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## Zoogeographic significance of Dmanisi large mammal assemblage

Saverio Bartolini-Lucenti <sup>a, b</sup>, Omar Cirilli <sup>a, c</sup>, Luca Pandolfi <sup>a</sup>, Raymond Louis Bernor <sup>d, e</sup>, Maia Bukhsianidze <sup>f</sup>, Francesco Carotenuto <sup>g</sup>, David Lordkipanidze <sup>f</sup>, Nikoloz Tsikaridze <sup>f</sup>, Lorenzo Rook <sup>a, \*</sup>



<sup>a</sup> Earth Science Department, Paleo[Fab]Lab, University of Florence, via La Pira 4, 50121, Firenze, Italy

<sup>b</sup> Natural History Museum, Geology and Paleontology Section, via La Pira 4, 50121, Firenze, Italy

<sup>c</sup> Dottorato di Ricerca in Scienze della Terra, University of Pisa, via S. Maria 56, 56126, Pisa, Italy

<sup>d</sup> Laboratory of Evolutionary Biology, Department of Anatomy, College of Medicine, Howard University, 20059, Washington DC, USA

<sup>e</sup> Human Origins Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, 20013, Washington, DC, USA

<sup>f</sup> Georgian National Museum, 3, Rustaveli Avenue, Tbilisi-0105, Georgia

<sup>g</sup> Department of Earth Sciences, Environment and Resources, "Federico II" University of Naples, Via Cinthia 21, 80126, Naples, Italy

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## ABSTRACT

We undertake a comparative mammalian zoogeographic analysis with the aim of revealing the extent to which the Dmanisi Early Pleistocene large mammal assemblage resembles, at the genus level, African, Arabian, and Eurasian localities of similar age. The inclusion of Old World Pliocene and Pleistocene mammalian faunas provides us with insights into the provincial origins of specific mammalian taxa and permits us to assess the relative affiliation of the Dmanisi mammalian faunas to other faunas in the Old World. Our analysis also allows us to consider hypotheses about the timing and direction of zoogeographic connections between western Eurasia and Africa during the Early Pleistocene. We utilize multiple zoogeographic analytical tools as a cross-comparison of Dmanisi with 42 other Eurasian and African mammalian-bearing localities between 2.7 and 0.7 Ma. Overall, we find that Dmanisi compares most closely with a subgroup of Greek, Italian, and Spanish localities that are slightly younger than Dmanisi itself. This could suggest a progressive dispersal from East to West of the large mammal communities during the late Early Pleistocene and the first occurrence at Dmanisi, and then later in Western Europe, of some taxa such as *Stephanorhinus* ex gr. *etruscus-hundsheimensis*, *Equus altidens*, *Bison georgicus*, *Soergelia minor*, *Megantereon whitei*, *Canis borjgali*, *Canis (Xenocyon) lycaonoides*. Dmanisi's habitats included drier areas, probably of open wooded savannah and grassland and by mountainous to semiarid rocky terrain. There is evidence that Dmanisi records short intervals of increased aridity in the middle part of the succession contemporaneous with the occurrence of *Homo*.

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## 1. Introduction

Dmanisi is located on an elevated wedge-shaped promontory at the confluence of the Pinesauri and Mashavera rivers, and it is famous for the outstanding discovery of the earliest skeletal record of hominins out of Africa (Gabunia et al., 2000; Lordkipanidze et al., 2013; Rightmire et al., 2017, 2019). The whole fossil-bearing sequence is strictly constrained between the Mashavera Basalt at its base (dated to 1.85 Ma; Ferring et al., 2011; Nomade et al., 2016) and the Olduvai/Matuyama transition (1.77 Ma; Ferring et al., 2011),

with the majority of the samples coming from layers dated to a short chronologic interval (1.77–1.76 Ma; Lordkipanidze et al., 2007; Ferring et al., 2011).

Geographically, Dmanisi is located between the two largest inland body waters of Eurasia, the Black and the Caspian seas. This region is characterized by a very heterogeneous landscape, with high mountains to the north (the Caucasus) and valleys. Biogeographically, Dmanisi is considered as the crossroads of different dispersal routes of past faunas. The fossil record found here documents that Dmanisi was the obligate ridge between the two water bodies for faunas dispersing along the Africa-Eurasia and Eastern-Western Eurasia axes. Although Dmanisi hosts the oldest occurrence of *Homo erectus* outside Africa, its fossil faunal composition is mostly Eurasian (Gabunia et al., 2001). Paleoenvironmental

\* Corresponding author.

E-mail address: [lorenzo.rook@unifi.it](mailto:lorenzo.rook@unifi.it) (L. Rook).

reconstructions of Dmanisi are important to understand its role during key Pleistocene dispersal events. The analysis of different floral proxies helped to distinguish between two subsequent phases of the Dmanisi's paleoenvironment. An early phase, coinciding with the Olduvai geomagnetic subchron, was characterized by forested and open ecosystems, typical of warm and humid conditions (Messager et al., 2010a). A second later phase is represented by a totally different environment with steppe-forest conditions. During this phase, there was a drastic reduction in precipitation at the end of the Olduvai geomagnetic subchron. The dominant biome was the so-called 'Savannahstan' which spread throughout eastern Africa and Southwest Asia (Dennell, 2010) once more arid conditions started appearing worldwide during the Pleistocene. This is the environment the first hominins most probably tracked while dispersing out of Africa into Eurasia and thus making Dmanisi one of their base camps in their route toward Eastern Asia (Carotenuto et al., 2016a).

Apart from the remarkable record of hominins, the site of Dmanisi has yielded a rich and diverse fossil coenosis with up to 54 vertebrate taxa, among which 45 belong to Mammalia (Lordkipanidze et al., 2007; Furió et al., 2010; Blain et al., 2014; Bernor et al., 2019; Bernor et al., 2021; Bernor et al., 2021; Cappellini et al., 2019; Krijgsman et al., 2019; Medin et al., 2019; Bartolini-Lucenti and Madurell-Malapeira, 2020; Bartolini-Lucenti et al., 2020; Bernor et al., 2021; Bartolini-Lucenti et al., 2022; Cirilli et al., 2020a, b; Pandolfi et al., 2021). The updated faunal list is given in Table 1. The biochronological correlation of the assemblage is congruent with the paleomagnetic and geochronological data (Ferring et al., 2011). Micromammal species recovered from Dmanisi are indeed typical forms of the mid-Early Pleistocene (late Gelasian–early Calabrian). The voles *Mimomys pliocaenicus*, *Mimomys ostramensis*, and *Tcharinomys tornensis* correspond to the late Villanyian–Early Biharian small mammal age of western Eurasia (Cappellini et al., 2019; Krijgsman et al., 2019). Concerning large mammals, the faunal assemblage is characterized by the occurrence of species that evolved in Europe during the early and middle Villafranchian such as *Mammuthus meridionalis*, together with species that originated in central or eastern Asia, such as some bovids (*Bison*) and cervids (*Praemegaceros*), or in Africa, such as *Homo*. The latter also dispersed in Western Europe during the late Villafranchian. The equids exhibit a relationship with Europe (*Equus stenonis*) and Eurasia (*Equus altidens*), with the latter apparently having an Asian origin.

The mammal community from Dmanisi has been object of several studies during the past decades, but no one analyzed the total faunal composition. The aim of this study is to compare Dmanisi with a broad suite of Pleistocene Eurasian and African mammalian faunas, assess their faunal similarities, and provide insights into times and directions of zoogeographic connections.

## 2. Materials and methods

To undertake zoogeographic comparisons between the Dmanisi large-mammal assemblage and other latest Pliocene and Early to early Middle Pleistocene localities from Africa, Europe and Asia (Fig. 1), we performed pairwise comparison using the genus-rank faunal resemblance indexes (GFRI). As with Lordkipanidze et al. (2007), we followed Bernor and Pavlakis (1987), Fortelius et al. (1996a, b), Bernor et al. (2001), Bernor and Rook (2008) and Bernor et al. (2009) for calculating both Dice's and Simpson's GFRI, with the addition of the closeness index (Geraads, 2010). Bernor (1978) found that calculations of species (SFRI) are 'noisy' owing to regional variation in use of species names and that GFRI are more robust (in fact, subsequent analyses cited earlier limited their

