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Small mammals (Insectivora, Rodentia, Lagomorpha) from the Early Pleistocene hominin-bearing site of Dmanisi (Georgia)

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ABSTRACT

Small mammals (insectivores, rodents, and lagomorphs) from Dmanisi are here reviewed for the first time and used as a tool for paleoenvironmental proxies. The small mammal faunal list is composed of shrews (*Beremendia fissidens*, cf. *Beremendia minor, Crocidura kornfeldi*), hamsters (*Cricetulus* sp., *Allocricetus bursae*), gerbils (*Parameriones* aff. *obeidiyensis*), murids (*Apodemus* cf. *atavus*), arvicolids (*Mimomys pliocaenicus*, *Mimomys* aff. *pusillus*), and pikas (*Ochotona* sp.). A paleoenvironmental reconstruction based on the habitat weighting method has been applied to the rodent assemblage. According to this method, the most common elements indicate an open-dry habitat (36.5%), followed by water edge (25.7%) and rocky (21.0%) elements. Open-wet (15.5%) and woodland elements (1.3%) are rare. Therefore, the habitat occupied by the hominids of Dmanisi was characterized by the prevalence of arid conditions, from steppe or semi-desert to open Mediterranean forest, with stony or rocky substrate and bushy areas. The presence of permanent aquatic environments is also documented. From a biogeographic point of view, the small mammal community from Dmanisi is composed mainly by Western or Central Asian elements, with a poor representation of European elements (*Mimomys*, *Apodemus*). It is concluded that Dmanisi hominins most possibly had ecological requirements which were different from those of the Early Pleistocene hominins from Western Europe, which settled on wetter habitats. It could be also possible that Dmanisi hominins entered Southern Caucasus at an interglacial phase before the deposition of the Dmanisi site.

1. Introduction

The Dmanisi site is located about 85 km southwest of Tbilisi, the capital city of the Republic of Georgia, on the northern slopes of the Lesser Caucasus (Fig. 1), near the village of Patara Dmanisi, at an altitude of 915 m asl. The site sits on a promontory of the Mashavera basalt, 80 m above the present-day water levels at the confluence of the Mashavera and Pinezaouri Rivers. The Early Pleistocene site of Dmanisi was discovered in 1983, under the ruins of the medieval town of Dmanisi. Excavations have yielded hominin fossils, a rich vertebrate fauna, and Mode I (Oldowan) stone artifacts. Occupation of the site began shortly after 1.85 Ma and is documented until about 1.77 Ma (Gabunia et al., 2000a; Vekua et al., 2002; Lordkipanidze et al., 2005, 2006, 2007; Ferring et al., 2011). The temporal and geographic setting and the preservation of at least five hominin individuals make Dmanisi a site that is crucial in understanding patterns of variation, biogeography, and evolution within early *Homo* (Lordkipanidze et al., 2013). Dmanisi deposits are divided into two major stratigraphic units: Stratum A and B. In the main excavation area 'Block 2', volcanoclastic fossiliferous alluvium, which overlies basalt, is approximately 2.5 m thick (Fig. 2). Dmanisi deposits have been considered as Early Pleistocene, about 1.8 Ma in age according to ^{40}Ar/^{39}Ar dating on Mashavera basalt (de

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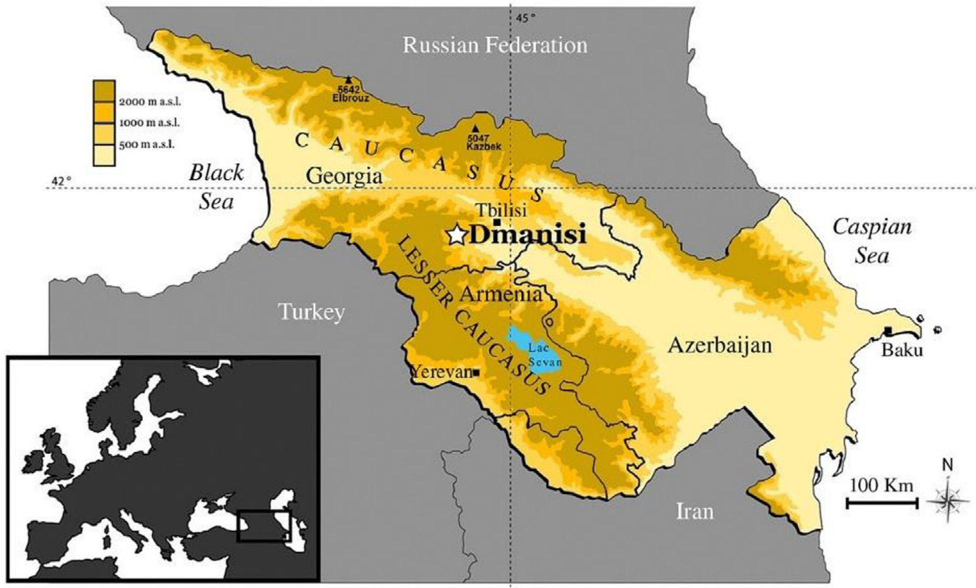

Figure 1. Dmanisi site location in regional context.

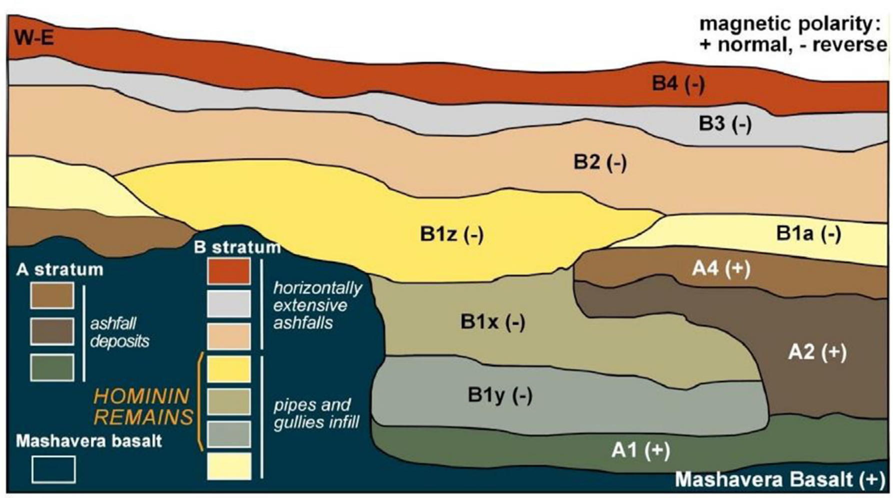

Figure 2. Schematic stratigraphic section of Block 2. Section is 10 m long, with ca. 1.8× vertical magnification (modified from Lordkipanidze et al., 2007).

