Large mammal exploitation in Late Middle Pleistocene China: a

comparison of rhinoceros & stegodonts at Panxian Dadong

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Abstract

This paper examines how studies of faunal assemblages from a hominin cave site, in conjunction with ecological data on extant taxa and comparisons with palaeontological localities and other hominin sites, can take our understanding from basic presence/absence lists to investigations of species-specific utilisation. The *Rhinoceros sinensis* and *Stegodon orientalis* components of the fauna from Panxian Dadong, a late Middle Pleistocene cave in the mountains of Guizhou Province, China, are relatively similar in their frequencies of skeletal elements represented, but the reconstructed age profiles are quite different. The *S. orientalis* remains are primarily from very young individuals while the *R. sinensis* elements are from prime age adults. These differences may be attributed to body size differences, transportability, and different uses of the two taxa for food and as sources of raw material.

1 Introduction

Palaeoanthropological research in China has a long and rich history. Similar to the progress seen in other countries, the application of archaeological science methodologies to Chinese localities has demonstrated a great potential for expanding our knowledge of past human behaviour. This paper examines how studies of faunal assemblages from a hominin cave site, in conjunction with ecological data on extant taxa and comparisons with palaeontological localities and other hominin sites, can take our understanding from basic presence/absence lists to investigations of species-specific utilisation.

The focus of this study is the large mammal component from Panxian Dadong, a karstic cavern with an interior chamber of over 8000 m². The cave is located in a mountainous region of western Guizhou Province (figure 1). Systematic investigations of Dadong began in the early 1990s and included two phases of excavation. The earlier excavations were the primary source of the taxonomic representation list; it is 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 (five isolated Homo sp. teeth) and carnivores (mustelids, foxes, hyenas, tigers, leopards). Other notable genera are large-bodied animals 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 some densely forested areas with bamboo during warmer periods.

The second phase of excavation investigated site formation processes, chronometric dating and palaeoclimatic reconstruction. In addition to the faunal assemblage, the Dadong deposits contain tools manufactured from chert, basalt and limestone, as



Figure 1 Map of China indicating location of Panxian Dadong

well some possible scrapers produced from rhinoceros teeth (Miller-Antonio et al 2000). Other indicators of human presence at the site include burnt bones, cut-marked bones and charcoal.

Our analysis of the Dadong faunal assemblage included examination of the differential density of faunal elements throughout the stratigraphic sequence (Schepartz et al 2003; Bekken et al 2004), taphonomic indicators of bone condition and human, carnivore or rodent damage (Schepartz et al 2003), and the age-at-death profiles of the stegodonts (Schepartz et al 2001, Schepartz et al 2005) and rhinoceroses (Schepartz & Miller-Antonio 2010). Our focus on the stegodonts and rhinoceroses stems from their importance in the faunal assemblage. They are the most common identified species: *Rhinoceros sinensis* comprises 24 per cent of the total elements identifiable to taxon, followed by *Stegodon orientalis* at 13 per cent (Schepartz et al 2003).

Rhinoceroses were probably an important prehistoric food source in China as they are found at over 80 per cent of the archaeological sites in the country (Tong 2001a, 2001b). This includes northern sites with *Dicerorhinus* and *Coelodonta*, the two-horned genera that were adapted to colder climatic conditions, and localities south of the Qinling Mountains where the *Ailuropoda-Stegodon* faunas of the Pleistocene include abundant examples of *Rhinoceros* sinensis. *R. sinensis* was a large species with a single horn and hypsodont (high-crowned) molars that are associated with grazing behaviours. The closest affinities of *R. sinensis* are with the more tropical rhinoceroses from India and Java (Colbert & Hooijer 1953).