assessment to GFRI). We selected 42 Old World latest Pliocene–Early and Middle Pleistocene localities (2.7–0.7 Ma) in our comparison with Dmanisi. The compiled matrix of genus occurrences (Table 2) is based on faunal lists and accounts published in the literature per each site used in the analyses (relevant references includes, among others, Teilhard de Chardin, 1940; De Giuli and Masini, 1986; Arribas and Palmqvist, 1998; Sotnikova et al., 2002; Abbazzi and Croitor, 2003; Palombo and Valli, 2003; Croitor and Kostopoulos, 2004; Gaudzinski, 2004; Martínez-Navarro, 2004; Mazza et al., 2004; Qiu et al., 2004; Delson et al., 2006; Lordkipanidze et al., 2007; Jin and Liu, 2009; Martínez-Navarro et al., 2009, 2012; Sotnikova and Titov, 2009; Geraads et al., 2010; Rook and Martínez-Navarro, 2010; Werdelin and Sanders, 2010; Kahlke et al., 2011; Rook, 2013; Rook et al., 2013, 2019; Wang et al., 2013; Madurell-Malapeira et al., 2014; Bartolini-Lucenti and Rook, 2016, 2018; Geraads, 2016; Gkeme et al., 2017; Koufos, 2018; Sahnouni et al., 2018; Bernor et al., 2019; Bernor et al., 2021; Breda et al., 2020; Cirilli et al., 2020a, b, 2021a; Jin et al., 2021; Bartolini-Lucenti et al., 2022). We revised and updated the few instances in which the original attribution was amended by a subsequent article. The entire Dmanisi fossil collection is kept in the S. Janashia Museum of Georgia, part of the Georgian National Museum (Tbilisi, Georgia). For taxonomic identification of the Dmanisi fauna, we used data from the literature, comparison with osteologic atlases (both for extant and fossil animals), as well as direct comparisons with extant and fossil taxa on reference museum collections (among others, the main collections we refer are those kept in the following institutions: American Museum of Natural History, New York, USA; National Museum of Natural History, Washington DC, USA; Hungarian Museum of Natural History, Budapest, Hungary; Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallés, Barcelona, Spain; Musée des Confluences, Lyon, France; Musée National d'Histoire Naturelle, Paris, France; Museum of Natural History, Geological and Paleontological section and 'La Specola' Zoology section, University of Florence, Italy; S. Janashia Museum of Georgia, part of the Georgian National Museum, Tbilisi, Georgia; Université Claude Bernard Lyon-1, Lyon, France).

The genus-level faunal resemblance index is calculated using Dice's (Sokal and Sneath, 1963), Simpson's (Simpson, 1943), and closeness index (Geraads, 2010) formulas. We utilize multiple indices for the sake of comparing results. These indexes have been largely used in paleontological literature (e.g., Flynn, 1986; and citations given earlier), and many scholars have maintained their robustness and validity for comparisons of fossil associations (Archer and Maples, 1987; Maples and Archer, 1988; Fortelius et al., 1996a, b; Geraads, 2010). The Dice's GFRI is calculated as  $2A/(2A + B + C)$  in which A is the number of genera shared by both faunas, B is the number of genera exclusive of the first fauna, and C is the number of genera exclusive of the second fauna. The Simpson's resemblance index is calculated with the formula  $A/(A + E)$  in which E is the smallest between B and C. The closeness index is calculated as  $A(A + B + C)/(A + B)(A + C)$  (where A, B, and C are the same as for Dice's and Simpson's indexes). The Dice's GFRI strictly takes into account the recorded taxa in both the compared sites, and thus, it is deeply affected by the preservation and record of the taxa in each site (Archer and Maples, 1987; Maples and Archer, 1988). This condition is somewhat relaxed in the Simpson's GFRI in which the number of different taxa between the sites considered by the index is limited to the smallest of the two. In this way, the effect of missing record is mitigated, although not removed (Fortelius et al., 1996a, b). Similarly, the closeness index is less affected by unequal sample representation in the analyzed sites (as expressed by Geraads, 2010).

**Table 1**

Updated faunal list from Dmanisi site (data revised and updated from the studies by Lordkipanidze et al., 2007; Blain et al., 2014; Cappellini et al., 2019; Krijgsman et al., 2019; Bartolini-Lucenti et al., 2020).

Class	Order	Family	Genus	Species and subspecies
Pisces	Salmoniformes	Salmonidae	<i>Salmo</i>	sp.
Amphibia	Anura	Bufonidae	<i>Bufo</i>	ex gr. <i>viridis</i>
Amphibia	Anura	Bufonidae	Anura indet.	
Reptilia	Testudinata	Testudinidae	<i>Testudo</i>	<i>graeca</i>
Reptilia	Squamata	Lacertidae	<i>Lacerta</i>	ex gr. <i>viridis</i>
Reptilia	Squamata	Colubridae	<i>Elaphe</i>	ex gr. <i>quatuorlineata</i>
Reptilia	Squamata	Natricidae	<i>Natrix</i>	sp.
Reptilia	Squamata	Colubridae indet.		
Aves	Struthioniformes	Struthionidae	<i>Struthio</i>	<i>dmanisensis</i>
Aves	Galliformes	Gallidae	<i>Gallus</i>	<i>dmanisensis</i>
Aves	Strigiformes	Strigidae	<i>Strix</i>	<i>gigas</i>
Mammalia	Insectivora	Soricidae	<i>Beremendia</i>	<i>fissidens</i>
Mammalia	Insectivora	Soricidae	<i>Sorex</i>	sp.
Mammalia	Lagomorpha	Ochotonidae	<i>Ochotona</i>	cf. <i>lagreli</i>
Mammalia	Lagomorpha	Leporidae	<i>Hypolagus</i>	cf. <i>brachygnathus</i>
Mammalia	Rodentia	Muridae	<i>Apodemus</i>	aff. <i>atavus</i>
Mammalia	Rodentia	Cricetidae	<i>Cricetulus</i>	sp.
Mammalia	Rodentia	Cricetidae	<i>Allocricetus</i>	<i>bursae</i>
Mammalia	Rodentia	Arvicolidae	<i>Tcharinomys</i>	<i>tornensis</i>
Mammalia	Rodentia	Arvicolidae	<i>Mimomys</i>	<i>pliocenicus</i>
Mammalia	Rodentia	Gerbillidae	<i>Parameriones</i>	aff. <i>obeidiensis</i>
Mammalia	Rodentia	Hystricidae	<i>Hystrix</i>	<i>refossa</i>
Mammalia	Primates	Hominidae	<i>Homo</i>	sp.
Mammalia	Carnivora	Canidae	<i>Canis</i>	<i>borjgali</i>
Mammalia	Carnivora	Canidae	<i>Vulpes</i>	<i>alopeoides</i>
Mammalia	Carnivora	Canidae	<i>Canis (Xenocyon)</i>	<i>lycaonoides</i>
Mammalia	Carnivora	Ursidae	<i>Ursus</i>	<i>etruscus</i>
Mammalia	Carnivora	Mustelidae	<i>Lutra</i>	<i>simplicidens</i>
Mammalia	Carnivora	Mustelidae	<i>Pannonictis</i>	<i>nestii</i>
Mammalia	Carnivora	Mustelidae	<i>Martes</i>	sp.
Mammalia	Carnivora	Mustelidae	<i>Meles</i>	sp.
Mammalia	Carnivora	Hyaenidae	<i>Pachycrocuta</i>	<i>brevirostris</i>
Mammalia	Carnivora	Felidae	<i>Lynx</i>	<i>issiodorensis</i>
Mammalia	Carnivora	Felidae	<i>Acinonyx</i>	<i>pardinensis</i>
Mammalia	Carnivora	Felidae	<i>Panthera</i>	<i>onca georgica</i>
Mammalia	Carnivora	Felidae	<i>Megantereon</i>	<i>whitei</i>
Mammalia	Carnivora	Felidae	<i>Homotherium</i>	<i>latidens</i>
Mammalia	Proboscidea	Elephantidae	<i>Mammuthus</i>	<i>meridionalis taribanensis</i>
Mammalia	Perissodactyla	Equidae	<i>Equus</i>	<i>stenonis</i>
Mammalia	Perissodactyla	Equidae	<i>Equus</i>	<i>altdiens</i>
Mammalia	Perissodactyla	Rhinocerotidae	<i>Stephanorhinus</i>	sp. 1
Mammalia	Perissodactyla	Rhinocerotidae	<i>Stephanorhinus</i>	sp. 2
Mammalia	Artiodactyla	Cervidae	<i>Pseudodama</i>	<i>nestii</i>
Mammalia	Artiodactyla	Cervidae	<i>Praemegaceros</i>	<i>obscurus</i>
Mammalia	Artiodactyla	Cervidae	<i>Cervalces</i>	cf. <i>gallicus</i>
Mammalia	Artiodactyla	Cervidae	<i>Arvernoceros</i>	<i>insolitus</i>
Mammalia	Artiodactyla	Suidae	<i>Sus</i>	sp.
Mammalia	Artiodactyla	Giraffidae	<i>Palaeotragus</i>	cf. <i>priasovicus</i>
Mammalia	Artiodactyla	Bovidae	<i>Bison (Eobison)</i>	<i>georgicus</i>
Mammalia	Artiodactyla	Bovidae	<i>Gallogoral</i>	<i>meneghinii sickenbergii</i>
Mammalia	Artiodactyla	Bovidae	<i>Capra</i>	<i>dalii</i>
Mammalia	Artiodactyla	Bovidae	<i>Soergelia</i>	cf. <i>minor</i>
Mammalia	Artiodactyla	Bovidae	<i>Praeovibos</i>	sp.
Mammalia	Artiodactyla	Bovidae	<i>Pontoceros</i>	<i>surprine</i>
Mammalia	Artiodactyla	Bovidae	Antilopini indet.	

