



The Pliocene–Pleistocene succession of Kvabebi (Georgia) and the background to the early human occupation of Southern Caucasus

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ABSTRACT

This article analyzes and discusses the chronological and zoogeographic context of the Pliocene site of Kvabebi in order to shed light into the background of the early human occupation of Eurasia, as evidenced by the early Pleistocene site of Dmanisi. New paleontological and paleomagnetic research has allowed this site to be placed in a reverse interval which can be identified as chron 2An.1r. The age of this site is therefore close to 3.07 Ma, coeval to the Hadar beds of the Afar Depression and slightly older than the last hipparionine faunas in Europe, such as Villarroja in Spain. The fauna of Kvabebi is composed of a number of species common to Europe and Asia, but also includes others with African affinities, such as *Kvabebihyrax kacheticus*, *Protoryx heinrichi*, *Parastrepsiceros sokolovi* and *Gazella postmitilini*. However, the presence these species cannot be explained as the result of a Pliocene dispersal from Africa, but rather as the last remnants of the so-called Greek-Iranian province.

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1. Introduction

Recent findings of well-preserved hominid remains at the Georgian early Pleistocene site of Dmanisi have raised the question of the timing and nature of the first hominid dispersal out of Africa (Gabunia et al., 2000; Vekua et al., 2002; Lordkipanidze et al., 2005). The fauna from Dmanisi includes a variety of species of different zoogeographic significance and origin. In addition to early homo, a number of species have been claimed as having African origins, such as *Mammuthus meridionalis* and *Paramerion* aff. *obeidiensis*. However, given the geographic position of Georgia, at the crossroads of Africa and Eurasia, it is a matter of debate as to whether the presence of African species is linked to the hominid dispersal or whether there was an African faunal background previous to that dispersal. It has been suggested that this first departure from Africa may have happened well before the Pliocene–Pleistocene boundary, at about 3.0–3.5 myr ago, when the Saharan–Arabian desert barriers did not yet exist (Dennell and Roebroeks, 2005). Furthermore, it has been argued that if australopithecines such as *A. bahrelgazali* were distributed throughout

the woodland and savanna belt between the Atlantic and the east African basins, why would they not have been on the grasslands of western Asia? (Dennell and Roebroeks, 2005). In this context, the Georgian middle Pliocene site of Kvabebi (UTM coordinates 8559383, 4591003, 426 m) takes an outstanding significance due to its richness and chronological position prior to the Dmanisi fauna.

The first fossil remains from Kvabebi were reported in 1962, when G. Avakov found the first vertebra of a large-hoofed mammal. Immediately after this discovery, a number of field campaigns were undertaken by the Institute of Paleobiology of the Academy of Sciences of Georgia. The excavations produced a huge collection of large vertebrates which later became the subject of a monograph (Vekua, 1972).

2. Regional setting

The Kvabebi site (Fig. 1) is located in the Sighnaghi region of Eastern Georgia, in the area surrounding Kvabebi Mountain to the south of the village of Magaro. This mountain forms the southern edge of the Iori Plateau, where the Iori river valley is located. The Kvabebi section is part of the sedimentary infill of the Kura Basin, which developed as a northward inland ingression of the Caspian, and is part of the Akchagylian Basin (Popov et al., 2006). Since the late Neogene, the basin has been bordered by the Greater Caucasus, the Lesser Caucasus and the Talysh ranges, to the NE, SW and SE,

