THE WISDOM OF THE AGED AND OUT OF AFRICA I

Martha Tappen

Abstract
The hominin lineage made a transition from a geographically constrained population endemic to Africa to the most widespread mammalian species able to occupy the entire globe. Currently, the best evidence for the initial geographic expansion beyond the lower latitudes is preserved at the lower Pleistocene site of Dmanisi in Georgia. Anthropologists have often speculated about the causes of the first expansion, known as “Out of Africa I.” Hypotheses of “initial kicks” for the expansion include changes in environment, the spread of African-like biomes, changes in hominin food-acquisition strategies, increased diet breadth, changes in technology or social factors such as the nature of intragroup interactions, as well as increases in brain size and body size. In this paper, these ideas are considered using the evidence from Dmanisi. In terms of the preserved evidence, it appears that intrinsic behavioral qualities of Homo must have been the most important factors in the first peopling of Eurasia. Evidence suggests that the Dmanisi hominins had primary/early access to animal carcasses, probably through hunting, and more individuals survived into old age, which likely increased not only population growth but also group cohesion and the accumulation of knowledge.

Paleohabitats are significantly different from contemporary hominin sites in Africa, and there are virtually no mammalian species in common except some carnivores that occupied huge geographic ranges across most of the Old World before, during, and after the Dmanisi hominin dispersal. The hominin expansion was not accompanied by other African faunas. Furthermore, the lack of suids, monkeys, hippopotamus, and crocodiles indicates a novel landscape that the hominins had to negotiate. Therefore, climatic hypotheses of the spread of African biomes north are not supported. In physically significant qualities such as brain and body size, the hominins are in between H. habilis and H. erectus and so do not indicate a stepwise change at this point.

Introduction
Ofer Bar-Yosef has a notable talent for picking the most significant questions in archaeology and targeting them with his fieldwork. He also sends his students to fill in gaps in the record. Some of the many grand issues in human evolution that Bar-Yosef writes about extensively are the first and later dispersals of humans from Africa into Eurasia. In this paper, I discuss hypotheses related to the first geographic expansion out of Africa, as indicated by what is preserved at the Dmanisi site in Georgia.

The greatest hurdle for a good understanding of the peopling of the higher latitudes is discerning which gaps in the fossil record represent real absence of hominins, and which gaps are a result of poor preservation and poor data recovery by archaeologists and paleoanthropologists. Vast
areas are underexplored, many sites are not well dated, and others have ambiguous evidence (Dennell and Roebroeks 2005). The outline of what happened and when it happened may therefore change, and widely held ideas today may need to be revised significantly as more sites are found. We must support and encourage fieldwork to improve this situation and continue to improve information recovery in the next decade. For now, I will proceed with the evidence as it exists today.

From our African-ape and australopith ancestry, hominins first began to spread beyond Africa about 1.8 Ma. Well-dated Lower Pleistocene sites are scattered far and wide across Asia, some of the earliest in the northern Chinese Nihewan Basin (Wang et al. 2005; Zhu et al. 2001) and in Indonesia (Swisher et al. 1994). For decades, the site of 'Ubediya, where Bar-Yosef worked extensively, has been one of the earliest sites known out of Africa, with well-accepted faunal chronological dates of over one million years, perhaps even 1.4 Ma (Bar-Yosef 1994; Bar-Yosef and Goren-Inbar 1993; Tchernov 1987, 1992a, 1992b). In Europe, the Spanish sites of Barranco Leon-5, and Fuente Nueva-3, and Atapuerca/Trincheras Elefante (Oms et al. 2000; Parés et al. 2006) and early Italian sites, including Pirro Nord (Arzarello et al. 2007), are also slightly younger than Dmanisi.

**Dmanisi**

Dmanisi in Georgia currently is the earliest site beyond Africa that has abundant evidence of hominins, fauna, and stone tools all associated together with reasonably good dates (Lordkipanidze et al. 2006; Vekua et al. 2002). Its stratigraphic situation and vertebrate taphonomy point to deposition that was rapid and did not involve much transport (Tappen et al. 2007). The presence of several hominin individuals at Dmanisi from a single population in the same geographic location and from a very short time range allows examination of variation in morphological traits (Rightmire et al. 2006). The "paleodeme" of the hominins at Dmanisi includes a minimum number of five individuals, several with cranial and postcranial remains (Table 3.1; Lordkipanidze et al. 2007). For these reasons, Dmanisi has become a new anchor point of understanding Out of Africa I (Anton and Swisher 2004; Anton et al. 2002; Dennell and Roebroeks 2005; Mithen and Reed 2002; Nikitas and Nikita 2005; Stiner 2002). There has been some debate as to whether some of the fossils are located within the Olduvai subchron (Stratum A, at about 1.81 Ma; de Lumely et al. 2006) or only within paleomagnetically reversed Stratum B immediately after it (between 1.78 and 1.76; Vekua et al. 2002; Lordkipanidze et al. 2006). This is resolved with new paleomagnetic analyses (Ferring et al. in prep). Although there are still no capping radiometric dates, the geological and paleontological evidence indicates Stratum A was deposited within the Olduvai Subchron and Stratum B was deposited immediately after the Olduvai subchron (Lordkipanidze et al. 2006), and the temporal and spatial associations between the various types of information (hominins, fauna, tools, pollen) are robust. Many of the other important early Out of Africa sites such as 'Ubediya, and Fuente Nueva and Barranco Léon in Spain are younger by several hundred thousand years and contain their own evidence, which differs from Dmanisi. Importantly, the faunal evidence from Dmanisi differs from the above-mentioned early sites in Europe and Asia, so they may represent later excursions out of Africa, in keeping with the idea that there are some real gaps in occupation of
Table 3.1 Hominin individuals from Dmanisi based on cranial remains