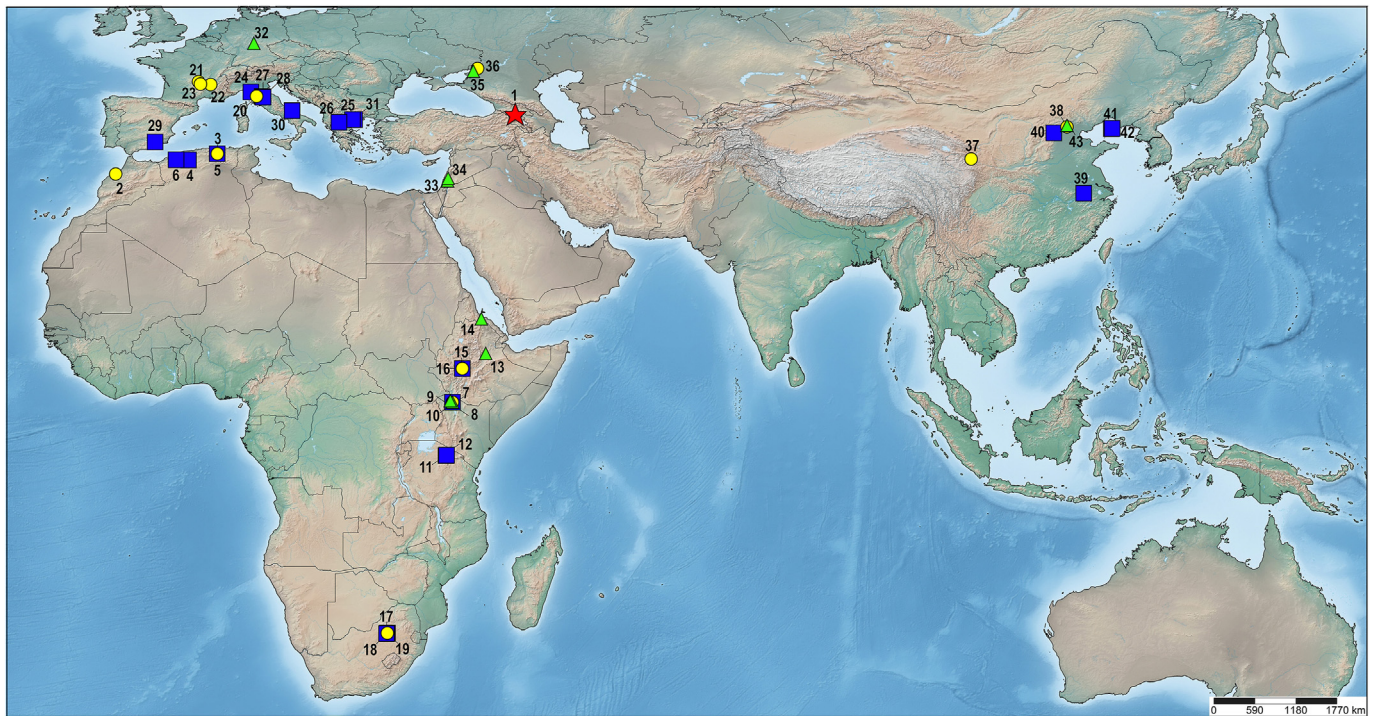
Three of the oldest and most similar localities to Dmanisi were selected to cross-test pairwise affinities to the other Old World sites.

### 2.1. Classifying Dmanisi according to faunal composition

To measure the proximity of Dmanisi to other fossil localities considered in this study, we used some methods and algorithms capable of calculating statistical classifications of sites according to their taxonomical compositions.

First of all, we tested if the taxonomical differences between the fossil sites in our study were statistically related to either or both temporal and geographical factors. Toward this aim, we performed

a Mantel test to assess any relationship between the taxonomical distance matrix measured by the Dice Index and both the geographic and age distance matrices measured between all the fossil sites. More specifically, the kind of analysis we performed is able to test the relationship between a response matrix and a predictor matrix while taking into account the effect of a second predictor matrix by means of permutations. Hence, we at first tested the relationship between the taxonomic distance and the geographic distance by accounting for the effect of the temporal distance and then we repeated the same analyses, this time by accounting for the effect of geographic distance on the relationship between taxonomic and temporal distance matrices. In addition, because we expected that the African sites would have accrued the



**Figure 1.** Map of the Old World showing the considered localities in the present study. Localities are grouped in chronological cluster: circles are localities dated 2.70–2.01 Ma; squares, sites between 2.0 and 1.2 Ma; triangles are localities between 1.19 and 0.70 Ma. Red star is the location of Dmanisi. Localities are those listed in Table 2: 1 = Dmanisi (Georgia); 2 = Ahl al Oughlam (Morocco); 3 = Ain Boucherit (Algeria); 4 = El Kherba (Algeria); 5 = Ain Hanec (Algeria); 6 = Tighenif (Algeria); 7 = Upper Burgi Member, Koobi Fora Formation (Kenya); 8 = KBS Member, Koobi Fora Formation (Kenya); 9 = Okote Member, Koobi Fora Formation (Kenya); 10 = Nariokotome Member, Nachukui Formation (Kenya); 11 = Olduvai Bed 1 (Tanzania); 12 = Olduvai Bed 2 (Tanzania); 13 = Daka Member (Ethiopia); 14 = Buia (Eritrea); 15 = Members C–F, Shungura Formation (Ethiopia); 16 = Members G–K, Shungura Formation (Ethiopia); 17 = Sterkfontein Member 4 (South Africa); 18 = Sterkfontein Member 5 (South Africa); 19 = Kromdraai (South Africa); 20 = Montopoli (Italy); 21 = Roca-Neyra (France); 22 = Saint Vallier (France); 23 = Senéze (France); 24 = Olivola (Italy); 25 = Libakos (Greece); 26 = Gerakarou (Greece); 27 = Poggio Rosso (Italy); 28 = Casa Frata (Italy); 29 = Venta Micena (Spain); 30 = Pirro Nord (Italy); 31 = Apollonia 1 (Greece); 32 = Untermassfeld (Germany); 33 = Ubeidiya (Israel); 34 = Geshen Benot Ya'aqov (Israel); 35 = Taman Faunal Complex (European Russia); 36 = Khapry Faunal Complex (European Russia); 37 = Longdan locality (China); 38 = Zhoukoudian locality 18 (China); 39 = Renzidong Cave (China); 40 = Xiashagou, Classic Nihewan (China); 41 = Jinyuan Cave Lower fauna (China); 42 = Jinyuan Cave Upper fauna (China); 43 = Zhoukoudian locality 1 (China).

contribution of geography on determining taxonomic distances between fossil sites, we repeated the mantel tests this time by using Eurasian fossil sites only. We anticipate here that the Mantel tests provided significant results when considering both the whole record and the reduced sample of Eurasian sites. As expected, the geographic component explaining taxonomical differences between sites was higher when considering African fossil sites than when including Eurasian localities (see Results section). As a consequence, we considered Eurasian fossil sites only in all the subsequent analyses to have a more balanced effect of both space and time in assessing the taxonomic proximity of Dmanisi to the other Eurasian sites.

As a first classification algorithm, we performed a cluster analysis on the occurrence matrix of all the considered assemblages by applying a bootstrapping cluster analysis (hereafter BCA). Bootstrapping cluster analysis is a partitioning methodology that is useful to test the robustness of the clustering results. It was used in recent studies (Raia et al., 2009; Carotenuto et al., 2016b) to statistically identify Pleistocene communities of Eurasian large mammals. This methodology starts by performing a first clustering of items by means of the unweighted pair group method with arithmetic mean algorithm (UPGMA; Sokal, 1958) to generate a reference cluster of the original data set in which the fossil localities are grouped according to their taxonomic similarity. The result of this analysis is the reference clustering. The following steps of this methodology aim to assign a probability value to each partitioning level of the original data in the

reference clustering. As a second step, a sample of the original data (i.e., the fossil localities with their taxonomic composition) is randomly chosen. This sampled data set is then used to feed a new UPGMA cluster analysis, which yields a new cluster. If the reference clustering (i.e., the results yielded by the UPGMA with the original data) is made by groupings that are really sharp, then we expect that very similar clusters are yielded by the UPGMA performed with a sample of the original data. Then, a similarity index ( $G^*$ ) is computed between the reference and the sample clustering. This index can range between 0 (if the two clusters are totally different) and 1 (if the clusters generated with the original and sampled data coincides). The  $G^*$  is then compared with the expected similarity value between reference and sample-based clustering ( $G^\circ$ ) under the null hypothesis that the sampled data set is a truly random sample of the original data. We repeated 1000 times the procedure of resampling the original data set, performing as many UPGMAs on sampled data and computing similarity indices. In the end, if the probability that  $G^*$  is higher or equal to  $G^\circ$  is higher than the significant level ( $p(G^\circ \leq G^*)$ ;  $\alpha = 0.05$ ), the partitioning levels of the reference cluster analysis are sharp (refer to the study by Pillar, 1999 for a detailed explanation of the algorithm). We calculated BCA by using the package 'pvclust' v. 2.2–0 (Suzuki et al., 2019) for R v. 3.6.0 (R Core Team, 2020).

