Taphonomy, Life History, and Human Exploitation of *Rhinoceros sinensis* at the Middle Pleistocene Site of Panxian Dadong, Guizhou, China

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ABSTRACT

Rhinoceros remains are commonly found in Chinese Pleistocene archaeological localities. This study examines the characteristics of the *Rhinoceros sinensis* sample from Panxian Dadong, a karst cave in the mountains of western Guizhou province, with a mammalian fauna in association with stone artefacts and human remains from the late Middle Pleistocene (MIS 6-8). The distribution of skeletal elements shows a predominance of foot (metapodial and phalanges) and lower limb (carpals and tarsals) bones, while the dental age-at-death profile, constructed using dental eruption and tooth wear data, is characterised by a high frequency of prime age adult teeth. There is little taphonomic evidence for the involvement of non-human carnivores or natural agencies in the formation of the faunal assemblage. Instead, it appears that human activities were responsible for the unexpected prevalence of prime age adults. Copyright © 2008 John Wiley & Sons, Ltd.

Key words: China; Middle Pleistocene; rhinoceros; age-at-death profile; taphonomy

Introduction

A principal research objective for investigators of Palaeolithic cave sites is to understand site formation processes and the use of caves by hominins and other animals. One key source of information is the accumulated animal fossil remains. Faunal analysis has proven to be an essential component of site formation studies, and it is particularly informative when bioturbation and diagenesis obscure finer-level stratigraphic

Rhinoceroses are found at approximately 80% of all archaeological sites in China (Tong, 2000, 2001b), suggesting they were an important prehistoric food source. There were northern representatives of the Rhinocerotidae, including Dicerorhinus and Coelodonta, that were two-horned and adapted to colder climatic conditions. To the south of the Qinling Mountains, the Ailuropoda-Stegodon faunas of the Pleistocene include abundant examples of Rhinoceros sinensis, a large species with a single horn and the hypsodont (high-crowned) molars that are associated with grazing species. Its closest affinities are with the more

distinctions within travertines, breccias or clays, or when no site structures or features are discernible.

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tropical rhinoceroses from India and Java (Colbert & Hooijer, 1953).

Although rhinoceros are commonly found in the Pleistocene cave deposits of southern China, the process by which they became elements of faunal assemblages is rarely studied. Generally, they are just identified and included in faunal lists that describe paleontological localities and archaeological sites. This paper describes the detailed taphonomic and mortality analysis of late Middle Pleistocene R. sinensis material excavated from Panxian Dadong cave in Guizhou province, southern China. The clear presence of humans at Panxian Dadong is documented by five isolated teeth and numerous stone tools made of limestone, chert and basalt (Miller-Antonio et al., 2004), tools made of R. sinensis teeth (Miller-Antonio et al., 2000), and cutmarks, percussion damage and burning on faunal material (Schepartz et al., 2003). The evidence for human activity and rhinoceros fossils throughout the stratigraphic sequence at Dadong makes it crucial to evaluate the possible role played by humans in the formation of the rhinoceros sample.

R. sinensis is well represented in the Dadong fauna and comprises 24% of the total mammalian collection identifiable to taxon. The diversity of mammalian species represented at Dadong indicates that a variety of habitats were available in the vicinity of the cave (Schepartz et al., 2003; Bekken et al., 2004). R. sinensis, like many other rhinoceroses, apparently had the flexibility to withstand extremes of climate and the ability to exploit a wide range of plant foods (Osborn, 1903).

Our interest in rhinoceroses at Panxian Dadong is part of a larger faunal analysis designed to: (1) provide information on the palaeoenvironment of upland southern China during the Middle Pleistocene; (2) investigate the interactions between prehistoric humans and mammalian species; and (3) clarify the role of humans, carnivores and natural geological processes in the formation of the Panxian Dadong faunal assemblage. This paper builds upon our previous study of the taphonomy and mortality profile for the proboscidean *Stegodon orientalis* (Schepartz *et al.*, 2005) which identified a striking predominance of young animals that were most likely brought into the cave through hominin activities. Here we

test the hypothesis that the same pattern applies to *R. sinensis*.

Regional setting and site characteristics

Little is known about the Middle Pleistocene palaeoenvironment of upland southern China in comparison with the well-studied loess sequences of north China. While many of the karst caves of Guizhou remain unexplored, Dadong was the focus of geological, palaeontological, and archaeological investigations for over ten years (detailed in Huang et al., 1995, and special volumes of Acta Anthropologica Sinica 16(3), 1997, and Asian Perspectives 43(2), 2004) because of its deep stratigraphic sequence, the abundance of fossil mammals, and associated archaeological materials. It preserves late Middle Pleistocene deposits that provide palaeoenvironmental context for the periods when human activities are documented (Karkanas et al., 2008).

