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STONE AGE INSTITUTE PUBLICATION SERIES

NUMBER 2

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# BREATHING LIFE INTO FOSSILS:

Taphonomic Studies in Honor of  
C.K. (Bob) Brain



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COVER CAPTIONS AND CREDITS.

*Front cover, clockwise from top left.*

*Top left:*

*Artist's reconstruction of the depositional context of Swartkrans Cave, South Africa, with a leopard consuming a hominid carcass in a tree outside the cave: bones would subsequently wash into the cave and be incorporated in the breccia deposits. © 1985 Jay H. Matternes.*

*Top right: The Swartkrans cave deposits in South Africa, where excavations have yielded many hominids and other animal fossils. ©1985 David L. Brill.*

*Bottom right: Reconstruction of a hominid being carried by a leopard. © 1985 Jay H. Matternes.*

*Bottom left: Photograph of a leopard mandible and the skull cap of a hominid from Swartkrans, with the leopard's canines juxtaposed with puncture marks likely produced by a leopard carrying its hominid prey. © 1985 David L. Brill.*

*Center: Photo of Bob Brain holding a cast of a spotted hyena skull signed by all of the taphonomy conference participants. © 2004 Kathy Schick, Stone Age Institute.*

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# CHAPTER 7

## ARE YOU IN OR OUT (OF AFRICA)? SITE FORMATION AT DMANISI AND ACTUALISTIC STUDIES IN AFRICA

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MARTHA TAPPEN, DAVID LORDKIPANIDZE, MAIA BUKSHIANIDZE, REID FERRING AND ABESALOM VEKUA

### ABSTRACT

Researchers from all over the world use the actualistic studies conducted in Africa to interpret the formation of faunal localities. Aspects of applying African models to the early Pleistocene faunas from Dmanisi in Georgia are discussed. Currently, there is no compelling evidence that the mammalian taxa from Dmanisi migrated from Africa at the same time as *Homo*. Preliminary analyses of taphonomic and stratigraphic evidence indicate that Dmanisi has a complex, but not a long taphonomic history. Several taphonomic agents were involved in modifying the fauna and hominin fossil assemblage, rather than one agent predominating, yet the bones accumulated relatively rapidly. Hominins left cut marks, carnivores left tooth marks, and porcupines gnawed some of the bones. Many specimens seem to have little alteration at all, including no weathering, no evidence for geologic transport (rounding or microstriations), and remain as articulated subunits, but not as whole animals. In many ways Dmanisi does not fit classic models of human habitation sites, hyena dens, or mass death sites. Specifically, the areas excavated at Dmanisi so far do not have enough stone tool damage to be primarily accumulated by hominins, nor do they have as much carnivore tooth scoring as modern dens. Detailed spatial analysis of taphonomic modifications is still underway, and may allow spatial parsing of the site into areas by taphonomic agent.

### INTRODUCTION

The interpretations of fossil bone assemblages derive from observations of the taphonomic journeys of present day animal remains. While actualistic studies

of taphonomy are conducted all over the world, most have been conducted in Africa, where parks conserve relatively healthy ecosystems retaining large carnivores that are key preburial taphonomic agents, and where the early archaeological record begins. But how universally can the observations from actualistic studies conducted by Africanists be applied to localities outside of Africa? Which features of bone accumulation and modification are robust enough to be generalized, with constrained amounts of variation possible or probable? This question is important to untangling the ecology of hominins and the taphonomic histories of early Palaeolithic sites found outside of Africa, and gets to the heart of factors that allowed the original range expansion into higher latitudes, because it requires precise paleoecological and behavioral reconstruction. Was the initial spread of *Homo* beyond the australopithecine geographic range due to the spreading of African-like biomes, or was it due to novel, intrinsic behaviors of *Homo*? In this paper we discuss some of these issues, and make some comparisons between the paleoecologic and taphonomic record of the early Pleistocene site of Dmanisi, in Georgia (Trans-Caucasus), and actualistic taphonomic studies in Africa. We outline some of the major taphonomic characteristics of Dmanisi, and argue that the signature from the site as a whole is not a good match for our archetypal models of bone formation processes of hominin sites, carnivore dens, or porcupine dens. We compare some key taphonomic features to time-averaged attritional death bone deposition studies as models for predation arenas from Africa to Dmanisi. While there are still more analyses to conduct, the predation arena model also does not fit Dmanisi's signature in some key ways.

## DMANISI: GENERAL BACKGROUND

Dmanisi is located around a thousand miles from of the NE tip of Africa at 41° N latitude, south of the Caucasus Mountains in Georgia. Numerous hominin fossils have been found in direct association with a large assemblage of mammalian fauna and simply flaked stone tools. David Lordkipanidze leads the excavations with an international team of principal investigators including the authors of this paper, with Philip Rightmire of SUNY Binghamton, Marcia Ponce de Leon and Christophe Zollikofer of the University of Zurich, and others. The hominin occupations date to the earliest Pleistocene, shortly after the Olduvai Normal Subchron which ended at 1.78 mya (Van Couvering, 1997). Geological and paleobiological evidence suggests that these levels with Mode 1 tools date to before 1.7 mya, and are closer to 1.77 mya (Gabunia and Vekua, 1995; Gabunia et al., 2000; Vekua et al., 2002).

Today rainfall, seasonality and habitat characteristics in Georgia vary greatly with elevation and from west to east. Eastern Georgia tends to be drier and have a more continental pattern, while in Western Georgia the weather has a more Mediterranean pattern. The site is in the South Central region (Kvemo Kartli Province) at an elevation of 915 meters above sea level. The region around Dmanisi has a good deal of topographic relief with hills and valleys that would have enhanced the potential for a mosaic of habitats, and the fauna indicate there were both wooded and open areas (Gabunia et al., 2000). Dmanisi is an open air site on a promontory overlooking the confluence of the Pinazauri and Mashavera rivers. These rivers have eroded down, in place, through 80–100 meters of basalt since the early Pleistocene, leaving the site high above them today (Figure 1).

Determining what processes accumulated the fossils



Figure 1. Dmanisi Promontory, above the confluence of the Mashavera and Pineazauri Rivers. The Medieval fortress and church can be seen in the back of the isthmus, the Paleolithic excavations are located in the middle of the plateau among the trees. With thanks to Ken Garret.

is the core taphonomic question at Dmanisi. The site has eight species of large predator in direct association with *Homo erectus sensu lato*, thus Bob Brain's celebrated question of "The hunter or the hunted?" is immediately *apropos*. Interestingly, there are several other analogies to the South African karstic cave sites that Brain so carefully deciphered: some of the bones accumulated in underground hydraulically formed pipes that eventually breached the surface, which can be thought of as mini-analogs to karstic cave formation, and many of the bones were introduced into the pipes by predators.

The stratigraphy of the site is being worked out by Reid Ferring of the University of North Texas, with preliminary dating by Carl Swisher, and detailed work continues. On top of basalt that dates to within the Olduvai subchron, there are two main strata, A and B. The A layers are normal and from within the Olduvai subchron, and the B layers were deposited immediately after this; they have reversed polarity and so post-date 1.78 myr. A series of hydraulic pipes formed within the A sediments, creating tunnels that then were filled with bones as well as reversed B1 sediment. Microstratigraphic analysis by Ferring indicates that pipes filled and some collapsed, forming low spots and then small drainage runnels. As of now, his evidence indicates that most of the hominins as well as artifacts and the majority of the fauna come from within these pipes and from on top of pipes that had collapsed and thus would have been low-lying land surfaces and small sediment traps when bones were deposited. The B2 stratum sediment that was deposited above also contains fauna and Mode 1 tools. Later a post depositional carbonate zone (K) was formed that sealed in the lower deposits of the site, especially the lower pipes and pipe collapses, protecting the bones from compaction and preserving them well (Vekua et al., 2002, Figure 2). It seems that the complex configuration of the microstratigraphy at the site was caused by the very complicated configuration of the surface of the underlying basalt, causing the small drainages and pipes to form. Bones accumulated in especially dense concentrations where the basalt is low lying.