<table>
<thead>
<tr>
<th>Individual</th>
<th>Age estimation</th>
<th>Main reason</th>
</tr>
</thead>
<tbody>
<tr>
<td>I (D2280)</td>
<td>adult</td>
<td>no teeth, synchondrosis not preserved, but adult size and shape, inferred from cranial sutures</td>
</tr>
<tr>
<td>II (D2282/D211)</td>
<td>young adult</td>
<td>$M_1$ just reaching wear</td>
</tr>
<tr>
<td>III (D2600)</td>
<td>older adult</td>
<td>Severe wear on all teeth, including $M_3$s</td>
</tr>
<tr>
<td>IV (D2700/D2735)</td>
<td>subadult</td>
<td>$M_3$’s partly erupted, root 30%, $M_3$ crypt on right, congenitally absent on left, unfused sphenoccipital synchondrosis</td>
</tr>
<tr>
<td>V (D3444/3900)</td>
<td>older adult</td>
<td>tooth loss and resorption of alveolar region</td>
</tr>
</tbody>
</table>

Data for "main reason" from de Lumley et al. 2006; Lordkipanidze et al. 2006; Rightmire et al. 2006.

... Eurasia and sporadic episodic dispersals (Bar-Yosef and Belfer-Cohen 2001b). With that in mind, I will discuss out of Africa hypotheses in light of the Dmanisi evidence alone.

**Hypotheses**

Many hypotheses are discussed in the literature regarding the causes of the first peopling of the higher latitudes into Eurasia from Africa. An inventory of these hypotheses reveals that many of the fundamental characteristics of humans that have evolved since the split with the other African apes are the same as those that have been proposed as instrumental in our range expansion. Hypothesizes include climate change, encephalization, habitual and efficient bipedality, hunting, scavenging, technology, fire, language, and trade (Foley 2001; Gabunia et al. 2001; Roebroeks 2001; Roebroeks and van Kolfschoten 1995; Shipman and Walker 1989; Walker 1984). These hypotheses are alternative but not mutually exclusive, which makes testing their relative importance all the more complex. To target these anthropological questions, I find it useful to divide these hypotheses into groups stressing the importance of “extrinsic” and “intrinsic” evolutionary forces. Extrinsic hypotheses include those that encompass factors that are external to *Homo*, in other words, that involve main causes that do not emphasize changes in human adaptations or human agency. With these hypotheses, *Homo* could remain essentially biologically and culturally the same as their immediate African forbearers, but through expansion of their prime habitat, their geographic range increased. In contrast, using the term “intrinsic hypotheses” highlights the evolution of new traits and behaviors within the hominin lineage, and the probability of their moving into a new “adaptive zone” sensu G. G. Simpson, that allows their geographic expansion into higher latitudes. While environmental changes and evolutionary changes within *Homo* are not mutually exclusive, I find the dichotomy useful for bringing out evidence of anthropologically important changes in *Homo*. In this paper, I consider many of these hypotheses in light of the evidence from Dmanisi.

**Extrinsic Hypotheses and the Large Mammal Community at Dmanisi**

Three examples of extrinsic hypotheses proposed to have important influence on *Homo*’s
ability to spread include (1) climate change causing the expansion of African biomes with *Homo* more or less tagging along, (2) other ecological changes, such as within the carnivore guild facilitating the expansion, and (3) changes in disease vectors (Arribas and Palmqvist 1999; Bar-Yosef and Belfer-Cohen 2001a, 2001b; Tchernov 1999; Turner 1992, 1999). It is well known and documented that climate change was notable in the Plio-Pleistocene, with fluctuations resulting in widespread drying and cooling at the end of the Pliocene (DeMenocal 1995). With climate and habitat oscillations, *Homo*, along with other African faunas, could make it out of Africa when circumstances were favorable – the “green light” model of Vrba (1995) – which would have allowed general expansion of African species/habitats beyond continental Africa (Tchernov 1998). If climate change caused the spread of African faunas northward, with *Homo* as a “fellow traveler,” other African mammal species should be present at Dmanisi.

**Spread of African Biome?** There are statements in the literature that some African species are at Dmanisi (e.g., Anton and Swisher 2004; Gabunia et al. 2000), but none of the large mammalian taxa from Dmanisi (Table 3.2) have compelling evidence that they spread out of Africa at 1.8 Ma, except *Homo* (Tappen et al. 2007). The genera at Dmanisi resemble European Late Villafranchian mammal faunas, with the highest similarity values with W. European “Late Villafranchian” assemblages. What similarities exist between Dmanisi and African assemblages are mainly due to the co-occurrence of common carnivore genera (e.g., *Homotherium, Megantereon, Pan-thera*) or, among herbivores, widespread genera like *Equus* (Lordkipanidze et al. 2007). Inspection of the paleontological record shows that the Dmanisi giraffids of the subfamily Palaeotraginae, the ostrich *Struthio*, and even *Pachycrocuta* and *Megantereon* are either from Eurasia, endemic to Georgia, or so widely distributed in space and time that the record of where they are “from” is ambiguous (Tappen et al. 2007). Perhaps the strongest case for a large mammal species represented at Dmanisi coming out of Africa at the Plio-Pleistocene border has been made for *Megantereon whitei* (Palmqvist et al. 2007), but its precursor, *Megantereon cultridens*, is widely distributed in Eurasia and the number of sites and specimens is few, and furthermore the validity of the taxon is in doubt by some. All in all, it does not make compelling evidence.