Dadong is located on the western Guizhou Plateau (25°37′38″N, 104°44′E; Figure 1), a region where continuous ranges of peaks contain numerous caves. Dadong is the middle of three interconnecting caverns stacked within a 230 m high hill approximately 1630 m ASL. The entrance is presently located 32.4 m above the valley floor as a result of recent uplift of the plateau; during the late Middle Pleistocene, it would have been closer to the valley floor and near the confluence of three small rivers that drained into the porous limestone of the lower cave. A later collapse produced a smaller pitfall entrance at the back of the cave.

Dadong's 8000 m² main chamber contains a clastic sequence of flowstones, finegrained clays and silt, consolidated gravels, and large limestone blocks. Uranium-series (U-series) dates (Shen et al., 1997) and electron spin resonance (ESR) dates (Rink et al., 2003; Jones et al., 2004) of tooth enamel samples suggest that most of the excavated levels at Dadong were deposited between 130–300 ka. The stratigraphic layers (Figure 2A) document an environmental sequence with substantial climatic fluctuations (Karkanas et al., 2008) corresponding to marine isotope stages (MIS) 6–8. The faunal assemblage at Dadong shows the loss of more temperature-sensitive

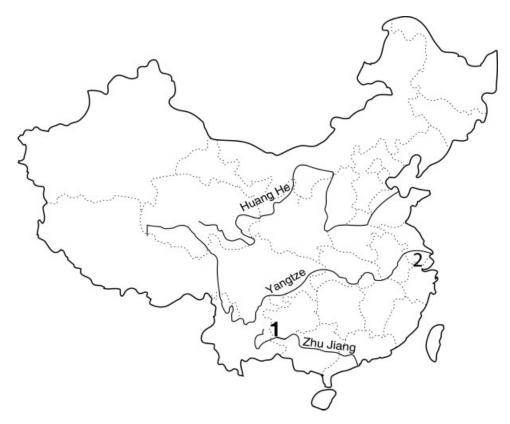


Figure 1. Map of China showing locations of (1) Panxian Dadong and (2) Nanjing.

species such as non-human primates during colder periods, while the hardier stegodonts and rhinoceroses persist throughout the sequence.

The Dadong faunal sample consists of a variety of species that are characteristic of the Ailuropoda-Stegodon faunas of Middle Pleistocene southern China (Zhang et al., 1997; Pan & Yuan, 1997; Schepartz et al., 2003). There are many ungulates (cervids, small and large bovids, pigs) and lesser numbers of primates (macaques, colobines and hominins) and carnivores (mustelids, foxes, hyenas, tigers, leopards, pandas). Other notable genera are large-bodied ungulates that would not ordinarily frequent caves, such as Stegodon orientalis, Rhinoceros sinensis, and the giant tapir Megatapirus augustus. This range of species suggests that the Pleistocene environment was mixed woodland. In addition, the recovery of pandas, bamboo rats and colobine monkeys (Pan & Yuan, 1997) suggests the existence of some densely forested areas with bamboo during warmer periods.

Materials and methods

The Rhinoceros sinensis component

The mammalian faunal sample from Dadong (n = 7045) consists of 3.3% skull fragments, 12.5% isolated teeth and 84% postcranial elements. The sample is primarily characterised by fragmentary bone, and there are very few examples of articulated elements. The most common identified species is R. sinensis, which comprises 24% of the total elements identifiable to taxon, followed by Stegodon orientalis at 13% (Schepartz et al., 2003).

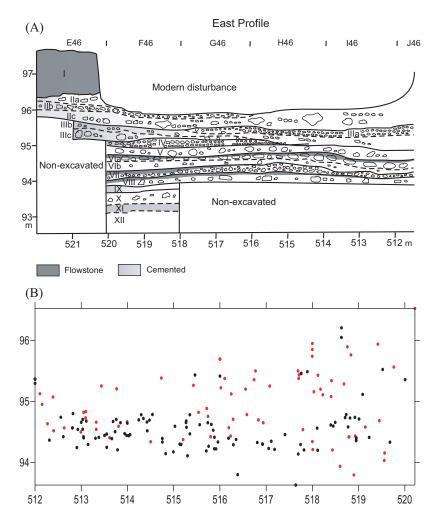


Figure 2. (A) Stratigraphic profile of Panxian Dadong excavations, drawn by P. Karkanas and adapted from Figure 5 in Karkanas *et al.* (2008). (B) Plot of excavated rhinoceros dental and skeletal elements. North is to the right. The *y*-axis is the depth in metres from the hypothetical surface of 100 m; the *x*-axis is a north–south range of the main excavation area in metres. Lighter circles are teeth, darker circles are bone.