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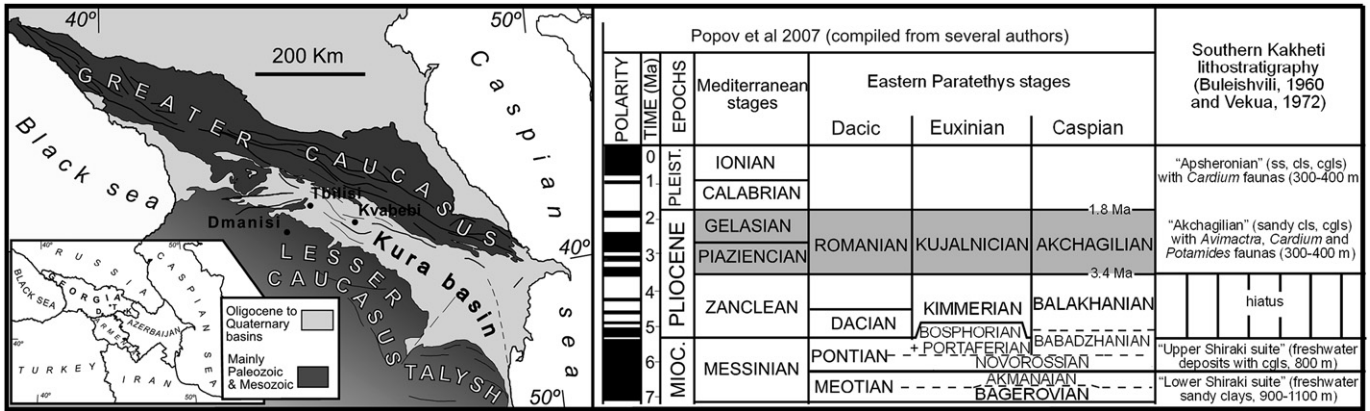


Fig. 1. Left: Location of Dmanisi and Kvabebi sites in the frame of the Neogene deposits of Southern Caucasus. Right: Eastern Paratethys stages and southern Kakheti lithostratigraphy. Note Akchagilian stage and equivalents in grey.

respectively. The section is in the middle part of the Akchagilian (Vekua, 1972), which is built up of 400–500 m of 'Sandy clays with conglomerate layers' that contain *Avimactra*, *Cardium* and *Potamides* (see Buleishvili, 1960).

The section described here is 170 m thick (Fig. 2). It starts at an elevation of 395 m above sea level and is slightly tilted to the NW. Southwards, it can be enlarged some 100 m at the base, where the sedimentary succession can be tracked in isolated outcrops,

