ash" level of Layer 8/9 near Locus G (Fig. 2), suggesting what may have been a focal point of hominid activity near the presumed eastern cave entrance where natural light would have been available. Abundant stone tools in Locus K, also near the eastern side of the cave,

Fig. 15. Evidence of carnivore damage on the Zhoukoudian Homo erectus fossil casts. (A) A superior view (posterior is to the top of figure) of a cast of the right parietal of ZDN Skull II (PA 17) from Locus D showing a long raking bite mark from the coronal suture to a line of breakage at the posterior margin of the parietal (toward the top of the figure). The bite mark deepens anteriorly and posteriorly. A V-shaped crack, filled with adhesive, is seen intersecting the bite mark approximately halfway along its length. (B) A posterior view of a cast of Femur I from Locus C. This specimen shows damage characteristic of bone chewed by modern hyenas. Damage was peri-mortem as indicated by the exposure of cancellous bone in the area of the greater trochanter (at three upper arrows), with damage extending anteriorly to include the area of the lesser trochanter. The femoral head is missing. A probable puncture bite mark is indicated at the lowest arrow. (C) The only element of the vertebral column of ZDN Homo erectus, an atlas missing its left side. A deep puncture bite mark is seen at arrow on its transverse process. This specimen derives from Locus I and is here considered associated with Skull VI (Individual II ["eye-one"]). (D) An anterior view of a cast of Skull II from Locus D. Arrows point to carnivore raking bite marks made on the left supraorbital torus, in a pattern very similar to that seen in Skull V (Fig. 14). (E) Internal view of Davidson Black's cast of the right parietal of Skull III (PA 16) showing the entrance point of a carnivore tooth (top arrow) through the bone. Non-comminuted fracture lines are seen radiating from the bite mark. A second, deeper entrance point of a carnivore tooth on the internal aspect of the skull can be seen at the middle arrow where the fragments of bone are comminuted. A third area of damage is seen at the lower arrow, which is damage that occurred after the cranium had been cracked opened and access gained to the internal surface. The arrow points to a puncture made from the inside at the end of a raking bite mark that was then used to lever off fragments of bone at the parietal margin (at the lower left in the figure). These fragments were recovered in excavation and reconstructed. (F) Postero-inferior view of the occipital of ZDN Skull III (PA 16) showing a long incised bite mark (at arrow). This surface defect in the bone did not extend through the entire thickness of the bone, unlike a post-mortem break. This bite detached bone fragments of the inferior occipital, posterior to the foramen magnum, thus demonstrating carnivore damage to this area. Fragmentation between inner and outer tables of bone, documenting that the damage was peri-mortem, may be seen at the inferior termination of the bite mark. Damage to the foramen magnum area was earlier hypothesized by Weidenreich (1939) and others to have been due to hominid cannibalism. (G) Lateral view of a cast of Adult Mandible I from Locus A. Arrows point to spalling of the inferior corpus, damage characteristic of hyenas in which mandibular bone is cracked off to gain access to the medullary cavity and marrow. This specimen also shows the "wishbone" pattern of breakage at the mandibular symphysis resulting from hyenas breaking the bone at this point in order to gain access to the tongue musculature. (H) ZDN Femur V (from Locus M), showing breakage characteristic of hyaenid modification. The bone also shows the smooth contours and acid-etched damage characteristic of regurgitated bone, and thus records not only carnivore damage of *Homo erectus* remains, but actual ingestion. (I) Two fragments of Femur VI, articulated to show the two carnivore bite marks (at arrows) that broke the femur open. These fragments were excavated 1 m apart in square F-2 of Locus M (Weidenreich, 1941: 100-104; see Fig. 9) and are re-articulated here from two separate casts. (J) The distal end of the Locus G clavicle showing a bone flake incident to peri-mortem breakage consistent with a carnivore chewing on the distal end of the bone at the attachment sites of the deltoid and trapezius muscles. This bone flake was made when the bone was fresh and its damage is interpreted as resulting from levering the broken bone shaft lateral to this point up against this medial, remaining fragment. Weidenreich (1943: 76-77, fig. 33) interpreted this damage as due to "the bite of a carnivore." We interpret this damage as associated with carnivore bone breakage, but clearly not a depressed bite mark. Scale bars=1 cm.

