Akhalkalaki: The Taphonomy of An Early Pleistocene Locality in the Republic of Georgia

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As part of our investigations into the potential of the Republic of Georgia for providing information on early hominin occupation of Eurasia, we report here on Akhalkalaki, a large late Early Pleistocene locality located along the lower slopes of a Miocene andesitic cone. Originally excavated in the 1950s as a palaeontological site, it was re-opened in the 1990s and stone tools were found associated with the fauna, suggesting that it is also an archaeological occurrence. Excavations in the 1950s and 1990s uncovered thousands of bones of an early Galerian fauna, including the remains of new species of Hippopotamus, Equus, and Canis (Vekua, 1962, 1987) and dominated by the remains of Equus suessenbornensis. We present the stratigraphy of the site, which together with faunal correlations and reversed paleomagnetics indicates an age most likely in the late Matuyama Chron, probably between 980,000 and 780,000 years ago. Taphonomic analysis suggests that the fauna was deposited and buried over a short time period, and was heavily modified by carnivores, but we cannot demonstrate involvement by hominins. Based on evidence of abundant krotovina (animal burrows filled with sediment) and the lack of definitive evidence for hominin modification to the bones, the stone tools at the site may have been mixed in with the older fauna. The taphonomic characteristics of the Akhalkalaki bone assemblage are not readily explained with reference to assemblage formation processes developed with actualistic studies that have been mostly conducted in Africa, including carnivore dens, predator arenas, human hunting and scavenging, mass deaths, or attritional bone deposition. Because of extreme anthropogenic modification of the present environments, the temperate setting, and the presence of mainly extinct taxa, local models based on actualistic studies cannot approximate the mammalian ecology reflected in the Akhalkalaki bone assemblage. A few comparisons are made with preliminary taphonomic observations from Dmanisi, an Early Pleistocene Homo ergaster site not far away.

Keywords: PLEISTOCENE TAPHONOMY, REPUBLIC OF GEORGIA.
Introduction

The Republic of Georgia, located along the southern slopes of the Caucasus Mountains, has become the focus of archaeological and palaeoanthropological interest due to the recent discovery and subsequent dating of several early Homo cf. ergaster fossils at the Lower Palaeolithic site of Dmanisi (Dzaporidze et al., 1991; Gabunia & Vekua, 1995; Gabunia et al., 2000). These important discoveries have altered debates surrounding the earliest evidence for Homo beyond the confines of Africa, and have stimulated new interest in conducting research within this archaeologically rich, yet poorly understood region. This paper reports on the excavations at the Early Pleistocene locality of Akhalkalaki, Amiranis Gora, in the Georgian Republic that were carried out during the 1950s and the 1990s. The research of the 1990s was originally instituted as part of our programme to investigate the timing and nature of the initial extra-African dispersals of Homo and the adaptive capabilities of early members of our genus. Research at Akhalkalaki has provided valuable data on the taphonomic forces influencing Lower and Middle Pleistocene sites within the Caucasus and the role these forces play in faunal assemblage composition and distribution at sites within the region. It reiterates the need for all Palaeolithic sites to be studied from a taphonomic perspective.

Initially conceived as an archaeological investigation, several lines of evidence suggested that the assemblage was not cultural, and the recent research at Akhalkalaki has been focused on the taphonomic factors affecting the composition and distribution of finds within the site. The following questions have been addressed at Akhalkalaki: (a) what is the age of the sediments and fauna?; (b) what were the main agents of accumulation of the faunal remains?; (c) are these deposits essentially the same as those excavated by previous researchers, with the same palaeontological and taphonomic characteristics?; and (d) what role, if any, did hominins play in the depositional history of the locality? The detailed taphonomic study presented here addresses these issues and proposes what we feel to be the most likely interpretation of the site. Several alternative models considered here are hominin activity, mass and attritional death, and carnivore denning.

History of Palaeontological Research and the First Archaeological Investigations

Palaeontological excavations

The Pleistocene open-air locality of Akhalkalaki is located on the Paravani Plateau in the southern Georgian Republic (Figure 1). It is situated at c. 1725 m AMSL on the western slope of the Amiranis
Figure 2. Map of the Paravani Plateau and the Paravani Gorge.
Gora (AG), a steep Mio-Pliocene andestic cone standing 190 m above the southeastern edge of the Paravani Plateau in the southern Republic of Georgia (Figures 2 & 3). The Paravani Plateau has a semi-arid continental climate with a mean annual temperature of 5·5°C and precipitation of 500–600 mm. The January average temperature is 8°C and that of July is 16·5°C. Palaeontological excavations conducted at Akhalkalaki by A. Vekua in the 1950s and 1960s led to the discovery and subsequent description of a rich fauna dominated by Equus su¨ssenbornensis in Early Pleistocene lacustrine deposits (Vekua, 1962, 1987). Over 4000 bones representing six orders and 21 mammalian species were recovered in these investigations. Vekua classified this fauna as representative of a steppe environment, as many of the species are found in steppes today or are primarily grazers (e.g., Citellus (=Spermophilus), Vormela, Mammutthus, Equus, Hippopotamus). An open steppe reconstruction is further supported by the presence of palaeobotanical remains of Lithospermum (=Buglossoides) arvense. There are also xerophilic, thermophilic terrestrial molluscs—Laminia papyroides and Helicella (Xeropicta) derbentina. Many of the vertebrates are capable of inhabiting a wide range of habitats including Erinaceus, and Lepus europaeus.

Akhalkalaki is a significant Pleistocene locality in Eurasia. Vekua named several new species of large vertebrate found there including Canis tengisii, Hippopotamus georgicus (a large hippo with terrestrial tendencies), and Equus hipparionoides (a smaller and rarer species than E. su¨ssenbornensis that was possibly endemic to the Caucasus). Like the archaeological excavations discussed below, Vekua’s work uncovered many skeletal elements in articulation and also noted that the bones from many different taxa were found “heaped up with no evident traces of selective deposition” (Vekua, 1987: 66). The bones were reported to be well fossilized, without evidence of rounding. These data, coupled with a lack of evidence of hominin activity in the vicinity, led Vekua to conclude that the Akhalkalaki assemblage represented a mass death probably instigated by the degradation of grasslands and watering holes due to frequent volcanic activity in neighbouring regions. Such loss of habitat would “pack” the remaining, unaffected environments with refugee populations, thus leading to epidemics, starvation, and increased predation by carnivores (Vekua, 1987: 92). The faunal distribution observed at Akhalkalaki is explained by Vekua as being due to post-mortem hydraulic forces washing carcasses from
near lakeshore positions into the lake itself where they were subsequently buried. Many finds were reported to exhibit evidence of carnivore and rodent gnawing, and these data were used to support the interpretation presented above.

**Archaeological Investigations**

Because of the richness of the palaeontological layer at Akhalkalaki, its presumed Lower Pleistocene age, and the abundance of Palaeolithic artefacts found across the Paravani Plateau, M. Gabunia began archaeological investigations there in 1992. Hoping to discover evidence of early hominins in the region, she began by conducting test excavations several meters south and upslope of Vekua’s original excavations. These small excavations continued each summer until 1994, at which time Georgia experienced political, economic and social upheavals at the end of a civil war.