Because the BCA is built on the occurrences matrix that includes the Dmanisi assemblage, we decided to perform another classification method that can be calibrated with all the fossil





Menelikia									X	X	X						X	X	
Redunca									X	X									
Gazella	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X	
Gazellospira									X	X	X	X	X				X	X	
Gallogoral	X										X	X	X						
Procamptoceras											X	X	X						
Pontoceros	X												X				X		
Spiroceros																		X	X
Budorcas																		X	X
Antidorcas										X	X	X						X	X
Antilope																	X		
Antilospira																			X
Parantidorcas		X																	
Madoqua																			
Tragelaphus	X																		
Taurotragus				X	X	X	X	X	X	X	X	X	X						
Syncerus																			
Pelorovis	X	X	X	X	X	X	X	X	X	X	X	X	X						
Cephalophus																			
Makapania																			
Pelea																	X		
Simatherium																			X
Boopsis																			X
Bubalus																			X
Bos																			X
Leptobos																			X
Praeovibos	X																		X
Soergelia	X																		X
Bison	X																		X
Hemibos																			X
Aepyceros																			X
Rabaticeras																			X
Bouria																			X
Nitidarcus																			X
Numidocapra		X	X																
Metacervolus																			X
Muntiacus																			X
Cervavitus																			X
Elaphurus																			X
Sinomegaceros																			X
Praemegaceros	X																		X
Metacervocerus																			X
Arvernoceros	X																		X
Croizetoceros																			X
Cervalces	X																		X
Megaloceros																			X
Eucladoceros																			X
Axis																			X
Dama																			X
Pseudodama	X																		X
Cervus																			X
Eostyloceros																			X
Procapreolus																			X

(continued on next page)

**Table 2** (continued)

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43					
<i>Capreolus</i>																																																
<i>Nippocervus</i>																																																
<i>Pliotragus</i>																																																
<i>Megalotis</i>																																																
<i>Capra</i>																																																
<i>Ovis</i>	X																																															

<sup>a</sup> List of the sites: 1 = Dmanisi (Georgia); 2 = Ahl al Oughlam (Morocco); 3 = Ain Boucherit (Algeria); 4 = El Kherba (Algeria); 5 = Ain Hanec (Algeria); 6 = Tighenif (Algeria); 7 = Upper Burgi Member, Koobi Fora Formation (Kenya); 8 = KBS Member, Koobi Fora Formation (Kenya); 9 = Okote Member, Koobi Fora Formation (Kenya); 10 = Nariokotome Member, Nachukui Formation (Kenya); 11 = Olduvai Bed 1 (Tanzania); 12 = Olduvai Bed 2 (Tanzania); 13 = Daka Member (Ethiopia); 14 = Buia (Eritrea); 15 = Members C–F, Shungura Formation (Ethiopia); 16 = Members G–K, Shungura Formation (Ethiopia); 17 = Sterkfontein Member 4 (South Africa); 18 = Sterkfontein Member 5 (South Africa); 19 = Kromdraai (South Africa); 20 = Montopoli (Italy); 21 = Roca-Neyra (France); 22 = Saint Vallier (France); 23 = Senéze (France); 24 = Olivola (Italy); 25 = Libakos (Greece); 26 = Gerakarou (Greece); 27 = Poggio Rosso (Italy); 28 = Casa Frata (Italy); 29 = Venta Micena (Spain); 30 = Pirro Nord (Italy); 31 = Apollonia 1 (Greece); 32 = Untermassfeld (Germany); 33 = Ubeidiya (Israel); 34 = Gesher Benot Ya'aqov (Israel); 35 = Taman Faunal Complex (European Russia); 36 = Khapry Faunal Complex (European Russia); 37 = Longdan locality (China); 38 = Zhoukoudian locality 18 (China); 39 = Renzidong Cave (China); 40 = Xiashagou, Classic Nihewan (China); 41 = Jinyuan Cave Lower fauna (China); 42 = Jinyuan Cave Upper fauna (China); 43 = Zhoukoudian locality 1 (China).

assemblages, with the exclusion of Dmanisi, and then we applied the derived model to classify Dmanisi according to a spatiotemporal criterion, as explained in the following.

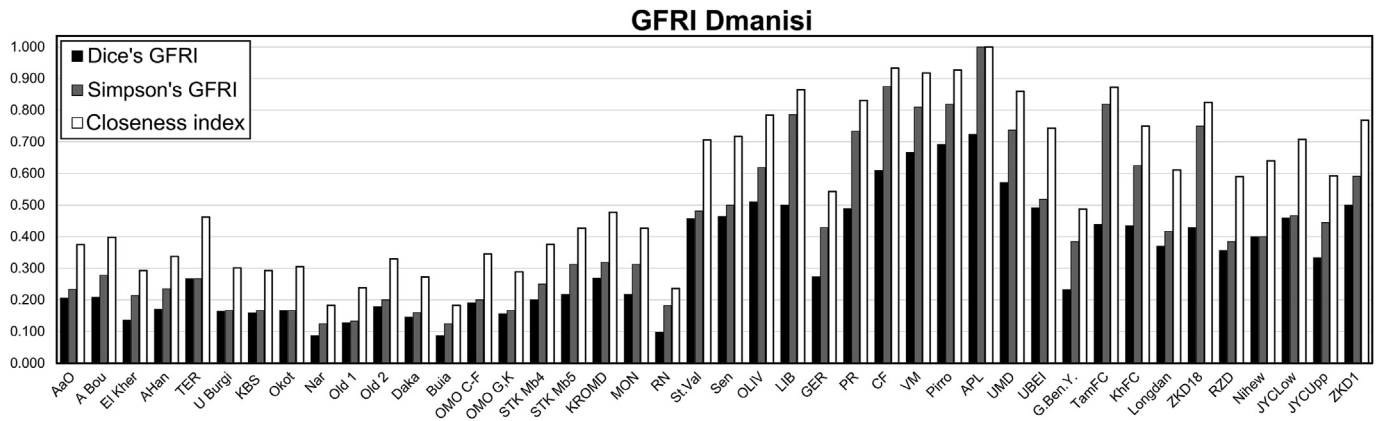
First of all, we grouped all the localities, but Dmanisi, according to their geographic and temporal position when compared with Dmanisi, that is, spatiotemporal classes. Indeed, we created the following classes: OlderEast = localities older and located east to Dmanisi; OlderWest = localities older and placed west to Dmanisi; YoungerEast = localities younger and east to Dmanisi; YoungerWest = localities younger and west to Dmanisi. Then, we computed the taxonomic distance matrix between all the localities (including Dmanisi) in our data set by using the (Dice) Bray–Curtis distance measure (suitable for binary occurrence matrices). As a further step, we performed a principal component analysis (PCA) on the distance matrix to reduce its dimensionality and any collinearity issue. We then considered only those PC axes that cumulatively explained 95% of the total variance. These PC axes were then used to feed a classification algorithm that we will explain later. Hence, we ruled out the Dmanisi PC scores and used all the remaining PC scores to train a model to later classify Dmanisi according to the previously defined spatiotemporal categories. Furthermore, to account for models' prediction accuracy and to reduce classes' imbalance effect, we calibrated our models by using only 50% of the complete data set and used the remaining localities as a testing data set to measure prediction's performance. We randomly sampled 50% of non-Dmanisi fossil localities 1000 times, and as a consequence, we trained as many models. As regards the kind of model we trained, we considered a multinomial log-linear regression fitted by means of artificial neural network (hereafter ANN). Multinomial log-linear regression is the multilevel version of the binomial log-linear regression for classifying more than 2 groups, whereas ANNs widely use machine learning algorithm inspired by the structure and organization of biological brains (Venables and Ripley, 2002). Very briefly, an ANN is made by layers of artificial neurons connecting the values of input variables (the PC axes in our case) to the output layer (the spatiotemporal groups we mentioned earlier). Combinations of predictor variables' values are weighted and transferred to neurons or output units and become a signal able to totally or partially activate the receiving units by means of an activation function. The activated unit, then, generates an output response. In a multinomial log-linear regression, this response is the probability for a given observation (PC scores of a particular locality in our case) to belong to a previously defined class (the spatiotemporal groups we created). This particular version of the multinomial log-linear regression stands on the training of a simple ANN directly connecting input variables to output classes. As mentioned earlier, we produced as many models as the subsets of data (1000). All these models were then used to predict the spatiotemporal groups that the Dmanisi site belongs to according to its faunal composition. For predictions, we only considered models with a predictive performance accuracy higher than 0.7 and with no unbalance of classes.