## BIOGEOGRAPHY OF THE DMANISI LARGE MAMMALS

The species composition of the fauna is the first evidence we address about both site formation and environments at Dmanisi. Did the Dmanisi hominins migrate out of Africa because of an expansion of African biomes, or from the agency of cf. *Homo erectus* itself? In the recent deliberations regarding the migration of hominins out of Africa, several mammalian paleontologists have discussed the importance of associated African faunas. For example, Tchernov suggested that "any hominid dispersal was a natural part of any emigration until the late Upper Pleistocene period." (Tchernov, 1998:80). Turner likewise stated that "The dispersion of *Homo* can be seen as part of larger pattern of dispersion by members of the

terrestrial mammalian fauna” (Turner, 1999). Rook (2004) has also pointed out a movement of African species, including *Megantereon*, *Theropithecus*, and *Hippopotamus* and suggested an association with *Homo*.



**Figure 2.** Excavations in 2003 in Block 2 at Dmanisi. At the top right in the lighter color sediments students can be seen excavating in the B2 sediments. Below this the carbonate layer can be seen. In the foreground, Georgian excavator David Takakishvili (in striped shirt) can be seen excavating in the darker B1x and y sediments. Just to the right of Takakishvili's shoulder is a round excavation pit where the skull 3444 was taken out in a block of sediments. He is sitting on the basal basalt, and the very rough, irregular and unweathered surface of the basalt is readily visible.

The association of African faunas with *Homo* out of Africa has been considered significant for several reasons, but especially because ‘Ubediya in the Levant was long been considered one of the earliest sites out of Africa, and it does indeed have African elements in its fauna, such as *Kolpochoerus olduvaiensis*, *Hippopotamus gorgops*, *Pelorovis olduwayensis*, *Crocota crocuta*, (Tchernov, 1992a, 1992b, 1999) and *Theropithecus* (Belmaker, 2002) although by far most of the fauna is Eurasian. These forms indicate a significant flow out of Africa into this corner of Eurasia, but this site is probably at least 400,000 years later in time than Dmanisi, and evidently represents a later dispersal event. These African species are also in Italy and Spain (at Pirro Nord, Fuente Nueva-

3 and Barranco Leon-5), but these sites likewise may be later in time than the Dmanisi. There is evidence for several influxes of hominins with fauna from Africa with later hominins also, for example the dispersal of early modern humans at Qafzeh are associated with an influx of African forms (Tchernov, 1998). But as discussed below, these associations are not in evidence for the expansion represented at Dmanisi.

Since the docking of Africa with Eurasia in the Early Miocene, there have been various moments when transfer of faunas was encouraged or discouraged by marine transgressions, the relative aridification of the Arabian Peninsula, and the Taurus-Zagros orogeny (Tchernov, 1998). There are several dispersals of African mammals that could be associated with the dispersal of hominins. In particular between 3.1-2.6 million years ago several bovid species spread out of Africa into Asia (Vrba, 1995). During this time there was a major retreat of the seas, called the ‘Acquatraversan erosional phase’ correlating with the ‘Elephant-*Equus*’ event in Eurasia (Azzaroli, 1995). Turner likewise stressed the late Pliocene as a time when hominin dispersion was most feasible (Turner, 1999). In this paper we take on the question with the perspective that if *Homo* spread due to a general emigration or spread of African savanna species and biomes, there would be several other large mammal species found at the site that had evidently had made it out of Africa about 2-1.7 million years ago. We therefore are addressing this question here from a strict and literal point of view: that the Plio-Pleistocene border was in fact the time when *Homo* made it out of Africa, and not earlier. There is a reasonable possibility that we will find earlier hominins, perhaps at the origins of tool use around 2.5 mya in Eurasia in the future, but here we proceed with the evidence that exists as it does today using the fauna directly associated with *Homo* at Dmanisi.

So are the Dmanisi large mammals directly from Africa (did these species recently emigrate to Eurasia)? Table 1 presents the current list of fauna identified from the Lower Pleistocene strata at Dmanisi. The list of taxa present is not yet static as each year of excavation we have found new species. For example, there are several new bovid species identified by Maia Bukhsianidze in the last year. Furthermore, some taxonomic assignments may be revised and more precisely defined as more and more detailed analyses take place within each taxon. Even with these caveats, important observations can be made about the Dmanisi taxa.

Starting with the herbivores, one can see immediately that for many of the lineages, such as the Equidae, Rhinocerotidae and Cervidae, an African origin is out of question. The stenoid representatives of the genus *Equus* Linnaeus, 1758 first appeared during the early Pliocene in North America. In the early Villafranchian they entered Eurasia (about 2.6 myr), where they passed through an adaptive radiation that led to the gradual displacement of the hipparions, that had been common until then, and then through Eurasia entered into Africa (Agu-

Table 1. Large mammal taxa from Dmanisi

Perrisodactyla OWEN, 1848
Equidae GRAY, 1821
<i>Equus stenonis</i> COCCHI, 1867
<i>Equus</i> sp. aff. <i>altidens</i> REICHENAE, 1915
Rhinocerotidae OWEN, 1845
<i>Stephanorhinus etruscus etruscus</i> GLOGER, 1841
Artiodactyla OWEN, 1848
Cervidae GRAY, 1821
<i>Cervus perrieri</i> CROIZET AND JOBERT, 1828
<i>Cervus</i> sp. (ex. gr. <i>Arvernoceros ardei</i> CROIZET AND JOBERT, 1828)
<i>Eucladoceros</i> aff. <i>senezensis</i> DEPÉRET
<i>Cervus (Dama)</i> cf. <i>nestii</i> MAJOR
Giraffidae, GRAY, 1821
<i>Palaeotragus</i> sp.
Bovidae GRAY, 1821
<i>Bison (Eobison) georgicus</i> BURCHAK-ABRAMOVICH AND VEKUA, 1994
<i>Gallogoral menighinii sickenbergii</i> KOSTOPOULOS, 1996
<i>Capra</i> sp. nov. sp.
<i>Sorgelia</i> cf. <i>minor</i> (MOYÀ-SOLÀ, 1987)
Ovibovini gen.et sp. indet
Antilopini gen.et sp. indet. (A)
Antilopini gen et sp. indet. (B)
Proboscidea ILLIGER, 1811
Elephantidae GRAY, 1821
<i>Mammuthus meridionalis</i> NESTI, 1825
Carnivora BOWDICH, 1821
Canidae GRAY, 1821
<i>Canis etruscus</i> MAJOR, 1877
Ursidae GRAY, 1825
<i>Ursus etruscus</i> CUVIER, 1812
<i>Ursus</i> sp.
Mustelidae SWAINSON, 1835
<i>Martes</i> sp. FRISCH, 1775
Hyaenidae GRAY, 1869
<i>Pachycrocuta</i> CROIZET, 1828
Felidae GRAY, 1821
<i>Lynx issiodorensis</i> CROIZET AND JOBERT, 1828
<i>Panthera gombaszoegensis</i> KRETZOI, 1938
<i>Megantereon cultridens</i> CUVIER, 1824
<i>Homotherium crenatidens</i> FABRINI, 1890

earliest representatives of bison (the oldest is *Bison sivalensis* Lydekker ex. Falconer M.S. 1868, 1878 from Pinjor zone of Upper Siwaliks, late Pliocene), Caprinae: *Gallogoral menighinii sickenbergii* (Kostopoulos, 1996)—the genus *Gallogoral* Guérin 1965 is known only from European Plio-Pleistocene sites (MN17-MN18) and supposedly has Asian origins (Guérin, 1965), *Capra* sp. nov. sp.—perhaps the oldest representative of the genus *Capra* Linnaeus, 1758 known so far in the world (The first undoubted remains of *Capra* are known from Petralona, Greece, Rissian, [Sickenberg, 1971, Tsoukala, 1991]), the genus *Capra* is considered to have originated in Eurasia, during the Plio-Pleistocene (Pilgrim, 1947). The Ovibovini (*Soergelia* cf. *minor* and Ovibovini indet.) is likewise an Eurasian group. Furthermore, the two representatives of Antilopini reveal affinities to the Eurasian spiral horn antelopes (Bukshianidze, 2005).