From the total number of identified specimens (NISP) of 285 rhinoceros elements, we analyse 224 specimens that are identifiable to tooth class or skeletal element (the remaining 61 elements are tooth fragments). The sample consists of teeth (n = 121), skull (n = 3), and postcranial elements (n = 100). Rhinoceros material is found throughout the sequence of excavated strata, as indicated in a vertical distribution of all the piece-plotted specimens (greater than 2.5 mm) (Figure 2B). It is important to stress that none of the skeletal elements were found in articulation or could be conclusively associated with each other.

Skull bone is surprisingly rare given the large number of teeth present and the high likelihood that dense portions such as the mandibular corpus would be preserved relative to some of the more fragile skeletal elements. In terms of counts of elements, the postcrania are clearly dominated by foot bones (metapodials and phalanges) and lower leg bones (carpals and tarsals) (Figure 3). Among these, phalanges are the most frequently recovered elements.

Seven post-cranial specimens (i.e. 7%) are from immature animals; two of the femoral portions may represent the same individual. A minimum

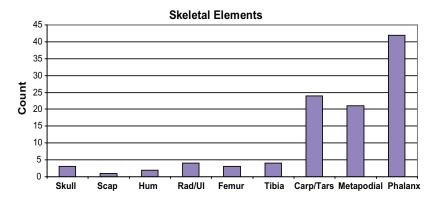


Figure 3. Skull and post-cranial representation of rhinoceros elements. This figure is available in colour online at www.interscience.wiley.com/journal/oa.

number of individuals (MNI) based on the counts of the non-dental elements is 4, although this must be viewed as a low estimate of the number of individuals present because it does not factor in skeletal maturation criteria.

Rhinoceros tooth classes and tooth eruption sequence

Over the course of rhinoceros evolution the anterior dentition has gone from having specialised cutting and shearing functions to being more rudimentary and highly variable. The living Asian species retain a tusk-like lower incisor, while the African species only have greatly reduced incisors (Ballenger & Myers, 2001). By the Pleistocene most rhinoceros dentitions became dominated by a series of large grinding premolars and molars (Osborn, 1903; Koulmann & Koulmann, 1970). The permanent dentition of R. sinensis lacks canines and has small upper and lower incisors (I1 and I2) and a small first premolar (P1) that is frequently not present. These teeth are rarely preserved in the palaeontological record of China (cf. Colbert & Hooijer, 1953; Tong, 2001a, b); it follows that most analyses focus on the posterior dentition which includes the remaining premolars (P2-4) and three molars (M1-3). Maxillary premolars and molars are similar in morphology: both have large buccal ectolophs and lingual meta- and protolophs separated by a deep valley that widens as the tooth wears (Osborn, 1903).

The permanent M3 is the most distinctive of the maxillary teeth, having a triangular rather than a square or rectangular shape (Figure 4, Stage 3 wear). The mandibular premolars and molars have two crescent-shaped or columnar lophs (termed the metalophid and hypolophid) that form posterior and anterior valleys (Osborn, 1903; Colbert & Hooijer, 1953) (Figure 5). The mandibular tooth classes are very difficult to distinguish, particularly when isolated worn teeth are evaluated.

R. sinensis also has four deciduous cheek-teeth. In the literature these are alternately referred to as deciduous molars (cf. Colbert & Hooijer, 1953), deciduous premolars (Tong. 2001a) or simply deciduous (D) 1–4 (Guérin, 1980). We use the latter terminology here. The deciduous teeth erupt in the following sequence, as summarised in Tong (2001a): D2, D3, D1, and finally D4. Occasionally, D1 erupts after D4. The permanent tooth eruption sequence is generally: M1, M2, P2, P3, P4 and M3 (Groves, 1967; Borsuk-Bialynicka, 1973; Guérin, 1980, as cited in Tong, 2001a). The most variable teeth are D1, which can be retained into young adulthood, and M2 which always erupts before P4. The most reliable teeth for ageing on the basis of the eruption sequence are M1, P4 and M3 (Tong, 2001a). In terms of relative age assessment, living rhinoceroses are classified into neonates (including animals from birth to less than 1.5 years), juveniles (1.5–4 years), subadults (4–6 years) and adults (over 6 years) (Foster, 1965). The cows