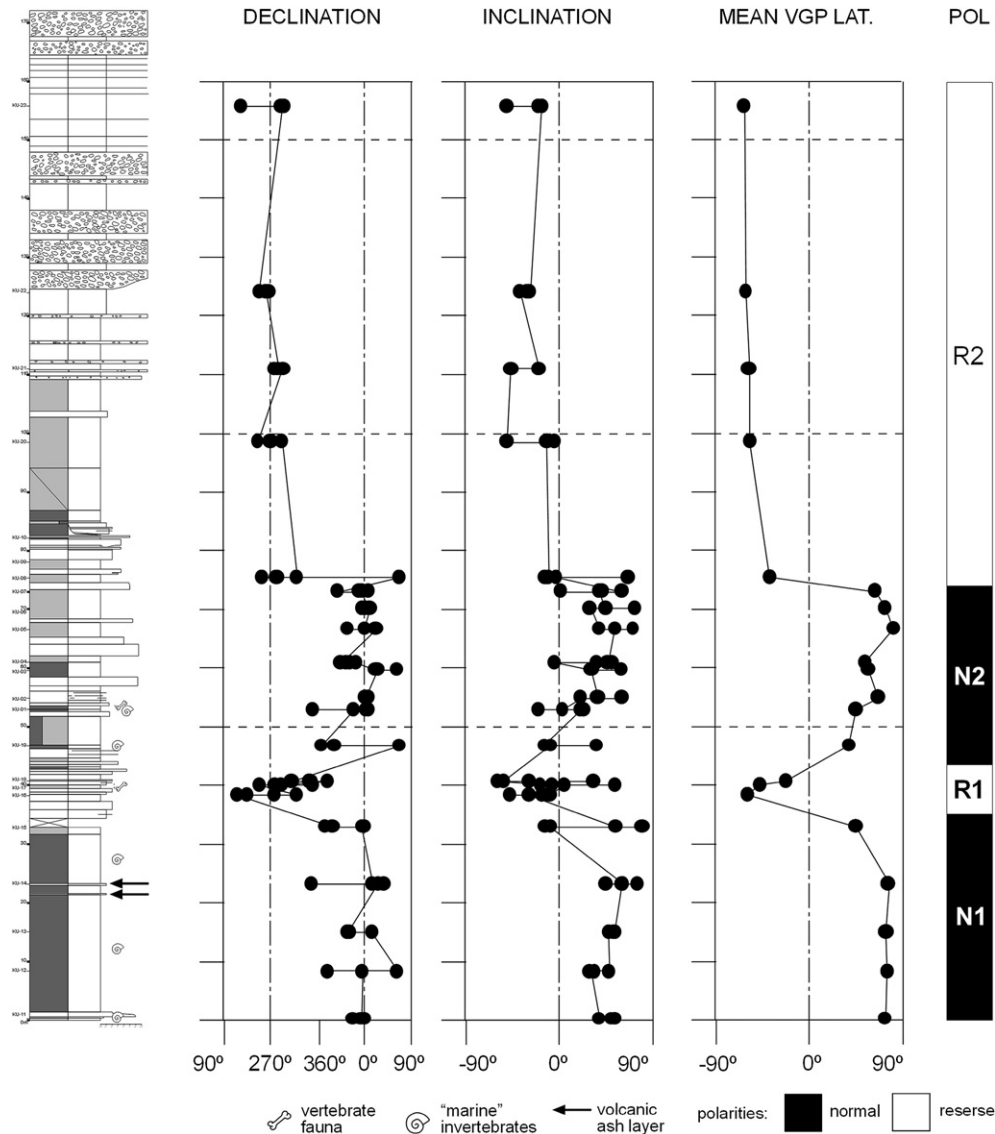


Fig. 2. Lithostratigraphy and paleomagnetism of the Kvabebi section.

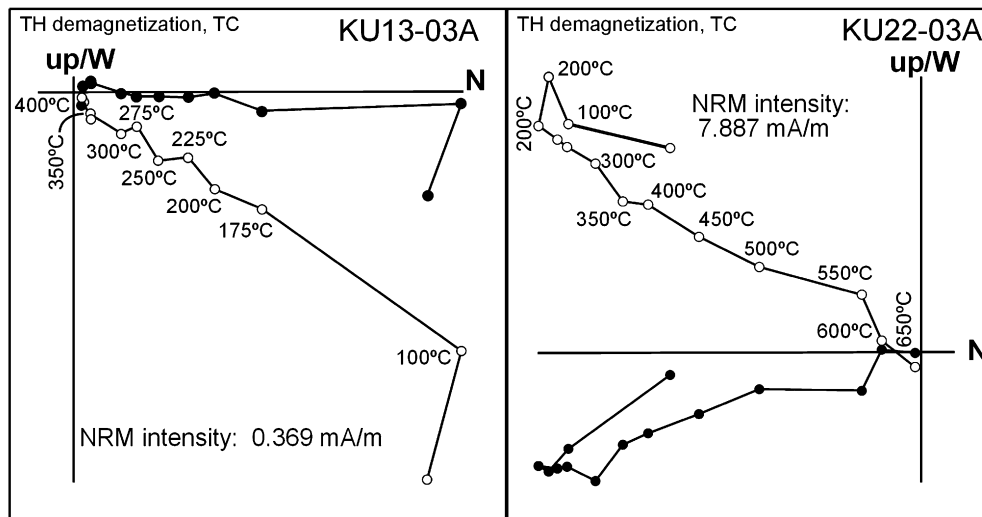


Fig. 3. Examples of demagnetization plots with normal and reverse polarity (left and right, respectively).