Not only were the genera and species different from those found at African hominin sites, the mammalian community structure was not like the African sites either. Several key African elements are missing from Dmanisi. At virtually all African hominin sites suids are present, often with the remains of several individuals from four or more species; yet after two decades of excavation at Dmanisi, we still have not recovered any pigs. Suids would have significant ecological interaction with hominins because they could be prey, but probably more importantly as food competitors. Bears (*Ursus etruscus*) were abundant in the Georgian habitats and would have similarly had much dietary overlap with the hominins. Perhaps the niche overlap of bears and *Homo* excluded pigs from the area.

There have been no monkeys uncovered at Dmanisi. Monkeys became rare in the Pliocene of Europe, with only semiterrestrial cercopithecoid species remaining. Their decrease likely signals deciduous trees, seasonal fruiting, cooling, drying, and discontinuous canopies (Eronen and Rook 2004). In fact, monkeys became rare in Europe near the time that hominins expand into
the region. Clearly, drying, cooling, and increased seasonality must have been more severe in the northern latitudes than in Africa, where monkeys remain. In Africa, meanwhile, monkeys are present at most hominin sites contemporary with Dmanisi, and would have been food competitors and probably prey for these hominins in Africa. While the African cercopithecoid Theropithecus is present at 'Ubediya (Belmaker 2002) and in the early Pleistocene of Spain and Italy, it remains absent from Dmanisi.

There are no hippopotamuses or crocodiles in the Dmanisi fauna either. In fact, there are virtually no aquatic taxa. The sediments containing the fossils include minor gullying, but are not lacustrine or fluviatile derived and so few aquatic species would be expected. However, paleolandscape reconstruction by Ferring indicates rivers and possibly a lake about a few hundred meters away from the fossil deposits. Hippopotamus bones can be found as far as 5 km away from permanent water, based on neotaphonomic landscape survey in Parc National Virunga (Tappen 1995), and so hippos may be truly absent from the Dmanisi habitats, rather than being missing due to the subaerial nature of the sediments. There is no doubt that crocodiles and hippos made life by the water dangerous for hominins in Africa (Njau and Blumenschine 2007).

In terms of numbers of individuals, the large herbivores are more commonly cervids than bovids at Dmanisi. Cervids are the most frequently encountered large mammal taxon at the site. Cervids tend to be browsers and mixed feeders, but they occupy a wide range of habitats (Geist 1999). In contrast, the most common large herbivores in African sites are bovids. Ecomorphological work aimed at interpreting the habitat preferences of cervid taxa at Dmanisi would be very informative.

<table>
<thead>
<tr>
<th>Table 3.2 Large mammal taxa from Dmanisi</th>
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<tbody>
<tr>
<td><strong>Carnivora</strong></td>
</tr>
<tr>
<td>Canidae</td>
</tr>
<tr>
<td>Canis etruscus</td>
</tr>
<tr>
<td>Vulpes alopecoides</td>
</tr>
<tr>
<td>Ursidae</td>
</tr>
<tr>
<td>Ursus etruscus</td>
</tr>
<tr>
<td>Ursus sp.</td>
</tr>
<tr>
<td>Mustelidae</td>
</tr>
<tr>
<td>Martes sp.</td>
</tr>
<tr>
<td>Meles sp.</td>
</tr>
<tr>
<td>Hyaenidae</td>
</tr>
<tr>
<td>Pliocrocuta perrieri</td>
</tr>
<tr>
<td>Pachycrocuta sp.</td>
</tr>
<tr>
<td>Felidae</td>
</tr>
<tr>
<td>Lynx issiodorensis</td>
</tr>
<tr>
<td>Acinonyx pardinensis</td>
</tr>
<tr>
<td>Panthera onca sp. (= gombaszoegensis)</td>
</tr>
<tr>
<td>Megantereon megarantereon</td>
</tr>
<tr>
<td>Homotherium cretanidens</td>
</tr>
<tr>
<td><strong>Proboscidea</strong></td>
</tr>
<tr>
<td>Elephantidae</td>
</tr>
<tr>
<td>Mammutus meridionalis</td>
</tr>
<tr>
<td><strong>Perissodactyla</strong></td>
</tr>
<tr>
<td>Equidae</td>
</tr>
<tr>
<td>Equus stenonis</td>
</tr>
<tr>
<td>Equus aff. altidens</td>
</tr>
<tr>
<td>Rhinocerotidae</td>
</tr>
<tr>
<td>Stephanorhinus etruscus</td>
</tr>
<tr>
<td><strong>Artiodactyla</strong></td>
</tr>
<tr>
<td>Cervidae</td>
</tr>
<tr>
<td>Cervus (Pseudodama) cf. nestii</td>
</tr>
<tr>
<td>Cervus abelomi</td>
</tr>
<tr>
<td>Eucladoceros aff. tegulensis (= senezensis)</td>
</tr>
<tr>
<td>Giraffidae</td>
</tr>
<tr>
<td>Palaeotragus sp.</td>
</tr>
<tr>
<td>Bovidae</td>
</tr>
<tr>
<td>Bison (Eobison) georgicus</td>
</tr>
<tr>
<td>Gallogalrus meneghinii sickenbergei</td>
</tr>
<tr>
<td>Capra</td>
</tr>
<tr>
<td>Soergelia cf. minor</td>
</tr>
<tr>
<td>Ovibovini indet.</td>
</tr>
<tr>
<td>Pintoceros sp.</td>
</tr>
<tr>
<td>Antilopini indet.</td>
</tr>
</tbody>
</table>