The faunal assemblage uncovered by Gabunia between 1992 and 1994 differed little from that described by Vekua in his earlier work, but these new excavations led to the discovery of six andesite artefacts (Gabunia, 2000) that were associated with the fauna. Gabunia and her colleagues concluded that the material found at Akhalkalaki was archaeological in nature and that hominins probably played a role in the formation and composition of the site (Gabunia et al., 1994). Since those excavations, Akhalkalaki has made its way into the literature as one of the few Early Pleistocene archaeological localities known in the Caucasus (Liubine & Bosinski, 1995). Given that little was understood of the site’s complex taphonomic history at the time, Gabunia’s conclusions concerning the agents of accumulation were not unreasonable.

**The 1995–1996 excavations**

In 1995, D. S. Adler was invited to the Georgian Republic to participate in a new international collaborative project at Akhalkalaki. The main goals of this project were to expand the archaeological excavations of Gabunia; to collect new palaeontological, sedimentological, and palynological samples for analysis; and to attempt to verify the archaeological nature of the site. These excavations, which spanned 5 weeks in 1995 and 2 weeks in 1996, covered a 26 m² area that straddled Gabunia’s earlier excavations and led to the recording and recovery of over 500 fossil specimens (Figures 4 and 5). The excavation was conducted in square metre units with each find, regardless of size, being recorded in three dimensions and illustrated *in situ*. Although sieving was not conducted, the loose, fine-grained nature of the sediments combined with careful excavation allowed recovery of the vast majority of bones. For example, in one instance we recovered a series of unfused caudal bones of a juvenile canid. All finds were washed, labelled, and reconstructed at a nearby laboratory, with final taxonomic designations provided
by Vekua at a later date. No lithic artefacts were discovered during either season of intensive excavation. The central question became whether or not the faunal material was in any way the result of hominin activities.

Stratigraphic observations made during the 1995 season and earlier by Ferring indicated clearly that the site had experienced severe bioturbation following deposition. Disturbances are evidenced by the ubiquity of decayed roots and ancient and recent rodent
The sediments at the site are part of the Plio-Pleistocene suite of volcanogenic deposits exposed in and near the Paravani Gorge, which has been incised up to 200 m below the Paravani Plateau (Figure 7; Gabunia et al., 2000). The lower part of the gorge exposes thick Pliocene mafic dolerites; the youngest of these, the Akhalkalaki Dolerite, is dated to c. 2.9 Ma and is overlain by up to 60 m of fluvo-lacustrine deposits called the Diliska Formation. Those deposits are capped by the c. 2 Ma old Korki Dolerite.

The sediments above the Korki Dolerite form an extensive mantle across the Paravani Plateau. Those deposits are thicker on the east side of the Paravani Gorge, merging with alluvial fans and colluvial aprons along the base of the Andesitic hills marking the eastern edge of the plateau. Near Diliska, these sediments include thick diatomite beds overlain by c. 15 m of gravel with interbeds of cryoturbated silt and reworked volcanic sands attributed to serial deposition by glacial meltwaters.

The Akhalkalaki excavations have been conducted in a broad amphitheatre-shaped depression which appears to be a borrow pit for the factory below the site (Vekua, 1987: Figure 1). Cobble and boulder-rich colluvium forms an apron around the base of the AG, which is over 7 m thick in the excavation area. These colluvial deposits are conformably overlain by 50–100 cm of black gravely silt, thought to be Holocene, based on soil profiles, and possibly related to the 19th century terracing associated with reforestation efforts.

Three excavation blocks at the site were aligned downslope. Block 3 was backfilled and not available for inspection. Block 1 was nearest to the vertebrate fossil concentration excavated previously by Vekua and was briefly described by CRF in 1993. At that time it was connected to Block 2 by a narrow trench passing under a fence. Block 2 was studied in 1993 and 1995 by CRF, and samples for palaeomagnetic analysis were collected in 1995 by CS. Two backhoe trenches were also dug by CRF. Trench 1 was completed in 1993 and Trench 2 in 1995. The profiles from Trench 2, Block 2, located 9 m south of the 1995 excavation, provide the most complete stratigraphic section of the locality that was present before the commercial quarrying removed overburden and revealed the fossil fauna (Figure 8, Table 1). The sediments in this section are colluvium derived from the weathered andesite cone, mixed with Plio-Pleistocene ash. There is no physical evidence that the sediments at the locality itself are lacustrine (Vekua, 1987). However, a nearby lake would not be unusual, since lacustrine basins have been present over different parts of the Paravani Plateau from the Pliocene to recent.

The silty matrix of Stratum III contains numerous differentially weathered andesitic boulders and smaller clasts. A weakly expressed, calcareous soil B horizon (Bkb) coincides with the major bone concentrations in Block 2. The degree of soil development suggests that only a brief interval of surface stability preceded and possibly accompanied the bone accumulation. The downslope, linear patterning of bones in Block 2 suggests they accumulated in the head of a small gully. Minor erosion of the surface of the bone accumulation would have been likely, especially in these quite soft sediments. However, the andesite cobbles and boulders in these sediments must have been deposited differently than were the bones. The andesite clasts do not appear to be concentrated as a lag deposit from surface erosion. Rather, their presence in the fine-grained matrix, as well as their dispersed positions, suggest mass movements, either as periodic debris flows or as

Geologic Context of the Akhalkalaki Fauna

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burrows (Figure 6). It was within one of these burrows that Gabunia discovered an andesite artefact in 1994. The other five andesite artefacts may have come from similarly disturbed contexts, but these biogenic features remained unidentified prior to 1995. Therefore the origin and context of these artefacts is thrown into question. Further complicating the situation was the discovery of numerous andesite artefacts resting on the modern, stripped surface surrounding the excavation. These andesite artefacts are typologically similar to and exhibit the same type and degree of patination as those reported to have been discovered within the bone-bearing deposit during the 1992–1994 excavations. Following the 1995–1996 excavations conducted by Adler, Gabunia began a survey around the entirety of Amirans Gora. In total she found 14 more andesite artefacts, in various contexts, similar to the six previously discovered at the Akhalkalaki locality between 1992–1994 (Gabunia, 1998, 2000). These artefacts also exhibited patination similar to that mentioned above but their stratigraphic location has not been correlated directly with the main locality described here. Gabunia (1998, 2000) reports that these materials are representative of the Acheulian and Mousterian epochs.

The Taphonomy of Akhalkalaki 1373

Figure 6. View of the 1995 excavation. Krotovina in the soil can be seen as linear discolorations in the sediments in the walls of the excavation.
downslope creep. No evidence of cryoturbation was seen in the profiles, and the positions and orientations of the bones do not indicate any post-depositional disturbance other than surface erosion. Cryoturbated sediments with reversed polarity occur down valley near Diliska, but the stratigraphic correlation between these loci has not been established yet (Gabunia et al., 2000). The bone-bearing surface was buried quickly, in part explaining the good preservation of the assemblage.