although these are not included in the scope of this study. The section we examined displays a general regressive trend. The section presents several sandstone layers, including the layer at meter 40 containing the Kvabebi site. Two consecutive volcanic ash-fall layers are found 17m below the paleontological site. The upper part of the section (110–170 m, i.e., the Kvabebi cliffs) is formed by a succession of alluvial reddish-brown sediments (mudstones, sandstones and conglomerates) with no marine fauna. The lower part (from the base to 110 m) is built up of a succession of brownish or bluish laminated mudstones. The bluish color is indicative of transgressive pulsations of a marine affinity as evidenced by its Pliocene (Akchagylian) age mollusk fauna, which include *Avimactra subcaspia*, *Avimactra venjukovi*, *Cardium dombra vogdti*, *Cerastoderma pseudoedule*, *Avicardium cucurtense* and other typical Akchagylian mollusks (Djikia, 1968). Ostracods are also present, represented by *Cyprideis punctillata*, *Condona combibo*, *Leptocytere gubkini*, *Loxoconcha laevatula* and others (M. Vekua, pers. com.). Moreover, foraminifera include *Bolivina textularoides*, *B. aksacia*, *Streblus beccarii* and others (O. Janelidze, pers. com.).

According to geochronological information, the Kvabebi section has been dated to the middle Pliocene (Chumakov et al., 1992; Adamia et al., 2002). Unfortunately, no detailed data have been provided except for the age value itself, which is said to be “around 2.5 Ma”

Fossil bones from Kvabebi are generally found anatomically disconnected. Most of the bones are isolated, display no evidence of carnivore damage and may be very well preserved (weathering stages 0–4 in the sense of Behrensmeyer, 1978). Kvabebi site is the result of accumulation due to tractive processes in a fluvial influenced environment. Bones and bone fragments are reworked and more or less scattered within sandstones and shales. Locally they seem to be roughly grouped in two levels vertically separated 1 m. Mixed with bones, some bivalves and mollusks (of marine affinity, see below) are also found Table 1.

3. Materials and methods

In recent years a joint Georgian-Spanish team conducted by A. Vekua and J. Agustí began re-prospecting and re-excavating the Kvabebi section. This process has given rise to new data, which is summarized here in this paper. Regarding the assemblage of vertebrate fauna from the site, the revised list of which is now as follows: *Testudo cernovi transcaucasica*, *Ioriotis gabunia*, *Struthio transcausicus*, *Hystrix cf. primigenia*, *Nyctereutes megamastoides*, *Eucyon*

sp., *Ursus minimus*, *Lynx issiodorensis*, *Homotherium davitashvili*, *Puma pardoides*, *Dinofelis abeli*, *Chasmaportetes lunensis*, *Propotamochoerus provincialis*, *Eucladoceros sp.*, *?Pseudalces sp.*, *Procapreolus sp.*, *Ioribos aceros*, *Protoryx heinrichi*, *Oryx (Aegoryx) sp.*, *Parastrepsiceros sokolovi*, *Eosyncerus ivericus*, *Gazella postmitilini*, *Hipparion rocinantis*, *Stephanorhinus megarhinus*, *Kvabebihyrax kachethicus*, *Anancus arvernensis* (Vekua, 1972, Hemmer et al., 2004).

Furthermore, in order to constrain the age of Kvabebi, a paleomagnetic analysis was conducted on the series. Despite few paleomagnetic results by L. Vekua have been mentioned from Kvabebi (see Hemmer et al., 2004), no detailed geochronological information is available. Our paleomagnetic analysis consisted of field sampling (with a drilling machine) from more than 20 levels. We obtained a minimum of three cores from each sampled level (basically mudstones and few fine-grained sandstones). The laboratory work comprised measuring remanence at several temperatures. Susceptibility changes were also monitored throughout the procedure in

Table 1

Minimum Number of Individuals (MNI) and number of identified specimens (NISP) from Kvabebi site.

Taxa	NISP	MNI
<i>Nyctereutes megamastoides</i>	70	9
<i>Eucyon sp.</i>	1	1
<i>Ursus minimus</i>	2	1
<i>Lynx issiodorensis</i>	8	1
<i>Homotherium davitashvili</i>	7	1
<i>Puma pardoides</i>	2	1
<i>Dinofelis abeli</i>	1	1
<i>Chasmaportetes lunensis</i>	1	1
<i>Hystrix cf. primigenia</i>	2	1
<i>Propotamochoerus provincialis</i>	37	8
<i>Eucladoceros sp.</i>	6	3
<i>?Pseudalces sp.</i>	6	2
<i>Procapreolus sp.</i>	9	4
<i>Ioribos aceros</i>	234	28
<i>Protoryx heinrichi</i>	72	17
<i>Oryx (Aegoryx) sp.</i>	1	1
<i>Parastrepsiceros sokolovi</i>	84	14
<i>Eosyncerus ivericus</i>	3	2
<i>Gazella postmitilini</i>	80	9
<i>Hipparion rocinantis</i>	83	8
<i>Stephanorhinus megarhinus</i>	53	16
<i>Kvabebihyrax kachethicus</i>	11	5
<i>Anancus arvernensis</i>	35	4
Total	808	138