Therefore, there is little or no evidence for an expansion of African fauna simultaneous with the Dmanisi hominin dispersal, signifying that the factors that allowed Homo's dispersion did not greatly affect the biogeography of the other
mammals that were part of the habitat of *Homo* when it was restricted to Africa. *Homo*’s initial spread is on its own and thus demands an explanation referring to *Homo*’s ecological niche and adaptations that is distinctive from some kind of generalized environmental change and biogeo-graphic spread.

Dmanisi’s paleohabitats are reconstructed as grasslands and mixed habitats including forests (Gabunia et al. 2000), which fits the concept of widely dispersed grasslands across Africa into China as the *Homo* habitat, or “Savanahstam” (Dennell and Roebroeks 2005). However, the particulars of the habitat as indicated by the fauna signify a very different landscape for hominins to negotiate than they did in Africa, and lumping all savannas together may be less informative and create false stereotypes rather than working in a sophisticated way with the variation that is known to exist (Tappen 2001). Grassland ecosystems are heterogeneous ecosystems, and tropical and temperate grasslands have differing properties in terms of species richness, net productivity, and mobility of large fauna (Marean 1997; Tappen 2001). The Eurasian mammalian taxa would have had their own behavioral traits that would not be the same as they would have been in Africa.

**Carnivore Guild Hypotheses.** Hominins entering the carnivore guild is important at many levels (Foley 2001), and *Homo* was at least occasionally eating meat at Dmanisi (below). The hypothesis that changes in carnivore species left more or less meat for scavengers and affected the ability of hominins to colonize Europe (Turner 1992, 1999) does not apply to Dmanisi as originally stated, because many of the proposed significant changes in taxa occurred later in time. Still, the importance of carnivore–carnivore interaction is important regarding the abilities of carnivores to invade new regions, and changes in the carnivores, especially *Megantoreon*, are still considered by some to be important factors in allowing *Homo* to disperse (Palmqvist et al. 2007). The latest morph of this hypothesis is that *Megantoreon* whitei was less able to consume meat as thoroughly as *Megantoreon cauridens*, due to decreased biomechanical power in the chewing apparatus, and so it left more meat for scavenging hominins. But since both *Megantoreon* species could consume meat and neither were bone crunchers, it is not convincing that the smaller biomechanical advantage of *M. whitei* would result in more meat left on bones. In fact, studies of modern day carnivores consuming meat and bone suggest that the main factor in how much food is left on carcasses is the number of animals feeding, i.e., carnivore population density and competition. Both at African sites and at Dmanisi there was a large number of carnivore species with different body sizes, including members of the conical-toothed and sabre-toothed cats, hyenas, canids, and, in Georgia, ursids. Predation on hominins and competition for carcasses could have been high on both continents but most likely varied in intensity with local conditions and local variations in number of predators and in numbers of hyenas (Behrensmeyer 2007). Today, the amount of scavengable food left varies from Ngorongoro crater to the Serengeti, to Amboseli (which itself varies through time), to the Western Rift Valley, and it would have varied greatly from place to place within Eurasia. To the extent that skeletal element completeness reflects the degree of competition for carcasses, the relatively high number of complete bones or nearly complete bones at Dmanisi (Tappen et al. 2007) could reflect low competition levels.
Disease Vectors. In another extrinsic hypothesis, Bar-Yosef and Belfer-Cohen suggested that the expansion was facilitated by a decrease in zoonotic disease from "the disease-plagued belts of Africa" (Bar-Yosef and Belfer-Cohen 2001a, b). As this would decrease mortality and so allow population growth, it is another extrinsic hypothesis. On the other hand, species colonizing new areas often find themselves in environments containing different pathogens that they have not yet evolved resistance to, and new diseases could have impaired expansion. Either way, changes in disease patterns may have occurred, but most diseases are not evident skeletally and so will not be preserved. Although the evidence does not really test these ideas, it is notable that some of the Dmanisi hominins have evidence of disease. Many of the Dmanisi hominins have evidence of periodontal disease; the severe case is D3400/D3900 with extreme tooth loss and resorption of the alveolar bone (Lordkipanidze et al. 2006). The large mandible, D2600, also has severe periodontal disease and severe tooth wear (Gabounia et al. 2002). The D2700 cranium has a rotated and malformed left fourth premolar. Its mandible, D2735, has a small hole distal to the central incisor alveoli, which may also represent infection, as the hole does not have an outer table of bone that has been crushed in, as usually seen in pits made by teeth, such as when carnivores chew bones. It also has signs of decay at the cervix of $M_1$ (Rightmire et al. 2006).