Lumley et al., 2002), which underlies the fossil-bearing sediments. Stratum A consists of a series of at least four separate ash falls that conformably overlie the basalt. Stratum B deposits include horizontally extensive ash falls, as well as a complex of deposits that filled pipes and the gullies that formed along collapsed pipes (Ferring et al., 2011). Stratigraphic studies revealed that all the hominin remains come from the base of Stratum B1, dated to ca. 1.77 Ma, based on $^{40}Ar/^{39}Ar$ dates, paleomagnetic and biostratigraphic constraints (Lordkipanidze et al., 2007), as it is also the case of the small mammal material subject of this study.

Rodents and lagomorphs were the subjects of a previous contribution by Mouskhelishvili (1995), who recognized the following species: *Cricetus* sp., *Kowalskia* sp., *Meriones* aff. *tristrami, Mimomys* ex. gr. *reidi, Apodemus* sp., and *Ochotona* ex. gr. *minor.* The porcupine *Hystrix refossa* from Dmanisi was described by Vekua et al. (2010). Although a more updated faunal list was provided by Lordkipanidze et al. (2007), a detailed revision of the existing material from a systematic, paleobiogeographic, and paleoecological point of view has never been carried out. In this article, we tackle for the first time these issues, in relation to one of the first recognized *Homo* dispersal out of Africa.

2. Materials and methods

The small-mammal sample was collected from the archaeological site of Dmanisi, Republic of Georgia. All the sediment that was screen-washed comes from the main excavation area Block 2, from layer B1. The Dmanisi rodent assemblage includes 135 identified elements that correspond to a minimum of 29 individuals, representing at least six taxa. We do not have included *H. refossa* in this study because of the different sampling methodology (excavation) with respect to that of the small mammals (screen-washing). Fossils are owned by the Georgian National Museum, but currently are stored at the Institut Català de Paleoecologia Humana i Evolució

Social (Tarragona, Spain). In the laboratory, the microvertebrate remains were examined under a binocular microscope for taxonomic identification. The nomenclature used in the descriptions of the teeth of Cricetidae and Gerbillidae is that of Freudenthal et al. (1994). The dental nomenclature and measuring methods for the studied material of Muridae follow van der Weerd (1976) and Martín-Suárez and Freudenthal (1993), respectively. The nomenclature used in the descriptions of the teeth of Arvicolidae is that of Van der Meulen and Zagwijn (1974). Dentognathic nomenclature and measuring methods for the Soricidae follow Reumer (1984).

To reconstruct the environment at Dmanisi, we have applied the method of habitat weighting (e.g., Blain et al., 2008, 2014; Piñero et al., 2016), distributing each rodent taxon in the habitat(s) where it is possible to find them at present (for extant species) or where they are assumed to have lived in the past (for extinct species). The habitats were divided into five types: open land in which dry and wet meadows are distinguished, woodland and woodland-margin areas, surrounding water areas and rocky areas. Each species was given a maximum possible score of 1.00, which was broken down according to the habitat preference of that species, so that if an animal occurred in more than one habitat type, its score was proportional to its habitat preference. To implement the habitat weightings method, it was necessary to calculate the proportions of each taxon in the assemblage.

3. Systematic paleontology

Order Eulipotyphla Waddell, Okada, and Hasegawa, 1999
Family Soricidae Fischer von Waldheim, 1817
Genus *Beremendia* Kormos, 1934
Beremendia fissidens Petényi, 1864
(Fig. 3A–G)

Holotype Not available. Petenyi (1864) quoted the species for the first time under the name '*Crossopus fissidens*' without designating a holotype. The genus *Beremendia* was erected by Kormos in 1934. However, he never provided a formal diagnosis but only a description, from which Reumer (1984) extracted several diagnostic characters.

Syntypes 6 maxillae and 37 mandible fragments (V 61.1585), housed at the Hungarian Natural History Museum from Budapest (Hungary) according to Pálfy et al. (2008).

Type locality Beremend 1 (Hungary).

Age range Early Pliocene (Mammal Neogene zone [MN] 14, Ruscinian) to Middle Pleistocene in Europe (Rzebik-Kowalska, 1998) and Early Pliocene to Early Pleistocene in Asia (Storch et al., 1998; Zazhigin and Voyta, 2019).

Geographic range Europe and Asia (Rzebik-Kowalska, 1998; Storch et al., 1998).

Referred material *Beremendia fissidens* is represented at Dmanisi by one complete maxillary with left I^1–M^2 and right A^1–M^3 dental rows, one left anterior side of the maxilla preserving the I^1–A^4 row, one fragmented right I1, one labial fragment of a right M^2, and one right hemimandible with the complete row I_1–M_3 (A_1 loose).

Remarks The teeth are pigmented at their cusps. The upper incisor is strongly fissident and the talon is invariably worn in the three specimens available. There are four upper antemolars, progressively decreasing in size from A^1 to A^4. The P^4, M^1, and M^2 are rather stout and they show a moderate posterior emargination. The M^3 is reduced to a triangular-shaped tooth in occlusal view, being wider than longer. The maxillary bone is robustly built. The lachrymal foramen is wide. The zygomatic process is rather short but wide and stout. The tip of the coronoid process of the mandible is tilted anteriorly. The articular process is twisted in posterior view with respect to the ascending ramus. The coronoid spicule is labially protruding. The P^4 has a lingual basin. The lower incisor is acuspulate and it bears a well-delimited groove running along the medial side of the tooth.

cf. *Beremendia minor* Rzebik-Kowalska 1976
(Fig. 3H)

Holotype Fragmentary right mandible with P_4–M_3 and processes except angular process (specimen ZZSiD, No. MF/1513) stored at the Institute of Systematic and Experimental Zoology (Kracow, Poland; Rzebik-Kowalska, 1976).

Type locality Rębielice Królewskie 1 (Poland).

Age range Early Pliocene (MN14, Ruscinian) to late Early Pleistocene (ca. 800 ka; Reumer, 1984; Botka and Mészáros, 2014).

Geographic range Europe (Rzebik-Kowalska, 1998; Zazhigin and Voyta, 2019).

Referred material cf. *Beremendia minor* is represented by one left side of a maxillary preserving A^4–M^2 row.

Remarks The teeth are stained at the tip of their cusps. The overall construction of the teeth is not as robust as seen in *B. fissidens*, but these teeth have rather a faint aspect. *Beremendia minor* shows teeth with less rounded cusps and sharper crests than its larger congeneric counterpart, *B. fissidens*. The identification of this species is left at a tentative level (cf.) because the teeth of the only specimen found are somewhat smaller than those frequently reported in literature.