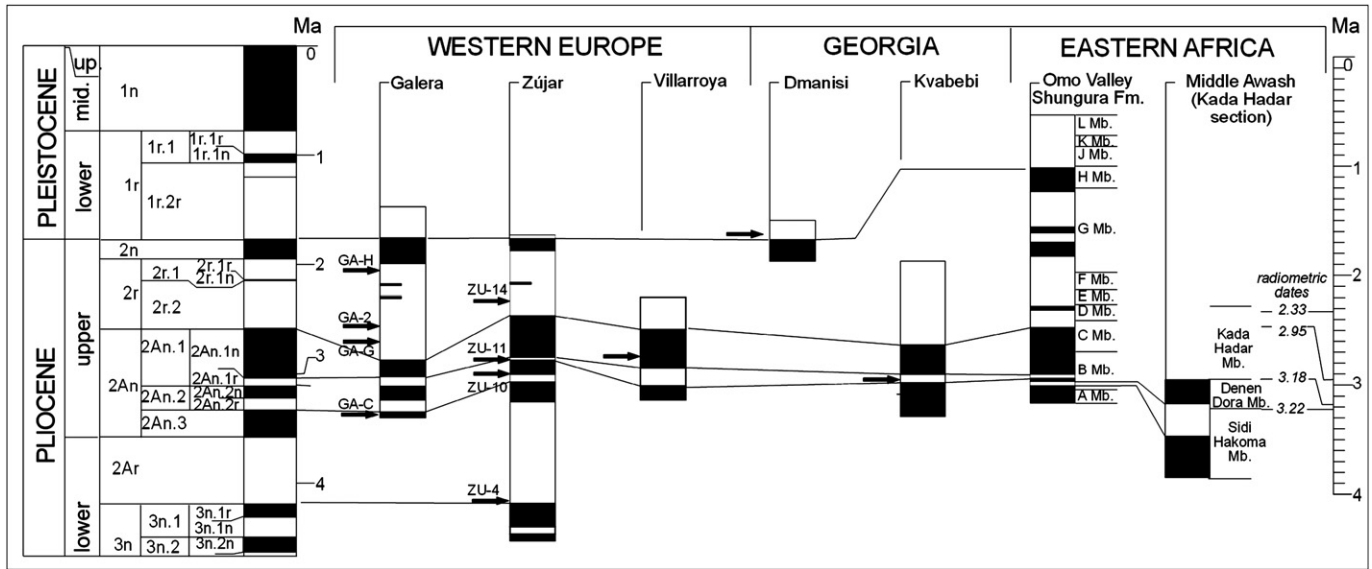


Fig. 4. Magnetostratigraphic correlation of the Dmanisi and Kvabebi sites with other well-calibrated Pliocene–Pleistocene sections from Africa and Western Europe. Chronology for Kada Hadar Member by Renne et al., 1993. See text for references of the other sections.

order to detect mineralogical changes. Some samples were also demagnetized by alternating fields.

4. Results

Demagnetization plots along the section show clear patterns with normal and reverse polarities. The upper third of the Kvabebi section exhibits higher magnetization intensities than the rest of the section. The paleomagnetic behavior of the samples is relatively stable and allows for the calculation of characteristic remanent magnetization components (ChRM). The samples included two components, generally defined as above and below approximately 100 °C. A linear component generally directed toward the origin of the demagnetization diagram can be removed in most cases. Several facts suggest that our characteristic remnant magnetization components are true primary acquired remanents. First, we observed that polarity changes are not related to lithology. Second, we discarded all ambiguous samples with low intensities or unstable behavior. Finally, the integrated magnetobiostratigraphic succession from Kvabebi was found to be fully consistent with other long records in Western Europe.