Due to the present African distribution of Giraffids it is important to stress that the small giraffid from Dmanisi belongs to the genus *Palaeotragus* Gaudry 1861. The origin and early stages of the evolution of the genus are not clear but it seems to go extinct in Africa at the end of Miocene, while from the end of middle Miocene to the end of Pliocene this genus has a wide distribution in the Old World (Godina, 1979). The Dmanisi

irre et al., 1997; Lindsay, 1997; Eisenmann, 2004). For the Rhinocerotidae, *Stephanorhinus etruscus* Falconer 1868 represents a typical species characteristic the entire Villafranchian (MN16-MN19) of Europe and Middle Asia. (Fortelius et al., 1993). The Cervidae is of course an autochthonous Eurasian group. Cervids have sometimes spread into North Africa, but are fundamentally Eurasian.

All the bovid taxa from Dmanisi are palearctic: *Bison (Eobison) georgicus* (= *Dmanisibos georgicus* Burchak-Abramovich and Vekua, 1994) is one of the

*Palaeotragus* is one of the last representatives of this genus and its affinities should be looked for among the Eurasian Palaeotraginae.

The earliest (Ethiopian) representatives of *Mammuthus* (sensu Maglio, 1973) migrated into Eurasia in the Early Pliocene (Palmqvist et al., 1999; Lister and van Essen, 2002, 2004; Kahlke, 2003). The Dmanisi *Mammuthus meridionalis* is a typical representative of the European Villafranchian, and one of the primitive forms of the archidiscodonts' Eurasian evolutionary lineage (Vekua, 1995; Gabunia et al., 2000) leading through

the steppe mammoth—*Mammuthus trogontherii* to the woolly mammoth—*M. primigenius*.

Carnivores as possible “fellow travelers” are of special interest. Many of the Villafranchian carnivores, especially the canids, ursids, and mustelids, do not have African roots and are essentially Eurasian. Others are so widespread that it may be premature to trace their speciation events and dispersals without more fossil sites.

Among the carnivores found in Dmanisi the small wolf-like Canid—*Canis etruscus* Major 1877 is the most abundant. The present level of knowledge of the history of the genus *Canis* does not allow unambiguous localization of its place of origin. The taxon represented at Dmanisi—*Canis etruscus*—appears in Eurasia at the limit of middle and late Villafranchian. This species is strictly Eurasian and is in the evolutionary line leading to extant *C. lupus*. The spread of *Canis etruscus* and the extinction of the racoon dog *Nyctereuntes megamastoides* Pomel 1842, marks the “wolf event” and represents a main faunal turnover in the course of the Villafranchian (Azzaroli, 1983). This event occurred at the time interval between the Reunion and the end of the Olduvai magnetic subchrons (Azzaroli et al., 1988). In Europe the first arrival of this species is registered in Olivola faunal unit (MN18, Azzaroli et al., 1988, Azzaroli, 1983). Among Georgian localities, *Canis etruscus* is first registered in Diliska (2.2 ma) followed by Kotsakhuri (1.8–1.9 ma), Dmanisi (1.75 ma) and Tsalka (early lower Pleistocene, Vekua, 1991; Vekua et al., 1985). *Canis etruscus* is thus not among the possible fellow travelers of early *Homo* in its migration out of Africa.

Furthermore, the Eurasian origin of mustelids (*Martes* sp.) and ursids (*Ursus etruscus*, *Ursus* sp.) is not doubted. The genus *Martes* Pinel, 1792 is exclusively palearctic, known from numerous Eurasian sites including several species starting from Miocene (MN3) up to present (Fortelius, 2003). *Ursus etruscus* Cuvier 1823 represented at the site is a typical Villafranchian European form (Rustioni and Mazza, 1992). It first appears in MN16–Lower Villafranchian and is present up to the end of MN19.

The Dmanisi hyena belongs to the genus *Pachycrocuta* Cretzoi. The roots of the genus *Pachycrocuta* are not clear, either a Eurasian or African origin is possible (Howell and Petter, 1980). In the case of Dmanisi it is important to stress that the first representatives of the genus are present in Eurasia from the Ruscinian (MN15 localities such as Sera en Voke, Lyana, Odessa Catacombs summarized in Sotnikova, 1989). During the earlier Villafranchian, *P. perrieri* Croizet and Jobert 1828, a species derived from this stock became the dominant hyena in western European and circummediterranean faunas (Howell and Petter, 1980) and was then replaced by larger hyena *P. brevirostris* Aymard, 1864, a species closely allied to *P. perrieri* from which it differs by its larger size (Howell and Petter, 1980). The place of origin of *P. brevirostris* is also unclear: it is “difficult to determine whether *P. brevirostris* originated in Asia or Africa,

though the age determinations presently known suggest an African origin” (Torre et al., 1992). *P. brevirostris* is present in Africa before 3 Ma (Turner, 1992). Later on it appears in Asia - Pinjor zone, India indicating an age not earlier than 2.5 Ma (Torre et al., 1992). To summarize, the origins and migration of *Pachycrocuta* species need to be more precisely defined.

There are at least four species of felid at Dmanisi. *Panthera gombaszoegensis* Kretzoi, 1938 identified in the Dmanisi fossil assemblage represents one of the earliest appearances of this species. The earliest appearance of this *Panthera* is registered from Late Villafranchian European localities such as: Olivola, Upper Valdarno, Tegelen, and Erpingen. Supposedly this species originated in the western palearctic (Hemmer, 1981) and although it is very close to the basal forms of the genus *Panthera*, the place of the origin of the genus *Panthera* is not clear: Africa after Howell and Petter (1976), Sotnikova (1989), and Asia after Hemmer (1981). The Dmanisi species is unknown in Africa (Turner, 1992) and is strictly Eurasian.

*Lynx issiodorensis* Croizet and Jobert 1828 is a typical late Pliocene early Pleistocene form and has a vast geographical distribution (Africa, Eurasia, N. America). An African origin of the genus is possible, as the oldest remains of the genus (*L. issiodorensis*) are known from the Pliocene site of Langebaanweg, South Africa, > 4 myr, (Hendey, 1974) but they are also present in the Pliocene of Europe (at Etouaires, more than 3.3 Ma, and at the Odessa catacombs, the age of which is considered to be older than of Etouaires [Sotnikova, 1989]). However, since the finds in Europe are much more numerous than in Africa, the opposite point of view—an Eurasian center of origin, can be also supported (Sotnikova, 1989). There is an important time interval between the first appearance of the species and Dmanisi, and in the Caucasus *Lynx issiodorensis* is identified in Kvabebi, an Early Villafranchian fauna, from the middle-late Pliocene of Georgia, Vekua (1972), so the Dmanisi species of *Lynx* was already present at this earlier time.

From the late Pliocene (the limit of Rouscinian and Villafranchian faunal zones) the genus *Homotherium* Fabrini, 1890 appears almost simultaneously all over the Old World (Turner and Anton, 1997; Sotnikova, 1989), seeming to originate in Eurasia. The Chinese early Pliocene *Machairodus* Kaup 1883 species are hypothetical ancestral forms of *Homotherium* (Sotnikova, 1989), and consequently migration from Eurasia into Africa is supported. However, *Homotherium* appears in the African Pliocene at Langebaanweg as well (Hendey, 1974), and thus an African origin is certainly possible, more so as genus *Machairodus*, its most likely ancestor, is also present there (Turner, 1990). All previously described species now are united into one species by some authors (*H. crenatidens* Fabrini, 1890—after Ficcarelli, 1979 and *H. latidens* Owen, 1846—after Turner, 1997) and this idea is widely accepted among paleontologists. Although *Homotherium* could have an African origin it is clear that

as *Homotherium* is present in Eurasia since the late Pliocene times there is no reason to see the Dmanisi form as newly appeared form. In addition, it should also be mentioned that the genus is present in Georgia since the earlier Kvabebi fauna (Vekua, 1972; Sotnikova, 1989).