Discussion *Beremendia* remains are known from more than 150 localities of 20 countries from Eurasia (Botka and Mészáros, 2014), where it is a rather frequent taxon in the small mammal assemblages from the earliest Pliocene to the Middle Pleistocene (Rzebik-Kowalska, 1998; Storch et al., 1998; Zazhigin and Voyta, 2019). The genus contains four valid species (*B. fissidens, B. minor, Beremendia pohaiensis,* and *Beremendia jiangnanensis*). The most widely distributed are *B. fissidens* (Early Pliocene–Middle Pleistocene) and *B. minor* (Early Pliocene–Early Pleistocene), representing the genus in Europe and Asia, whereas the other two species with a lesser number of occurrences, namely *B. pohaiensis* (middle Pliocene–Early Pleistocene) and *B. jiangnanensis* (Early Pleistocene), have only been found in Asia (Voyta et al., 2020). Until recently, the co-occurrence of *B. fissidens* and *B. minor* was limited to Pliocene sites (see data in Rzebik-Kowalska, 1998). However, Botka and Mészáros (2014) reported specimens of both species also from the Early Pleistocene Hungarian site of Somssich Hill 2 (ca. 900 ka). The purported presence of a small form of *Beremendia* in Early Pleistocene layers from Hungary and Georgia is baffling. Further research and new fossils are required to shed some more light in this issue.

On the other hand, the paleobiological profile of *Beremendia* is controversial. In first approaches, the species of this genus were regarded as opportunistic elements (Reumer, 1984; Popov, 2003). Other than that, the species *B. fissidens* has been sometimes considered as an indicator of nearby open water bodies by some authors (e.g., López-García et al., 2014), or typical of gallery forest or bushy vegetation on the sides of rivers and lakes (Botka and Mészáros, 2014). Nevertheless, such approaches have been carried out using indirect methods, so the resulting inferences must be taken with some reservations. In the last years, the scientific debate has turned to explain the opportunistic character of the genus *Beremendia* by means of the likely usefulness of the venom capabilities deduced from the typical lingually grooved lower incisors of its species. For some authors, this trait indicates that *Beremendia* was adapted to hunt on large prey, probably vertebrates (Cuenca-Bescós and Rofes, 2007; Rofes and Cuenca-Bescós, 2009; Bennàsar et al., 2015). Others alternatively consider the venomous capabilities to be adaptive in providing a careful injection to smaller

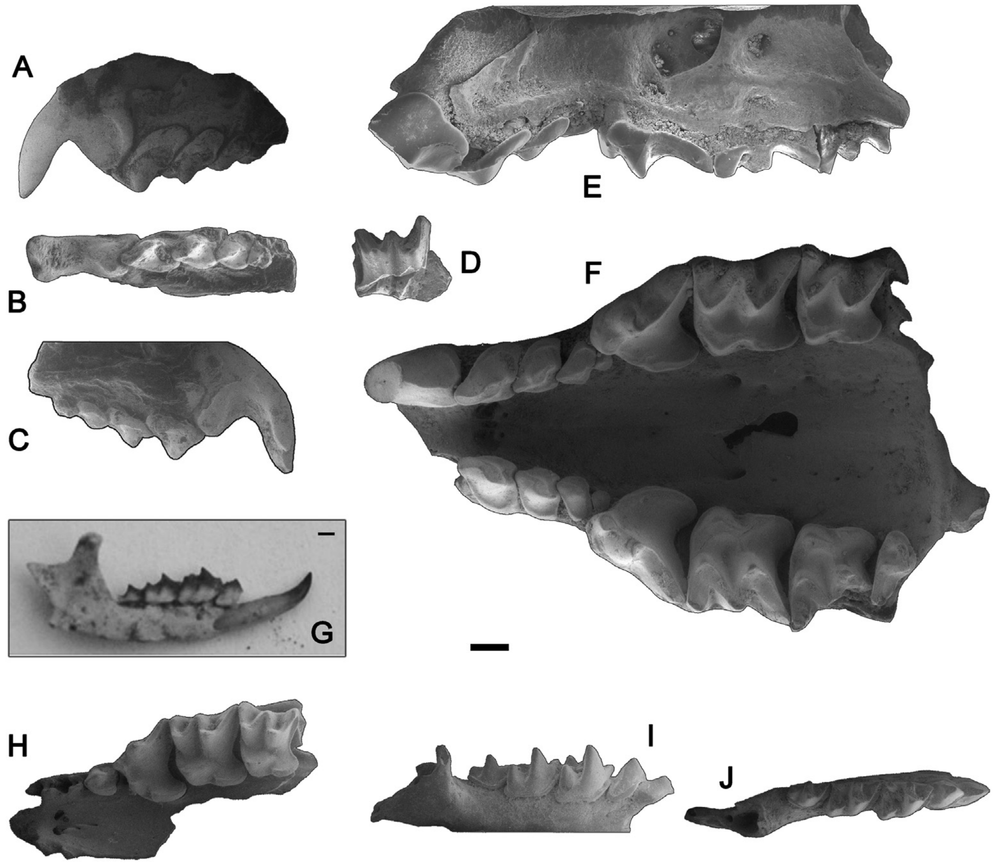

Figure 3. Soricidae from Dmanisi. Left I^1–A^4 row of *Beremendia fissidens* in labial (A), occlusal (B), and lingual (C) view. Labial fragment of a right M^2 of *Beremendia fissidens* (D). Maxillary of *Beremendia fissidens* with left I^1–M^2 and right A^1–M^3 dental rows in left labial (E) and occlusal (F) view. Right hemimandible of *Beremendia fissidens* with I_1–M_3 row missing the A_1 (G). Unfortunately, this specimen is currently lost and only this picture, which was taken in the field by Lorenzo Rook right after the specimen was unearthed, is available. The scale bar in this case has been deduced by indirect methods and it roughly equals 1 mm. Left fragment of a maxillary of cf. *Beremendia minor* with A^4–M^2 row (H). Right broken hemimandible of *Crocidura kornfeldi* with A_1–M_3 row (I and J). The scale bar equals 1 mm.

(and nonstruggling) prey to hoard them in comatose state, a predator strategy to face the environmental unpredictability (Furió et al., 2010; Furió, 2017; Zazhigin and Voyta, 2019). Some of the present authors find the second option more suitable, because according to its masticatory apparatus and dental wear, *Beremendia* was highly specialized in feeding on coleopterans and gastropods. The induction of victims into a comatose state permits their hoarding for a longer time, thus decreasing the risk of starvation in the case they were dead. Such strategy would have been extremely important to thrive in Dmanisi during the genesis of the site, as volcanic eruptions much likely resulted in frequent episodes of food shortage for long periods. Nonetheless, the debate about the use of venom in shrews is still open to new evidence and hypotheses (e.g., Kowalski and Rychlik, 2018; Moya-Costa et al., 2018) and they will be all useful in the forthcoming years to reach an integrative view of the ecological profile of *Beremendia* as claimed in Furió (2017).