The prehistoric use of stegodonts, and proboscideans in general (Gaudzinski et al 2005), is less clear. Close relatives of the ancestors of contemporary elephant genera Loxodonta and Elephas, stegodonts were present from the late Miocene through the Pleistocene of Asia. They are known to have persisted until quite recently (Saegusa et al 2005). The exploitation of a dwarf species is described for Liang Bua on Flores, Indonesia as late as 12 ka (Van Den Bergh et al 2008). Stegodon is the most common genus, with S. orientalis having the greatest temporal range and geographical distribution (Zong 1995; Saegusa 1996; Takahashi & Namatsu 2000:figure 4). The importance of Stegodon in Chinese mammalian faunas is reflected in the term 'Ailuropoda-Stegodon assemblage' that is commonly used to refer to southern Chinese faunas of the Pleistocene. Stegodonts are known from many Middle and Late Pleistocene Chinese cave sites that also contain Homo erectus (Hexian, Jianshi, Tangshan) or early Homo sapiens remains (Maba, Tongzi, Tubo, Nalai, Tiandong, Liujiang, Shuicheng and Jiande) (Han & Xu 1989; Mu et al 1993; Bakken 1994). Open-air Homo erectus sites with stegodont material include Gongwangling, Chenjiawo, Shangnabang at Yuanmou, and Yunxian (Dong et al 2000). Many more Chinese sites yielding stone tools, but lacking hominin fossils, attest to the possible interactions of prehistoric human populations and stegodonts. To date, there are no localities that resemble the proboscidean single carcass sites in other regions where the remains of largely intact carcasses are associated with stone tools (Gaudzinski et al 2005). The use of stegodonts (and other species) as food resources is generally assumed, but few of the Chinese faunal assemblages have been critically evaluated to assess whether there is specific evidence for hominin exploitation of the animals.

Gaudzinski et al (2005), in their review of Palaeolithic uses of proboscideans, determined that there is limited direct evidence for use of elephants as food sources. While this may be due to the decreased likelihood of stone tool cutmarks on such large-bodied and thickskinned animals, a striking finding of their survey was the growing body of evidence that elephants were exploited as raw material sources. Increasing numbers of sites in Europe and North America are yielding tools made on proboscidean bones and tusks. These artefacts were often fabricated using the same production techniques applied to lithic raw materials. More common uses of proboscideans include the Upper Palaeolithic ivory art objects and structures comprised of mammoth bones. At Panxian Dadong, we found interesting differences in the age-at-death profiles for the rhinoceroses and stegodonts that may reflect their relative importance as food and raw material sources. To explore this possibility, we evaluate the Dadong results by comparing them to faunal assemblages from a palaeontological locality and other archaeological sites. We also consider how proboscidean and rhinoceros ecology and body size may contribute to our findings.

2 Environmental record, chronology and taphonomic considerations

2.1 Setting and stratigraphy

The western part of the Guizhou Plateau where Panxian Dadong Cave is located is composed of Carboniferous and Permian limestones, basalt, shale, sandstone, and coal formations. The general elevation ranges between 1400 and 2000 m. The cave is a sinkhole formation that resulted from neotectonic uplift and the drainage of underground rivers. The Dadong deposits are a good candidate for palaeo-environmental reconstruction for several reasons. The deposits form a small low angle fan that is directly connected to the entrance and the outside environment. Therefore, the main source of sediment input is well defined and the sequencing of flowstones versus clastic deposition that occurred in Dadong is considered excellent for reconstructing environmental conditions in caves. Capping flowstones preserved the integrity of the stratigraphy and prevented postdepositional mixing and slumping (Karkanas et al 2008).

The northern profile of the excavation (figure 2) illustrates this sedimentary sequence of clastic sediments with thin intercalating capping flowstones and a top layer of thick flowstone. In the lower parts, the clastic sediments are mainly massive silts changing to alternating bedded gravels, clay-rich deposits, and boulder lags. At Dadong, extensive flowstone formations and intercalated clastic sediments are closely associated with intensive freeze-thaw activity. This reflects cold and wet environmental conditions. By contrast, clastic sediments are lacking in the eastern profile. The iron and manganese crust preserved in these strata is the result of bacterial activity and the breakdown of organic material. These layers were formed under probable humid warm climatic conditions when the soil on the hills above the cave was



Figure 2 Northern profile. Note the fine-grained nature of the lower part, the boulder and gravel-rich middle section, and the flowstone formations of the upper part. The total height is 5 m. (From Karkanas et al 2008)

stable enough to support a tree cover (Karkanas et al 2008).