*Megantereon cultridens* Cuvier 1824 is the second Machairodontinae species present in Dmanisi, it is smaller than *Homotherium*, and as a rule coexisted with the latter. The genus *Megantereon* Croizet and Jobert 1828 first appears at 4.5 Ma in the North America in the Bone Valley Formation, Florida (Berta and Galiano, 1983). *Megantereon* disperses from North America before 3.5 Ma and spreads all over the Old World. In Europe the oldest remains of the genus are known from the very end of Ruscinien (Catacombs of Odessa, Sotnikova, 1989). The first record from China is from Yushe basin Shansi province (Teilhard and Leroy, 1945) that corresponds the early Villafranchian of Europe; in India from Pinjor zone of Upper Siwaliks (Pilgrim, 1932) corresponding the late Pliocene, and this genus is also known from Java (Koenigswald, 1974). In Africa the oldest remains of the genus is dated ~ 3.5 Ma deposits of the Nachukui Formation south of the Turkwel River in West Turkana, Northern Kenya (Werdelin and Lewis, 2000). The genus lasts up to the end of the Villafranchian in Europe, in central Asia to the end of early Pleistocene, and in America to the Holocene, where most probably it gives rise to the extant genus *Smilodon* Lund 1842. Initially a number of *Megantereon* species were described, but in a comprehensive review of the systematics of *Megantereon* in the New and Old World, Turner (1987) considered *M. cultridens* Cuvier 1824 to be the only valid species of this genus. While some authors consider that the genus *Megantereon* comprises three species: *M. cultridens* Cuvier 1824 (North America, Asia, Europe) and its descendants on the one hand in the Indian subcontinent—*M. falconeri* Pomel 1853 and on the other hand in Africa—*M. whitei* Broom 1937 (Martinez-Navarro and Palmqvist, 1995, 1996). According these authors the latter species (*M. whitei*) colonizes Europe (it is present at European sites: Dmanisi, Venta-Micena and Apollonia) at the time of the Plio-Pleistocene boundary, and the spread of this species is probably related to the first arrival of *Homo* in Eurasia. The question whether the Dmanisi *Megantereon* has an African origin or not greatly depends on the sufficiency of the taxonomic importance of the observed morphological characters for the identification of new species. The main considerations for the separation and identification of the species *M. whitei* according to the above mentioned authors is on the tendency of reduction of p3 and p4 and the longer diastema between p3 and p4. It should be stressed that the reduction of p3 and p4 is the general character of *Megantereon* (Sotnikova, 1989). The judgment based on such a small set of rather variable characters is not yet convincing.

The giant ostrich—*Struthio dmanisensis* (Burchak-Abramovich and Vekua, 1994), is of special interest, it is very close to the Olduvai *Struthio olduvaiensis* in size,

but giant ostrich populations are widely distributed in Eurasia in Pliocene, and they are known from the Caucasian region as well: Kvabebi—*Struthio transcaucasicus* (Vekua, 1972), Taribana (Gabunia and Vekua, 1963), Late Pliocene, and Palan-Tukan in West Azerbaijan late Pliocene (Burchak-Abramovich, 1953). Therefore it is more reasonable to consider Dmanisi ostrich within the context of late Pliocene populations of giant ostriches in the Caucasian region.

Thus, the large animals that coexisted with *Homo* in Dmanisi are either purely Eurasian taxa or taxa that have migrated out of Africa a long time before the *Homo* has reached Eurasia. Most lineages can immediately be recognized as deeply Eurasian (Cervidae, Ursidae, Mustelidae). Some confusion has arisen in perception because those who have taken a cursory look at the faunal list have noted lineages that have extant relatives in Africa (*Struthio*, Giraffidae, Hyaenidae). Other taxonomic assignments, such as within the Bovidae, have recently been revised. Finally, the fossil record of the felid taxa present at the site is so broad in space and time, that answers to questions of origins and of dispersals are premature.

The implications of the fact that *Homo* is the only large mammalian African species among Eurasian forms are very important and need to be emphasized. It shows that something vital and intrinsic to *Homo* lead to this early phase of dispersal. Of course, *Homo* had to make it out of Africa when it was possible to make it out of Africa. Nonetheless, *Homo* at Dmanisi without other African taxa suggests *Homo* was able to extend on their own. Even if in the future some of the species are demonstrated to have simultaneously dispersed from Africa, the Dmanisi fauna can not be considered to be a real extension of “Africa-ness.”

In addition, there are some key taxa that are present in nearly every East African hominin site that are entirely absent from the Dmanisi fauna to date. These are the suids, monkeys, hippopotami, and crocodiles. These species would have interacted in significant ways with hominins. Crocodile and hippopotamus could have been a significant danger to hominins when near water, and pigs and monkeys would have been food competitors and perhaps prey. The lack of pigs and monkeys may indicate habitats where tree cover was less than continuous. Also notable is the scarcity of aquatic species at Dmanisi, which are so common in East African hominin sites. Dmanisi indicates a significant broadening of habitats occupied by *Homo* and supports hypotheses that base the biogeographic spread on intrinsic characteristics of *Homo*.

Would this Eurasian fauna require different strategies in the behavior and ecological adaptations of the hominins? We do not know surely how cold it became during winter in Georgia in the Plio-Pleistocene, but there may have been significantly more seasonality in temperatures than nearer to the equator. Like Africa, there were both carcass producing felids and bone destroying carnivores.

Would hominins have to change meat acquisition strategies in a habitat with a greater number of cervids than bovids? To some extent we know that predators adapt mainly to prey size, but still there were probably many behavioral differences in the faunas that would have changed hominin food procurement strategies, and research should focus on these issues. Studies on the ecomorphology of escape behaviors of extant and extinct cervids is currently being conducted by Sabrina Curran of the University of Minnesota will help elucidate aspects of these questions.

## GENERAL TAPHONOMIC OBSERVATIONS OF DMANISI

Over the past decade of excavations in the Paleolithic levels at Dmanisi, thousands of fossil bones have been recovered, and excavations continue each summer. Taphonomic observations and analysis are preliminary. For example, many bones from the last seasons are still encased in hard matrix, and therefore some have yet to be fully identified. All specimens are being examined for surface modifications under magnifications between 5-50x (usually 10-20x). Enough of the assemblage has been systematically examined ( $N > 2000$ ) to make some important taphonomic characterizations of the fauna, although final frequencies of bone modifications are not yet known. This paper discusses preliminary observations on surface modifications and bone damage, while mortality profiles and skeletal element frequencies will be reported in subsequent papers.

The Dmanisi fauna in the units below the carbonate horizon (K) is very well preserved, and many bones have survived unbroken. The area below the carbonate horizon typically includes the A strata (normal) and the lower portions of the B1 stratum (reversed), although K formed in various layers depending on the location in the site. The bone surfaces are well preserved with little subareal weathering: For the site overall, Seventy-two percent of the specimens are unweathered, i.e. they are in weathering stage 0; 21% are in stage 1, and 5% are in stage 2 (stages after Behrensmeyer, 1978). The lack of weathering indicates the bones were removed from subaerial exposure rapidly after death of the animals, perhaps immediately, or within a year or two.

Detailed spatial analyses are being conducted, and all specimens are being recorded in three dimensions using a total mapping station that allows computerized three-dimensional presentation. These images will be forthcoming in future papers by the team, along with detailed parsing of taphonomic features by microstratigraphic layers. Some general patterns are evident, for example, above and within the carbonate horizon, the bone assemblage is less well preserved than below it, largely because of longer subaerial exposure (more weathering), and the precipitation of carbonates within weathering cracks in bones causing splitting. In general bones and artifacts are more evenly scattered above the carbonate

layer especially in the B2 layer, while very dense clumps of bone occur in the pipe fills and gullies of B1 sediment within A2. It is in these latter areas that the hominins are mostly found, and Mode 1 artifacts are directly associated with these dense concentrations (as well as above them). Figure 3 shows one view of a dense concentration of bone including the new edentulous hominin mandible uncovered in 2003 (Lordkipanidze et al., 2005).



Figure 3. Dense pocket of bone, including vertebrae and long bones of herbivores as well as the edentulous hominin mandible D3900.

Most bones are not articulated, but articulated body segments are not uncommon, and in addition bones of the same body segment are very often found near one another. Examples of articulated units include long (e.g., 10 or more) and short (e.g., two) units of vertebrae (including two hominin cervical vertebrae found articulated), an entire hindlimb of a lagomorph, and partial to whole limbs of large herbivores and carnivores. These specimens were deposited while ligaments still survived, and the partially articulated carcass segments indicate that during the preburial phase they were separated from other body portions (Figure 4).