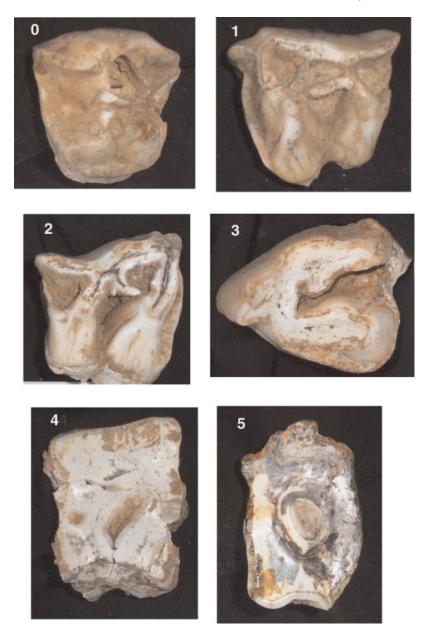


Figure 4. Wear stages (0-5) and examples of maxillary tooth morphology. This figure is available in colour online at www.interscience.wiley.com/journal/oa.

reach sexual maturity by six years, the bulls are fully mature at 7–10 years, and the lifespan may encompass 45 years (Ballenger & Myers, 2001). Table 1, derived from data on the extant African species of *Diceros bicornis* (black rhinoceros) and *Ceratotherium simum* (white rhinoceros), presents the posterior tooth eruption sequence for these different age cohorts. From the table, the

following major distinctions in dental development can be summarised:

- (1) neonates and animals less than 1.5 years old have only deciduous teeth;
- (2) early juveniles have worn deciduous teeth and permanent molars with beginning stages of wear;



Figure 5. Specimen 99D F46:455 mandible with LP3, RP2-P4. This figure is available in colour online at www. interscience.wiley.com/journal/oa.

- (3) late juveniles have highly worn D1s and D4s, and P2s and P3s with little wear:
- (4) subadults have P4s with little wear and unworn M3s:
- (5) adults are characterised by the greater stages of premolar and molar wear.

This information can be used, in conjunction with tooth wear data, to develop an age-at-death profile for the Dadong rhinoceroses.

The total count of rhinoceros maxillary and mandibular teeth at Dadong is 70 and 51, respectively (Figures 6 and 7). Few of the teeth are preserved in jaws, but one of the most complete examples is a large mandible with the right P2-P4 and left P3 (Figure 5). Among the tooth classes, premolars are most frequent at Dadong. There are only two maxillary D1s in the sample. These are small teeth often retained into adulthood and heavily worn. They are rarely preserved as individual teeth. We will focus primarily on the posterior maxillary dentition due to the larger sample size and the greater precision in recognising tooth class distinctions for maxillary teeth. The minimum number of individuals (MNI) based on the highest frequency tooth category (14 maxillary P2s) would be 7, but a higher MNI is suggested by the presence of 7 maxillary M3s and 4 maxillary D4s. As animals do not retain M3s and D4s concurrently and none of these teeth have good antimeres in the sample, a dental MNI of 11 is a better estimate.

Table 1. Tooth eruption and age cohorts (modified from Tong, 2001a)

Teeth present	Key features	Age cohort (yrs)
D1-D4 D1-D4, M1-M2 D1?, D4, P2-P3, M1-M2 P2-P4, M1-M3 P2-P4, M1-M3	Deciduous teeth only Deciduous teeth and permanent molars D4 not yet replaced M3 erupted but not in use M3 in use	Neonate (<1.5) Early juvenile (app. 1.5–3) Late juvenile (app. 3–4) Subadult (4–6) Adult (>6)

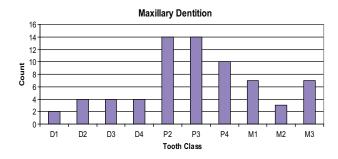


Figure 6. Distribution of maxillary tooth classes (n=70). This figure is available in colour online at www.interscience. wiley.com/journal/oa.

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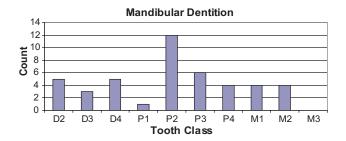


Figure 7. Distribution of mandibular tooth classes (n = 51). This figure is available in colour online at www.interscience. wiley.com/journal/oa.

It should be emphasised that these MNI estimates are based upon analysing the Dadong sample as a single entity without stratigraphic divisions. Interestingly, if the dental sample is divided into upper (n = 35) and lower (n = 39)subsamples following what appears to be a potential gap in the spatial distribution of piece-plotted elements around the elevation of 95 m (Figure 2B) and corresponding roughly to the division between layers V and IV (Figure 2A), the frequencies of deciduous teeth, premolars and molars are basically the same for each subsample (upper: 37% deciduous, 29% premolars, 34% molars; lower: 38% deciduous, 28% premolars, 33% molars), and the combined MNI determination remains the same as that for the combined sample.

Table 2 includes descriptive statistics for the Dadong maxillary sample. Basic comparison with data published in Colbert & Hooijer (1953) suggests that R. sinensis at Dadong is similar in size to their study collection, although our measures do not correspond exactly with their system of measurement (they measured at the base of crowns; we measured maximum BL and MD measures across the crown and perpendicular to each other). In addition to what is reported in the table, we have one deciduous incisor that is heavily worn. The crown height and mesiodistal length are the measures most affected by agerelated changes as the tooth is used. The variability in the buccolingual measures, as seen in the relatively high standard deviations, is probably best explained as representing size variation due to sexual dimorphism.