2.2 Chronology and palaeoclimate

Absolute age estimates for the sedimentary deposits of Dadong include Uranium-series ages from speleothems and coupled Electron Spin Resonance (ESR)/U-series ages for fossil teeth. The oldest speleothem formations from the lower part of the clastic sequence averaged to about 330 ka (Shen et al, 1997). These sediments accumulated during a glacial period, Marine Isotope Stage (MIS) 8, when seasonal freezing temperatures through the winter months prevailed in the cave. Frost action was interrupted by humid, probably milder periods where calcite was deposited in frost cracks, and there was a variable water table. The densest accumulations of anthropogenic material occur in these layers. As we move up in the sequence, coupled ESR/U-Th dates on mammalian teeth suggest a minimum age of about 157 ka placing the formation of these sediments within glacial MIS 6. The uppermost cap of the flowstone is dated with U-Th to ca 130 ka (Rink et al 2003, Jones et al 2004). Thus, the main part of the flowstone corresponds to the lower part of MIS 6. A sample from the uppermost layer preserved 10 cm of the flowstone that is not affected by frost action. This suggests that flowstone formation continued into the ensuing interglacial but with reduced intensity.

The Dadong sedimentary record supports the scenario of high effective precipitation during intervals of the glacial periods. These were also characterised by low temperatures and reduced vegetation cover. This contrasts with the other speleothem studies in the area that record enhanced precipitation only during very warm interstadials. This difference is observed because Dadong is situated at the boundary between the Indian and east Asian monsoons and belongs to a different precipitation regime than the rest of subtropical southern China. The cave sequence provides strong indications of enhanced monsoons during glacials with temperatures much lower than today.

2.3 Taphonomy and depositional environment

The faunal record at Dadong provides additional evidence for the climatic conditions prevailing during the formation of the deposits. The frequent intercalation of flowstones and calcified and non-calcified clastics, with the former building extensive caps on the underlying clastic deposits, assures that artefacts and bones are more or less contemporaneous with the enclosing strata. Formation processes of each layer, however, include transport and reworking along distances restricted to their lateral and horizontal extensions. Some crude lateral sorting is evident from a preliminary analysis of the sizes of the bone in each layer, although taphonomic surface analysis of the assemblage precludes extensive post-depositional alteration of the fauna.

Nevertheless, during interglacials the combina-

tion of reduced sedimentation, enhanced bacterial activity, and the associated production of acidic waters would have resulted in the dissolution of bones accumulated on the cave floor. Interestingly, there are no indications of enhanced dissolution of the carbonates (limestone clasts, flowstones, etc). Furthermore, widespread chemical alteration in the form of phosphate mineralisation that normally occurs in cave environments, and is partly attributed to bone dissolution, is not recorded in any of the Dadong layers. Some smaller bones that accumulated during the formation of the weathering crusts might have dissolved away, but the evidence does not support dissolution to any extent that would alter the faunal composition (results of analysis by P Karkanas, personal communication 2006).

In a previous study (Paraso et al 2006), we examined the spatial and temporal relationships among all of the excavated materials (stone, bone, teeth and charcoal) from six 2m x 2m squares, the deepest of which represents 4m of deposits. Our goal was to evaluate changes in archaeological materials over time by comparing high and low density layers in order to distinguish patterns that might reflect the natural sedimentation processes or human activities. Figure 3 illustrates



Figure 3 Two dimensional plot of artefact (lithics, bones and teeth) position by excavation depth (z) along a north-south axis. North is to the right. Unit squares (for example, I46) are 2x2 metres. Note that most artefacts are from depths ranging between 94.25 and 96.5 m

the vertical distribution of all piece-plotted materials and the density differences at specific levels in the excavation. We determined that the upper levels were significantly richer in basalt and chert artefacts; these levels also contained significantly greater frequencies of bone with cut marks, percussion damage and burning. We interpret this as probably indicating an increased intensity in the occupation of the cave, but we recognise that assigning a single causative factor to these patterns is not straightforward.