As a result (Figs. 2 and 3) the calculated ChRM directions define four successive magnetozones (normal 1 to reverse 2; see N1, R1, N2, R2 in Fig. 2). The Kvabebi site falls within the reversed polarity interval R1. The polarity zones observed in the Kvabebi section can be correlated with the Geomagnetic Polarity Time Scale (Cande and Kent, 1995) based on the available biochronological data and the polarity reversal pattern (Fig. 4).

The mammal community from Kvabebi, largely dominated by Eurasian taxa, allows for a close correlation to the well-calibrated European biochronological scale. A number of elements are shared with sites such as Triversa in Italy, Les Etouaires in France and, especially, with Villarroya in Spain: *Anancus arvernensis*, *Stephanorhinus megarhinus*, *Hipparion rocinantis*, *Chasmaportetes lunensis*, *Nyctereutes megamastoides*, and *Hystrix aff. primigenia*. Above all, the presence of the equid *Hipparion rocinantis* indicates that the Kvabebi fauna predates the first occurrence of the genus *Equus* in Western Eurasia. *Hipparion rocinantis* was defined as *H. crusafonti* at the early Late Pliocene site of Villarroya, and is considered a very advanced *Hipparion* species, which disappeared just before the entry of the first representatives of *Equus*. Villarroya, the type-locality of

Hipparion crusafonti, is placed within chron 2An.1 n (Fig. 4), a datum that immediately predates the first occurrence of *Equus* in Eurasia, established in the uppermost part of the same chron or at the base of the Matuyama chron (Agustí and Oms, 2001). Therefore, the reverse interval at which the Kvabebi site is placed should be older than the Gauss–Matuyama boundary.

On the other hand, the Kvabebi assemblage presents a number of typical Late Pliocene, early Villafranchian elements, such as *Hipparion rocinantis*, *Pseudalces* sp., *Nyctereutes megamastoides*, *Lynx issiodorensis*, *Homotherium davitashvili*, a derived *Eucyon* species, and others. Therefore, it should be younger than the Ruscinian–Villanyian (or Villafranchian) boundary, established in the Guadix–Baza Basin between the chrons C2An.2r and C2An.2 n (Agustí et al., 2001a,b; Oms et al., 1999). We therefore correlated the N1, R1, N2 and R2 polarity intervals with chrons 2An.2 n, 2An.1r, 2An.1 n and 2r, respectively (Fig. 4). The Kvabebi site should have an age bracketed by the polarity reversals of chron 2An.1r, i.e., 3.04 and 3.11 Ma (Cande and Kent, 1995). Thus, an age of approximately 3.07 Ma is assumed for the Kvabebi site, coinciding closely with that of Shamar in northern Mongolia, a *Hipparion* site dated at 3.1 myr that also contains a derived *Eucyon* form (Vislobokova et al., 1995; Sotnikova and Rook, in press).

5. Discussion

As stated in the previous section, several elements from Kvabebi correspond to taxa of Eurasian affinities. In addition to the above-mentioned *Hipparion rocinantis*, this is also the case of *Anancus arvernensis*, *Stephanorhinus megarhinus*, *Proptamochoerus provincialis* and most of the carnivores: *Nyctereutes megamastoides*, *Lynx issiodorensis* and *Chasmaportetes lunensis*. *Chasmaportetes* is a genus that was widespread in the Old World and North America during the Pliocene–Early Pleistocene. Most authors consider all the Eurasian representatives as *Chasmaportetes lunensis*, a geographically and chronologically wide-ranging species (Kurtén and Werdelin, 1988; Rook et al., 2004). Other taxa can be considered as local variants of Eurasian genera. This is the case, for instance, of *Iribobis aceros* (closely related to *Leptobis*) and *Dinofelis abeli*. Although the genus *Dinofelis* originates in Africa where it has a long fossil record (Werdelin and Lewis, 2001), its occurrence out of the African continent has been documented since the late Miocene in