Genus *Crocidura* Wagler, 1832
Crocidura kornfeldi Kormos, 1934
(Fig. 3I–J)

Holotype A skull with partial dentition (of which the left A^4 got lost after 1934; specimen Ob. 3686), stored at Magyar Állami Földtani Intézet (MAFI, Hungarian State Geological Survey; Budapest, Hungary; Reumer, 1984).
Type locality Villány 3 (Hungary).
Age range Late Pliocene (MN16, Villányian) to Middle Pleistocene (Reumer, 1984; Rzebik-Kowalska, 1998).
Geographic range Europe (mostly Mediterranean area and some Central European countries; Rofes and Cuenca-Bescós, 2011).
Referred material *Crocidura kornfeldi* is represented at Dmanisi by one right hemimandible with A_1–M_3 row (broken ascending ramus).
Remarks The genus *Crocidura* is frequently regarded as an indicator of mild climates according to the preferences of its present-day representatives (Reumer, 1984; Rofes and Cuenca-Bescós, 2011; Furió et al., 2015). Not by chance, the genus is widely distributed on the entire African continent and the southern part of Eurasia, with presence in many Indonesian islands. The northern -and colder- parts of the continent are not suitable for the development of *Crocidura* species because of their metabolic rates, which are rather slow if compared with their red-toothed counterparts, the Soricinae (Rofes and Cuenca-Bescós, 2011).

The case of *C. kornfeldi* is of special interest because of the African origin of the genus and its arrival to the European continent during the Plio-Pleistocene (Reumer, 1984). The spatial distribution of the species ranges from the late Pliocene Greek localities of Tourkobounia 3 and 5 (MN16–MN17) till its last occurrences in Spain (Botka and Mészáros, 2016). Although the exact moment of colonization of Eurasia is unknown, some models describe a progressive migration from the East to the West of Europe (Rzebik-Kowalska, 1995; Rofes and Cuenca-Bescós, 2011). It is noteworthy that this species is present in the small mammal assemblages of the Spanish localities of Fuente Nueva 3, Barranco León, and Sima del Elefante, all of them recording the earliest evidence of human occupation (Rofes and Cuenca-Bescós, 2011; Agustí et al., 2015; Cuenca-Bescós et al., 2016; Furió et al., 2018). In a similar way, many of these Biharian sites where *C. kornfeldi* is present (Furió et al., 2007, 2015; Piñero et al., 2015, 2020, 2022) have also provided the oldest European finds of other African elements such as *Hippopotamus* or *Theropithecus*. Therefore, most probably *C. kornfeldi* followed these large mammals (*Hippopotamus*, *Theropithecus, Homo*) in their dispersal into Eurasia.

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer von Waldheim, 1817
Genus *Allocricetus* Schaub, 1930
Allocricetus bursae Schaub, 1930
(Fig. 4A, B)

Holotype No formal holotype was designed by Schaub (1930), but it is usually considered the upper maxilla figured in that paper (Schaub, 1930: fig. 13) as the holotype of the species.
Type locality Fortyogoberg bei Brassó (Rumania).
Age range Early and Middle Pleistocene (Chaline, 1972; Cuenca-Bescós, 2003).
Geographic range Europe and Israel (Cuenca-Bescós, 2003; Tchernov, 1986).
Referred material *Allocricetus bursae* is represented at Dmanisi by two mandibles and isolated upper and lower teeth.
Remarks *Allocricetus bursae* from Dmanisi coincides in size and shape with other representatives of this species from southwest Asia and eastern Europe, such as Ubeidiya II23, Kozi Grzbiet, Zamkova Dolina Cave, or Verbeshnitsa. This species, closely related to *Cricetulus migratorius*, has been usually interpreted as an inhabitant of moist steppes of Asian origin, becoming a common component of the late Early Pleistocene to the late Middle Pleistocene Western Eurasian rodent communities.

Genus *Cricetulus* Milne-Edwards, 1867
Cricetulus sp.
(Fig. 4C, D)

Remarks *Cricetulus* sp. is the third most abundant small mammal species at Dmanisi. The teeth fit the morphology of the genus *Cricetulus*. However, its size is considerably larger than the Pleistocene populations of the extant species *Cr. migratorius*, such as those from the sites of Krak des Chevaliers, in Syria, Bacho Kiro, Nietoperzowa, Mamutowa and Qesem caves, as well as Zhoukoudian in China. The Dmanisi species also differs from this species in the weakly subdivided or crest-like anteroconid. In this way, it is close both in size and morphology to the populations of *Tscherskia*, often recognized as a subgenus within *Cricetulus*. Today, the species *Tscherskia triton* is found in northeastern China, Manchuria, Korea and the Ussuri region of southeastern Siberia. However, representatives of this genus have been also reported from the Holocene of Bastam, in Iran (*Tscherskia rusa*; Nord-west, Aserbeidschan; Storch, 1974), suggesting a much wider geographical range during the Pleistocene. Tchernov (1986) described a similar population as *Cricetus cricetus* (size of *Cricetus cricetus nanus*) at the Early Pleistocene site of Ubeidiya. However, both the species from Ubeidiya and that from Dmanisi are smaller than *Cricetus cricetus*, as well as the subspecies *Cri. cri. nanus*, differing also in their morphology. The living *T. triton* is a burrowing species that is usually found in dry, open landscapes.