Determination of dental age wear stages

Rhinoceros teeth develop several characteristic features as they wear. The initial changes involve blunting of crests and the beginning of dentine

Table 2. Descriptive statistics of maxillary dentition sample

Tooth	n	Mean	SD	Range
D1 MD BL HT D2 MD BL HT	2 2 2 1 1	26.2 23.9 21.4 30.5 30.3 23.2	1.414 7.85 0.354	25.2–27.2 18.4–29.5 21.1–21.6
D3 MD BL HT	2 1 1	39.4 43.8 40.5	3.182	37.1–41.6
D4 MD BL HT P3 MD BL HT P4 MD BL HT M1 MD BL HT M2 MD BL HT M3 MD BL HT	4 4 3 15 16 16 11 1 1 9 9 9 6 6 6 3 3 3 6 6 5	46.9 50.8 51.8 30.7 35.7 25.5 38.2 45.9 31.8 40.7 56.6 21.2 49.1 60.3 29.8 51.3 53.3 30.7 43.9 48 32	10.315 7.507 24.239 2.24 4.82 8.562 3.799 5.8 17.646 4.514 5.474 5.979 3.695 5.013 5.091 1.301 7.209 8.056 6.25 6.547 4.932	34.2–55.4 42.1–59.3 24–68.7 27.4–35.2 21.5–40.4 12.8–47.9 30.8–43.1 35.7–51.8 9.7–61.5 33.3–48.3 48.5–63.7 11.3–34.1 47.2–55 54.4–67.8 21.3–35.1 50–52.6 45–58 21.6–37 34.2–49.7 41.7–56.4 25.5–37.5

MD, mesiodistal length; BL, buccolingual breadth; HT, crown height.

exposure along the crest ridges. In contrast to the relatively flat advanced wear of the mandibular dentition, the maxillary teeth develop strongly sloped or dished occlusal surfaces as wear progresses on the meta- and protolophs. The anterior premolars (P2s) tend to wear flat and to eradicate the crest features more completely. With age, the mesial-distal length of all teeth is significantly reduced due to interproximal wear, and the enamel is often missing from the mesial and distal surfaces of heavily worn teeth. Based on this wear information, we scored individual teeth on a 0-5 scale, as listed below, to facilitate age estimates. Higher scores reflect greater levels of wear. Figure 4 provides examples of the wear stages. Louguet (2006) recently published another attritional ageing system for Rhinocerotid teeth. While it is fundamentally the same as our methodology in terms of the recognition of the wear processes, the scoring is reversed and therefore not directly comparable to our system:

0: no wear or an unerupted tooth;

- 1: edge of crests show very slight wear;
- 2: edge of crests show dentine and flattening;
- 3: major dentine exposure but crest morphology still visible;
- 4: flat wear and major features of crest enamel are obscured;
- 5: wear to the root on the lingual side or strong scooped or sloping wear.

According to tooth eruption patterns (Table 1) and this wear scheme, the youngest rhinoceroses (neonates and animals aged less than 1.5 years) can be identified by the presence of unworn or slightly worn (stages 0–1) deciduous teeth. The use of the deciduous teeth for ageing is complicated by their continued presence in the mouth for several years; in some cases D1 and D4 may be in use throughout the juvenile phases (Tong, 2001a). Thus the presence of deciduous teeth alone is not evidence for very young ages and their wear scores must also be factored into an age-at-death profile. At the other end of the age spectrum, the presence of an M3 with any stage of wear indicates an individual in the adult age cohort.

Results

Deciduous teeth comprise 22% of the dental sample identifiable to tooth class. They demonstrate a range of wear scores that can be used for assigning them to the neonate and juvenile age cohorts. About 30% of the deciduous teeth are from neonates or individuals under 1.5 years of age, while 44% are heavily worn and represent late juvenile stage individuals (Figure 8). The permanent teeth also provide important information for the construction of the age-at-death profile. There are very few lightly used teeth in the permanent dentition (Figures 9 and 10). Maxillary teeth have predominantly higher scores, indicating that the majority are from adult animals. Conversely, the mandibular tooth scores show a pattern of less wear, with no teeth scored at Stage 5 (Figure 10). The difference between the maxillary and mandibular wear may be explained by taphonomic factors. It is unlikely

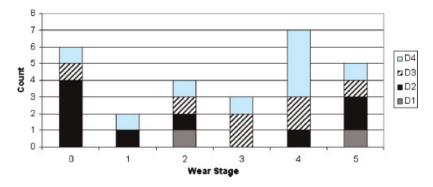


Figure 8. Wear stages for the deciduous teeth, maxillary and mandibular combined (n = 27). This figure is available in colour online at www.interscience.wiley.com/journal/oa.