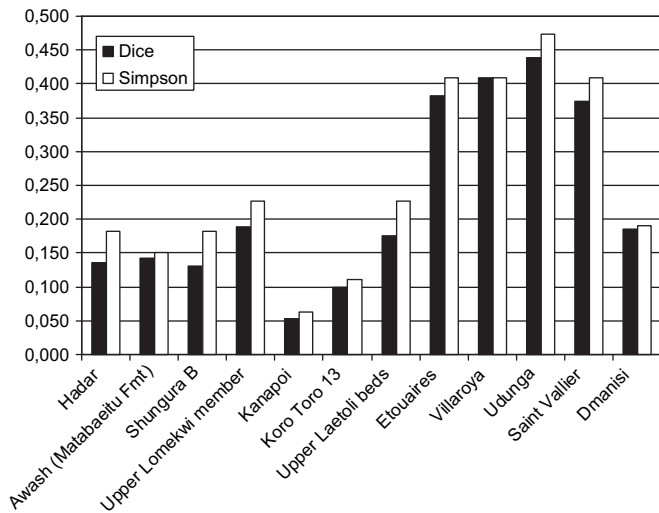


Fig. 5. Comparison of Genus-Level Faunal Resemblance Indexes (GFRI) illustrates the zoogeographical affinities of the Kvabebi large mammal fauna. GFRI are made using both Simpson's and Dice indexes. The Dice index is calculated as: $2A/(2A + B + C)$, where A is the number of taxa present in both faunas, B is the number of taxa present in fauna 1, but absent in fauna 2, and C is the number of taxa present in fauna 2 but absent in fauna 1. Simpson's faunal resemblance index and is calculated as: $A/(A + E)$ where E is the smaller of B or C (data source updated from Turner et al., 1999 and NOW database, public release 030717 available at <http://www.helsinki.fi/science/now/>).

Greek-Iranian province assemblages and it cannot be considered as coming from Africa during the time of Kwabebi. In addition to *Nyctereutes*, it was initially reported the occurrence of a canid taxon, which was referred to as ? *Canis* sp. (Vekua, 1972). The canid material available from Kvabebi confirms the occurrence of a form different from *Nyctereutes*, now better attributable to *Eucyon* sp. The documentation of the latest stages of this genus in Western Europe (where the genus seems not to have survived into the Late Pliocene) is a matter of some discussion (Spassov and Rook, 2006). The genus *Eucyon*, however, has been documented in the Late Pliocene in sites as widespread as Turkey, Tadjikistan, Kazakhstan and China (Spassov and Rook, 2006; Sotnikova and Rook, in press).

Interestingly, the first occurrence of a number of late Pliocene taxa in Western Eurasia is documented at Kvabebi. This is the case, for instance, of *Puma pardoides*, *Eucladoceros* sp. and *Pseudalces* sp. The case of *Eucladoceros* is particularly interesting, as the dispersal of this cervid in Western Europe has traditionally been linked to the spread of *Equus*. The datum of Kvabebi demonstrates that the *Eucladoceros* dispersal took place shortly before the spread of modern equids. This is also the case for the first representatives of elk in Western Europe (*Pseudalces*). However, some authors do not consider *Pseudalces* to be the ancestor of modern elk (Vislobokova et al., 2001).

In addition to the abovementioned European components, the fauna from Kvabebi presents a number of mammals of African affinities. This is the case of *Kvabebihyrax kacheticus*, *P. heinrichi*, *Oryx* sp., *Parastrepsiceros sokolovi*, *Eosyncerus ivericus*, *Gazella postmitilini* and possibly *Puma pardoides* (Hemmer et al., 2004). The most striking of these are the giant hyraxes of the genus *Kvabebihyrax*. Hyraxes are a typically African elements that today inhabit the rocky savannas and bushy woodlands of central and eastern Africa. In the Late Miocene, hyraxes entered Eurasia, where they have been found at a number of Vallesian sites (Can Llobateres, Soblay, Melambes, Esme-Akçakoy) (Golpe and Crusafont, 1981; Kotsakis, 1987) and Turolian sites (Garkin, Pikerimi, Samos and others, Almenara-M in Spain) (Kuss, 1976; Hünermann, 1985; Pickford et al., 1997). Despite its Middle Pliocene age, *Kvabebihyrax* seems closely related to the Late Miocene European genus