Two of the four published crania have small circular lesions on the cranial vaults. There are three dimples on the frontal and parietals of D2800, and D3444 likewise has two dimples. The dimples range in diameter from just under a centimeter to nearly two centimeters. Rightmire et al. (2006) suggest that the shallow pits on the D2880 cranium may be the result of (healed) blunt-force trauma, but other possibilities include tumors or some form of treponemal disease (Smith 2006). Dimples like these are found on several other hominin crania, for example, on the Zuttiyeh cranium from Israel (Patricia Smith, personal communication) and deserve more study.

**Intrinsic Hypotheses**

The suite of hypotheses in the "intrinsic" category include those that emphasize novel adaptations in *Homo*, such as technological advances, increased brain and/or body size, changes in socioeconomic behaviors (food sharing, division of labor), greater communication abilities (i.e., language, not discussed here), and increased diet breadth (food processing and or hunting/scavenging).

**Stone Technology:** Major changes in stone-tool technology were not central to the exodus out of Africa represented at Dmanisi. Dmanisi, as well as some of the other earliest sites in China (Wang et al. 2005; Zhu et al. 2001) and Java (Stone 2006), contains simply flaked tools, without handaxes, and generally can be called Oldowan. Dmanisi tools include some flakes and cores in direct spatial association with the hominin and mammal fossils. These tool types are least-effort types that result in sharp-edged rocks (Isaac 1986). Thus, hominins expanded their geographic range without the help of Acheulian tools and before the first Acheulian is known to have appeared in Africa circa 1.5 Ma (Asfaw et al. 1992). Later dispersals are now known to have included Acheulian tools; several of the earliest sites out of Africa, which were once thought to contain Pre-Acheulian industries, produced rare handaxes once sample sizes were larger (e.g., Gran Dolina TD6, the lower levels at
‘Ubediya). At ‘Ubediya and Gesher Benot Ya’qov, the African-like Acheulian indicates a new dispersal (Bar-Yosef and Belfer-Cohen 2001b). In any case, the Acheulian did not replace the Oldowan, rather handaxes were additive (Bar-Yosef and Belfer-Cohen 2001b; Monnier 2006; Villa 2001).

There are very large numbers of unmodified cobbles throughout the site, which, according to Ferring, must be manuports rather than naturally occurring (Figure 3.1). As unmodified cobbles, they cannot be seen as an advance in technology, but their sheer abundance is striking, and the cobbles must have been important tools in the lives of these hominins.

**Controlled Fire.** The controlled use of fire is sometimes considered to be essential to moving to the higher latitudes, because it would provide needed warmth in the winter. Local conditions are critical to the preservation of such evidence, especially in open-air situations, such as much of the Dmanisi site. There is no evidence for use of fire recognized at Dmanisi as of yet: no hardened red patches and no burnt bones.

**Hunting and Scavenging.** If fruits are not available year-round at higher latitudes, many believe the hominins would have had to increase diet breadth by including more animal products, especially in the winter. In fact, the evidence from Dmanisi shows that the hominins were eating meat and, furthermore, had early access to carcasses, though the evidence is rare. Several conditions hinder finding evidence for meat consumption via surface modifications (tools marks) on the mammalian bone from Dmanisi. Although the fauna is very well preserved, some bone surfaces are coated in calcite that is very hard compared to the fossils themselves and adheres tenaciously. The calcite is often thicker and difficult to remove from the bone near the edges of breaks, where surface modifications are more likely to occur. Other surfaces have been destroyed by fungal etching ("root-etching," Figure 3.2). The fungi sometimes seem to be attracted to areas where the bone surface was already damaged, in such cases obliterating previous surface modifications. The fungal etching at Dmanisi is very distinctive from carnivore marks, not like that reported from Olduvai (Dominguez-Rodrigo and Barba 2006). The etching has a characteristic patterning and often exposes very white underlying bone. Furthermore, the bones are damp when first exposed during the excavation, and in this state, they are soft and easily damaged. We allow the bones to dry before preparation and cleaning because they become more durable, but some still get damaged. Despite these problems, we have several cut-marked specimens identified so far. They include defleshing marks on a cervid femur and on a humerus shaft fragment, marks on the distal radii of two bovids, and a few striation fields and hammerstone marks (Lordkipanidze et al. 2007; Tappen et al. 2007). Thus, although rare, there is evidence for meat removal on upper limb bones (femur-humerus) and middle leg bones (radius-tibia). Since large cats and hyenas rarely leave meat on upper limb bones (Dominguez-Rodrigo 1999, 2002; Pobiner 2007), those marks probably signal that the hominins had early access to carcasses, instead of access only after a large carnivore was finished eating. Some of the medium mammal bones appear to be smashed for marrow as well. This evidence, though rare for the site, supports theories that meat was part of the Dmanisi hominins’ diet and may well have been a critical factor in the spread of hominins.
Other Foods, Fat, and “Fallback.” In addition to increased meat consumption, changes in anatomy/physiology such as in the ability to accumulate fat could also help buffer seasonal variation in food supply (Atello and Wells 2002). Consumption of tougher fruits, pods, and tubers that survive severe seasons as edible, could also be important at high latitudes. The severe wear on the Dmanisi hominin teeth (below) may be an important signal of their diet in upper latitude winters, because such wear may indicate the use of hard, tough fallback foods that require a lot of chewing or need to be consumed in large quantities because of low nutritional value. Furthermore, tough fibrous foods that are processed in concentrated areas of the jaw can contribute to tooth loss (Cuozzo and Sauther 2006), a factor which should be considered as a possible explanation of for the amount of tooth
loss on the Dmanisi hominins. In addition to the cheek teeth, the anterior dentition tends to be heavily worn and so biting into tough foods as well as chewing is indicated (as well as the possibility of using the anterior teeth as tools.) Studies on the microwear on the Dmanisi hominin teeth will be very enlightening.