### 3. Results

#### 3.1. Genus-level faunal resemblance index and closeness index for Dmanisi

The results of the pairwise comparisons using the Dice's and Simpson's genus-level faunal resemblance indices and the closeness index between the association of Dmanisi and those of selected latest Pliocene and Early to early Middle Pleistocene localities of the Old World are reported in Figure 2. In this graph, it is clear that Dmanisi has an affinity with Eurasian sites, as opposed to African ones. Particularly the highest values of both indexes are





**Figure 2.** Histograms showing the degree of similarities resulting from the pairwise comparison between Dmanisi and other selected localities of the Old World, using both Dice's (black), Simpson's genus faunal resemblance index (dark grey), and the closeness index (white). Dmanisi shows clear resemblance with Eurasian late Villafranchian mammal faunas. Abbreviations: AaO = Ahl al Oughlam (Morocco); ABou = Ain Boucherit (Algeria); El Kher = El Kherba (Algeria); AHan = Ain Hanec (Algeria); TER = Tighenif (Algeria); U Burgi = Upper Burgi Member, Koobi Fora Formation (Kenya); KBS = KBS Member, Koobi Fora Formation (Kenya); Okot = Okote Member, Koobi Fora Formation (Kenya); Nar = Nariokotome Member, Nachukui Formation (Kenya); Old 1 = Olduvai Bed 1 (Tanzania); Old 2 = Olduvai Bed 2 (Tanzania); Daka = Daka Member (Ethiopia); Buia = Buia (Eritrea); OMO C–F = Members C–F, Shungura Formation (Ethiopia); OMO G–K = Members G–K, Shungura Formation (Ethiopia); STK Mb4 = Sterkfontein Member 4 (South Africa); STK Mb5 = Sterkfontein Member 5 (South Africa); KROMD = Kromdraai (South Africa); MON = Montopoli (Italy); RN = Rocca-Neyra (France); St. Val = Saint Vallier (France); Sen = Senèze (France); OLIV = Olivola (Italy); LIB = Libakos (Greece); GER = Gerakarou (Greece); PR = Poggio Rosso (Italy); CF = Casa Frata (Italy); VM = Venta Micena (Spain); Pirro = Pirro Nord (Italy); APL = Apollonia 1 (Greece); UMD = Untermassfeld (Germany); UBEI = 'Ubeidiya (Israel); G.Ben.Y. = Gescher Benot Ya'aqov (Israel); TamFC = Taman Faunal Complex (European Russia); KhFC = Khapry Faunal Complex (European Russia); Longdan = Longdan locality (China); ZKD18 = Zhoukoudian locality 18 (China); RZD = Renzidong Cave (China); Nihew = Xiashagou, Classic Nihewan (China); JYCLow = Jinyuan Cave Lower fauna (China); JYCUpp = Jinyuan Cave Upper fauna (China); ZKD1 = Zhoukoudian locality 1 (China).

with the late Villafranchian and even Epivillafranchian localities of western Eurasia such as Apollonia 1, Venta Micena, Pirro Nord, Casa Frata, Taman Faunal Complex, and Untermassfeld. High values are also shared with Libakos (Greece), Poggio Rosso (Italy), and by Eastern European, Near East, and Asian localities older than Dmanisi such as Taman and Khapry Faunal Complexes (European Russia), Ubeidiya (Israel), Jinyuan Cave Lower Fauna (China), and Zhoukoudian Locality 18 (China). In contrast, African localities have lower affinities with Dmanisi, despite their age (i.e., older or younger than Dmanisi). The highest GFRI and closeness index values among the Africa localities are found in Kromdraai (South Africa), Dice's GFRI = 0.269, Simpson's GFRI = 0.318, and closeness index = 0.477, albeit still rather low. Kromdraai ranks as the twenty-second and twenty-third most similar locality to Dmanisi (Table 3), respective to the Dice's and to the Simpson's and closeness indices (same position).

### 3.2. Genus-level faunal resemblance index and closeness index for three coeval Old World sites

Figure 3 shows the GFRI and closeness indexes values for three of the most similar sites to Dmanisi, from Europe (Olivola), Asia (Jinyuan Cave Lower Fauna), and Africa (Sterkfontein Member 5), whereas the Supplementary Online Material (SOM) Tables S1–S3 show the ordered values for the three sites. As for Olivola, the most similar associations are Casa Frata, Poggio Rosso, Senèze, and St. Vallier. It should be noted that some Asian sites, roughly coeval to Olivola, for example, Zhoukoudian Locality 18, Xiashagou, and Jinyuan Cave Lower Fauna, also have fairly high indices (Fig. 3). Jinyuan Cave Lower Fauna is similar to other chronological coeval Chinese localities such as Xiashagou or Longdan, but some Western European localities are also close to Jinyuan Cave Lower Fauna. Among these are Olivola (as noted earlier), Poggio Rosso, and Casa Frata. A lower degree of similarity with Jinyuan Cave Lower Fauna can be identified with Apollonia 1, Khapry Faunal Complex, Pirro Nord, the Taman Faunal Complex, Ubeidiya, and Zhoukoudian Locality 1 (Fig. 3). The histograms of the comparison with Sterkfontein

Member 5 in Figure 3 show high values of the indices only for the East and South African sites. The highest values are those of Sterkfontein Member 4 (Dice's index = 0.778; Simpson's index = 0.875; closeness index = 0.963), Omo level G–K (Dice's index = 0.400; Simpson's index = 0.625; closeness index = 0.735), and Upper Burgi member from Koobi Fora (Dice's index = 0.383; Simpson's index = 0.536; closeness index = 0.690). Similarly, high values of Dice's and Simpson's GFRI as compared with Sterkfontein Member 5 are those of Omo C–F (Ethiopia), Okote (Kenya), and Olduvai 1 (Tanzania). For the closeness index, the highest values are the Upper Burgi member, Omo C–F levels, and Kromdraai.

### 3.3. Dmanisi classification according to faunal composition

The first set of Mantel tests yielded significant relationships either between the taxonomic and the temporal distance matrices when accounting for the effect of space ( $r = 0.167$ ;  $p(r < 0) = 0.002$ ;  $p(r > 0) = 0.945$ ;  $p(r = 0) = 0.002$ ) or between the taxonomic and geographic distance matrices when accounting for time ( $r = 0.415$ ;  $p(r < 0) = 0.001$ ;  $p(r > 0) = 1.000$ ;  $p(r = 0) = 0.001$ ). The second set of Mantel tests, performed by excluding the African fossil sites, provided significant relationships either between taxonomic and temporal distances when accounting for geography ( $r = 0.409$ ;  $p(r < 0) = 0.001$ ;  $p(r > 0) = 1.000$ ;  $p(r = 0) = 0.001$ ) or between taxonomic and spatial distances when accounting for time ( $r = 0.242$ ;  $p(r < 0) = 0.003$ ;  $p(r > 0) = 0.998$ ;  $p(r = 0) = 0.003$ ). Because the inclusion of African fossil sites increased the spatial component in the statistical relationships, we performed all the classification analyses by considering the Eurasian fossil sites only, as explained earlier.

The results of the BCA of the absence–presence matrix on the Eurasian localities are shown in Figure 4. The BCA yielded several small clusters. Numerical values indicate the percentage  $p$ -values supporting each branching node, in red and bold, those above 95%, whereas in blue those below this. The first distinction is between a large cluster of localities (node A) and a small group of late

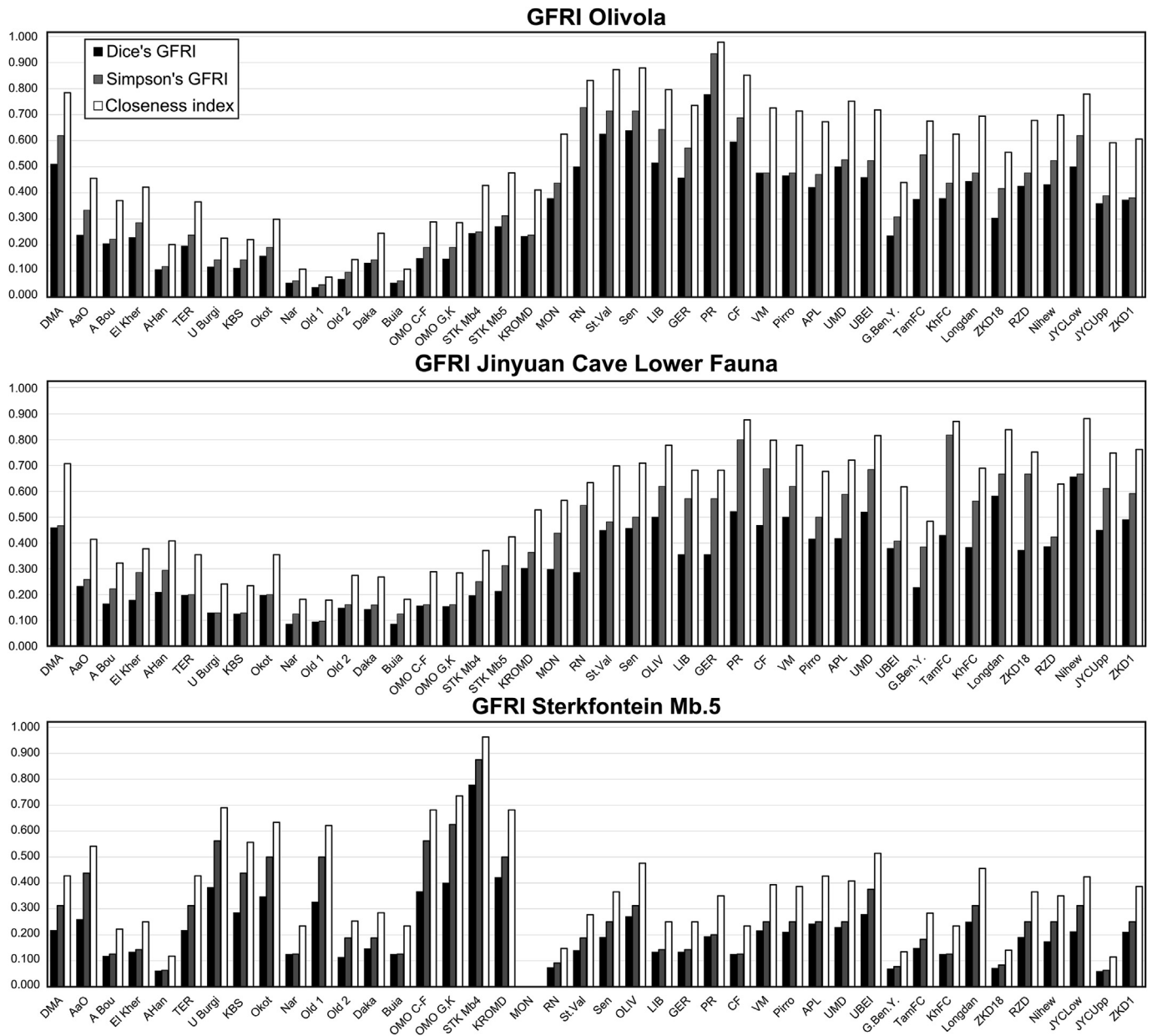
**Table 3**  
Resuming GFRI values for Dmanisi obtained applying different indexes (Dice's, Simpson's, and closeness index) as shown in Figures 2–3.