Pliohyrax (Pickford et al., 1997) and, therefore, its presence in Kvabebi fits better as a remnant of the Eurasian population of pliohyracids rather than the result of a Pliocene migration from Africa. A similar conclusion can be drawn from the analysis of most of the bovid fauna from Kvabebi. Therefore, species such as *P. heinrichi*, *Parastrepsiceros sokolovi* or *Gazella postmitilini* appear as local equivalents of forms that have their roots in the so-called Pliocene faunas (Gentry and Heizmann, 1996). In contrast, the presence of *Oryx* sp., *Eosyncerus ivericus* and possibly *Puma pardoides* at Kvabebi could indicate a real dispersal event from Africa.

However, on the whole, the Kvabebi African elements appear as the last remnants of the late Miocene Subparatethyan or Greek-Iranian province (Bernor, 1984; de Bonis et al., 1992; Vekua and Lordkipanidze, 2008), rather than the result of a middle Pliocene migration from Africa. In this case, the southern Caucasus may have acted as a refuge area to those Miocene species. This does not mean that a faunal connection with Africa did not exist at that time, since reported fauna from Northern Africa in the late Miocene to early Pliocene include a high number of elements that were also characteristic of the Greek-Iranian province. For instance, a significant part of the mammal assemblage of Sahabi, in Lybia, is composed of taxa that were common to the Greek-Iranian province (Boaz et al., 1987), such as the bovids *Miotragoceros*, *Prostrepsiceros* and *Leptobos*, the amebelodontid gomphothere *Amebelodon* and the whole carnivore taxocoenosis (*Machairodus*, *Chasmaportetes*, *Hyaenictitherium*, *Adcrocuta*, *Viverra*, *Indarctos*, *Agriotherium*).

6. Conclusions

It has been suggested that much of the current savannah fauna did not evolve *in situ* from early and middle Miocene African mammals, but migrated from more northern latitudes in the Late Miocene, replacing the previous forest endemic dwellers (Maglio and Cooke, 1978). More specifically, with the drying out of Africa between 8 and 7 Ma, large mammals from the Greek-Iranian province may have colonized the lower latitudes, their adaptations to a sclerophyllous woodland (hypsodont teeth, cursorial skeletons) acting as pre-adaptations (Gould and Vrba, 1982) to a savannah biome (Solounias et al., 1999; Gabunia and Vekua in Vekua and Lordkipanidze, 2008). This was probably the case of bovids, giraffids, equids, hyenas, and rhinos. In the case of hominids, the similarities between the recently described *Nakalapithecus* and *Ouranopithecus* from Greece seem to support this scenario (Kunimatsu et al., 2007). Therefore, we might hypothesize that the progressive drying of the Greek-Iranian province led the fauna from this region to concentrate in two refuge areas, northern and eastern Africa to the south, and south Caucasus to the east, which would explain the "African" character of the Kvabebi fauna. However, by the time of the deposition of the Kvabebi beds, these two refuge areas were already disconnected, as demonstrated by the absence of common elements between the Georgian site and the coeval Hadar levels in the Afar Depression. This is why the large mammal assemblage of Kvabebi compared with coeval East African sections such as Hadar, Shungura B or Lomekwi shows rather low similarity index (Fig. 5).

Moreover, almost none of the African species from the Kvabebi site are part of the subsequent Dmanisi fauna and the similarity index for the two faunas is quite low (Vekua, 1995; Lordkipanidze et al., 2007). Therefore, Kvabebi cannot be regarded as the African background to Dmanisi. The presence of the first hominids out of Africa in Southern Caucasus can be better related to the set of climatic and faunal events associated with the late Pliocene onset of the first Northern Hemisphere glaciations that would characterize the whole Quaternary.

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