Brain and Body Size. Brain and body size are some of the most important biological variables that we are able to reconstruct in hominin species, as they relate to so many other variables such as dietary needs, sociality, home-range size, and life-history variables. Hypotheses about the role of increased brain size and out of Africa stem from ideas regarding increased intelligence and behavioral flexibility for a primate to adapt to new environments. However, a large increase in brain size over *H. habilis* is not indicated in the Dmanisi hominins, whose cranial capacities are between 600 cc and 775 cc, overlapping with the range of *Homo habilis* and smaller *Homo erectus sensu stricto* specimens. Of course, brain size needs to examined in light of body size, and recent calculations of encephalization quotients are 2.6–3.1, which are more in line with *H. habilis* than with *H. erectus* (Lordkipanidze et al. 2007).

Increased body size correlates with home-range size, as efficiency in bipedal locomotion correlates with longer lower limbs (Anton and Swisher 2004; Anton et al. 2002; Shipman and Walker 1989). New body-mass estimates from postcranial remains suggest that the largest individual was about 49 kg, the smaller adult was about 40 kg, and the subadult was about 41 kg. The Dmanisi hominins thus are not tall like the Nariokotome specimen, which had, out of necessity, become the postcranial model of early Pleistocene *Homo ergaster*. As true for many traits, the Dmanisi hominins are between traditional *H. habilis* and *H. erectus* or African *H. ergaster* specimens in brain and body size. New smaller-sized *Homo erectus* from Ilert, Kenya (Spoor et al. 2007), and later from Olorgesailie (Potts et al. 2004) suggests smaller-sized individuals were part of the populations in Africa, too.

The wide range in body size begs the question of whether the variation at Dmanisi is due to sex or population or species differences. Were they more dimorphic than had been proposed for early African *H. erectus* (McHenry 1994)? There remains a range of opinions as to the number of species they constitute (*H. habilis, ergaster, erectus, georgicus*); many conclude that there is one variable species represented (Lordkipanidze et al. 2006; Rightmire et al. 2006), and others suggest that the variation is too great to encompass a single species (Skinner et al. 2006). The taphonomic and geological evidence that they are all from a very short time range and from the same place must be included in these deliberations. They are all from within Layer B1, but microstratigraphic evidence shows slight differences within B1 (B1x, B1y, and B1z). These microstratigraphic layers represent minor infilling and gullying events that occurred in rapid succession within a very short time range (Lordkipanidze et al. 2007). This evidence contradicts the interpretation that there was a single catastrophe. The overall context suggests a single species but cannot exclude the possibility of there being more. If they do represent a single species, then most of the variation is due to sex and age. The very large size of the D2600 mandible indicates that a high degree of sexual dimorphism is retained. If the variation in body mass is due to sex, males were on the order of 20 percent larger than females. The idea that sexual dimorphism was severely reduced with early out of Africa *Homo* (Aiello
and Wells 2002; Leonard and Robertson 1994; McHenry 1994) is not supported.

**Age of Death and Increased Life Span.** The pace of human life histories has slowed down, with slower maturation rates, delayed reproduction, and adults living long lives, often into old age. The biocultural ramifications of this life-history pattern are huge, and it is important to consider these factors for the Dmanisi paleodeme. Here I would like to consider the evidence for increased longevity. There is considerable debate about rate and patterns of growth and maturation in australopiths and early Homo (Dean et al. 2001). Age assessments of younger individuals depend on patterns and rates of maturation, which are influenced by body and brain size. Once an individual is mature, assessing age based on tooth wear can be imprecise because of variable hardness and abrasiveness of food in the diet and because proximity to abrasive substrates varies between populations and increases rates of wear. Problems are circumvented to a certain degree in assigning ages at death when very gross age categories are used such as juvenile, prime adult, and old adult (Caspari and Lee 2004). With these categories, a reasonable statement about the age-of-death profile represented by the Dmanisi hominins can be made.

We can assign the Dmanisi hominins to broad age categories of subadult (third molars not in wear), prime adult (third molars in wear), and older (severe wear). There is one subadult (D2700/D2735), one young adult (D211/D2282), a presumed prime adult (D2280, inferred from cranial suture closings; de Lumley et al. 2006), and two individuals that were old when they died (D3444/3900 and D2600). Although it is possible that D3444/D3900 was toothless earlier in life than expected because of disease, it is likely an older individual. The large D2600 mandible has all adult teeth and severe wear on all his surviving teeth, including third molars. The high gradient of tooth wear between first and third molars on this specimen and the presence of wear on the anterior teeth of D211, despite its subadult status, suggests the rate of tooth wear was high for the Dmanisi paleodeme (Van Arsdale 2006). Van Arsdale, in fact, suggests this individual may have been a prime-aged adult rather than old. However, the periodontal disease and the possibility that the teeth were used on very fibrous structures (perhaps, for example, working the teeth hardest near the fulcrum of wear near M1 and P4), make it difficult to age this individual. Even with relatively rapid tooth wear, D3444/D3900 and D2600 have every indication of being old adults, and here are considered likely to be over 35, but exactly how much older is not known.