Fully one third of the bones plotted from Dmanisi are whole (unbroken), and many that are broken retain a substantial portion of the original element. There are also several hundred long bone shaft fragments, but the assemblage is not nearly as comminuted as at most archaeological sites. This pattern of many whole or minimally fractured bones contrasts with most other early hominin archaeological sites at Olduvai and East Turkana, where typically 70-95% of the fauna are non-identifiable fragments (Potts, 1988; Bunn, 1997, [although perhaps with the new emphasis on including more detailed analysis of shaft fragments would render larger portions of these assemblages identifiable, (e.g., Marean et al., 2001)]). The fragments at Dmanisi often retain identifiable landmarks, and were not further crushed by sediment compaction below the K horizon. However, recent comparisons by Villa et al. of late Pleistocene European hyena dens and Middle and Upper Paleolithic cave sites suggests increased breakage and decreased identifiability should not be considered a characteristic of archaeological sites when contrasted with hyena dens (Villa et al., 2004). The numbers reported here from Dmanisi are of plotted specimens and do not yet include the fragments of bone less than 2 cm in length recovered from screen-

ing. (The screened bones have been examined but the tallies are not yet complete.) Most often, breaks on bones at Dmanisi occurred while the bone was still fresh: 50% of the breaks have curved outlines and typically have oblique fracture edges. A further 21% are “intermediate” in character (categorization after Villa and Mahieu, 1991). Post-fossilization breaks are uncommon, except for those breaks that inevitably occurred during the excavation of the often delicate fossils within hard matrix. Dmanisi’s pattern of whole bones and large fragments is partially due to the protection from sediment compaction by the carbonate horizon, but also reflects relatively little breakage during the primary accumulation.

Together the evidence of little weathering, articulated units, and relatively little breakage indicates that bones were rapidly deposited after the deaths of the animals and



Figure 4. *Articulated hind limb of a size 2 bovid, Gallogoral with unfused epiphyses, an articulated pelvis can also be seen.*

that there was little subsequent movement. The lack of much post-fossilization breakage and the relatively brittle nature of the fossils further confirms that there was no substantial geological displacement. The larger scale issues of fluvial transport of bones (Behrensmeyer, 1988; Behrensmeyer, 1991; Behrensmeyer and Quade, 1993; Behrensmeyer, 2002) are absent from Dmanisi, where only short distance water transport in pipes or small gullies was possible. There are only a handful of specimens from the site that have evidence of abrasion indicative of trampling or geological transport, and the bones are not in fluvial sediments. If the bones were washed together, it was from trivial distances on the scale of meters, and therefore there must have been another bone concentrating mechanism for their initial accumulation.

Some other commonly acknowledged bone accumulating mechanisms are unlikely to have been significant at Dmanisi. Porcupines were present at the site, but less than 2% of the specimens examined so far are ro-

dent gnawed. Rare specimens of *Hystrix* are present, but, based on the actualistic studies by Brain (1981), the levels of gnawing are relatively low, and the bones are too unweathered to suspect that a large portion of the Dmanisi fauna was accumulated by porcupines. So far there is no geological evidence for a deep fall that would trap large animals. Although the top of the A sediments into which the hydraulic pipes formed has been eroded, it seems that where most of the pipes breached the surface the pipes would have been on the order of one meter and possibly two meters deep, and so did not have the depth required to trap large animals. In this area of repeated volcanic activity, there were repeated ashfalls devastating the land suggesting that mass death could have also contributed to the site. If so, one expects many entire carcasses, and catastrophic age profiles of the fauna. A consideration of the mortality profiles will be presented in another paper by the team, but the separation of carcasses in units suggests consumption by predators, which will be the main consideration here. Thus, in the absence of evidence for transport by geological processes, or the possibility of a drowning event, or even much trampling, the separation of carcass parts into units and their aggregation was likely caused by carnivores and/or hominins.

## HOMININS

With plenty of hominin fossils, stone tools, and manuports present, we know hominins were living at the site or in the immediate vicinity; but how much of the bone assemblage was accumulated by hominins? The most secure method for identifying hominin involvement is via surface modifications by stone tools such as cut marks, striae fields, and percussion marks (Potts and Shipman, 1981; Bunn, 1982; Isaac, 1983; Blumenshine and Selvaggio, 1988; Potts, 1988). For the analysis at Dmanisi, surface modifications such as scores and pits are described in terms of their cross sectional shape, presence of microscopic striations, and other morphological features; size; location on the bone (using a 20 unit system for long bones, similar to that used by (Marean and Spencer, 1991); and orientation in respect to the long axis of the bone. Interpretation of the cause of the marks (e.g., tool, tooth, trampling, etc.) is then made and recorded in a separate category from the descriptions, along with a confidence rating of the interpretation of 1 (certain) 2 (most likely) or 3 (possibly). Tappen has been very conservative with cut mark identifications because the surfaces of the bones are not hard and are easily scratched during excavation and preparation. Often preparation or excavation marks are easily distinguished from ancient marks, but

if marked when the bone is still damp from being in the ground, the coloration difference is often masked. When the bones are washed in water, sediment can be moved into preparation scratches and give them the appearance of being old. For these reasons great caution is taken when identifying cutmarks or assessing the antiquity of scores, and the cleaning methods of each bone are tracked to the degree possible. Most bones are cleaned by light brushing or an aircrusher, and then sometimes rinsed in water. Data are collected on whether tenacious matrix, calcrete, manganese, or root marks that coat or pass through surface marks. If they do, the marks are confidently considered to be ancient. This conservative method is necessary at Dmanisi because of the texture and hardness of the fossils.

Using this procedure, there are less than ten scores and pits from Dmanisi that are interpreted as ancient tool marks, and approximately 20 that are classified as certainty level 2 tool marks. Some of these tool marks can be seen in Figure 5. Several conclusions can be drawn from this small amount of tool mark evidence from the site. First, because of the low frequency of tool marks, hominins were unlikely to have been the main bone accumulators at the site. As more of the assemblage is viewed and spatial analysis is conducted, there may nonetheless be locations within the site that can be attributed to hominins, and our team is looking at this issue because of its potential for giving us more behavioral information. Second, some of the marks represent filleting marks for removal of meat from prime meat bearing bones, such as the femur and humerus (e.g., Figure 5 a,b). These marks show that hominins had early access to the carcasses, and that these carcasses were not first consumed by large cats or hyenas, who leave little edible meat (Domínguez-Rodrigo, 1999; Domínguez-Rodrigo, 2002). Third, other marks represent pits from hammerstone blows for marrow removal.

Both carnivores and humans create notches when breaking long bone shafts to obtain marrow, and these resulting notches on shaft fragments overlap in size and shape substantially (Capaldo and Blumenschine, 1994). There is a tendency for dynamic hammerstone impact to create broader and more arcuate notches than those created by carnivore teeth, although overlap in size is substantial; and the platform angle of the negative flake scar may be more acute. At Dmanisi most notches can be explained as carnivore notches. The mean breadth to width ratio of notches on shaft fragments is 6.27 mm (N = 39), which falls between the ratio of notches studied by Capaldo and Blumenschine created by carnivores and those by hammerstone. Dmanisi has more variation in shape than their experimental carnivore and hammerstone sample (sd = 9.77), as expected if more than one process broke the bones. Fracture Angles are still to be measured. There are a few striae fields and pits with associated