Dice's index			Simpson's index			Closeness index		
1	APL	0.723	1	APL	1.000	1	APL	1.000
2	Pirro	0.692	2	CF	0.875	2	CF	0.933
3	VM	0.667	3	Pirro	0.818	3	Pirro	0.927
4	CF	0.609	4	TamFC	0.818	4	VM	0.917
5	UMD	0.571	5	VM	0.810	5	TamFC	0.873
6	OLIV	0.510	6	LIB	0.786	6	LIB	0.864
7	LIB	0.500	7	ZKD18	0.750	7	UMD	0.860
8	ZKD1	0.500	8	UMD	0.737	8	PR	0.831
9	UBEI	0.491	9	PR	0.733	9	ZKD18	0.825
10	PR	0.489	10	KhFC	0.625	10	OLIV	0.784
11	Sen	0.464	11	OLIV	0.619	11	ZKD1	0.768
12	JYCLow	0.459	12	ZKD1	0.591	12	KhFC	0.750
13	St.Val	0.456	13	UBEI	0.519	13	UBEI	0.743
14	TamFC	0.439	14	Sen	0.500	14	Sen	0.717
15	KhFC	0.435	15	St.Val	0.481	15	JYCLow	0.708
16	ZKD18	0.429	16	JYCLow	0.467	16	St.Val	0.706
17	Nihew	0.400	17	JYCUpp	0.444	17	Nihew	0.640
18	Longdan	0.370	18	GER	0.429	18	Longdan	0.611
19	RZD	0.357	19	Longdan	0.417	19	JYCUpp	0.593
20	JYCUpp	0.333	20	Nihew	0.400	20	RZD	0.590
21	GER	0.273	21	G.Ben.Y.	0.385	21	GER	0.543
22	KROMD	0.269	22	RZD	0.385	22	G.Ben.Y.	0.487
23	TER	0.267	23	KROMD	0.318	23	KROMD	0.477
24	G.Ben.Y.	0.233	24	STK Mb5	0.313	24	TER	0.462
25	STK Mb5	0.217	25	MON	0.313	25	STK Mb5	0.427
26	MON	0.217	26	A Bou	0.278	26	MON	0.427
27	A Bou	0.208	27	TER	0.267	27	A Bou	0.398
28	AaO	0.206	28	STK Mb4	0.250	28	STK Mb4	0.375
29	STK Mb4	0.200	29	AHan	0.235	29	AaO	0.375
30	OMO C–F	0.190	30	AaO	0.233	30	OMO C–F	0.345
31	Old 2	0.179	31	El Kher	0.214	31	AHan	0.337
32	AHan	0.170	32	Old 2	0.200	32	Old 2	0.330
33	Okot	0.167	33	OMO C–F	0.200	33	Okot	0.306
34	U Burgi	0.164	34	RN	0.182	34	U Burgi	0.301
35	KBS	0.159	35	U Burgi	0.167	35	KBS	0.293
36	OMO G–K	0.156	36	KBS	0.167	36	El Kher	0.293
37	Daka	0.145	37	Okot	0.167	37	OMO G–K	0.289
38	El Kher	0.136	38	OMO G–K	0.167	38	Daka	0.272
39	Old 1	0.127	39	Daka	0.160	39	Old 1	0.238
40	RN	0.098	40	Old 1	0.133	40	RN	0.236
41	Nar	0.087	41	Nar	0.125	41	Nar	0.183
42	Buia	0.087	42	Buia	0.125	42	Buia	0.183

Abbreviations: Aao = Ahl al Oughlam (Morocco); ABou = Aïn Boucherit (Algeria); AHan = Aïn Hanec (Algeria); TER = Tighenif (Algeria); APL = Apollonia 1 (Greece); Buia = Buia (Eritrea); CF = Casa Frata (Italy); Daka = Daka Member (Ethiopia); El Kher = El Kherba (Algeria); G.Ben.Y. = Gescher Benot Ya'aqov (Israel); GER = Gerakarou (Greece); JYCLow = Jinyuan Cave Lower fauna (China); JYCUpp = Jinyuan Cave Upper fauna (China); KBS = KBS Member, Koobi Fora Formation (Kenya); KhFC = Khapry Faunal Complex (European Russia); KROMD = Kroomdrai (South Africa); LIB = Libakos (Greece); Longdan = Longdan locality (China); MON = Montopoli (Italy); Nar = Nariokotome Member, Nachukui Formation (Kenya); Nihew = Xiashagou, Classic Nihewan (China); Okot = Okote Member, Koobi Fora Formation (Kenya); Old 1 = Olduvai Bed 1 (Tanzania); Old 2 = Olduvai Bed 2 (Tanzania); OLIV = Olivola (Italy); OMO C–F = Members C–F, Shungura Formation (Ethiopia); OMO G–K = Members G–K, Shungura Formation (Ethiopia); Pirro = Pirro Nord (Italy); PR = Poggio Rosso (Italy); RN = Roca-Neyra (France); RZD = Renzidong Cave (China); Sen = Senèze (France); St. Val = Saint Vallier (France); STK Mb4 = Sterkfontein Member 4 (South Africa); STK Mb5 = Sterkfontein Member 5 (South Africa); TamFC = Taman Faunal Complex (European Russia); U Burgi = Upper Burgi Member, Koobi Fora Formation (Kenya); UBEI = 'Ubeidiya (Israel); UMD = Untermassfeld (Germany); VM = Venta Micena (Spain); ZKD1 = Zhoukoudian locality 1 (China); ZKD18 = Zhoukoudian locality 18 (China).

Calabrian ones (node C). The latter small group includes Gesher Benot Ya'aqov, Ubeidiya, Jinyuan Cave Upper Fauna, and Zhoukoudian Loc. 1 (in order of increasing similarity; Fig. 4). In the large group, the first cluster to branch out is the one made of European localities of Gerakarou (node F) and the couples of Montopoli and Roca-Neyra (node L) and of St. Vallier and Senèze (node T). The latter couple has a high supporting *p*-value (Fig. 4). On the opposite side, Renzidong is the most different locality of the large cluster at node B, followed by Khapry and Taman Faunal complexes (node O). These east European localities have a rather high percentage *p*-value of 93. The following grouping of localities is supported by the second highest *p*-value of the analysis (node E). The Chinese localities of Longdan, Xiashagou, and Jinyuan Cave Lower Fauna (node M) are grouped together and supported by the highest percentage *p*-value (shared with node P). The other

Chinese locality, Zhoukoudian Loc. 18, is instead located at the base of a cluster of western Eurasian localities and Dmanisi. The latter sites are separated into two clusters. The first one (node N), relatively supported (92 percentual *p*-value), includes Libakos and the Italian faunas of Casa Frata, Olivola, and Poggio Rosso. Opposite to this group, there is a cluster of late Villafranchian (late Early Pleistocene) localities (node P), strongly supported in the analysis (percentage *p*-value of 98). The site of Dmanisi is included in the last cluster. Particularly, Dmanisi is positioned at the base (node S) of the small cluster made up of Apollonia 1 and Venta Micena (node W), whereas Pirro Nord and Untermassfeld group with one another (node U). This supports a closer resemblance between all of these five sites but also that the association of Dmanisi is closer to Venta Micena and Apollonia 1 as compared with Pirro Nord and Untermassfeld.