Family Gerbillidae Alston, 1876

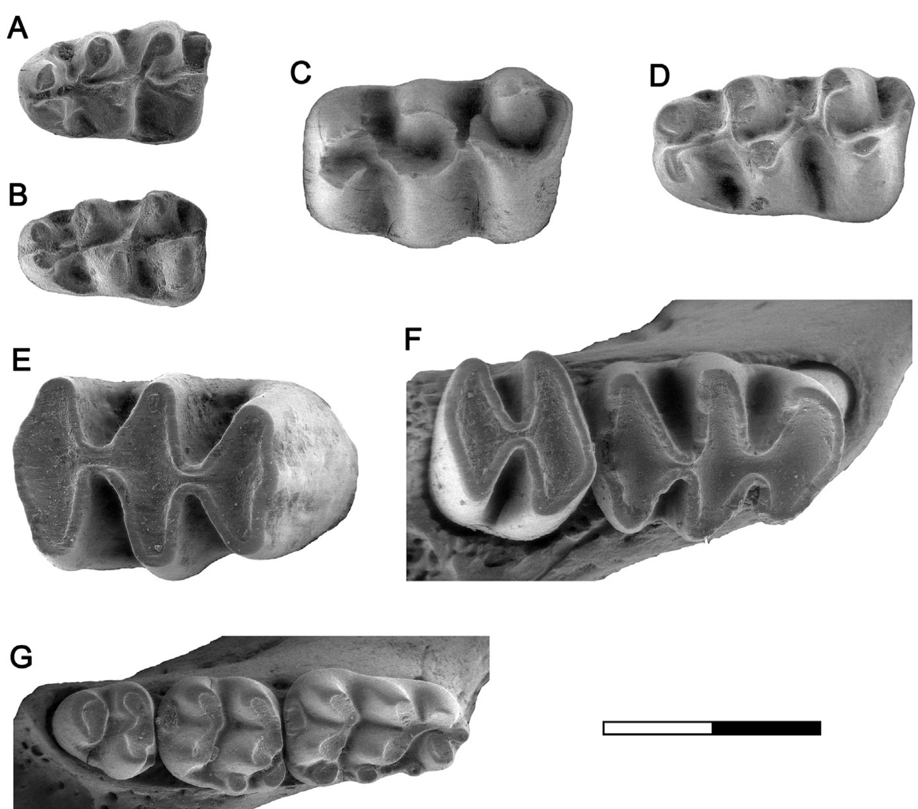

Figure 4. Rodents from Dmanisi. A) Left M_1 of *Allocricetus bursae*. B) Left M_1 of *Allocricetus bursae*. C) Left M^1 of *Cricetulus* sp. D) Left M_1 of *Cricetulus* sp. E) Right M^1 of *Parameriones* aff. *obeidiyensis*. F) Right M_1–M_2 of *Parameriones* aff. *obeidiyensis*. G) Right M_1–M_3 of *Apodemus* cf. *atavus*. Scale bar represents 2 mm.

Genus *Parameriones* Heptner, 1937
Parameriones aff. *obeidiensis* Haas, 1966
(Fig. 4E, F)

Holotype Incomplete mandible with M_1, M_2, M_3 (specimen HUJ.P.U.1001, illustrated in Haas, 1966: pl. XII, fig. 28). Housed at Hebrew University, Jerusalem.
Type locality Ubeidiya (Israel).
Age range Early and Middle Pleistocene (Tchernov and Chetboun, 1984; Tchernov, 1986).
Geographic range southwest Asia (Israel and Syria; Tchernov and Chetboun, 1984).
Referred material A total of 57 molars belonging to *Parameriones* aff. *obeidiensis* have been recovered from the site of Dmanisi.
Remarks The genus *Parameriones* was defined by Heptner (1937), including the species *Meriones persicus* and *Meriones rex*. However, Tchernov and Chetboun (1984) 'rediscovered' and redefined that genus based on the previously described *Meriones obeidensis* Haas (1966) from Ubeidiya. The same species was identified by Tchernov (1968) in several karst fissure fillings of the Middle Pleistocene age. The study of the fossil gerbils from the Ubeidiya formation has shown that *Parameriones obeidiensis* is characterized by a mixture of primitive and derived features that do not fit the genus *Meriones*. According to Tchernov (1986), although belonging to the group of *Meriones*, this species probably represents a dead-end evolutionary line within the gerbil radiation. Comparison between Dmanisi and Ubeidiya show that Dmanisi *Parameriones* is smaller than the one from Ubeidiya, which is an indication of size increase through time. From a paleoecological point of view, *Parameriones* aff. *obeidiensis* is the most abundant small mammal species from Dmanisi. *Parameriones* was a grassland animal, much more like the modern *Meriones tristrami*.

Family Muridae Illiger, 1811
Genus *Apodemus* Kaup, 1829
Apodemus cf. *atavus* Heller, 1936
(Fig. 4G)

Holotype Right mandibular fragment with M_1 and M_2 (Heller, 1936: tab. X, fig. 2), stored at the Senckenberg Museum (Frankfurt, Germany).
Type locality Gundersheim (Germany).
Age range Latest Miocene to Early Pleistocene (Rietschel and Storch, 1974; Fejfar and Storch, 1990; Colombero et al., 2014).
Geographic range Western Europe to China (Cai and Qiu, 1993; Martín-Suárez and Mein, 2004; Knitlová and Horáček, 2017).
Referred material *Apodemus* cf. *atavus* is represented at Dmanisi by a single left mandible with M_1, M_2, and M_3.
Remarks The molars display the typical features observed in the lower teeth of *A. atavus* (see Heller, 1936): small size, protoconid–metaconid pair connected to the lingual lobe of the anteroconid, presence of accessory labial cuspids on the M_1, and large posterior heel in M_2 protruding over the outline. Rietschel and Storch (1974) gave as diagnostic criterion of *A. atavus* that the posterior accessory cuspid of M_2 is large, which contrasts with the absence of the posterior accessory cuspid in the studied M_2. However, Martín-Suárez and Mein (2004) discarded this criterion as diagnostic for *A. atavus* when observed that this cuspid is highly variable in size among the material of this species from the localities of Schernfeld (Germany) and Balaruc 2 (France). The size of the material from Dmanisi is very similar to that of the populations of *A. atavus* from Notio 1 (Greece; Hordijk and de Bruijn, 2009), Csarnota 2 (Hungary; van der Weerd, 1976), Moreda 1, Rambla Seca-A1, Belmez-1 (Spain; Castillo Ruiz, 1990), Alozaina (Spain; Aguilar et al., 1993), Mas Rambault 2 (France; Aguilar et al., 2002), Monte Peglia (Italy; Van der Meulen, 1973), Monte la Mesa (Italy; Marchetti et al., 2000), Hambach (Germany; Mörs et al., 1998), Frechen (Germany; Van Kolfschoten et al., 1998), and Jura Neuchâtel (Switzerland; Bolliger et al., 1993), among others. According to both the morphological and biometrical criteria, we assign the studied mandible to *Apodemus* cf. *atavus*. The scarcity of remains led us to use an open nomenclature.
Discussion Mouskhelishvili (1995) recognized the presence of *Apodemus* sp. at the site of Dmanisi. Later, Gabunia et al. (2000b) and Gabunia et al. (2001) referred to the murid of this site as *Apodemus* cf. *dominans* and *Apodemus dominans*, respectively. Agustí and Lordkipanidze (2011) quoted this species as *Apodemus* aff. *atavus*. *Apodemus atavus* and *A. dominans* are considered to be extreme phenotypes of a single species by several authors, *A. dominans* being a junior synonym of *A. atavus* (Fejfar and Storch, 1990; Martín-Suárez and Mein, 2004; Minwer-Barakat et al., 2005; García-Alix et al., 2008; Colombero et al., 2014). *Apodemus atavus* has a very wide geographical distribution throughout the Palaearctic region, spreading from Western Europe to China (Cai and Qiu, 1993; Martín-Suárez and Mein, 2004; Knitlová and Horáček, 2017). Its chronological range extends from the latest Miocene to the Early Pleistocene (Rietschel and Storch, 1974; Fejfar and Storch, 1990; Minwer-Barakat et al., 2005; Sala and Masini, 2007; García-Alix et al., 2008; Colombero et al., 2014). This species has a relatively conservative morphology, with little variation between the oldest and the youngest populations (Martín-Suárez and Mein, 2004; Minwer-Barakat et al., 2005). Some authors considered *A. atavus* as a direct ancestor of the extant *Apodemus sylvaticus* (Rietschel and Storch, 1974; Fejfar and Storch, 1990; Martín-Suárez and Mein, 1998).