In the fossil record of australopiths and early Homo from Africa, older individuals are rare (McKinley 1971). Caspari and Lee (2004) assessed the proportions of older to younger adult individuals over the course of hominin evolution. They found few older individuals in the australopith taxa when compared to later middle Pleistocene Homo and especially modern humans. They report of the eleven “habilines” in their sample that all are categorized as young adult and none are categorized as old. For the australopiths, which are much better sampled than habilines, only 12 percent are old, and 25 percent of early/middle Homo are old (Caspari and Lee 2004). They appropriately emphasize that the age at death increases most dramatically for Upper Paleolithic humans. But here I call attention to the evidence from Dmanisi, which may indicate that the beginning of this trend started during the early period of the Out of
Africa expansion of hominin populations. The presence of two old individuals out of five is really striking. Why are there so many older individuals? Do the two of five Dmanisi hominin fossils suggest a higher number of individuals surviving to old age in the Dmanisi paleodeme compared to a chimp model or to the earlier hominin record? Of course, the sample size of five is much smaller than we need. To help resolve that issue, we are continuing to excavate at the site each summer.

Nonhuman primates sometimes survive into old age (and sometimes with severe tooth loss), but the percentage that do so is not high. The presence of some nonhuman primates with nearly the same amount of tooth loss as exhibited in D3444/D3900 demonstrates that primates can continue to live with severe antemortem tooth loss without intentional care (Caspers and Lee 2004; Cuozzo and Sauther 2006; DeGusta 2002). But note that extreme degrees of tooth loss can be quite rare in the other primates, for example, the lemurs of the Cuozzo and Sauther study have the highest known rate of tooth loss of any primate, and only two individuals out of more than eighty had tooth loss on the level seen in D3444.

In chimpanzees, mortality is higher than in human hunter-gatherers, and chimpanzees also senesce earlier (Hill et al. 2001, 2007). Hill et al. (2001) conducted a comprehensive analysis of ages at death from all five of the major chimpanzee field sites. Of 284 deaths where age was known or could be well estimated, 62 percent died by age 12, 31 percent died as prime adults, and only 8.6 percent survived past 35 years. Some chimpanzees live well into old age and thus the question of the significance of the number of old individuals at Dmanisi becomes a probability statement. To test the null hypothesis that the rate of old individuals is the same for the chimpanzee sample as for the Dmanisi sample versus the alternative that the rate for Dmanisi is higher, a bootstrap approximation with B=10000 samples to the exact distribution of the chi-square test with the function chisq.test in the program R was used. The significance level for this one-sided test was 0.034. Thus, the chances of sampling the Dmanisi rate of two old individuals out of five in nonhuman primates that are old/with severe tooth loss are low (but, of course, not impossible considering the likelihood of sampling error).

Could there be a taphonomic bias in the Dmanisi record towards (or against) older individuals that was not present in earlier hominin sites? Death assemblages are not the same as the living-population structure but do sample survivorship curves (Caughley 1966). We can assess some biasing mechanisms known to occur for or against age groups in the fossil record. We know juveniles with smaller, less mineralized bone do not preserve as well as adults do. There can be bias against old adults due to bone mineral depletion (Hawkes and O'Connell 2005; O'Connell et al. 1999), but due to increased robusticity in earlier hominins, this bias is less likely to be a significant factor than it is in modern humans. Predation is probably the most common cause for a bias toward old individuals above and beyond what is present in a life assemblage in mammals (see references cited in Stiner 1994). However, considering the frequent evidence for chewing by carnivores on so many of the australopith and early Homo fossils, the role of predation in forming the earlier hominin fossil record was strong for this earlier time period that has few old adults. If similar numbers of australopiths and Homo cf. habilis were surviving to old age in the Pliocene, they
too would have older individuals represented in the death assemblages. In other words, there is no a priori taphonomic reason that there would be a larger bias toward the old at Dmanisi than there would be for australopiths or earlier Homo.

From a zooarchaeological perspective, the Dmanisi hominin ages would be considered to form an attritional or U-shaped age profile, because the most vulnerable individuals, the young and the old, are better represented than prime adults. From this perspective, the age profile could be used to support ideas that the hominins were predated upon, or died from attritional causes, rather than representing a catastrophic event. It is important to note that age profiles are evidence for death mechanisms but are not diagnostic without other taphonomic evidence (Stiner 1994). The taphonomic evidence from the site in general indicates that there were multiple bone-deposition and bone-modification processes, including by humans (as evidenced in cut marks and some of the bone breakage), but carnivores were an even more important bone concentrating mechanism at the site (Tappen et al. 2007). Important to the discussion here is that evidence for carnivore modification to the hominin bones is ambiguous (Tappen in prep), and the evidence from skeletal elements present suggests that some hominins were not consumed by predators (at least that they were not consumed in a pattern that matches the pattern of leopards consuming baboons). Experimental work by Pickering (Carlson and Pickering 2003; Pickering 2001a, b) shows that leopards usually consume clavicles, sterna, and upper ribs first, and these elements rarely survive. Clavicles of two individuals, as well as upper ribs are present at Dmanisi, suggesting that these individuals were not consumed or predated upon.