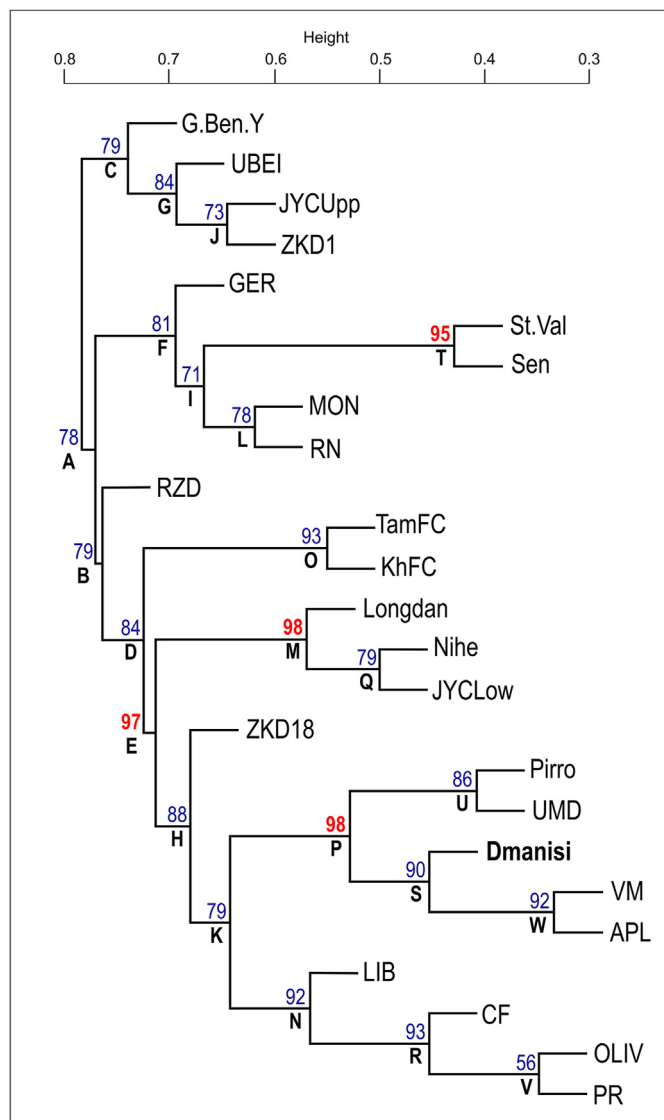
**Figure 3.** Different patterns of similarity of three of the most similar sites to Dmanisi from Europe, Asia, and Africa. Abbreviations: AaO = Ahl al Oughlam (Morocco); ABou = Ain Boucherit (Algeria); AHan = Ain Hanec (Algeria); TER = Tighenif (Algeria); APL = Apollonia 1 (Greece); Buia = Buia (Eritrea); CF = Casa Frata (Italy); Daka = Daka Member (Ethiopia); DMA = Dmanisi (Georgia); El Kher = El Kherba (Algeria); G.Ben.Y. = Gescher Benot Ya'aqov (Israel); GER = Gerakarou (Greece); JYCLow = Jinyuan Cave Lower fauna (China); JYCUpp = Jinyuan Cave Upper fauna (China); KBS = KBS Member, Koobi Fora Formation (Kenya); KhFC = Khapry Faunal Complex (European Russia); KROMD = Kroomdrai (South Africa); LIB = Libakos (Greece); Longdan = Longdan locality (China); MON = Montopoli (Italy); Nar = Nariokotome Member, Nachukui Formation (Kenya); Nihew = Xiashagou, Classic Nihewan (China); Okot = Okote Member, Koobi Fora Formation (Kenya); Old 1 = Olduvai Bed 1 (Tanzania); Old 2 = Olduvai Bed 2 (Tanzania); OLIV = Olivola (Italy); OMO C-F = Members C-F, Shungura Formation (Ethiopia); OMO G-K = Members G-K, Shungura Formation (Ethiopia); Pirro = Pirro Nord (Italy); PR = Poggio Rosso (Italy); RN = Roca-Neyra (France); RZD = Renzidong Cave (China); Sen = Senéze (France); St. Val = Saint Vallier (France); STK Mb4 = Sterkfontein Member 4 (South Africa); STK Mb5 = Sterkfontein Member 5 (South Africa); TamFC = Taman Faunal Complex (European Russia); U Burgi = Upper Burgi Member, Koobi Fora Formation (Kenya); UBEl = 'Ubeidiya (Israel); UMD = Untermaßfeld (Germany); VM = Venta Micena (Spain); ZKD1 = Zhoukoudian locality 1 (China); ZKD18 = Zhoukoudian locality 18 (China).

As regards the classification based on the multinomial log-linear regression via ANN, we found that 451 of 1000 models had a predictive performance accuracy higher than 0.7 (mean accuracy = 0.795; SD = 0.06) and 432 models were built upon unbalanced classes (mean accuracy = 0.797; SD = 0.06). We used these 432 models to classify the Dmanisi PC scores according to the four spatiotemporal groups. Dmanisi site was classified into the following categories with the related frequency: YoungerEast (1 time) and YoungerWest (431 times).

#### 4. Discussion

##### 4.1. Faunal composition and zoogeographic comparisons

Besides its reputation as having the oldest fossilized skeletal remains of hominins outside of Africa, the outstanding faunal record of Dmanisi (Table 1) at a geographic crossroad to Eurasia and Africa underscores the importance of this Early Pleistocene locality at both regional and intercontinental scales. The diverse mammal



**Figure 4.** Dendrogram resulting from the bootstrapping cluster analysis (BCA) based on the presence/absence genera matrix of 23 localities across Eurasia. Numbers represent the percentage *p*-values supporting the node: values below 95% are in blue, whereas those above 95% are in bold red. Abbreviations: APL = Apollonia 1 (Greece); CF = Casa Frata (Italy); G.Ben.Y. = Gescher Benot Ya'aqov (Israel); GER = Gerakarou (Greece); JYCLow = Jinyuan Cave Lower fauna (China); JYCUpp = Jinyuan Cave Upper fauna (China); KhFC = Khapry Faunal Complex (European Russia); LIB = Libakos (Greece); Longdan = Longdan locality (China); MON = Montopoli (Italy); Nihe = Xiashagou, Classic Nihewan (China); OLIV = Olivola (Italy); Pirro = Pirro Nord (Italy); PR = Poggio Rosso (Italy); RN = Roca-Neyra (France); RZD = Renzidong Cave (China); Sen = Senéze (France); St. Val = Saint Vallier (France); TamFC = Taman Faunal Complex (European Russia); UBEI = 'Ubeidiya (Israel); UMD = Untermassfeld (Germany); VM = Venta Micena (Spain); ZKD1 = Zhoukoudian locality 1 (China); ZKD18 = Zhoukoudian locality 18 (China).

faunal association of Dmanisi records the transition from middle to late Villafranchian, with relevant implications for the post Olduvai-event faunas in Western Europe (Rook and Martínez-Navarro, 2010). Several of the recorded elements are well known from Early Pleistocene contexts in western Eurasia, such as *M. meridionalis* (typical form), *E. stenorhinus*, *Palaeotragus priasovicus*, *Gallagheria meneghinii*, *Stephanorhinus* spp., *Acinonyx pardinensis*, *Homotherium latidens*, *Lynx issiodorensis*. The absence of typical Middle Villafranchian elements in the faunal association, such as raccoon dogs (*Nyctereutes* ex gr. *megamastoides*), within the huge number of fossils recovered supports the idea of a younger

mammal age for the locality. Another European late Villafranchian taxon recovered at Dmanisi is the typical open country adapted horse *E. altidens* (refer to the study by Vekua, 1995; Bernor et al., 2019, Bernor et al., 2021). Indeed, the Dmanisi fauna is also peculiar for the presence of some more modern taxa, which anticipates the faunal turnovers that took place in Europe and Near-Middle East in the first half of the Calabrian stage (1.8–1.5 Ma). The same is observed in western Eurasian localities belonging to the Faunal Unit of Tasso (Rook et al., 2013) similar to the Mygdonia Basin (Koufos, 2014; Konidaris et al., 2015) but also in the younger sites, for example, Venta Micena (Arribas and Palmqvist, 1998), Pirro Nord (Rook, 2013), and Ubeidiya (Gaudzinski, 2004; Martínez-Navarro et al., 2009, 2012). This is exemplified by the relatively early appearance of the carnivores characteristic of late Villafranchian and Epivillafranchian times, for example, *Pachycrocuta brevirostris*, *Panthera onca georgica*, and *Megantereon whitei* (Martínez-Navarro and Palmqvist, 1995; Hemmer et al., 2010). The same can be said of some artiodactyls (e.g., *Soergelia*, *Pontoceros* and *Bison*) as their occurrence at Dmanisi marks one of their earliest European appearances from their Asian dispersal center. *E. altidens* has its earliest known occurrences at Dmanisi, and there are competing hypotheses of its geographic origin (Bernor et al., 2001). Nevertheless, the time of arrival of the same genera into western and southern Europe is dated somewhat later (middle Calabrian, around 1.6 Ma; Rook and Martínez-Navarro, 2010). These observations are confirmed by the pairwise comparison between the association of Dmanisi and the selected localities of the Old World as shown in Figure 2 and Table 3. The similarity in genus composition between Dmanisi and Eurasian sites is striking. On the contrary, the degree of resemblance with the association of Plio-Pleistocene of Africa is rather limited. Eurasian localities that show the greatest affinity to Dmanisi are those of the European late Villafranchian and Epivillafranchian. Among these are Apollonia 1, Venta Micena, Pirro Nord, Casa Frata, Taman Faunal Complex, and Untermassfeld (De Giuli et al., 1986; Kahlke et al., 2011; Rook, 2013; Madurell-Malapeira et al., 2014; Koufos, 2018). Much of this similarity is due to the rich diversity of carnivores (e.g., *Homotherium*, *Megantereon*, *Panthera*; refer to the study by Bartolini-Lucenti et al., 2022) and also other taxa such as, for example, *Equus* (refer to the study by Bernor et al., 2021), *Stephanorhinus* (refer to the study by Pandolfi et al., 2021), *Pseudodama*, *Bison*, and *Soergelia*. The occurrence of other Eurasian elements supports high values of taxonomic similarity of sites such as Libakos (Greece), Poggio Rosso (Italy), Khapry Faunal Complexes (European Russia), Ubeidiya (Israel), Jinyuan Cave Lower Fauna (China), and Zhoukoudian Locality 18 (China). Taxa supporting this affinity include *Canis*, *Equus* (in all of them), *Mammuthus* (in all except for ZKD18; Martínez-Navarro et al., 2009, 2012; Kahlke et al., 2011; Jin et al., 2021), *Pachycrocuta* (in all except for Ubeidiya, Martínez-Navarro et al., 2009), and *Martes*, *Meles*, *Canis* (*Xenocyon*), and *Ursus* (in the latter two; Teilhard de Chardin, 1940; Jin et al., 2021). Dmanisi lacks some Asian taxa such as *Paracamelus* and *Elasmotherium* (see Table 1). The marked difference between older and younger African localities and Dmanisi is mainly due to the absence in the Dmanisi fauna of some artiodactyls, such as bovids of typical African tribes (Alcelaphini, Hippotragini, Tragelaphini, Reduncini, etc.) and of warthog-like suids that thrived in African localities (Werdelin and Sanders, 2010). The most similar African locality to Dmanisi is the South African locality of Kromdraai, yet these GFRIs are rather low (Fig. 2; Table 3). The application of the same indices to three selected localities roughly coeval to Dmanisi and coming from Europe (Olivola), Asia (Jinyuan Cave Lower Fauna) and Africa (Sterkfontein Member 5) is informative for the degree of affinities of these sites as compared with the other Old World localities, as shown in Figure 3.