Karkanas et al (2008) reported evidence for freezethaw activity and depositional hiatuses that surely affect the patterning of archaeological materials through the Dadong deposits. A comparison of two trenches in the cave suggests that unconformities are not always of the same duration. Sedimentation can occur in some areas while a depositional hiatus is taking place elsewhere. This makes the interpretation of anthropogenic versus non-anthropogenic factors quite complex. In addition, it was apparent that deposits close to the cave walls were subject to a greater degree of rock debris and fragmentation from roof fall and wall erosion, in part as a result of drainage patterns during heavy rainfall. In the field and in the laboratory analyses, P Karkanas observed that sorting of sediments took place laterally from the cave walls toward the center of the main chamber, probably reflecting these natural weathering processes (as seen in the distribution of artefacts in figure 3).

This very complex depositional environment constrains our interpretation of the archaeological materials. While we demonstrated a differential representation of raw material through time (Miller-Antonio et al 2004), we do not regard the evidence at Dadong as specifically indicative of its use as a workshop for the manufacture of basalt and chert tools or rhinoceros tooth tools. We do hypothesise that humans utilising the cave were experimenting with a variety of raw materials that could have included stone resources, faunal resources, and perhaps other materials like hardwoods and bamboo.

3 Materials and methods

3.1 Sample composition and age-at-death

The mammalian faunal sample from Dadong (n= 7045) consists of 3.3 per cent skull fragments, 12.5 per cent isolated teeth and 84 per cent postcranial elements. The sample is primarily characterised by fragmentary bone, and there are very few articulated

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elements. For our studies of the rhinoceros and stegodont elements, we followed the following procedures to construct age-at-death profiles:

- 1 assignment of teeth to wear stages
- 2 use of wear stages and developmental/eruption data to create age cohorts
- 3 bar graph plots of population age structure to evaluate the mortality profiles (following Haynes's [1991] modeling of proboscidean data).

Due to the limited sample sizes that result when the assemblage is divided by stratigraphic levels, and the relatively unrefined scope of our chronometric dates, we analysed the faunal components as a single sample. We assumed that time averaging would affect our study but negate some of the effects of using the entire sample (cf Haynes 1991). Initial analyses of temporally subdivided components suggest that the demographic and skeletal element patterns discussed below are characteristic of the entire sequence, although a few factors, such as bone versus tooth representation, show some differences by stratum.

Rhinoceros material is found throughout the Dadong sequence. 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 or os petrosum 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). Among these, phalanges are the most frequently recovered elements. From the total number of identified specimens (NISP) of 285 rhinoceros elements, we analysed 224 specimens identifiable to tooth class or skeletal element (the remaining 61 elements are tooth fragments). The sample consists of teeth (n=121 or 54 %), skull (n=3), and postcranial elements (n=100). An MNI based on the most numerous dental elements and their developmental co-occurrence in the same dentition is 11 individuals. Using a system of dental attrition and dental eruption, we were able to construct an age-at-death profile from the dental elements with five age classes: neonate, early juvenile, late juvenile, subadult, and adult. The Dadong rhinoceros component has a predominance of prime age adults (figure 4) (Schepartz & Miller-Antonio 2010).



Figure 4a



Figure 4b

The stegodont elements are similarly found throughout the Dadong strata. The sample consists of 215 isolated or fragmentary teeth, four skull fragments (the most numerous single element), and 38 postcranial elements yielding an NISP of 257. The postcrania include 10 axial elements and 28 appendicular elements, with foot and ankle elements as the most numerous category- as seen in the rhinoceros elements. However, that is where the similarities in the representation of these two genera end. Isolated teeth or tooth fragments are the dominant elements (over 81 per cent, as compared to slightly over half for the rhinoceroses). This difference is undoubtedly due to the fragile nature of stegodont teeth. The molars and premolars are composed of buccallingual or transverse crests (lophs) with intervening valleys that are common postmortem fracture sites.