A major feature of these deposits is the number of large krotovina throughout the section. These all appear to be rounded to subrounded in section, range from 10–25 cm in diameter, and have variable fills, suggesting multiple generations of burrowing. Most of the burrows appear to be subhorizontal, although several have fairly steeply dipping orientations. There are two types of mammals represented in the Akhalkalaki fauna that may have been responsible for these large krotovina—the marmots and/or the badgers. Notoriously fossorial, these animals dig burrows up to 15 m long and several metres below the surface. Both are fond of rocky soil and marmots particularly select high places with expansive views to burrow. Marmots and badgers are represented in the site from the period of the Akhalkalaki fauna to the Holocene (Vekua,
Bioturbation by such fossorial animals can move archaeological materials significant distances vertically (Erlandson, 1984; Bocek, 1986). Unfortunately we neglected to collect samples for palaeomagnetic analysis from the krotovina, which could help in dating the disturbances. However, two samples from undisturbed sediments in the Block 2 south profile are both geomagnetically reversed, establishing a minimum age for the fauna of c. 0.78 Ma.

Faunal correlations

Faunal correlations are useful for dating the site in conjunction with the palaeomagnetic signals. Table 2 presents a list of the taxa identified in the 1950s and 1990s excavations. *Equus süssembornensis*, the predominant species, is considered to be a “typical early Galerian species” that replaced the earlier *E. stenonis* group (Aguirre *et al.*, 1997). It has been found
in bone breccias near Verona, and in the Forest Bed series near Norfolk (Azzaroli, 1989). It has also been found in Taman, Russia, Suessenborn (Vekua, 1987) and Dorn-Durkheim 3, Germany (Franzen, 1999); and Stranska Skala, Czech Republic (Musil, 1971). Mammuthus meridionalis and E. suessenbornensis are typically associated during MNQ 20 (Guerin, 1989). M. meridionalis is normally seen to precede M. trogontherii, but there is also evidence that these two species coexisted (Lister, 1996). The Villafranchian-Galerian transition is thought to have occurred between 1·0–0·9 myr As the paleomagnetic signal at the level of the fauna is reversed, it suggests that Akhalkalaki is within the Matuyama Reversed Chron, between 1·78 Ma and 0·78 Ma. The paleomagnetic data combined with the faunal correlations suggests a date between the end of the Jaramillo Normal Subchron ending at 0·98 myr and the Brunhes Normal Chron beginning at 0·78 myr. Less likely, although possibly, the site could date prior to the Jaramillo subchron.

Taphonomic Analysis

Interpreting the palaeoanthropological and palaeoenvironmental significance of Akhalkalaki lies in understanding how the fossil accumulation was created and modified, how the animals died, and the processes that subsequently altered the assemblage. We assess what physical and biological processes were involved in the creation and alteration of the site through a series of analyses of species representation, bone surface alterations, skeletal element proportions, and mortality. Carnivore modification of the assemblage is extensive, and a series of modern day analogs documented by taphonomists, such as mass deaths, attritional deaths, and predation arenas are used for comparative purposes.

The fauna was originally catalogued by Vekua, who identified skeletal element and taxon. M. Tappen gathered taphonomic information on bones from the...
1992, 1993, 1994, and 1995 excavations; this subsample totalled 293 specimens and is referred to throughout the paper as the "taphonomic subsample". The taphonomic subsample represents 53% of the total number of bones catalogued by Vekua from the 1990s and is the subsample from which observations on bone surfaces, breakage, and skeletal element frequency and fragmentation analyses are based.

Excavations conducted in the 1990s at Akhalkalaki led to the recovery of an assemblage dominated by *Equus süssenbornensis* (75% of NISP [number of identified specimens]). The Artiodactyla include *Bos* and *Bison, Capra sp.* as well as cervid, probably *Dama*. The carnivores include *Felis sylvestris*, canids, and a large hyena. Thus, the species representation is less diverse but consistent with that found in the 1950s (Table 3).

**Preservation**

All of the fossils in the assemblage are identical, being creamy white in colour, having retained little or no collagen, and being very friable with powdery surfaces. The matrix adhering to the bone surfaces is also the same in each instance—a fine-grained, light brown sediment. These taphonomic features, colour and texture, and adhering matrix, along with detailed field observation are among the evidence indicating that the assemblage is not mixed from different layers and is a single coherent unit. There was no abrasion in the form of fine striations that occur as the result of bone transport across sediment. Furthermore, rounding and polishing of the surfaces is rare and not severe when found, occurring in 6% and 11·7% of the specimens, respectively.

Recognition of the amount of original bone surface that remains visible to the researcher is important if comparisons of frequencies of surface modifications are to be made with other palaeontological or neontological sites. For example, *Milo* (1998: 102) found 160 surface modification frequencies must be considered minimums. The remaining surfaces were obscured either by matrix or erosion. Surface erosion usually took the form of excessive root etching (84% of the specimens). Post-depositional destruction by roots is ongoing at the site, as roots are still present and splitting the bones as they lie in situ.

The degree of surface weathering on bone is an indication of the length of time it was exposed on the surface before burial. The full array of subaerial weathering stages as defined by *Behrensmeyer* (1978) is not present at the site. Nearly all bones (93%) conform to weathering stage 0, with 4·4% assigned to weathering stage 1, and weathering stages 2 and 3 accounting for 1·3% and 0·9% of the bones respectively. No specimens were weathered beyond stage 3 (Table 4). This indicates that the bones were buried fairly rapidly after the death of the animals (*Behrensmeyer*, 1978; *Andrews*, 1995). In fact the bones corresponding to weathering stage 0 were likely buried within a year or two after death, possibly slightly longer if covered in dense vegetation. The percentages of weathering stage 0 are similar for all three major orders represented, suggesting that the individual animals from all the orders were deposited and buried within a short period of time.

**Fluvial transport**

The very narrow, elongated, and dendritic nature of the distribution of bone suggests that they could have been deposited in a small runnel (Figure 5). The long axis of bone distribution is along the slope of Amiranis Gora; the south (high) end of the site has bones deposited between 340 and 380 cm while at the lower end of the site the vertical distribution is between 300 and 370 cm above datum (Figures 9a & b). Thus, the strong orientation of the site follows the direction of the slope of the hill. However, no sedimentological difference was identified between the areas with bones and those areas devoid of bones that were immediately adjacent.