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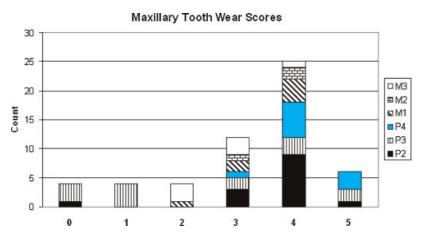


Figure 9. Distribution of wear stages for each tooth class of the maxillary permanent dentition (n=55). This figure is available in colour online at www.interscience.wiley.com/journal/oa.

that the Dadong dental sample lacks mandibular teeth with advanced wear. However, due to their morphology, those teeth are more likely to fragment when heavily worn and the resulting pieces cannot be assigned to tooth class. For this reason, we suggest that the maxillary tooth scores are more characteristic of the sample.

When both permanent and deciduous tooth scores are then assigned to the different age cohorts, an age-at-death profile for the sample shows some clear patterning. There are 8.3% of the teeth from neonates and animals aged less than 1.5 years, 5.8% from early juveniles, 27.3% from late juveniles, 9.1% from subadults and 49.6% from adults (Figure 11).

There are several factors complicating the construction of a dental age profile for this sample. Deciduous teeth are more difficult to

interpret than the permanent teeth. Since deciduous teeth are shed, the presence of isolated deciduous teeth does not necessarily indicate death of the individual or young age (although the sample does contain some unworn teeth without root resorption that could only come from carcasses of young animals). Figure 11 therefore represents the developmental age of some individuals in combination with age-atdeath information from carcasses. Another complication stems from the nature of the sample. Few specimens at Dadong can be associated with other teeth and must consequently be considered to represent individual elements. This bias, which is the largest source of potential error for this analysis, cannot be avoided when isolated teeth constitute the bulk of the sample. In addition, as discussed above, we

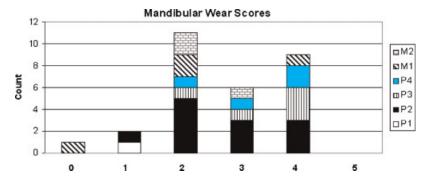


Figure 10. Distribution of wear stages for each tooth class of the mandibular permanent dentition (n = 30). This figure is available in colour online at www.interscience.wiley.com/journal/oa.

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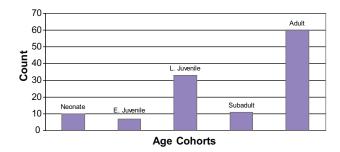


Figure 11. Distribution of age cohorts from individual teeth, deciduous and permanent combined (n = 121). This figure is available in colour online at www.interscience.wiley.com/journal/oa.

examined the sample as a whole without spatial or temporal divisions to maximise the sample size. This has important ramifications in the interpretation of the age-at-death profile, but the use of an unstratified sample probably does not introduce as much bias to this study as might be expected, because some degree of time-averaging is characteristic of all faunal assemblages from prehistoric sites that are the product of repeated events (Haynes, 1991).

Discussion

Mortality profiles

The two basic mortality profiles that archaeozoologists use to model population age structure are termed 'catastrophic' and 'attritional'. In a catastrophic profile, successive age classes contain fewer individuals because it represents a population's age structure at the time of death as the result of a non-selective event (such as a flood or fire). An attritional (normal or cemetery) profile is bimodal or U-shaped, with most individuals from the youngest and oldest age classes (Klein, 1982; Lyman, 1994). Both profiles assume that the populations do not exhibit dramatic fluctuations in births or survival, and are therefore stable and stationary. Haynes (1991: Figure 6.4) refined this classification by specifying four types of age profile in living and extinct proboscidean assemblages. In addition to attritional and bimodal distributions (Types A and B), he described another pattern (Type C) that is dominated by prime-age adults. This results from selective mortality affecting males only (for

example, killings by hunters interested in ivory), or from non-selective mortality affecting declining populations. His fourth distribution (Type D) shows no patterning and results from various causes, including insufficient sample size.