Family Arvicolidae Gray, 1821
Genus *Mimomys* Major, 1902
Mimomys pliocaenicus Major, 1902
(Fig. 5A–D)

Holotype Fragmentary left mandibular branch with M_1 stored at the Museo de Paleontologia di Firenze.
Original reference Forsyth Major (1902), on some mandibles and teeth of Pliocene voles (*Mimomys* gen. nov.) from the Norwich Crag in Thorpe and the Upper Val d'Arno.
Type locality Castelfranco di Sopra (Italy).
Age range Late Pliocene (Chaline and Laurin, 1986).
Geographic range Europe (Chaline and Laurin, 1986).
Referred material *Mimomys pliocaenicus* is scarcely represented at Dmanisi, having been recovered one M_1, one M_2, and one fragmented M^3.
Remarks Although very rare in Dmanisi (less than 1%), *M. pliocaenicus* is a highly significant element from a biostratigraphic point of view, as it is a characteristic element of the Late Pliocene (late Villanyian) faunas from Europe, predating the dispersal of the rootless microtine *Allophaiomys pliocaenicus* (a main event in the Early Pleistocene of Eurasia; Rabeder, 1981).

Mimomys aff. *pusillus* Méhely, 1914
(Fig. 5E–H)

Holotype No holotype was formally designed by Méhely (1914), but it is usually considered mandible Nagy. 6.2 with M_1, M_2, and M_3 (Méhely, 1914: fig. 11), as a valid holotype for this species. It belongs to the collections of the Magyar Állami Földtani Intézet (MAFI, Hungarian State Geological Survey; Budapest, Hungary).
Type locality Püspökfürdo, Oradea (Nagyvárad, Romania).
Age range Late Pliocene to Early Pleistocene (Rabeder, 1981).
Geographic range Europe (Rabeder, 1981).

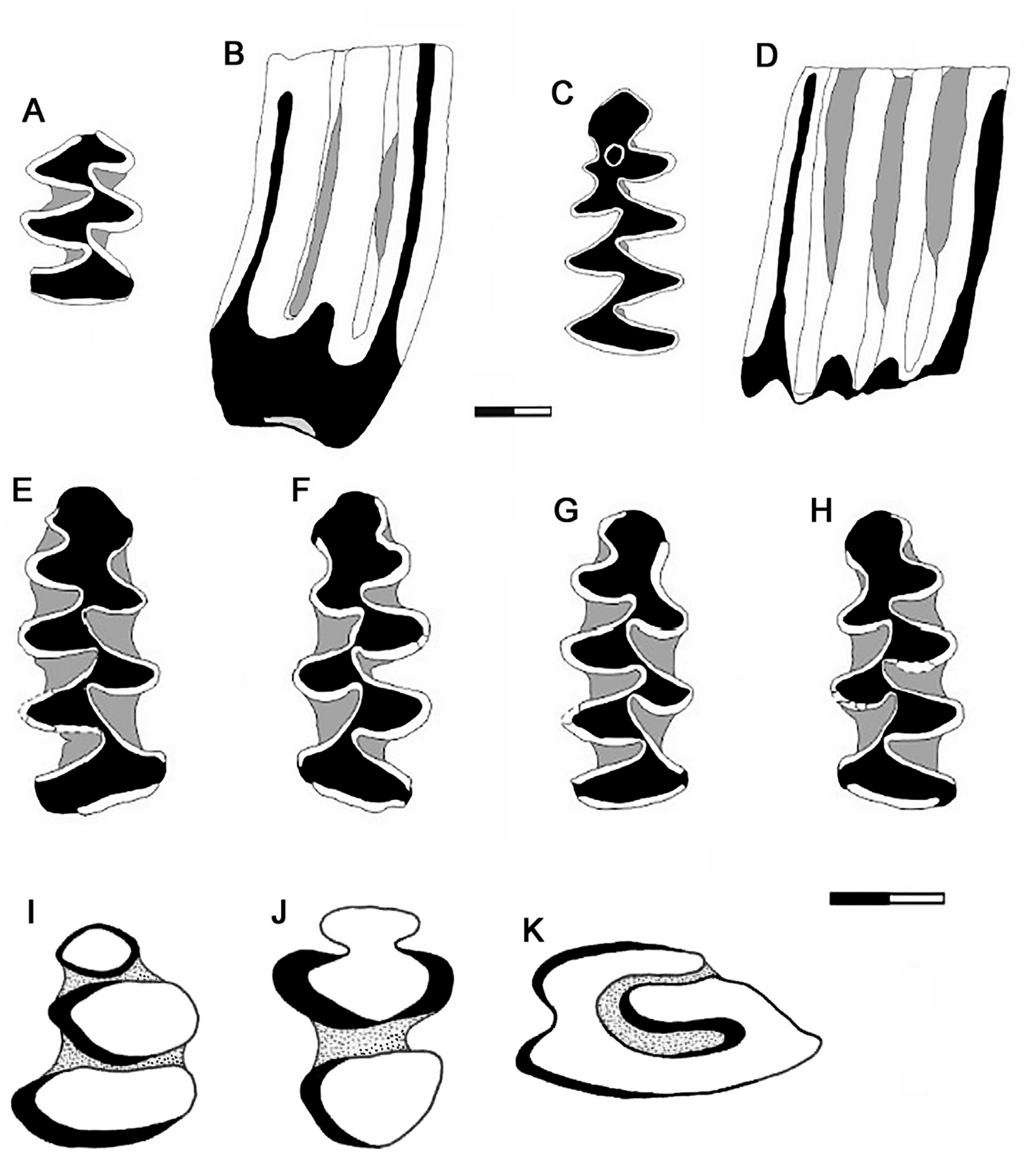

Figure 5. Arvicolids and lagomorphs from Dmanisi. A–B) Right M_1 of *Mimomys pliocaenicus* in occlusal (A) and lateral (B) views. C–D) Left M_1 of *Mimomys pliocaenicus* in occlusal (C) and lateral (D) view. E) Right M_1 of *Mimomys* aff. *pusillus* in occlusal view. F) Left M_1 of *Mimomys* aff. *pusillus* in occlusal view. G) Right M_1 of *Mimomys* aff. *pusillus* in occlusal view. H) Left M_1 of *Mimomys* aff. *pusillus* in occlusal view. I) Juvenile P_3 of *Ochotona* sp. in occlusal view. J) Juvenile P_4 of *Ochotona* sp. in occlusal view. K) Left P^3 of *Ochotona* sp. in occlusal view. Scale bar represents 1 mm. The upper scale bar goes with A–D, whereas the lower one goes with E–K.