Fluvial sorting of skeletal elements has not occurred. While ribs and vertebrae are among the most

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### Table 3. Representation of Mammalian Orders at Akhalkalaki, including all specimens from the 1990s excavation, and those only from the taphonomic subsample

<table>
<thead>
<tr>
<th>Order</th>
<th>1990s-NISP</th>
<th>%</th>
<th>Taphonomic Subsample-NISP</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Indet</td>
<td>36</td>
<td>6·5</td>
<td>10</td>
<td>3·4</td>
</tr>
<tr>
<td>Carnivora</td>
<td>30</td>
<td>5·4</td>
<td>12</td>
<td>4·1</td>
</tr>
<tr>
<td>Artiodactyla</td>
<td>70</td>
<td>12·6</td>
<td>40</td>
<td>13·7</td>
</tr>
<tr>
<td>Perissodactyla</td>
<td>415</td>
<td>74·9</td>
<td>231</td>
<td>78·8</td>
</tr>
<tr>
<td>Probosoda</td>
<td>2</td>
<td>0·4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rodentia</td>
<td>1</td>
<td>0·2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>554</td>
<td>100</td>
<td>293</td>
<td>100</td>
</tr>
</tbody>
</table>

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### Table 4. The frequency of weathering stages for the Taphonomic Subsample from Akhalkalaki for NISP, percentage in parentheses

<table>
<thead>
<tr>
<th>Weathering Stage</th>
<th>Artiodactyla</th>
<th>Carnivora</th>
<th>Perissodactyla</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>22 (88·0)</td>
<td>8 (88·9)</td>
<td>181 (94·3)</td>
<td>211 (93·4)</td>
</tr>
<tr>
<td>1</td>
<td>8·0</td>
<td>0</td>
<td>8 (4·2)</td>
<td>10 (4·4)</td>
</tr>
<tr>
<td>2</td>
<td>1 (4·0)</td>
<td>0</td>
<td>2 (1·0)</td>
<td>3 (1·3)</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>1 (11·1)</td>
<td>1 (0·5)</td>
<td>2 (0·9)</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td>9</td>
<td>192</td>
<td>226</td>
</tr>
</tbody>
</table>
transportable elements (Voorhies, 1969; Behrensmeyer, 1975) and so could have been washed away from the excavation area, skulls and teeth, which are considered to be lag elements, are also under-represented (see below). Thus there is a mix of elements from opposite transport groups present and missing from the site. However, articulated anatomical units (such as entire limbs) do have transport potential, and if bones were transported in articulation they would not show skeletal element sorting (Coard & Dennell, 1995). The linear spatial distribution of the faunal remains does suggest the bones were ultimately deposited in some sort of gully; however, that does not mean the bones were transported far (perhaps just from the banks nearby). The mean dip of bones was found to be only 12.8° (N=64, s.d. 8.17), indicating, along with a lack of trample marks, that post-depositional trampling was not important at this site (Hill & Walker, 1972; Andrews & Cook, 1985; Behrensmeyer et al., 1986; Gifford-Gonzalez et al., 1985; Fiorillo, 1989).

Orientations were taken for 229 elongated specimens from the map in Figure 5, and are shown as a mirror image rose diagram in Figure 10. An overall North–South orientation of bone is evident, following the linear distribution of the extent of the site itself, as it is oriented down the slope of the hill. There are shorter echoes at 90° and 45°. Experiments show that objects disturbed by running water tend to orient parallel or perpendicular to the orientation of flow (e.g., Schick et al., 1989). Here we have an additional peak at 45°.

Figure 9. (a). Vertical distribution of fossils in the 1995 excavation, south–north units. The projection includes all of the bones (see Figure 5) the y axis scale is equal to 50 cm, while the x axis scale is equal to 1 m. (b) Vertical distribution of fossils in the excavation, west-east units. Scale as in 9(a).
Surface modification

All bone surfaces were scanned for even “inconspicuous” marks (Blumenschine et al., 1996) under magnifications between 5 × and 20 ×. Bone surface modifications were difficult to assess because of the soft, friable condition of the bones. The bones’ texture also precluded making moulds for SEM analysis. Further, the bones were easily damaged during excavation and preparation, and so exhibited many preparatory marks. Uniform exterior and interior bone colour made it difficult to distinguish between ancient and recent marks. Still, no definitive cut marks or hammer stone blows were found on the bones. Rodent gnawing is rare in the Akhalkalaki taphonomic subsample (N=1). Only 20 specimens (8% of the taphonomic subsample, excluding teeth) exhibit unambiguous carnivore score marks. Considering that half of the original bone surfaces were not visible, the percentage of gnaw marked specimens in reality may have been twice this amount. Tooth pits sensu Binford (1981) are rare. However, the number of carnivore modified bones increases to about a third of the broken bones when one includes bones with breaks that are consistent with carnivore chewing (see next section).

Breakage patterns

A distinctive feature of the Akhalkalaki fauna is the remarkably high proportion of complete bones. In the taphonomic subsample, excluding teeth, 131 (52-6%) of the bones are complete, and most others were identifiable to taxon and element. This high proportion of identified specimens is evident in the figures presented by Vekua (1987) and also characterizes the

Figure 10. Mirror-image rose diagram of the orientation of the long axis of elongated specimens.
1990s sample, which were collected as part of a field strategy that emphasized recovery of small artifacts and bone fragments.

Breakage patterns are radically different between proximal and distal limb elements. One hundred percent of the upper (humerus-femur) and middle limb (radius-ulna and tibia) elements are broken, in contrast to much lower breakage rates for metapodials (58.5%), phalanges (25.0%), and podials (20.4%). The percentages of breaks among long bone elements are consistent with a general carcass consumption sequence: horse metapodials and phalanges, in particular, have little marrow, and there is little motivation for a carnivore (or hominin) to break them. Five of the eight vertebrae are whole, but four of them are canid caudal vertebrae (discussed below).

Common post-burial fragmentation of the friable bones, resulting mainly from compaction and root action, is indicated by rectilinear and stepped fractures (Figure 11). There are also several kinds of pre-fossilization bone breakage, including spiral fractures (on 23% of broken bones) that occur either alone or combined with jagged, irregular, or stepped breaks. The most common type of break of those that occurred in antiquity is the irregular break, occurring on 27% of broken bones. The irregular breaks show many changes in the vector outline, similar to what Hill (1989) called “sinuous gnawed edges” of hyena gnawed bone, or the “ragged” edges caused by leopards and hyenas described and illustrated by Brain (1981). Specimens such as these often do not exhibit scores, but are considered here to be clear evidence of carnivore gnawing.

The average maximum dimension of bone specimens in the taphonomic subsample is rather large: 11 cm (range, 1.6–33 cm). Hominins tend to break bone into smaller fragments than do hyenas (Brain, 1981; Bunn, 1983). The Akhalkalaki bone specimens are slightly larger than at Buca della Iena, which has been interpreted as a hyena den (Stiner, 1994).

**Skeletal element representation**

The relative frequencies of elements in the skeleton and their degree of breakage are some of the most important clues to the taphonomic history of a site. Table 5 presents the major skeletal element frequencies at Akhalkalaki. Skeletal element frequencies for the taphonomic subsample and the remaining bones are similar, \( r^2 = 0.69 \) (\( P < 0.01 \)), with the exception of radii, which are more commonly broken. The similarity in % MAU (minimum animal units) between the taphonomic subsample and the entire 1990s assemblage is also clear.

The Akhalkalki assemblage is characterized overall by a lack of axial elements (Figure 12). Skulls and teeth are greatly underrepresented while vertebrae and ribs are almost entirely lacking. Only small fragments of crania were recovered and there are no mandibles in the taphonomic subsample. Lower limbs from the radius-ulna and tibia down are the dominant elements of the site, with lower frequencies for the upper limbs, including the scapula, humerus, and femur.