Figure 4 Comparative age-at-death profiles for; (a) Dadong rhinoceroses and, (b) stegodonts. The y-axes are individual counts. The x-axes are age cohorts

During life the teeth wear down anteriorly and can fracture there as well. Thus, through normal dental attrition and postmortem taphonomic damage, the larger teeth with more crests are likely to be over-represented in analyses using fragmentary elements. The stegodonts also present a very different age-at-death profile in comparison with the rhinoceroses. The great majority of the teeth (approximately 75 per cent) are from the youngest animals in the 0–12 year cohort. Only two of the remaining 48 teeth can be definitively assigned to the 25–36 and 37–48 year cohorts; the others could be from animals between 13 and 60 years (figure 4) (Schepartz et al 2005).

The age-at-death profiles for the stegodonts and rhinoceroses are clearly different, and they appear to represent different population mortality models. A profile that has a predominance of prime-age adults

(termed Type C), as seen for the rhinoceroses, results from selective mortality affecting males only (for example, killings by hunters interested in ivory or antlers), or from non-selective mortality affecting declining populations (Haynes 1991). The question is whether the Dadong rhinoceroses are prime age animals rather than older, more vulnerable individuals. The dental sample lacks M3s in late stages of wear. We interpret this as an absence of teeth from advanced age adults and a predominance of teeth from prime individuals (see also Borsuk-Bialynicka 1973:15, table 4). There is also a sizeable representation of late juveniles and subadults - those who are presumably inexperienced and vulnerable to predation when they are no longer travelling under their mother's protection (Foster 1965). In contrast, the stegodont profile is either Type A or Type B of Haynes's classification. Type A is characterised by the greatest portion of individuals in the first category of subadults with each successive category represented by decreasing proportions. This pattern results from nonselective mortality in stable populations. Type B is bimodal. Although subadults predominate in this type as in Type A, there are few prime age adults. This type of profile results from selective mortality affecting mixed herds. Even if it were possible to assign all the stegodonts molars to age cohorts, as discussed above, the sample would still have a distribution that has predominantly younger individuals.

3.2 Research questions

In order to further investigate the different representation of these two genera, the following questions will be considered:

- 1 are there differences in the size and portability of carcasses or carcass elements that might explain the differences in the age-at-death profiles
- 2 are there ecological or demographic factors that might explain the age-at-death profiles
- 3 do other studies confirm the patterns observed at Dadong?

4 Results

4.1 Body weight and social group comparisons

Differences in the body weights of stegodonts and rhinoceroses may bear upon the patterns observed at Dadong. If these large animals died outside the cave (the most likely scenario), then it is unlikely that adult animals would be brought into the cave as complete carcasses. Processing and transportation of the carcass portions (the so-called schlepp factor) should be influenced by animal body size.

Asian rhinoceros species range from the smallest Sumatran rhinoceros (600–950 kg; 1–1.5 m shoulder height) and the Indian *R. unicornis* (similar in weight to the large African white at 1800–2700 kg, but slightly taller [1.75–2 m at the shoulder]) to the rare Javan *R. sondaicus* at 900–2300 kg and measuring 1.5–1.7 m at the shoulder (International Rhino Foundation Fact Sheet 2010). Rhinoceros infants weigh between 27–55 kg and grow rapidly. Some species reach over 450 kg in their first year.

Colbert and Hooijer (1953) regarded *R. sondaicus* as representing a model for the *R. sinensis* ancestor, and *R. unicornis* as the derived form. *R. sinensis* teeth are variable in size and are similar to both *R. unicornis* and *R. sondaicus* for certain measures although *R. sondaicus* teeth are usually smaller. Based on the humerus or femur, it appears that *R. sinensis* may have been shorter and somewhat lighter than the living Asian species. An estimate of 2000–2300 kg would seem a reasonable approximation for male adults.

Modern elephants are significantly larger than rhinoceroses and they are among the most sexually dimorphic mammals. Asian elephants, *Elephas maximus*, are smaller than the African forms. Females are typically 3000 kg, while bulls are 5000 kg and shoulder heights range from 2.5–3 m. Elephants infants are typically 100 kg (Meyers et al, 2008). Some stegodonts were among the largest of the extinct proboscideans. *S. orientalis* was not among the biggest, but it was probably similar in weight to *E. maximus* although somewhat shorter and stockier (**Osborn 1934**, Shoshani & Tassey 1996). *S. orientalis* bulls would be approximately twice the size of *R. sinensis* bulls.