tend to support this hypothesis (Fig. 7). After collapse of the roof of the cave in Layer 6 (Goldberg et al., 2001), this preferential eastern patterning of artifacts is, on present evidence, no longer seen. Locus H, especially, shows a high concentration of stone tools in the southwestern portion of Layer 3 (Fig. 4). Whether this change reflects a new single opening towards the south or west, or a much more open cave roof generally must await further data.

The presence of fire in the cave, albeit not attested to by wood-stoked hearths (Weiner et al., 1998; Goldberg et al., 2001), has also long been considered a hallmark of hominid presence in the cave. The ashes cited by earlier authors (Breuil, 1931; Black, 1931b) as indicative of fire at Zhoukoudian are now clearly seen both geochemically and sedimentologically as reworked loessic silt, and the carbon deposits earlier thought to indicate remains of charcoal are clearly laminated, waterlaid detrital deposits. However, it should be noted that there remains evidence of relatively abundant charred bone. Some of these bones were fresh when burned, as in the equid remains discussed above. Weiner et al. (1998) reported that 7 out of 278 fragmentary microfaunal specimens from Layer 10 were uniformly black in color and presented an infrared spectrum characteristic of burned bone matrix. Bohlin (1980), the second excavation head at Zhoukoudian after Zdansky, opined that blackened microfaunal remains that he had discovered represented disgorged owl pellets that fell into still-hot ash. Since there is no evidence of hot ash at the site, but the hypothesis of owl pellet accumulations is reasonable, it may be that a fire burned over the microfauna on the cave floor, charring it.

More puzzling is the evidence of discolored bone that resulted from burning already fossilized bone. Weiner et al. (1998) observed discolored bone among their samples from Locality 1 and undertook experiments to show that only heated fossil bone discolored in this manner. Why fossil bone was lying on the surface and why it may have been burned, either intentionally or incidentally, remains to be determined.

Recent sedimentological research by Goldberg et al. (2001) combined with our plotting of Locus G (Fig. 2) throws some light on the context of the presumed association of supposed charcoal and hominid remains at this locus. The carbon-rich blackened sediment found here and elsewhere was determined by Goldberg et al. (2001) to have been deposited in detrital micro-layers under standing water. Fossil hominid remains found in such clusters or pockets might well represent the remains of pools of standing water inside the cave used by hyaenids as cache sites for kills. This is a behavior observed in extant savanna-living African hyaenids, especially in conditions of inter-specific competition (Kruuk, 1972), and may also explain aspects of the fossil cave-living Pachvcrocutaassociated fauna at Venta Micena (Arribas and Palmqvist, 1998).

Conclusions

Our compilation of data from a number of sources has allowed us to present a threedimensional plot of the excavations at Locality 1 and the localization of the loci from which hominid fossils were recovered. At present an estimated 51 hominid individuals are represented at the site. The 3-dimensional grid presented here can be expected to assist archaeological and paleontological analyses in the future. Hominid fossils from Zhoukoudian Locality 1 have been heavily modified by hyaenids and represent allochthonous members of the bone assemblage. Patterning of hominid fossils suggests that hominid carcasses or body parts were transported into the cave and within the cave, and were extensively gnawed. A number of loci preserve individual hominids represented by isolated teeth without adherent bone, a pattern probably also best explained by hyaenid destruction. Despite recent geochemical and sedimentological studies that modify earlier interpretations of the use of fire at the site, there are signs that fire was used by hominids at Zhoukoudian. Stone tool distributions indicate transient hominid presence in the cave, as does evidence of burned fresh bone.

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