Differential bone density is widely recognized as one of the most important influences on skeletal element survival (Lyman, 1984, 1994). The selective loss, or low survivorship, of low-density bones can be the result of one or more factors. Carnivores prefer to chew on low-density (porous) bones because they are easier to break and contain more grease (e.g., Cruz-Uribe, 1991; Marean and Spencer, 1991; Marean et al., 1992; Blumenschine & Marean, 1993). Low-density bones are more easily destroyed by sediment compaction and diagenesis, and they are more easily transported, and lost, by flowing water. In the Akhalkalaki assemblage, however, bone mineral density does not help account for element frequencies. Figure 13 shows the maximum bone mineral density (BMD) for skeletal element portions of equids (data from Lam et al., 1999, Table 1) against frequency (MAU). Bone mineral density does not correlate significantly with MAU (\( r^2 = 0.0654 \), \( P = 0.116 \)). We controlled for the absence of mandibles here, which have the highest bone density, by examining the relationship between BMD and MAU for long
Table 5. Skeletal element representation at Akhalkalaki, organized by column A (taphonomic subsample) column B (unsampled) and column C the entire 1990s excavation assemblage (the sum of column A and B)

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<th>A2</th>
<th>A3</th>
<th>A4</th>
<th>A5</th>
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Raw data are presented as NISPs (number of identified specimens). MAUs (minimum animal units) are included to standardize element frequencies by their frequency in an animal’s skeleton. MAUs were calculated by dividing the number of elements by the number expected if an animal was represented whole. It differs from MNI (minimum number of individuals) by element because it does not distinguish between right and left side (see Lyman, 1994: 104–112 for discussion). Percent MAU is a measure of skeletal completeness calculated by setting the most frequently occurring element at 100%. This index is also known as % Survivorship, and allows comparison between assemblages of different sizes. In this case metapodials indicate the minimum number of animals represented at the site (20.75 individuals are 100% MAU). The %MAUs for the other elements are calculated as if one expected all 20.75 individuals to have been brought to the site whole. Although MAUs are usually calculated using MNEs rather than NISPs (Lyman, 1994), here MNEs cannot be calculated for the entire faunal assemblage but only from the taphonomic subsample. However, the correlation between estimates of MAU based on NISP and MNE for the taphonomic subsample is highly significant (r²=0.90 (p<0.001) supporting the use of NISP. MNEs were calculated by summing up portions of bones by skeletal element (e.g., for long bones, using a five categories vertically: proximal, proximal shaft, shaft, distal shaft, distal, after Marean and Spenser (1991); and 4 horizontal categories “anterior”, “posterior”, “medial”, “lateral”).

Many archaeological sites have skeletal elements that are biased toward lower limbs and skulls, especially for large species (Klein et al., 1999). Perkins & Daly (1968) developed the concept of the schlepp effect to explain the repeated observation that lower limbs tend to dominate archaeofaunas, suggesting that the feet would have been used as handles on the hide for transporting meat. There has been much discussion of this interpretation over the years. At some archaeological sites, lower limbs and skulls have been taken to indicate scavenging, after the original suggestion by Binford (1984; see also Stiner, 1994). In a recent paper, Bartram & Marean (1999) suggest that the dearth of
upper limb elements of large bovids common at archaeological sites (part of “the Klasies Pattern”) is due to the preferential destruction of these elements during marrow processing. Clouding the picture is the lack of attention given to long bone shaft fragments that are difficult to identify. Marean & Frey (1997) suggest that reverse utility curves are common because scientists base long bone abundance on long bone ends rather than shafts. While the lack of long bone shaft fragments may have some influence on the skeletal part frequencies at Akhalkalaki, the reverse utility curve of skeletal element representation is also based on axial elements. At issue is whether or not crania, mandibles, pelvis, vertebrae, ribs, and humeri and femora were originally present and were selectively destroyed, or were never introduced to the site.

One way to explore this question is to reconstruct the number of skulls that may have been originally at the site but were destroyed, achieved by calculating MNE for skulls based on isolated teeth. If there are many isolated teeth, the skulls from which they originated must have been destroyed by some taphonomic process. Although there are few skull fragments, isolated teeth and a few tooth rows suggest some were originally present at the site. Reconstructed MNE for missing crania based on isolated teeth is 5 (2 artiodactyls, 3 equids). There are no mandibles in the taphonomic subsample and as they are very dense bones, diagenesis would not have destroyed them at a particularly high rate, and carnivores generally leave at least the alveolar portion (Stiner, 1994). Reconstructed MNE for missing mandibles based on mandibular teeth is 6 (3 artiodactyls, 3 equids). These numbers are low enough to suggest that although there may have been a few skulls originally at the site, many more skulls were never present. Adding the “reconstructed missing skulls” based on teeth does not change the appearance of the classic reverse utility curve. In addition, the one large ungulate vertebra in the sample is delicate and well preserved, suggesting that other vertebrae, if originally present at the site, would have survived too. Furthermore, as already mentioned,
there are not as many small bone fragments as one might expect if bones were rapidly being destroyed in situ.

All of the above considerations indicate that many of the axial elements were never present within the area of excavation. These axial elements are of varying bone densities and transport potentials. Thus there are two alternatives. Carnivores could have consumed and destroyed the highest utility elements near where they killed or found the animals, and what remained after consumption was transported to this spot; or the site is the death site and the high utility elements were transported away from the site and eaten off-site. The evidence that most skulls were never present, and that there are few small bone fragments, suggests the former.

Traditionally, limb dominated skeletal part frequencies have been considered indicative of a transported assemblage rather than a death assemblage (Bunn & Kroll, 1986). Monahan (1998) has shown that among hunter-gatherers, the axial elements are transported at least as often as limbs. Hunter-gatherer field processing and transport decisions are based on many factors, such as group size and sharing considerations (Bunn et al., 1988; Marshall, 1994; O’Connell et al., 1988, 1990). For social carnivores, transport and consumption decisions can be nearly as complex as they are with humans, and are contingent upon factors such as the number of competing carnivores, the length of time they feed upon a carcass, and their degree of hunger (Haynes, 1980). Despite the variability in factors affecting the amount of food remaining on a skeleton, lower legs are by far the most common surviving skeletal elements at kill sites when carcass utilization is high (Haynes, 1980; Blumenschine, 1986). Adult heads are often too large to be dragged to carnivore dens (Scott & Klein, 1981). The skeletal part frequencies at Akhalkalaki thus suggest carnivores may have consumed or dragged away the most edible portions of carcasses and the remaining lower legs slumped into a small gully.