The other factor to be considered is the social grouping of the animals. Modern rhinoceroses are typically solitary feeders. Lone bulls and satellite males have ranges that overlap with the females and their young. Females reach maturity at five to seven years while males are not independent until ten years (Dinerstein 2003; International Rhino Foundation Fact Sheet 2010). This type of social organisation would make *R. sinensis* easier animals to exploit than the larger and more social stegodonts— if we assume that stegodonts, like all known proboscideans, lived

in groups comprised of several adult females and their sexually immature offspring (Sukumar 2003). The presence of numerous adult females and other subadult group members would have provided protection for infant stegodonts. Solitary males who periodically associate with the female groups would have been more vulnerable to predation, but their large body size would have generally discouraged prehistoric hominins from hunting them.

How do these data on body size and social groupings inform our analysis of the Dadong assemblage? We would predict that only the most valued portions of stegodonts would be transported, and most meat would be removed from a carcass at the site of death. Skulls might be exploited for the tongue and masticatory muscles, but only infant skulls would possibly be transported. Few postcranial bones would be expected in the Dadong fauna if stegodonts were used as a source of protein. However, the size of infants would not preclude their transport back to the cave as complete or nearly complete carcasses. Bones and molar teeth of adults would be much less likely to be represented because of their bulk and the difficulty of separating them from the carcass. Conversely, adult rhinoceros elements would be more likely to be transported. Only the more easily detached parts of the carcass, such as lower limbs elements (carpals, tarsals, metapodials, phalanges), would be expected in any quantity. Infant rhinoceros were also light enough that they could have been transported whole. Finally, we would predict the least representation of axial elements and upper limb portions for both of these species if whole animals were not present in the cave.

Different element frequencies would be predicted if stegodonts and rhinos were exploited for their value as raw material for tools rather than for their meat and fat. Proboscidean tusks, molars, long bone diaphyses, and ribs have been used in this manner (Gaudzinski et al 2005). Rhinoceros molars (Miller-Antonio et al 2000) and long bones could potentially have been sources of raw material in China, where lithic material in archaeological contexts is often of poor quality for knapping.

Figure 5 presents the proportional distribution of rhinoceros and stegodont skeletal elements. This comparison is interesting in light of our predictions. Stegodonts are most frequently represented by carpals and tarsals, but the relative scarcity of metapodials and phalanges is not expected. One possible explanation might be that those elements were processed for their marrow, and thus rendered unidentifiable, while the cancellous-filled carpals and tarsals were not. Several of the axial elements are from immature individuals, as are the majority of the dental elements. None of the stegodont elements have evidence of human processing, but five (approximately 3 per cent) were gnawed by porcupines. The rhinoceros skeletal elements are dominated by adult



Figure 5 Proportional distribution (%) of Dadong rhinoceros and stegodont skeletal elements. The Y-axis is %

foot elements, as would be predicted if meaty lower limb portions were transported back to the cave. Two of the three femurs are juvenile. A distal radius has a clear concentric compression area that is indicative of hominin processing (Schepartz & Miller-Antonio 2010), but no cutmarks are visible on the rhinoceros bones. Approximately 10 per cent of the bones and teeth have rodent or porcupine gnawing and one metapodial exhibits carnivore damage. Evidence for the action of natural forces, such water-rounding and weathering, is fairly rare for both the rhinoceros and stegodont bone elements (and for the entire assemblage), suggesting that these factors played a relatively limited role in shaping the Dadong assemblage (Schepartz et al 2003).

4.2 Comparison with other localities

One palaeontological locality that provides information about young stegodont vulnerability is Yanjinggou in Sichuan Province, China where the stegodont component is predominantly very young animals (Colbert & Hooijer 1953). The fossil assemblage was formed when animals fell into natural fissures. The traps seem also to have attracted many opportunistic carnivores, but there is no evidence for human activity (Bakken 1997). The Yanjinggou fauna provides evidence that the youngest stegodonts were more likely to be trapped, but the assemblage cannot be used to evaluate the expected proportions of skeletal elements because there was systematic collecting bias favoring highly diagnostic elements.