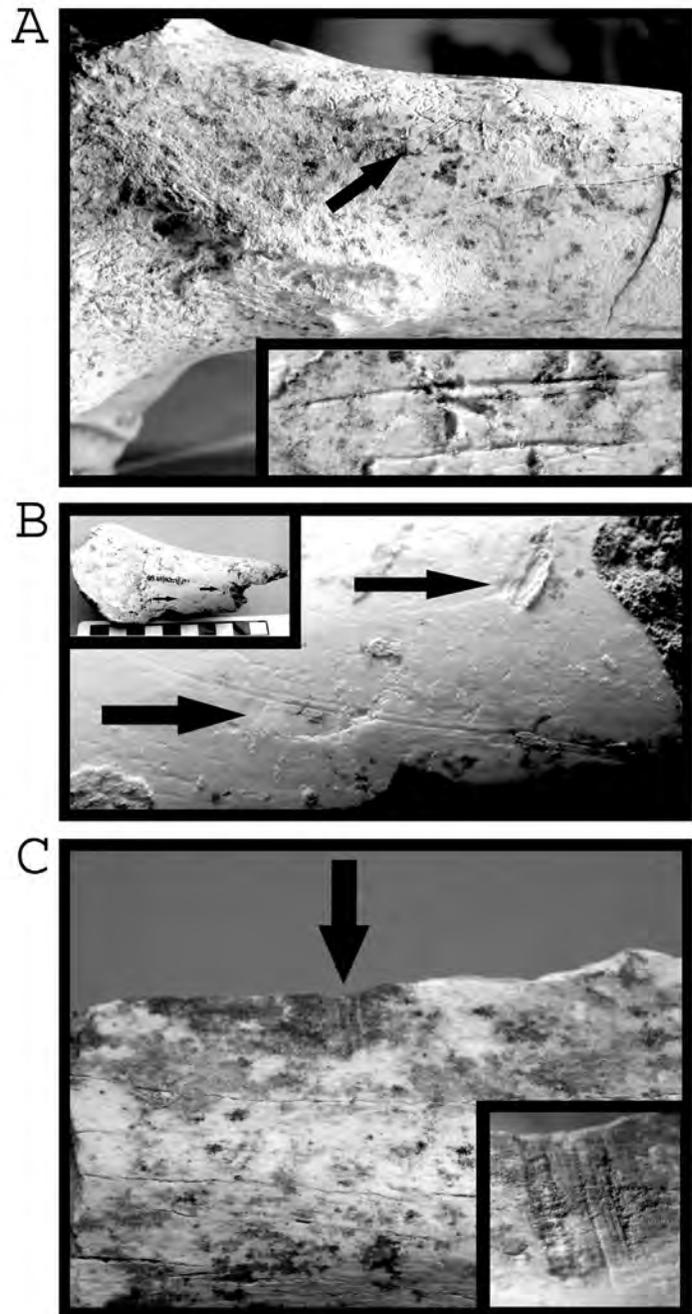


Figure 5.

- A. Cervidae size class 2 (classes after Brain, 1981) femur with stone tool cut marks on the distal lateral shaft. The location of the marks signifies meat removal rather than marrow processing. Inset: Close up of marks. Root marks and manganese cross the marks, indicating the tool marks are ancient. A barb, characteristic of tool marks, can be seen at the end of the lower mark.
- B. Long cut mark with internal striations on a proximal humerus midshaft fragment (includes distal portion of deltoid tuberosity). This mark was found under a calcrete layer that coated the bone. Note adjacent chop mark or tooth mark. Inset: View of entire fragment.
- C. Percussion striations on the edge of a long bone shaft fragment, for removal of marrow. Inset: close-up of striations, occupying an area of 7 by 3.5 mm.

striations that are indicative of hammerstone damage at the site (Figure 5c). A medium sized humerus shaft fragment is also illustrated with cut marks indicative of filleting meat, and also has a deep impact mark near the break that may indicate marrow removal by hominins, although striae are not present, and so it could also represent a pit caused by carnivore teeth (Figure 5b). This latter interpretation would suggest hominins filleted the meat before carnivores broke the bone.

## CARNIVORES

Carnivores could have used and expanded the piping features for denning (Tappen et al., 2002) and the presence of large carnivore coprolites indicates that super-predators were living directly at the site. Forty-five coprolites have been preserved; most are round and/or round with a pit—the morphology of hyena coprolites. Others are more elongated and may be coprolites of felids or canids. Evidently, conditions were right for coprolite preservation, but there are few compared to many den sites, such as San Teodoro Cave in Sicily where 68% of the nearly 6,000 plotted specimens are coprolites! (Marra, Villa et al., 2004), or Bois Roche, France (Villa and Bartram, 1996; Bartram and Villa, 1998; Villa, Castel et al., 2004); apparently they have documented latrine areas at these sites. Bones with clear signs of digestion by hyenas or other larger carnivores, which would include bones with thinned edges, pinholes, polish, and severe irregular erosion are rare at Dmanisi; only three positive identifications have yet been made of digested bone. This number could increase when the screened bone has been tallied, but preliminary examination does not suggest that a high percentage of screened bone was digested. (This contrasts sharply with percentages of digested bones in screen fractions at Bois Roche 87% and at San Teodoro 27% (Marra et al., 2004). Digested bones were also abundant at a modern den studied at Masai Mara and Arad, Israel (Peterhans, 1990).

Linear drag marks and pits caused by teeth on bone surfaces are the best evidence for carnivore activities. Indeed such marks are preserved at Dmanisi, but less frequently than in modern dens. Tooth scores and pits with a certainty level of 1 are on 6.1% of the

specimens analyzed, and adding those classified at the second level of certainty, brings the total number of carnivore marked specimens to 7.56%. A number of authors have remarked that ancient fossil dens have lower frequencies of gnawing than modern ones, often gnawing is found only on one or two percent of the bones (Cruz-Uribe, 1991; Pickering, 2002). The lack of congruence between actualistic and ancient assemblages suggests that multiple agents were involved at many of the ancient sites. Another explanation for this phenomenon noted by several authors is that less well preserved surfaces and very broken bones at archaeological sites relative to actualistic assemblages decreases the percentage of bones with observable gnawing (Milo, 1998). Dmanisi's bone surfaces are mostly well enough preserved to exhibit surface marks such as gnaw and cut marks. Still, there are portions of bone surfaces *not* visible to the analyst, caused by: 1) tenacious matrix, usually cemented on the surface by carbonates, 2) some exfoliation (flaking of the bone surface), or 3) post-depositional dendritic "root marks" (which are in fact likely saprophytic fungal rhizomes, N.C. Tappen, personal communication). The percentage of the bone surface that was visible and preserved well enough to exhibit cut marks and gnaw marks for each specimen was recorded using a quartile system (these estimations were made for periosteal and articular surfaces, not endosteal surfaces, which are not expected to have as many marks). On bones with less than 50% of their surfaces intact (36.2% of the specimens) 4.55% had carnivore gnaw marks, and 0.72% have tool marks; while on bones with 50% or more of their surfaces exposed and well preserved (63.8% of specimens) 9.26% had carnivore tooth marks and 3.5% have tool marks. Therefore, it is likely that some marks made by carnivores and humans are unobserved, and so reported frequencies should be considered minima.



Figure 6. Femur long bone cylinders from Dmanisi.

There are also bones with crenulated break edges and characteristic carnivore breakage, but without confirming surface scores or pits. When these are added to the tooth marked specimens, the number of carnivore-modified specimens increases by another 2.7%. Hyenas and other carnivores tend to gnaw soft ends of bones, and if they do not break through the shafts, the result is a long bone cylinder (e.g., Bunn, 1983; Potts, 1988), whereas humans tend to break long bones more often midshaft. Hyenas can break bones midshaft too, especially size class 2 and even 3 mammals. It is probably more rare for hominids to break off the ends without also breaking the bone in middle, and so bone cylinders are considered indicators of carnivore damage. At Dmanisi, femurs occur as cylinders more than of the other long bone elements examined so far. Of 56 femurs, 13 (23%) are long bone cylinders broken by carnivores, most likely hyenas (Figure 6).

In sum, carnivore damage is present on about 6–10% of non-tooth NISP, depending on how conservative one prefers to be. Dens, on the other hand, usually have at least 30% carnivore damage and often twice this amount or more (Bunn, 1983; Pickering, 2002; Marra et al., 2004). Therefore, although carnivore gnaw marks are more common than tool marks, they are not present in the high frequencies of modern dens (Figure 7).