The carnivores from Akhalkalaki display a different pattern of skeletal part frequencies than do the ungulates (Figure 15). Of the few post-cranial axial elements recovered, half are from carnivores, suggesting carnivores have a slightly different taphonomic history than the herbivores. In one instance, a rib and four articulated caudal vertebrae with unfused plates belonging to a juvenile canid were discovered in the same unit. (The position of the articulated caudal vertebrae can be seen in the centre of the plan map in Figure 5 in square 52–53 N/51–52 E.) Since unfused caudal vertebrae are so small and are normally very quickly consumed by carnivores, the fact that they are preserved at all is remarkable. That the bones are articulated in situ suggests ligaments were still attached at the time of burial. Some ungulate bones were semi-articulated,
suggesting that these bones also remained in position after soft tissue decay.

**Mortality**

Mortality curves based on age of death of animals may provide clues as to the cause of death and the taphonomic history of a site. At Akhalkalaki, one gets a different impression of mortality depending on whether one considers the post-crania or teeth. The post-crania do not exhibit a mortality curve traditionally associated with predation. The post-cranial bones from the taphonomic subsample indicate that there are few juveniles: most epiphyses are fused. Only five of the ungulate bones (MNI=1) have unfused epiphyses (a metacarpal, metatarsal, radius, humerus, and femur—all *Equus*), and only one element exhibits pathological growth common in older individuals. Perhaps this is not surprising since carnivores tend to consume juvenile post crania nearly completely. This pattern is similar to that expected from human hunting, whereas carnivores tend to generate faunal assemblages showing preferential predation on young and very old individuals (Stiner, 1994). However, ages of death are best if based upon teeth. Although the sample of equid teeth is small, it includes an MNI of two very old individuals with extremely low crown heights (they are too broken and eroded to measure exact heights) and three very young infants (deciduous cheek teeth not in wear or slight wear). There are no prime age adult equid teeth in the taphonomic subsample. Although the dental sample is small, for equids there is a trend toward the attritional death pattern, as only the most vulnerable are present. For artiodactyls, there is an MNI of three individuals represented in the teeth. There is a caprine prime adult (light wear on M3); a prime adult bovine (represented by two permanent upper premolars, worn) and one juvenile about 5 months old (M4 not yet in wear).

**Comparison of the 1950s’ and 1990s’ faunal samples**

Study of the 1950s’ sample in Tbilisi showed that the fossils were identical to the 1990s’ material in terms of completeness, patterns of fossilization, and surface features (the majority are weathering stage 0). The 1950s’ bones are also most commonly lower limb bones of *E. süssenbornensis*, with elements distal to the radius and tibia represented. Most bones were whole, and gnawing was not particularly common. Gnawing appeared to be more common on the smaller *E. hippopatonooides* than the larger *E. süssenbornensis*. There were also some tooth rows of young and old individuals, and there were few skulls. Some carnivores were also well preserved, for example, a nearly complete skeleton of a juvenile canid was recovered. So, like the 1990s’ sample, at least some of the carnivores and herbivores seem to have had different taphonomic histories that allowed some carnivore skeletons to be better preserved. The fact that these assemblages from the early and recent excavations are similar indicates that they represent a single unit, and suggests that fauna will continue to be found if excavations are extended between the two excavation areas. The ongoing destruction of the bones by roots suggests that the bones predicted to lie between the two excavation areas will be destroyed if they are not recovered soon.

**Formation of the Akhalkalaki faunal assemblage**

The mode of accumulation of the Akhalkalaki bones can be understood best in the context of comparisons with known bone accumulating agents. Although rodents were present at the site, their gnawing is relatively rare, and they are unlikely to have had a strong impact at the site. Likewise, physical aggregation of the bones through fluvial transport and downslope movement could have been only minimally involved as the initial cause of bone aggregation. The most likely agencies of bone accumulation are denning carnivores, mass death, and serial predation.

**Carnivore denning**

It is evident that carnivores heavily modified the Akhalkalaki fauna, and this raises the possibility that the site represents a den or lair. Carnivores frequently den in ravines and gullies where the changes in slope allow them to tunnel into the earth from the side. The spatial distribution of bones at the site suggests the possibility that it could represent a pocket of bones from within such a lair. Bones collected by carnivores in dens can be found in isolated elongated patches with preferred orientations, consistent with den passageways (Potts *et al*., 1988). However, the very large horizontal extent of the site, likely extending downslope to the areas excavated in the 1950s, seems larger than modern day denning areas. However, if landscape features conducive to denning persisted in the area for a long time, time-averaged reuse of the area could result in much larger bone accumulations than expected.

The following comparison with dens is based largely on Cruz-Uribe’s (1991) synthesis of taphonomic observations of modern and fossil hyena dens. Carnivore-accumulated assemblages do tend to have many carnivores represented, but in fact the amount varies from 0% (in rare spotted hyena dens) to 77% in striped and brown hyena dens. In contrast to Akhalkalaki, bear dens tend to have very high percentages of bear remains, exhibiting attritional mortality (Stiner *et al*., 1996). Human-accumulated assemblages, on the other hand, tend to have fewer carnivores-less than 13% of MNI. Carnivores and humans generally compete and often avoid each other (although sometimes humans selectively accumulate carnivore skeletons when after their fur). Carnivore remains are relatively common at Akhalkalaki, representing 15% of the MNI for the
1950s and 1990s excavations combined (Table 6), which is within the lower range of proportions found in modern dens. Natural traps also attract and accumulate carnivores that come to scavenge and then become trapped themselves. There is no evidence for a physical trap at Akhalkalaki. Where juveniles are reared, lairs may be expected to contain juvenile carnivores. There is one juvenile canid in the taphonomic subsample.

Gnawing damage on bone surfaces is expected on between 22–100% of the bones in modern den assemblages, whereas in fossil carnivore assemblages the frequency tends to be much lower. Only 20 (8%) of the specimens in the taphonomic subsample have carnivore gnaw marks. When these gnaw-marked specimens are added to those that have been clearly broken by carnivores the number of carnivore damaged specimens increases to 32 (12.8%). This is lower than found in modern hyena dens. There is a wide variety of carnivores at Akhalkalaki, and some species (e.g., felids) are perhaps less likely to have left as many marks as hyenas (Marean, 1989; but see Marean & Ehrandt, 1995). Linear gnaw marks at Akhalkalaki range from 2.7 mm to 0.74 mm in width. Marks of this size can be made by a carnivore the size of a fox or larger (Andrews & Jalvo, 1997). Some of the carnivores are quite large at Akhalkalaki (Homotherium, Panthera, Crocuta). Canis and especially Crocuta are the most likely candidates for having broken open some of the bones (Figure 16). There are no bones that show signs of carnivore digestion, and no coprolites are present in the taphonomic subsample.

Another feature of carnivore dens is the presence of complete long bone shafts lacking epiphyses (“bone cylinders”). These derive from carnivores gnawing leisurely on the ends of long bones, destroying the soft, grease-filled epiphyses. Four of 47 marrow bones (8.5%) in the Akhalkalaki taphonomic subsample can be classified as long bone cylinders. This is higher than the percentages of cylinders at the Amboseli hyena den (Potts, 1988), and so is within the range of denning carnivores. Long bone cylinders are less common in landscape assemblages, even those heavily modified by carnivores: for example, at Parc National des Virunga only about 3.8% of long bones were classified as long bone cylinders. Still, at Akhalkalaki the degree of gnawing and breakage is less than expected for a hyena den. Large numbers of complete metapodials are common in hyena assemblages and rare in human accumulated assemblages (Potts et al., 1988). Akhalkalaki has many complete metapodials.