There may have been similar fissures in the Panxian Dadong karstic region during the Middle Pleistocene. Dadong itself was a large, high-ceilinged cavern by that time, based on the dating of a large stalacto-stalagmite that had formed in the interior (Shen et al 1997). Young stegodonts may have become trapped or mired after wandering into the cave (J Shoshani pers comm 2001), but this seems unlikely during the times when humans were active there and the passage was dry (Karkanas et al 2008). Proboscidean dung has been recovered from dry cave sites in North America (Haynes 1991) and it may be inferred that they were seeking mineral salts from the sediments. With the abundant drainage systems on the Guizhou Plateau and in the Dadong valley (Karkanas et al 2008), stegodonts would probably not have had to venture into the cave to obtain water, but it might have been an attractive source of necessary sodium and calcium (Redmond 1982).

More comprehensive comparisons can be made with faunal assemblages from archaeological sites. An interesting case is the Late Pleistocene (95–12 ka) site of Liang Bua, famous for the diminutive *Homo floresiensis* remains. There is a sizeable *S. florensis insularis* subsp. nov. dwarf stegodont component that is associated with the hominins and stone tools (Van Den Bergh et al 2007). The stegodont NISP is 231 and



Figure 6 Comparison of stegodonts at Dadong and Liang Bua

	Dadong	Dadong	Liang Bua	DV I	DV I 5-8	DV II	Milovice
	Rhino	Steg	Stegodont	Mammoth	Mammoth	Mammoth	Mammoth
Skull	2.9	11.1	44.4	5.2	11.1	5.2	17.6
Sternum	0	2.8	0	0	0	0	0.2
Scap	1	0	10	6.6	11.9	3.4	7.2
Hum	2	2.8	3.7	6.1	12.4	2.6	5
Radius	2.9	5.6	1.2	3.5	2.2	0.9	2.7
Ulna	1	0	3.7	6.7	4.9	0	2.3
Vert	0	5.6	12.3	17	4	38.8	18.6
Innom	0	2.8	3.7	6.6	25.7	8.6	8.5
Femur	2.9	11.1	5	5.9	9.7	5.2	4
Patella	0	2.8	1.2	2	1.3	0	0.5
Tibia	3.8	2.8	2.4	5.7	5.3	5.2	4.7
Fibula	0	2.8	0	2.9	3.1	0	3.3
Carp/Tars	23	38.9	2.4	22.7	6.6	13.8	12.1
Metapod	20.2	5.6	7.4	0	0	10.3	8
Phalanx	40.4	5.6	2.4	9.3	1.8	6	5.3
NISP	104	257	81	1128	226	116	601

 Table 1
 Proportional representation of select bone elements

consists of 15.6 per cent skull and 65 per cent dental elements. In comparison with the S. orientalis remains from Dadong (figure 6 & table 1), the Liang Bua sample is characterised by many cranial elements and more axial elements (ribs are omitted from this comparison as exact numbers are not available, but they are described as being plentiful). Only 26.7 per cent of the 45 postcranial elements were from adults. Van Den Bergh et al, (2007) suggest an MNI of 47 individuals; 94 per cent were juveniles and 23 per cent of these were neonates. There is at least one vertebral fragment with cutmarks. Some of the elements display dissolution features on one side only. This is interpreted as possible evidence of diagenetic changes that might have resulted in the loss of more porous bones and juvenile elements. The higher frequencies of cranial and axial elements from young stegodonts at Liang Bua are more suggestive of entire carcasses in the cave, rather than the transportation of select body portions. Even the small Homo floresiensis individuals should have been capable of carrying entire neonate or younger dwarf stegodonts. The differences between the Dadong and Liang Bua stegodont assemblages might reflect a greater emphasis on stegodonts as a protein source at Liang Bua due to more successful abilities to exploit the animals at this temporally later site.