Our knowledge of carnivore gnawing frequencies in dens is mostly from modern hyena dens. At Dmanisi we have more remains of felids than of hyenas. Although felids sometimes den, they do so less often than

hyenas. It has been found that while felids break bones less than hyenas, there still tends to be abundant tooth marks (Martin and Borrero, 1997). At a *Homotherium* den in Texas 21% of bones had tooth marks (Marean and Ehrhardt, 1995). *Homotherium*'s very large size suggests that it had prey preferences for larger animals (e.g., for baby pachyderms, as seen in the Texas cave). It may have

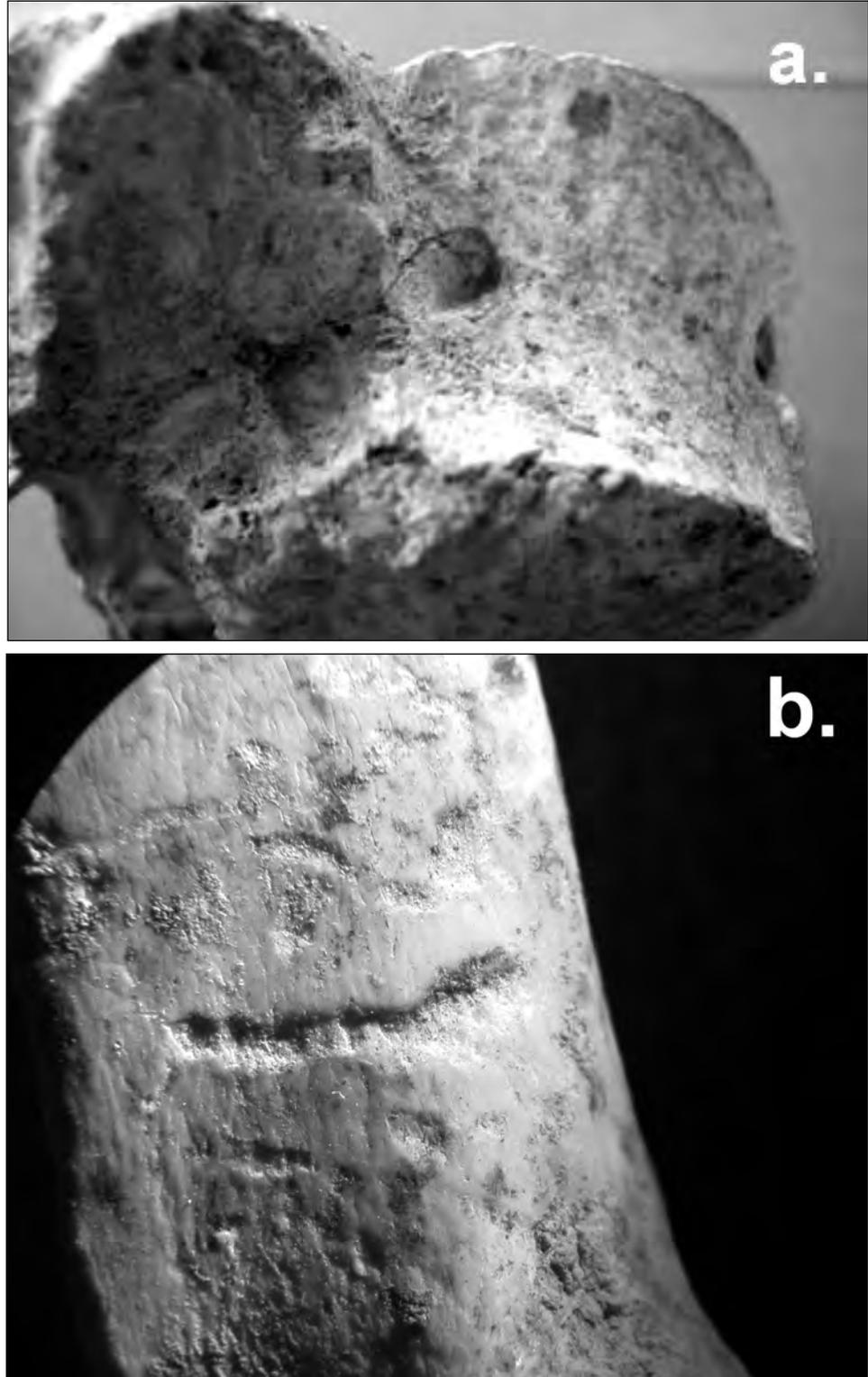


Figure 7. Carnivore tooth marks. a. Tooth punctures on a size class 2 thoracic vertebra b. Drag mark and tooth pits on the anterior portion of a cervid mandible.

been involved in some of the larger herbivore deaths and bone deposition at Dmanisi, (Tappen et al., 2002), but the majority of the fauna are from smaller size class 2 or 3 herbivores, and so *Homotherium* is less likely to have been the major agent at Dmanisi than hyenas and the other cats, such as *Megantereon* and cf. *Panthera gombazsogensis*. In a puma lair in South America 47% of isolated bones have carnivore damage, but articulated segments do not have as much marking, (Martin and Borrero, 1997) which would lower this percentage considerably. Thus, although carnivore denning is one of the probable causes of accumulation at Dmanisi, carnivore damage occurs at lower frequencies than expected at dens, so denning is likely only part of the explanation for the bone accumulation.

### PREDATION HOT SPOTS

In addition to denning, carnivores can create bone concentrations at what have been variously called “predator arenas,” “predation patches,” or “serial predation spots” (Behrensmeyer, 1983; Haynes, 1988; Tappen, 1995). These predation “hot spots” occur when there is an area on the landscape where predation is facilitated and therefore repeated frequently enough to accumulate bones in high densities. Predation hot spots are thought to require a special landscape feature that improves hunting success, because all studies conducted so far show that modern attritional deaths of medium and large mammals do not normally result in spatial concentrations of bone that mimic the high densities at large archaeological and paleontological sites. These lower spatial densities were found in Amboseli Park, Kenya (Behrensmeyer, 1975; Behrensmeyer et al., 1979; Behrensmeyer and Dechant-Boaz, 1980; Behrensmeyer, 1981, 1983, 1991), Ngorongoro Crater and Serengeti National Park, Tanzania (Blumenschine, 1989), Parc National des Virunga, in the Congo (Tappen, 1995; Tappen, 2001). Predation hot spot bone accumulations therefore require a change in elevation or some other geomorphological feature; a change in vegetation physiogamy such as a windy hilltop, a treeline, the bottom of a cliff, a drinking spot, or perhaps a natural cul de sac. Over a period of some years, repeated carnivore kills result in the bones of many animals concentrating in a restricted area. How common such predation hot spots are, how concentrated bones can become in such sites, and how often they have resulted in paleontological sites is still not well understood. For an accumulation to occur, predation rates, removal from sunshine and burial rates must be higher than subaerial weathering and the alternate wetting and drying that are so damaging to bone preservation (Behrensmeyer, 1983).

The Dmanisi site is located on a promontory on top of thick basalt that has been cut on two sides by the Mashavera and Pinezauri Rivers. The lava of the basal basalt flowed down the Mashavera River during the Olduvai normal event and when it reached the confluence

with the Pinezauri River, Ferring has documented that it blocked the river and created a lake. Thus, the promontory has always been an isthmus projecting out between either two rivers or between a river and a lake. Large hills further surround the locale. The area of the promontory today is about 13,000 sq m in area, and because the rivers have incised downward (rather than moving much laterally), in prehistoric times the size of the isthmus would have been similar. So a special landscape feature, as required by a serial predation patch, did indeed exist at Dmanisi. In one scenario, prey species could have wandered into this cul-de-sac, perhaps attracted to the smell of water, and found themselves ambushed with nowhere to escape on three sides. Another possibility is predators could have actively driven animals out on the promontory where they were relatively easy to catch. Hominins conceivably could have also used such a strategy, been the victims of such a strategy, or both.

The taphonomic signatures of predation hot spots are not well documented. As carnivore kill and consumption sites, but not dens, we can make predictions of their characteristics. At both dens and hot spots bones are accumulated by carnivores, and so many of their characteristics would be similar, and many of their differences in character would be related to being open air versus covered, analogous to comparisons of human open air versus cave sites. Table 2 considers some of these factors.