Referred material *Mimomys* aff. *pusillus* is the third most abundant species at Dmanisi, represented by 33 first lower molars.

Remarks The simple dental pattern of the small arvicolid species from Dmanisi fits that of a number of Early Pleistocene (late Villanyan) *Mimomys* species: *Mimomys tornensis, Mimomys tigliensis, Mimomys blanci* and *Mimomys pusillus*. *Mimomys tornensis* is present in several Early Pleistocene localities such as Schernfeld, Deutsch Altenburg 3, 10, 2C1 and 4B (Rabeder, 1981). In Deutsch Altenburg 2C1 and 4B, this species is found associated with *Allophaiomys*. *Mimomys tornensis* is the largest and more hypsodont species within this group, characterized by high dentine tracks and abundant crown cement in the reentrant angles (Jánossy and van der Meulen, 1975). *Mimomys tigliensis* from Tegelen is smaller and less hypsodont than *M. tornensis*, as evidenced by the lower dentine tracts and the less abundant crown cement. In addition, the Tegelen species present more variants with the *Mimomys*-ridge than *M. tornensis*. Therefore, *M. tigliensis* appears as a feasible ancestor of the latest Villanyian *M. tornensis.* Carls and Rabeder (1988) defined the subgenus *Tcharinomys* for this group of small *Mimomys* species with hypsodont molars and abundant crown cement. However, the small arvicolid species from Dmanisi differs from both *M. tornensis* and *M. tigliensis* in being considerably smaller and having less hypsodont molars. This taxon coincides with the species *M. blanci* and *M. pusillus*. According to Van der Meulen (1973), *M. blanci* from Monte Peglia (type-locality of this species) differs from *M. pusillus* because of the presence of an incipient fourth buccal salient angle (BSA 4) in some specimens and the complete absence of *Mimomys*-ridge in young individuals. For the moment, we cannot check these characters in the Dmanisi sample, although the length values fit better those of *M. pusillus* from Beftia 2 than those of *M. blanci*, which is somewhat smaller. *Mimomys pusillus* and related species were included in the new genus *Pusillomimus* by Rabeder (1981), which actually resulted a junior synonym of the genus *Microtomys* Méhely, 1914.

Order Lagomorpha
Family Ochotonidae Thomas, 1897
Genus *Ochotona* Link, 1795
Ochotona sp.
(Fig. 5I–K)

Referred material *Ochotona* sp. is represented at Dmanisi by a juvenile P_3, a juvenile P_4, a M_1, two P^3, and one M^1.
Remarks The juvenile P_3 presents a triangular shape. It is subdivided into three cuspids, as the anteroconid is isolated and the talonid is not connected to the trigonid. In lateral view, the P_3 shows the characteristic conical shape of the juvenile teeth. The juvenile P_4 presents a trigonid with lateral inflexions and is again isolated from a slightly smaller talonid. The P^3 has an ellipsoidal surface, with a poorly developed hypoflex. The paraflex is filled by cement.
Discussion As no adult P_3 has been found, it has not been possible to assign *Ochotona* sp. from Dmanisi to any of the already described species of this genus. *Ochotona* is quite common in several Pliocene and Pleistocene sites from Asia and Europe, from China (Zheng, 1976; Cai, 1989) to Mongolia (Qiu, 1987), Russia (Averianov and Tesakov, 1998), Czech Republic (Cermak, 2004), Greece (de Bruijn et al., 1970), and France (Chaline, 1972; Erbajeva et al., 2001). The present distribution of *Ochotona* includes Asia and North America, being found in areas of broken rock and talus that are surrounded by suitable vegetation. *Ochotona* is most commonly seen at the interface between meadow habitat and open rocky terrain (Hemmer et al., 2011).

4. Discussion

4.1. Paleobiogeography

The most common species in Dmanisi is the gerbil *Parameriones* aff. *obeidiensis*. The second most common species at Dmanisi is the hamster *Cricetulus* sp. Both *Parameriones* aff. *obeidiensis* and *Cricetulus* sp. can be related to species that have been found in the younger Paleolithic site of Ubeidiya. At this locality, a similar species of hamster was described as *Cricetus* sp. (size of *Cricetus cricetus nanus*). In contrast, in the Late Pliocene and Early Pleistocene sites in Europe, hamsters are usually represented by *Al. bursae*. Although present, this species is scarcely represented at Dmanisi. Typical European elements such as arvicolids of the genus *Mimomys* are quite rare at Dmanisi, with the exception of *Mimomys* aff. *pusillus*, a common arvicolid in Late Pliocene (late Villanyian) European faunas. A second arvicolid species, *M. pliocaenicus*, is very rare in Dmanisi. In contrast with other coeval sites in northern Caucasus like Muhkai 2 and Tizdar, the genus *Allophaiomys* is absent from the arvicolid association of Dmanisi. This absence can be explained based on the existence of different environmental conditions at both sides of the Caucasus, with a colder climate to the north. Another European element, the murid *Apodemus* cf. *atavus*, is again scarcely represented. None of the small mammal species from Dmanisi can be regarded as of African origin, with the possible exceptions of *Parameriones* aff. *obeidiensis* and *C. kornfeldi*. The most likely origin of the genus *Crocidura* is Africa (Butler, 2010), but Rofes and Cuenca-Bescós (2011) considered Asia Minor as an alternative source area. The geographic range of the living gerbil *Meriones*, closely related to *Parameriones*, certainly covers northern Africa. However, several species of *Meriones* are also present in Asia, ranging from Saudi Arabia, Turkey and Pakistan to Russia and China. Even the Saharan species *Meriones lybicus* reaches eastern Georgia today, as it is also the case for the Anatolian *Meriones tristami*. In the case of *Cricetulus* sp. from Dmanisi and Ubeidiya, either if it could be assigned to the (sub)genus *Tscherskia* or not, this hamster is of probable Asian or Western Asian origin. In its turn, many authors have considered the small-sized hamster *Al. bursae* as an eastern element. Therefore, we can conclude that the small mammal community from Dmanisi is composed mainly by Western or Central Asian elements, with a poor representation of European elements (*Mimomys*, *Apodemus*).

4.2. Paleoenvironmental context

As stated, by far, the most common species in Dmanisi is the gerbil *Parameriones* aff. *obeidiensis* (42%). Following *Parameriones* aff. *obeidiensis*, the most common element is the hamster *Cricetulus* sp. (26%). The third most common species is the small-sized arvicolid *Mimomys* aff. *pusillus* (25%). *Allocricetus bursae* is, in its turn, very rare (7%). The large-sized arvicolid species *M. pliocaenicus* is again very rare at Dmanisi (0.7%), as it is also the case of the murid *Apodemus* cf. *atavus* (1.3%; see Table 1). These last two European elements are usually associated with wooded or humid habitats.