In dens, attritional age profiles are common. As indicated above, although the sample size is small, the equid teeth at Akhalkalaki represent an attritional pattern of death, with only young and old individuals represented. However, post-crania represent the largest numbers of individuals, and these are overwhelmingly adult. Bovids include prime adult individuals.

There are dozens of European cave sites with large bone assemblages that can be attributed entirely or almost entirely to carnivore behaviour, but that also contain small numbers of stone tools (e.g., Stiner, 1994; Villa & Soressi, 2000). These have variously been interpreted as representing alternating occupations of carnivores and hominins, hominins scavenging from hyena dens or natural traps, or simply occasional occupation by hominins. Akhalkalaki is more similar in character to those sites interpreted as carnivore dens than those with extensive hominin involvement for several reasons, including a lack of burning, lack of unmistakable cut marks, and a very high ratio of NISPs to lithics (Stiner, 1994). Sites such as Bois

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</table>

*1950s based on Vekua, 1987: Table 1. 1990s other* is based on NISP rather than MNE, and thus is an approximation.
Roche, France, and Venta Micena, Spain, fit more comfortably with modern dens than does Akhalkalaki, because of high numbers of coprolites, many deciduous carnivore teeth, and numerous digested bones (Arribas & Palmquist, 1998; Villa & Soressi, 2000). The ratio of carnivore NISP to ungulate NISP at Akhalkalaki is also substantially lower than at any level at Buca della Iena, interpreted as a hyena den (0.06 versus 1.89–0.69 [Stiner, 1994: 78]), and frequencies of carnivore gnawing are lower at Akhalkalaki.

**Mass death**

“Mass death” is a bone accumulating process where many individuals die at once or over a short period of time. When a fossil assemblage includes many individuals of the same species, such that might represent a herd, and with all the specimens with the same weathering stage, one must seriously consider mass death as a possible bone-accumulating agent. Common causes of mass death include large drowning events of migratory animals while crossing rivers (commonly seen in East Africa today), mass starvation and epidemic disease, winter snow storms (Berger, 1983), volcanic eruptions and poisonous gases associated with volcanically active areas, and even falling o

![Figure 17. Percent survivorship of skeletal elements of Akhalkalaki compared to an attritional death landscape assemblage.](image)

tures that Akhalkalaki shares with mass death sites include the predominance of a single species (*E. süssenbornensis*), predominance of adults, low variation in weathering stages, many intact elements, and under-representation of bones with high marrow weights.

**Attritional death or serial predation**

The skeletal element frequencies at the site are significantly different from those of attritional death assemblages that accumulate slowly across landscapes through time. Modern attritional death, or natural (=minimally affected by humans) landscape bone assemblages have been well studied at Amboseli Park, Kenya (Behrensmeyer & Dechant-Boaz, 1980), Serengeti and Ngorongoro National Parks, Tanzania (Blumenschine, 1989), and Parc National Des Virunga, D.R. Congo (Tappen, 1995). Figure 17 compares percent survivorship of the skeletal elements of Akhalkalaki to those found in Tappen’s bone rain survey across a central African savanna and shows that there is no correlation ($r^2=0.006386$, $P=0.795$). Tappen’s skeletal element frequency data from the Congo have been found to correlate with those from the other well documented attritional death landscape assemblages from Amboseli Park, Kenya (Behrensmeyer, 1983) and the Serengeti and Ngorongoro in Tanzania (Blumenschine, 1989; Tappen & Laden, 1997). Cranial and mandibles dominate all the modern landscape assemblages; there are intermediate numbers of limb bones and a lack of podials and phalanges. The buried attritional landscape assemblage at Amboseli is also not like Akhalkalaki; it is dominated by vertebrae.
ogy are much more variable than what is present today related to climate, vegetation, and large mammal ecology remaining in reasonably high densities than in most areas (Tappen, 1995). Akhalkalaki may have afforded a special topographic situation where predation was unusually successful and so repeated. It may be that carnivores were attracted to the general area because the change in slope created by the volcanic cone would have created areas with easy access for digging dens and/or ambush. This would create a high density of carnivores in the area, and thus high bone deposition rates. Alternative terms for such situations are “predator arenas” (Behrensmeyer, 1983), or “serial predation” (Haynes, 1988). Sites that are good for ambush in open environments may be adjacent to waterholes (Binford, 1981, 1984), next to isolated large trees or lines of trees or other cover (perhaps the edge of volcanic cone?), and on high spots that tend to be windy where carnivores can move upwind of their prey and not be detected (Tappen, 1995). Such predator arenas have rarely been noted or studied by taphonomists, and the variability (e.g., in skeletal element representation) between the sites that have been studied is high. Pelves and skulls dominate the serial predation sites studied by Haynes, a pattern that certainly does not match Akhalkalaki. The predation arena by a large shade tree studied by Tappen (1990, 1995) was dominated by elements that are easily disarticulated: scapulae, mandibles, humeri, but also innominates; small bones such as phalanges are under-represented. This too does not match Akhalkalaki well.

Discussion and Brief Comparison with Dmanisi

The majority of actualistic data available on death and bone alteration in natural environments comes from Africa, where there are large game and large predators remaining in reasonably high densities than in most temperate regions. Yet environmental features clearly related to climate, vegetation, and large mammal ecology are much more variable than what is present today in Africa, and these features affect bone taphonomy. Taphonomic and ecological observations in more northerly climes indicate that large winter storms and harsh winters with much snow can be deadly to the large ungulates such as equids and cervids that inhabit these areas (Barnosky, 1985; Berger, 1983; Weigelt, 1989). Although species such as the hippopotamus at Akhalkalaki may suggest an environment that was relatively warm, the high latitude and altitude suggests that cold, deadly winters were a possible influence on mortality. Other variables affecting bone taphonomy vary with environmental situation. For example, mummification and dehydration may hamper disarticulation in some situations more than in others (Nasti, 2000). In environments where the number and variety of carnivores is low and competition is low, the moving of carcasses during feeding is uncommon (e.g., in the high altitude desert in Argentina (Nasti, 2000). It is interesting to note that bones that were evidently accumulated by large carnivores in the past tend to have lower frequencies of gnaw marks than actualistically studied dens (Cruz-Uribe, 1991). This suggests fossil “dens” may have more complicated taphonomic histories than such a name implies. Just as all bones in an archaeological site may not have been introduced by hominins, not all bones in palaeontological dens may have been introduced by carnivores.