It is informative to compare the Dadong rhinoceros and stegodont components with European sites that have evidence for intensive exploitation of megafauna communities. While such localities are potentially important for our purposes, the complexity of using other's data makes such comparisons challenging. Unfortunately, we found no data on rhinoceros components that are directly comparable to the Dadong assemblage, but there is growing evidence that large rhinoceros genera were exploited by hominins. For example, the Middle Palaeolithic mammal assemblage from Taubach, Germany includes at least 76 rhinoceros individuals (mostly *Stephanorhinus kirchbergensis*). Over 1200 elements were analysed and 8 per cent of these were cutmarked. The pattern of cut-marking indicates selective exploitation of the tongue, removal of the head, separation of the lower limb segments, and meat removal from the long bones and feet. The largest age class was 1-year olds (33 per cent) (Bratlund 1999). Despite some problems with sample biases, Dusseldorp (2009) suggests the site may also reflect hominin hunting of other megafauna including proboscideans.

Recent investigations of some mammoth faunas in Europe provide much relevant data that can be directly compared with Dadong. The Mammuthus primigenius sample from the Vogelherd Aurignacian deposit contained an estimated 28 mammoths (Niven 2001). Cranial elements comprise 72.4 per cent of the skeletal sample, and approximately 2500 ivory fragments were also recovered. This would suggest that the skulls, in addition to the meatier portions of the body, were valued. The age-at-death profile reflects the presence of many young animals along with adults from all age cohorts. Younger adults (13-36 vears) are the least represented groups. Niven (2001) considers the Vogelherd mammoth assemblage as example of the probable use of proboscideans for raw materials. fuel. and food.

Four Moravian Gravettian (Mid-Upper Palaeolithic) faunal assemblages have been re-examined. Three bone heaps from Dolní Vêstonice and a mammoth 'hut' site at Milovice were compared (Svoboda et al



Figure 7 Proportional representation (%) of select bone elements. Ribs are omitted from the analysis. Dadong Rhino= Panxian Dadong Rhinoceros sinensis, Dadong Steg= Panxian Dadong Stegodon orientalis, Liang Bua Steg= Liang Bua Stegodon florensis insularis subsp. nov, DVI Mammoth= Dolní Vêstonice I Mammuthus primigenius, DVI 5-8 Mammoth= Dolní Vêstonice I Kjökkenmöddings (bone deposit) 5-8 Mammuthus primigenius; Milovice Mammoth= Milovice G Mammuthus primigenius

2005). These assemblages, with their representation of skeletal elements in nearly expected anatomical frequencies, provide evidence for exploitation of entire mammoth carcasses rather than selective transportation (table 1; the most frequent elements are highlighted in bold). The contrasts with the Dadong stegodon and rhinoceros components are clearly indicated by the differences in vertebral and innominate representation at the European sites (figure 7 & table 1) – in contrast to the most numerous distal limb elements at Dadong.

5 Conclusions

The analysis and interpretation of faunal assemblages is complicated by many factors that can produce confusing mortality profiles and skeletal element representations, or obscure the evidence for hominin exploitation. The rhinoceroses and stegodonts at Panxian Dadong have relatively similar frequencies of specific skeletal elements, but their age-at-death profiles are quite different. In the absence of significant carnivore use of the cave, differential exploitation by hominins may be the major cause of these differences. Based on the evidence from extant taxa, we would predict that the group-living stegodonts would be more difficult to hunt and their larger body size would make carcass processing more labour-intensive. Fewer of the adult elements should be transported to the cave, although portions of the very young might be of manageable weight. The higher frequencies of young stegodont teeth (and cranial portions at Liang Bua) might be a by-product of transporting the skulls for the tongues, musculature, tusks, and teeth. The possibility that proboscidean bone might also be of value as a raw material for tools, as documented in later European sites, needs to be explored further.

The rhinoceros bone component at Dadong is basically consistent with the selective schlepping of meaty distal limb segments from large, prime age adults. However, the predominance of teeth requires further explanation. Teeth could have been brought into the cave simply because they were components of skulls that were processed for their tongues, marrow and fat; they could have been valued as raw material; or they could merely be 'over-represented' due to their high durability.

The European megafaunal assemblages, with their great numbers of identifiable individual animals, highlight the differences in element representation at Dadong, where it is likely that complete carcasses of large adult animals were never present.

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