Applying Haynes's (1991) age profile interpretations to the Dadong rhinoceros data, several observations are relevant. A Type A profile might be expected in a time-averaged sample such as ours, but the Dadong distribution does not show this pattern. In contrast to a Type B bimodal profile, where a mode with substantial numbers of very young individuals is expected, we have only one clear mode of adults (almost half of the total sample). A Type C profile is the best fit. The question is whether these are prime age animals rather than older, more vulnerable individuals. There are several of the later sequence premolars, M1s and M2s, with advance wear scores, but there is a notable lack of M3s in Stage 4 or 5 wear. We interpret this as an absence of teeth from advanced age adults (Figures 9 and 10) and a predominance of teeth from prime individuals (see also Borsuk-Bialynicka, 1973: Table 4, p.15). There is also a sizeable representation of late juveniles and subadults - those who are presumably inexperienced and vulnerable to predation as they are no longer travelling under their mother's protection (c.f. Foster, 1965; Goddard, 1970).

Taphonomic indicators of accumulation and transport

Several activities could produce the rhinoceros assemblage at Panxian Dadong. The material may

have accumulated through five factors: the natural loss of deciduous teeth, the natural death of animals, water flow into the cave, transport by porcupines, or predation by large carnivores or humans. It is therefore important to examine each of these factors in light of what appears to be a differential representation of teeth from adult animals.

There is some question as to why rhinoceroses would naturally appear in a cave fauna. With abundant drainage systems on the Guizhou Plateau and rivers in the Dadong valley, they would probably not have had to venture into the cave to obtain water, but it might have been a source of mineral salts. Accidental deaths of young rhinoceroses might occur naturally in karst environments where natural fissure traps are formed through limestone dissolution. There may have been fissures in the Panxian region during the Middle Pleistocene. Dadong itself was a large, high-ceilinged cavern by that time, based on the dating of a substantial columnar speleothem (stalacto-stalagmite) that had formed in the interior (Shen et al., 1997). Young animals may also have become mired after wandering into the cave, but this seems unlikely during the times when humans were active there. Any of these natural processes whereby rhinoceroses could have been added to the Dadong assemblage would have produced a different signature from what is found - namely, more complete and extensive representation of skeletal elements.

The Dadong rhinoceros specimens show a variety of breakage and damage that suggests they were subject to minimal destructive or natural transport processes. A small number of bones appear chalky or surface weathered, and five elements display trampling damage. These changes may reflect diagenic processes as well as physical destruction. The low frequency of polish and rounding that can be attributed to water action (10 elements, or 3.5%) does not provide support for the idea that water transport was particularly important in Dadong. Overall, most of the rhinoceros sample was not substantially altered by natural processes, suggesting that these activities were not important factors in the formation of the assemblage. This is also true for the total faunal sample (c.f. Schepartz et al., 2003).

Furthermore, the rhinoceros sample shows minimal post mortem damage from animal processing. Rodents collect faunal elements that they gnaw to maintain their incisor functioning. Porcupines and small rodents were active in Dadong, especially during later time periods, but their damage to bones and tooth roots was fairly limited, affecting approximately 5% of the total sample (Schepartz et al., 2003). Only 10% of the rhinoceros sample exhibits rodent gnawing. This proportion is actually quite low when compared with faunal assemblages from other localities in the general region, such as Lang Trang from Vietnam, where almost all of the teeth exhibit gnawing damage (Vu The Long et al., 1996).

Big and small cats such as Chinese wild cats and tigers, hyenas, foxes and other small carnivores were present in Dadong. These species are rare (4% of the sample identifiable to taxon), and there are few that would have preyed upon animals the size of rhinoceroses. Scavenging carnivores, such as hyenas, could have transported portions of younger and smaller animals into the cave. This might have been particularly true in the case of elements that are left at kill sites, such as crania or lower limbs (c.f. Blumenshine, 1986; Lyman, 1994). Hence, scavenging might account for the high proportion of teeth in the assemblage, if scavengers were able to detach crania or mandibles. The numbers of foot elements might also be explained.

There is very limited evidence for carnivore damage on the Dadong bones (although this probably under-represents the possible extent of carnivore activity in the generation of bone assemblages; c.f. Lyman, 1994). One bone clearly displays carnivore chewing damage. The possible role of carnivores in the generation of the sample can also be evaluated by examining the ratio of carnivores to ungulates and herbivores. Carnivore-generated assemblages, such as den sites, ordinarily contain high frequencies of carnivore bone (Brain, 1981). The Dadong faunal sample falls outside the range of values observed for carnivore-generated den deposits (at 4.6%, or 55 carnivores to 1176 herbivores and ungulates, of the elements identified to taxon). The scarcity of carnivores at Dadong is notable, as it is a cave with side chambers and crevices suitable for denning. It could be that the current faunal

sample represents an area of the cave that was not extensively used by the carnivores, or that carnivore presence in the cave alternated with human activity phases (c.f. Stiner, 2002).