At Akhalkalaki, definitive signs of hominin modification are not recognizable on the bones, and carnivore tooth marks and breakage are at moderate levels. There is a notable lack of skulls and high utility elements at Akhalkalaki. The missing axial bones and upper limbs are likely to have not been introduced to the site in great numbers, but were likely consumed nearby, either dragged from the low utility elements left at the site, or consumed where the animals died, and the lower utility elements were moved to the site. This transport may have occurred over a short distance and likely would have happened in the context of feeding competition among the carnivores and/or small-scale physical displacement of the bones into a runnel. Although hominins and carnivores both prefer to consume the same portions of the animals, the lack of definitive evidence for hominins and the presence of carnivore modification suggest carnivores as the agents. Carnivores are known to drag bones in the context of feeding competition to lines of trees and other features that give them relative seclusion (Tappen, 1995). Mass death via starvation/winter storms, poisonous gas or even falling off a cliff is possible, which then would have attracted carnivore scavengers. However, in the case of mass death we would expect carcasses to be less well consumed than they are at Akhalkalaki (Haynes, 1980, 1985, 1988).

Feeding competition among carnivores is suggested by the many species of carnivore present at Akhalkalaki. Any of these species could have been scavengers, but considering the large body size of the prey, the most likely species to have hunted the equids and large bovids are Homotherium, Panthera, Canis, and Crocuta. The sabre tooth is not considered to be a big bone crusher, and the missing elements such as the upper limbs suggest Crocuta was involved. If Canis hunted the equids, then they were in large packs of 8–14 individuals because prey size is so large (Haynes, 1985: 63). In fact, the large size of the prey suggests the other three species were more likely the predators.
However, which species hunted, and which scavenged from the site is not discernable at this time.

At Akhalkalaki, we can reasonably infer that many individuals of a variety of species died in a relatively short period of time and were buried rapidly. We can also conclude that hominins were involved little in the history of this fauna; that there were enough large carnivores relative to the rate of accumulation of carcasses to consume the best portions of the carcasses and yet not consume the lower quality pieces. Likely, limbs were removed and dragged short distances away from the axial skeleton to be consumed in a less competitive location, and the lower, less nutritious portions abandoned. The spatial configuration suggests short distance movement by gravity and washing into a small runnel on the side of the volcano. Colluvium then buried the bones.

Akhalkalaki is one of several sites being examined by us as part of an effort to assess the potential of the Republic of Georgia to yield significant information about the first extra-African dispersal of Early and Middle Pleistocene hominins. The Akhalkalaki fauna is important in terms of biozonation, palaeoenvironments, and archaeological taphonomy. We have presented new data, including the results of palaeomagnetic and detailed taphonomic studies. However, the majority of the Akhalkalaki fauna does not seem to have been accumulated by hominins as there are no definitely hominin modifications (cut marks or hammer stone blows) recognizable on the bones. Instead, the faunal remains appear to have been modified, and likely collected, by carnivores. There are six artifacts associated with the fauna, but it appears that some (and perhaps all) of these artifacts worked their way into the faunal layer from the surface via rodent burrows and are not contemporaneous with the fauna.

It is also possible that these artifacts were discarded by hominins prior to the deposition and burial of the fauna and that the eventual association is entirely fortuitous. Given that other stone tools are present near and around the excavation area reported here (Gabunia, 2000), and that artifacts and hominin fossils have been discovered nearby at the older locality of Dmanisi, hominins may have been present on the Paravani Plateau at this time. Yet the excavations conducted in 1995–1996 and this taphonomic study do not speak to this presence. Such a situation is not at all uncommon in sites of this age, where hominin population densities are presumed to have been low and archaeological signatures thus ephemeral. There are many Palaeolithic sites with a few stone tools and many animal bones, the majority of which have been accumulated by carnivores, or other non-hominin agencies. These sites have been interpreted in many ways, including ephemeral occupation by hominins, scavenging by hominins, and post-depositional mixing of stone tools with behaviourally unassociated bones (Villa & Soressi, 2000; Stiner, 1994).

The physical dimensions of the bone accumulation are reminiscent of those from Dmanisi and the nearby site of Diliska (Ferring et al. in preparation), in that they all are discretely linear in plan view, with a significant vertical dimension (from c. 25 cm upslope to c. 75–80 cm downslope). These distinctive spatial distributions may be the result of steep topography (Akhalkalaki) or, in the case of Dmanisi, may indicate accumulation of these bones in “tunnels” (Gabunia et al., 2000; Ferring et al., in preparation).

To date, little taphonomic analysis has been undertaken on the Dmanisi fauna or other archaeological faunas from this region, and our study of Akhalkalaki is one step toward greater use of taphonomic methods in the region. Although the Dmanisi site has yielded over 1000 lithic artifacts, no undisturbed occupation surfaces have been defined, and the vast majority of the fossils and many of the artifacts have been recovered from large cavities that intruded into older deposits at that site. The human mandibles, calvaria, and crania were found in these features, while the human metatarsal was recovered from an overlying, but contemporaneous erosional surface. In addition, there is increasing evidence now for occupation at Dmanisi in sediments attributed to the Olduvai Normal Subchron. The pocket of bone that included the human mandible (D211) was 50–70 cm thick. In Stratrum A (formerly Unit V) in the profile in Building 11, the largest exposure of the intrusive, tunnel-like features is c. 6 m long and 23–53 cm high. Although geologic processes such as piping are being investigated as formative agents, the size and shape of the tunnel-like features are also within the range of burrows made by some modern animals, and this hypothesis needs investigation.

Carnivore species make up 25-85% of the species excavated from Dmanisi (Vekua, 1995: 86). Carnivores in life typically make up a very low percentage of the biomass and of the number of species in modern environments (Eisenberg, 1980, 1981). The most common concentrator of rare carnivore bones is competitive behavior by carnivores, and so the presence of carnivores beyond that expected in the living community is a possible indicator of a lair (Klein & Cruz Uribe, 1984; Cruz-UrIBE, 1991). The other features known to aggregate carnivore skeletons are natural traps that attract scavengers. The first hominin mandible was found in direct association with two species of sabre tooth cat (Megantereon megantereon and Homotherium sp.), a bear (Ursus etruscus) and a Canis specimen (DzparaZite et al., 1991). The presence of a juvenile Pachycrocuta at Dmanisi (Vekua, 1995: 95) is suggestive of a den belonging to that species. Furthermore, based on behavioural analogies to their extant relatives three of the species of carnivore from Dmanisi, Canis, Ursus and Pachycrocuta are, likely to have occupied dens. Finally, there is the exceptional presence of articulated axial skeletal remains, complete skulls and mandibles, and numerous coprolites. These
observations suggest that carnivores played a significant and possibly dominant role in the accumulation and modification of the Dmanisi fauna. However, brief observation of the bones indicates that, like at Akhalkalaki, carnivore scoring is not particularly common. The presence of artifacts indicates that continued study at Dmanisi is required to establish the taphonomic history of the fauna vis à vis hominin and carnivore agents.

The taphonomic history of the Akhalkalaki fauna provides a critical comparative record for the taphonomic assessment of Dmanisi. The fact that the Akhalkalaki fauna does not meet all of the major expectations for a carnivore assemblage based on African analogies highlights the present and future need to develop models for the Palaeolithic zoarchaeology of different regions, including the Caucasus.

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