As a result of application of the habitat weighting method, the distribution of the relative abundances of rodent taxa and their habitat preferences (Table 2; Fig. 6) indicates a dominance of open dry meadows (36.5%) and rocky habitats (21%). The rodent assemblage also indicates open herbaceous habitats with some humidity requirements (15.5%) and areas surrounding water (25.7%). Therefore, the rodent association from Dmanisi suggests the presence of an open, steppic environment in the vicinity of Dmanisi, although the scarce arvicolid and murid representation would indicate the existence of wooded areas (1.3%) not far away from this steppic landscape.

The vertebrate paleontological information provides strong evidence of the existence of a fairly differentiated landscape pattern around the site of Dmanisi. The flat river valley would have contained open water bodies and areas of wet ground throughout the year. Other parts of the valley floodplain were covered by gallery forests. Paleoenvironmental data indicate a semi-dry and warm climate during this time, similar to the present-day Mediterranean climate, with small rivers or water bodies and lakes and rich animal and vegetable resources. These results agree with those for large mammals, amphibian, reptiles (Blain et al., 2014) and the paleobotanical analysis (Klopotovskaja et al., 1989; Kvavadze, 1997; Messager et al., 2010), which indicate a significant water stress suggesting a period of increased aridity contemporaneous with human occupation of the site. It must be considered that the local environment was affected from time to time by volcanic episodes and ash falls.

4.3. Implications for the early hominin dispersal out of Africa

Analysis of paleoenvironmental conditions of the small vertebrate associations from several Early Pleistocene sites led Agustí et al. (2009) to conclude that presence of hominids was strongly influenced by climatic parameters, namely high pluviosity and relatively warm temperatures. The small mammal assemblage from Dmanisi corroborates this last respect, but not the former one,

Table 1
Rodents from Dmanisi in number of identified specimens (NISP).

Species	NISP	%
Parameriones aff. *obeidiensis*	57	42.0
Cricetulus sp.	35	26.0
Allocricetus bursae	7	5.0
Mimomys pliocaenicus	1	0.7
Mimomys aff. *pusillus*	33	25.0
Apodemus cf. *atavus*	3	1.3
Total	135	100

Table 2
Relative abundances of each rodent taxon from the early Pleistocene site of Dmanisi, with the distribution of their potential habitats.

Species	Habitat				
	OD	OW	W	R	WE
Parameriones aff. *obeidiyensis*	0.5	–	–	0.5	–
Cricetulus sp.	0.5	0.5	–	–	–
Allocricetus bursae	0.5	0.5	–	–	–
Mimomys pliocaenicus	–	–	–	–	1
Mimomys aff. *pusillus*	–	–	–	–	1
Apodemus cf. *atavus*	–	–	1	–	–

Abbreviations: W = woodland and woodland-margin areas; R = rocky areas; OD = open dry meadows; OW = open wet meadows; WE = water-edges.

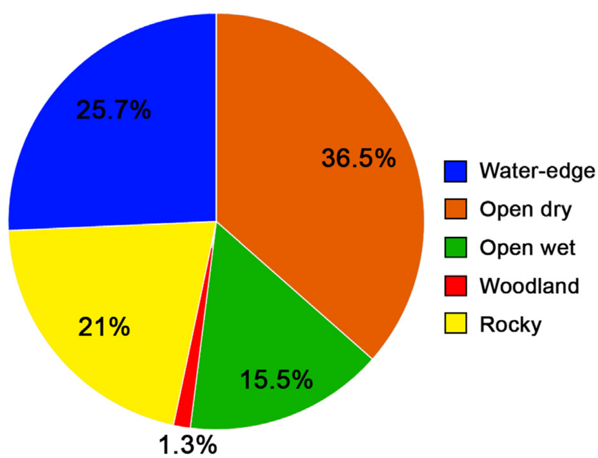

Figure 6. Pie chart illustrating the distribution of the habitats at Dmanisi according to the ecological preferences of the rodent species.

indicating the prevalence of dry, steppic conditions. In this way, the results of this paper agree with those of Blain et al. (2014). A plausible explanation for this disagreement between Dmanisi and other European Early Pleistocene sites could lie on the ecological requirements of the Dmanisi hominins, being in this way behaviorally different from the ones that later settled on Western Europe, at sites like Barranco Léon and Fuente Nueva 3 (Guadix-Baza Basin) or Sima del Elefante (Atapuerca karstic complex). However, an alternative interpretation is also possible. Agustí and Lordkipanidze (2019) proposed a scenario in which the first out of Africa can be explained based on the woodland regression in Eastern Africa and the spread of savanna. In this way, Southern Caucasus could have acted as a kind of biotic refugium for those hominin populations, as it has been also the case for many other species. However, the Early Pleistocene at ca. 1.8 Ma is marked by increasing aridity, with quite unfavorable conditions for dispersal throughout the southwest Asia to reach Southern Caucasus. In contrast, hominin dispersal would have been more feasible at an earlier time, at the base of the Pleistocene (Agustí and Lordkipanidze, 2011). If this scenario is correct, the Dmanisi hominins could have reacted in the same way as the Western European Early Pleistocene hominins, entering Southern Caucasus in an interglacial phase before the deposition of the Dmanisi site.

5. Conclusions

The small mammal community from Dmanisi is composed of three insectivore species (*B. fissidens,* cf. *B. minor,* and *C. kornfeldi*), six rodent species (*Parameriones* aff. *obeidiensis*, *Cricetulus* sp., *Al. bursae*, *Mimomys* aff. *pusillus*, *M. pliocaenicus*, and *Apodemus* cf. *atavus*) and one lagomorph (*Ochotona* sp.). From a biogeographic point of view, the small mammal community from Dmanisi is composed mainly by western or Central Asian elements, with a poor representation of European elements (*Mimomys*, *Apodemus*). From a paleoecological point of view, most of the taxa suggests the presence of arid environments, from steppe or semi-desert to open woodland, with stony or rocky substrate and bushy areas, which indicate a semi-dry and warm climate during the hominin occupation, similar to the present-day Mediterranean climate. However, the presence of *Apodemus* cf. *atavus* evidences the existence of forested areas around the Dmanisi site. The presence of *Mimomys* is also indicative that small temporary, water bodies could have been present. These new data are in accordance with the previous paleoenvironmental proxies (paleobotanical and paleontological data) that indicate a period of increased aridity contemporaneous with human occupations of the site and support the presence of open, dry environments. In this respect, Dmanisi hominins differ from the Early Pleistocene hominins from Western Europe, which use to appear in wetter environments, avoiding the dry ones. This may indicate different ecological requirements among the two populations. A second alternative explanation would be that Dmanisi hominins entered Southern Caucasus at an interglacial phase before the deposition of the site.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgments

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