Evidence for hominin activity and selection for prime age adults

Although the above factors may have contributed to the formation of the Dadong faunal assemblage, we suggest that none of them were the single or primary source of accumulation. As the material is found in association with stone tools and hominin fossils, humans probably played some role in their accumulation. There is an excellent example of human-produced modification on a distal portion of a rhinoceros radius that has a bashed concentric fracture in the centre of the shaft (Figure 12). Bones from other species also have stone tool cutmarks, impact fractures,



Figure 12. Distal radius with concentric impact fracture. This figure is available in colour online at www.interscience. wiley.com/journal/oa.

and burning that we attribute to hominin activities. Burning is the most common alteration, occurring on 3% of the bones. Although it is impossible to rule out other explanations for the impact fractures and burning, the co-occurrence of these features with cutmarks (and the lack of their co-occurrence with carnivore damage) strengthens our interpretation of them as resulting from hominin behaviour.

Evaluating the human role is complicated, as they could have acted as hunters or scavengers. The large size of rhinoceroses means that any processing of their carcasses might entail behaviours that reduce the carrying load. For example, data on recent elephant hunters verify that they spend considerable time and energy processing at the kill site. They consume on-site, or smoke and dry meat to decrease its carrying weight (Fisher, 1993). If the Dadong rhinoceroses died or were killed away from the cave, which is highly probable, the problem of transport could result in similar signatures for human hunting and human or carnivore scavenging.

The age structure of the rhinoceros dental sample, with its predominance of prime age animals' teeth, sheds light on the possible role of hominins in its formation. Numerous studies of fossil faunal assemblages attribute profiles dominated by prime age adults to human activity (Gaudzinski & Roebroeks, 2000; Steele, 2003). For several species, the fact that the more difficult to procure animals are targeted has been explained as the result of exploiting them for special resources such as antler or tusk.

Tong (2001a) studied the fossil assemblage of Dicerorbinus mercki from the Middle Pleistocene Nanjing Man site in South China. He reported that most of the rhinoceros remains were from very young or juvenile animals (74% deciduous teeth still preserved in maxilla or mandibular bone). Tong argued that humans are the only natural predators of rhinoceroses due to the large body size of even the juvenile animals, which can approach 500 kg (Bigalke et al., 1950, as cited by Tong, 2001a). Thus he viewed the Nanjing assemblages as the product of human hunting. The age-at-death profile and taphonomy of the rhinoceroses at Dadong contrast strongly with that observed by Tong. We have isolated teeth from adult animals and very few cranial fragments with or without dentition. If human activities are responsible for the rhinoceroses in the Dadong assemblage, a very different selective strategy is involved. Given the distribution of skeletal elements in our rhinoceros sample, we cannot make a compelling argument for active hunting rather than scavenging by hominins. However, we suggested elsewhere that the large molar teeth may have been a raw material for tools (Miller-Antonio et al., 2000). It follows that the overall larger size and greater crown height of young adult teeth would make them best suited for this purpose. Sizeable mandibles are often smashed for their marrow at kill or scavenging sites, and that might explain their limited representation at Dadong. This could also explain why there is a scarcity of cranial remains but an abundance of teeth in the assemblage (Schepartz et al., 2003).

The small number of teeth and bones from neonates, young animals less than 1.5 years of age, and young juvenile rhinoceroses at Dadong may reflect a taphonomic bias against the preservation of more fragile elements (c.f. discussion in Steele, 2003). A comparison between the rhinoceros and stegodont representation at Dadong is informative with regard to this issue. The distribution of skeletal elements is extremely similar for both of these large-bodied species, yet their dental mortality profiles are very different as few adult stegodonts are represented (Schepartz et al., 2005). The preservation of so many young stegodont remains indicates no selective bias against individuals from the youngest age classes, and supports our interpretation of deliberate procurement of elements from adult rhinoceroses.

Conclusions

The analysis and interpretation of the Panxian Dadong rhinoceros dental and skeletal material illustrates that the sample consists largely of teeth from prime age adults (almost 50%), although individuals from all age cohorts (neonates and animals under 1.5 years, early juveniles, late juveniles, subadults and adults) are represented. This pattern deviates from the attritional distribution expected from natural mortality of a wild population. It also does not fit the catastrophic death assemblage pattern.

Based on the available archaeological, faunal and taphonomic data, the rhinoceros faunal assemblage at Dadong is predominantly a result of hominin activities (either hunting or scavenging). Almost certainly, other collection agents (carnivore, rodent, or geological processes) played some role in its formation. The rhinoceros assemblage is distinctive in that it differs from the observed pattern at the Nanjing Man site and also the mortality profile for Stegodon orientalis at Dadong, both of which are characterised by a higher prevalence of younger animals. This unexpected finding is supportive of our earlier hypothesis that rhinoceros teeth were sought for use as a raw material for tool-making. This study supports the results of other taphonomic work (Schepartz et al., 2003) that suggests that humans played an important role in the formation of the Dadong faunal assemblage.

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