The presence of older individuals at Dmanisi may really be significant and may signal an important change in the rate of survivorship into old age, which must have been mediated through important changes in behavior. Increases in longevity can be associated with greater potential lifetime fertility (Lahdenpera et al. 2004; O'Connell et al. 1999) and can occur through decreased childhood or adult mortality (Kaplan and Robson 2002). The population growth that must have accompanied the range expansion out of Africa (Bar-Yosef and Belfer-Cohen 2001b) may have been mediated by this increase in survivorship. Interrelationships between body size, brain size, maturation rates, and longevity are significant (Kaplan and Robson 2002). Since the Dmanisi hominins are in between earlier Homo and later Homo erectus in so many ways, including brain and body size, we can hypothesize that they were also in between their life-history parameters such as surviving to old age, too.

The increased survivorship of kin would have changed many aspects of social and economic interactive behavior. Recent experiments on the likelihood that chimpanzees will provide food to another chimpanzee, at no cost to themselves, indicated that chimpanzees are more or less indifferent to others (Silk et al. 2005), while even more recent experiments have shown that altruism is present (Warneken et al. 2007). While chimpanzees sometimes help the injured, there is a relative expansion in human prosocial behavior. The increased average degree of relatedness among individual hominins in groups where the ascending generation is present would increase the likelihood of kin-based altruism. Increases and changes in social interaction, cooperation, reciprocity, food sharing, increased division of labor, trade, etc. are behaviors that we know increased in human
evolution, and would change, in fundamental ways, how hominins interacted with the environment. The increased numbers of elderly at Dmanisi, if real, presages these changes in hominins, but rather than emphasizing the need of the elderly for care, emphasis should be placed on the contribution of older individuals and the resultant changes that would echo throughout the residential group. The elders would increase the numbers of close kin within the group, promoting prosocial behaviors across generations in both directions. Older individual's "memories function as repositories of information" allowing for increased transgenerational transfer and hence accumulation of knowledge and cultural development (Kaplan and Robson 2002; Rosenberg 2004).

Longevity and survivorship into old age is often discussed in the context of emphasizing the role of one sex over the other. On the one hand, there is the role of grandmothers as alloparents increasing the reproductive success of their daughters (O'Connell et al. 1999; Voland et al. 2005). On the other hand, the role of increased hunting success in older, more experienced males is certainly relevant (Gurven et al. 2006). This later model is a version of the "embodied capital model," where the feeding niche requires a long learning period. For either sex, the benefits of having older individuals in the groups could be enormous.

Hill et al. (2007) state that both the grandmother hypothesis and the embodied capital hypothesis "identify adaptations that provide additional benefits once a significant portion of the population begins to survive to older age" (p. 452, italics original) but that neither model accounts for why there is a decrease in early adult mortality (10-39 yrs) in humans (hunter-gatherers). They point out that a decrease in early-adult mortality should produce a longer growth period, later sexual maturity, and later onset of senescence. Longer-lived organisms tend to have low vulnerability to predation, accidents, and disease in their adult years, and they suggest that care for the sick and injured is mostly responsible for the initial improvement in early-adult survival, and link those behaviors to homebase and food-sharing behaviors.

The evidence from Dmanisi suggests that the increase in survivorship to old age may have been an important initial step in these interrelationships and that it was significant enough to allow change from an ecologically and geographically constrained species to a more cosmopolitan one. If more hominins were escaping predation at this point in time, it could set the stage for the evolution of lengthened life-histories stages and longevity. This hypothesis requires extensive scrutiny through multiple lines of evidence. Rather than emphasizing older females over older males (or vice versa), the role of older individuals of both sexes would have strong effects on human adaptations and on the reproductive success of hominins.

Summary
A series of hypotheses for out of Africa are considered from the evidence preserved and identified so far at Dmanisi in Georgia. Extrinsic hypotheses involving the spread of Homo with other African mammal dispersals are not supported, and ideas that the carnivore-guild structure changed in a way that expedited hominin dispersal are not compelling. Although there is evidence for disease among the Dmanisi hominins, the evidence does not directly test Bar-Yosef's and Belfer-Cohen's ideas of release from zoonotic disease as the mechanism of increasing survivorship. Furthermore, the basic
stone-tool kit does not appear to be novel, and there is no evidence for fire. Body and brain size appear similar to Homo habilis hominins, larger than australopiths, but not as large as the model Nariokotome gave us for Homo ergaster. The Homo ergaster (= Nariokotome) body size has been central to hypotheses of out of Africa but is not found at Dmanisi and should be adjusted in future models. Since body and brain are smaller than those of H. ergaster, this “in-between” state was still large enough allow increase in the ranging capacities of these hominins. The degree of sexual dimorphism in body size remained high.

The severe seasonality of resources at high latitudes would have placed strong selection pressures on the Dmanisi hominins. Meat eating by hominins is evident at the site, and furthermore, as there was defleshing of meat on upper limbs of ungulates, it appears that there was early access to carcasses, which probably indicates hunting. Plant fallback foods that were tough and fibrous are likely also to be important as displayed by the heavy wear on the teeth.

The representation of two old individuals at Dmanisi from a sample of five (40 percent old) signals important new behaviors at the time of the Dmanisi hominin range expansion. That there was an accompanying population increase with the spread out of Africa is logical to the idea of range expansion. In terms of direct evidence from this first excursion to higher latitudes, a key adaptation may have been an increase in younger and adult survivorship. With adults living to older age, learning from their experience, greater social cohesion, sharing among relatives, and of course, alloparenting were increased and became central to hominin adaptations.

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