Landscape attritional death assemblages such as in the studies cited above include the bones of vertebrates that died from many processes, including disease and predation. However, such assemblages are comprised largely of the remains of mammals consumed by predators, and in many ways the taphonomic features of bones at predation hot spots will be simply concentrations of bones with the signature of attritional death bone deposition across landscapes (Behrensmeyer, 1983). Furthermore, since landscape bone deposition studies have yielded large samples of bones, they more likely incorporate the variation possible for predation hot spots than do the very small samples we have from such hot spots. Carnivore gnawing frequencies, bone cylinder frequencies, and weathering rates of an attritional death bone deposition study by Tappen conducted in Central Africa are compared here to these taphonomic features at Dmanisi. The actualistic landscape study was in Parc National des Virunga (PNV) along the Semliki River at the base of the Western Rift Valley of the Congo to Dmanisi (Tappen, 1995, 2001). PNV is a semi-arid savanna, with non-migratory ungulate populations: principally reduncines especially the kob (*Kobus kob*), waterbuck (*Kobus ellipsiprymus*) and reedbuck (*Redunca redunca*). Buffalo (*Synceros caffer*), bushbuck (*Tragelaphus scriptus*), sitatunga (*Tragelaphus spekii*) warthog (*Phacochoerus aethiopicus*) and hippopotamus (*Hippopotamus amphibius*) are also abundant. Lions (*Panthera leo*), spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*) are the large predators common in the park. As an ex-

Table 2. Some predicted characteristics of carnivore dens compared with predation hot spots

Characteristic	Den	Predation Hotspot
Landscape feature <sup>1</sup>	Hole or cave	Various possibilities
Spatial Distribution	Concentrated by edges of feature	More diffuse
Bone transport <sup>2</sup>	Bones transported further	Bones less transported
Carnivore surface modification <sup>3</sup>	More gnawing? More juvenile gnawing	Less gnawing ? Less juvenile gnawing
Numbers of Juvenile carnivores <sup>4</sup>	More juvenile carnivores	Fewer juvenile carnivores
Weathering Stages <sup>5</sup>	Little weathering	Variation in weathering
Coprolites <sup>6</sup>	Coprolites better preserved	Coprolites present but fewer
Trampling	By carnivores only	Also by large ungulates

1. Discussed in the text.

2. Since by definition predation hot spots represent a place of repeated carnivore kills, there would be less transport from the kill than in dens, and hot spots would have the signature of kill sites multiplied several times. Behrensmeyer predicted that relative to dens at hotspots there would be more vertebrae and fewer skulls, which tend to get transported (1983). This would vary with the size of the prey and the number of carnivores competing (Tappen, 1995).

3. While both dens and predation hot spots are carnivore consumption areas, there may be lower frequencies of carnivore gnawing in predation hot spots than in dens. This would be predicted based on less time spent at the site and therefore less chewing on bones picked up again and again. Continuing investigation by Behrensmeyer (this volume) of bone deposition and modification at Amboseli Park over 25 years indicates that the amount of carnivore competition, and the relative number of hyenas, largely dictates the degree of bone destruction by carnivores. Gnawing by juveniles would be higher in maternal dens. This would be evident in more narrow tooth scores and smaller, less deep tooth punctures, evidence of mouthing, and perhaps more gnawing on soft cancellous bones with fewer breaks in shafts, and possibly more bone cylinders relative to long bone shaft fragments if the juveniles were unable to break bones.

4. Maternal dens would have more juvenile carnivores present (e.g., Stiner, 1994).

5. A time-averaged open air situation, accumulated over several years, predicts significant weathering, and a large variation in weathering stages at hot spots. Dens, on the other hand, would contain bones immediately removed from ultraviolet light, and thus would have fewer signs of subaerial weathering.

6. Coprolites in the open would be destroyed more quickly than in the closed situation of a den.

tant African habitat, there are no mammalian species in common with Dmanisi, and the bone assemblages are only comparable to the extent to which the taphonomic characteristics compared are shaped simply by a landscape with super predators and ungulates of a variety of body sizes.

Fifteen percent of NISP display clear traces of carnivore gnawing in the PNV attritional death landscape assemblage. This percentage of NISP displaying tooth marks should be considered a minimum at PNV,<sup>1</sup> whereas actualistic studies of hyena dens suggest usually between 38–100% of specimens have tooth marking (summarized in Pickering, 2002). Using these attritional death bone assemblage data as a proxy for predation hot spots, shows that hotspots have fewer tooth marks than do dens, yet still more than that of Dmanisi.

At PNV, 10% (N=13) of the MNE of 133 femurs were “long bone cylinders”—which is a lower frequency than observed at Dmanisi. This could be because the relative size of the long bones to the power of the carnivores’ jaws are greater in PNV, or perhaps trampling reduced long bone cylinders to shaft fragments very easily in the PNV open air situation. We should be able to resolve this issue as the investigation of Dmanisi proceeds.

Another factor that could discriminate between hot spots and dens is variation in weathering stages, because in dens most bones are removed from the most severe weathering agent, the sun, while open-air landscape attritional death assemblages typically would have longer exposure. The frequencies of weathering stages of bones at PNV were: Stage 0–19%, Stage 1–25%, Stage 2–18%, Stage 3–22%, Stage 4–11%, Stage 5–5 %. The bones are fairly evenly distributed throughout the stages, until Stage 4 and 5 where there is a decrease. This pattern is congruent with the concept of bones being continuously added to the landscape, with increased chance of burial or obliteration by trampling the longer they are exposed. It contrasts sharply with the Dmanisi pattern presented above, where it was shown that weathering is uncommon and varies little at the site, and so time averaging of attritional deaths across an open air landscape seems unlikely at Dmanisi. However, attritional deaths by carnivores are a possibility if the carcasses fell into the pipes immediately, perhaps in a “Transvaal-Cave” type of scenario (Brain, 1981; Brain, 1993). In this scenario Dmanisi was an habitual eating site of large carnivores, and preserved bones fell into the hydraulic pipes and/or were quickly buried in the low spots.

## DISCUSSION

Like with so many Stone Age sites, reconstructing the taphonomic puzzle of Dmanisi site formation has been inspired and informed by Bob Brain's taphonomic and actualistic research in South Africa. While there are still many analyses to be done and questions to be answered about Dmanisi site formation, initial observations reported here are indicative of some of the processes involved and suggest further lines of inquiry.

The large species present in the Dmanisi fauna are Eurasian, and most if not all did not leave Africa 1.8 myr at the time the evidence for the expansion of *Homo* at Dmanisi indicates. There is the possibility that some species, such as *Megantereon*, may have dispersed from Africa at this time, but the evidence now is ambiguous. There is, of course, also the possibility that some African species will be identified at Dmanisi, and the early Pleistocene is a well-known period of drying in Europe and Africa, so climate change is likely to have been important. But clearly the Dmanisi hominins are in a very different kind faunal community than they are at the Early Stone Age sites from Africa. From the perspective of the immediate region around Dmanisi, *Homo* significantly expanded its range of ecozones, and the spread of African-like fauna is not the main correlate or determinant. Adaptations of *Homo* must have significantly changed, and we should consider that there may be too much stress on the "fellow travelers" concept (Turner, 1984) and not enough on the agency of *Homo* in deliberations on this topic.

Geological evidence shows the Dmanisi fauna was buried within a series of open air ashfalls as well as portions deposited in hydraulic pipes and into gullies that formed over collapsed pipes. Bone modifications indicate that hominins contributed to but were not the main accumulators of bones at the site, and there is considerable evidence that carnivores were important taphonomic agents at the site. Nonetheless, the presence of some cut marks, abundant Mode 1 tools and manuports, speaks to hominins' presence directly at the site. Furthermore, the location of defleshing marks on the shafts of a humerus and femur add to the growing body of data that hominins at this time period had early access to meat, and were not only passive scavengers of abandoned carnivore kills.

Comparisons of weathering to attritional landscape bone assemblages indicate that the site was probably not formed merely as an attritional death hot spot. Still, the geomorphological position of the site on an isthmus between bodies of water likely contributed to the attraction of the area for hominins, predators, and prey. The frequency of carnivore marks and toolmarks co-occurring on bone may be the best indicator of the level of interdependence on the same carcasses by hyenas and hominins (Egeland et al., 2004), and may through our further analyses, indicate the amount of direct interaction, resource competition, close encounters, etc. that occurred at the site between carnivores and hominins. Our continued work on the taphonomy of the site, of the

hominins themselves, and parsing of microstratigraphic units, spatial analyses, and skeletal element frequency and mortality profiles will surely inform us of these important issues as the excavations and analyses progress.

## NOTES

<sup>1</sup> The PNV gnawing counts include only bones with "conspicuous tooth marks" (Blumenschine et al., 1996), as identifications were made in the field without the aid of a microscope. The percent gnawed does not include rib fragments, the vast majority of which had ragged breaks which were attributed largely to carnivore chewing. Nor does it include long bone shaft fragments, or "bone flakes." These shaft fragments were often found as small piles with no epiphyseal ends, and were found distributed across the landscape, sometimes by themselves and sometimes within larger bone patches. At the time of the survey they were simply tallied, and noted if some of the group had evidence for gnaw marks. There were 298 of these bunches of shaft fragments.

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