### Genus-level faunal resemblance index Olivola pairwise comparison

In the case of Olivola, the closest associations are those of the middle Villafranchian, that is, Senèze and St. Vallier (Palombo and Valli, 2003; Delson et al., 2006), and of the beginning of the late Villafranchian like Poggio Rosso or Casa Frata (De Giuli and Masini, 1986; Mazza et al., 2004; Rook and Martínez-Navarro, 2010; Rook et al., 2013). Nevertheless, a certain degree of similarity with some roughly coeval Asian sites can also be noted, for example, Zhoukoudian Locality 18, Xiashagou, and Jinyuan Cave Lower Fauna (Teilhard de Chardin, 1940; Wang et al., 2013; Jin et al., 2021).

### Genus-level faunal resemblance index Jinyuan Cave pairwise comparison

Jinyuan Cave (recently described in detail by Jin et al., 2021) is a rich site in northeastern China. In the case of the Early Pleistocene levels (i.e., Lower Fauna), the fossil association is, as expected, similar to other chronological coeval Chinese localities such as Xiashagou or Longdan (as noted by Jin et al., 2021; see in addition, in the studies by Qiu et al., 2004; Wang et al., 2013). Nevertheless, a relatively high degree of similarity is also visible with the western European localities of Olivola (as evidenced earlier), Poggio Rosso, and Casa Frata (De Giuli and Masini, 1986; Rook et al., 2013). To a lesser extent, Jinyuan Cave Lower Fauna resembles the Khapry Faunal Complex, close in age (Sotnikova et al., 2002; Kahlke et al., 2011), or the younger sites such as Pirro Nord, Apollonia 1, Ubeidiya, the Taman Faunal Complex, and Zhoukoudian Locality 1 (Martínez-Navarro et al., 2009, 2012; Kahlke et al., 2011; Rook, 2013; Koufos, 2018; Jin et al., 2021). At a larger geographical scale, Olivola and Jinyuan Cave Lower Fauna share numerous genera, as exhibited by their GFRI scores (Fig. 2). This is due to the common occurrence of genera such as *Mammuthus*, *Equus*, *Stephanorhinus*, and *Sus*. These Eurasian taxa appeared during the late Pliocene and the beginning of the Early Pleistocene (Pandolfi et al., 2015, 2017; Rook et al., 2019; Cirilli et al., 2020b). Other similarities include carnivorans, whose descendants became common elements in subsequent faunas, for example, *Canis* and *Panthera* (as also shared with Dmanisi; Hemmer et al., 2010; Bartolini-Lucenti et al., 2020). Different is the case of Sterkfontein Member 5 (Fig. 3), whose GFRI histogram shows, as in other South African localities, a generalized pattern of low similarity indexes with all the considered Old World localities, with no particular regional affinity, if not with East and South African sites.

### Genus-level faunal resemblance index Sterkfontein Member 5 pairwise comparison

The highest values in comparison with Sterkfontein Member 5 are, as expected, those of Sterkfontein Member 4 (Dice's index = 0.778; Simpson's index = 0.875; closeness index = 0.963), the member slightly older from the same site (Werdelin and Sanders, 2010). Regarding the East African sites, the two most similar localities are Omo level G–K (Dice's index = 0.400; Simpson's index = 0.625; closeness index = 0.735) and Upper Burgi member from Koobi Fora (Dice's index = 0.383; Simpson's index = 0.536; closeness index = 0.690), both somewhat younger than Sterkfontein Member 5 (Werdelin and Sanders, 2010; Werdelin and Lewis, 2013). Other sites having slightly lower values are Omo C–F (Ethiopia), Okote (Kenya), Olduvai 1 (Tanzania), and Kromdraai.

This pattern of reduced similarity between geographically distant sites could be explained by analyzing the genus composition. On the one side, Kromdraai shares with these African localities the presence of numerous primate taxa (e.g., *Paranthropus*, *Papio*, and even *Homo*). On the other side, abundance of the carnivore genera (e.g., *Homo*, *Dinofelis*, *Megantereon*, *Canis*) is shared by the South African sites, Kromdraai and Eurasian localities. In the three comparisons of Figure 3, the highest GFRI values for Dmanisi are with Olivola (Dice's = 0.51, Simpson's = 0.619, and closeness index = 0.796).

**Clustering and classification of fossil localities** Although Eurasian sites shared about 33% of their genera with the African localities, this was not enough to equalize the faunal composition of the two

continents, as explained by the Mantel tests. This is an indirect proof that geographic corridors between the two continents filtered many taxa. The contribution of both geography and time still explains the taxonomical differences when considering Eurasian sites only. The impact of both temporal and spatial differences between Eurasian fossil sites was then confirmed by the other analyses we performed.

Indeed, the cluster analysis yielded some interesting grouping patterns (Fig. 4). The most different localities within the selected Eurasian ones are the Israeli Gesher Benot Ya'aqov and Ubeidiya and the Chinese Jinyuan Cave Upper Fauna and Zhoukoudian Loc. 1. These localities are all late or latest Calabrian in age. Furthermore, Ubeidiya and Gesher Benot Ya'aqov have important connections with the African faunas, as represented by the occurrence of taxa such as *Camelus*, *Gazella*, *Hippopotamus*, and *Pelorovis*, still maintaining certain affinity with Eurasian association in the presence of *Stephanorhinus* and *Ursus*. Zhoukoudian Loc. 1 and Jinyuan Cave Upper Fauna are separated mainly on the basis of some peculiar and exclusive taxa in comparison with the other localities here selected. Those include *Bubalus*, *Cuon*, *Palaeoloxodon*, *Protoryx*, *Sinomegaceros*, and *Spiroceros*. The following cluster includes middle-late Villafranchian localities of western and southern Europe. In this cluster, faunas are grouped for the close age and geography of the sites (e.g., Montopoli and Roca-Neyra, around 2.6 Ma; and St. Vallier and Senèze between 2.4 and 2.2 Ma). Gerakarou seems to have an affinity with these older localities for the occurrence of taxa such as *Croizoceros*, *Gazella*, *Gazellospira*, *Eucladoceros*, *Leptobos*, *Metacervoceros*, and *Pliocrocota*. After this small cluster, Renzidong sticks out. Unlike the other, its several peculiar taxa include *Ailuropoda*, *Herpestes*, *Hesperotherium*, *Megaviverra*, *Sinomastodon*, and *Tapirus*. Two other subgroups to branch out before the two large groups that separates at node K are those of Khapry and Taman FC (node O) and of the Chinese localities of Longdan, Xiashagou, and Jinyuan Lower Fauna (node M). In the former case, the grouping is based on the geographic position of the two sites and the co-occurrence of numerous taxa in both complexes. The Chinese localities of the lower Jinyuan Cave fauna, Longdan, and Xiashagou are correlated to the Nihewanian age (2.6–1.6 Ma; Wang et al., 2013), and their clustering seems to be due to the co-occurrence of several carnivore genera (*Canis*, *Meles*, *Pachycrocuta*, *Ursus*) and some ungulates (like *Equus* and *Cervus*). Zhoukoudian Loc. 18 branches out before the two clusters of European late Villafranchian localities (2.0–1.0 Ma; Rook and Martínez-Navarro, 2010) mainly from central and Mediterranean Europe. The Chinese site is included in this cluster for the numerous carnivore taxa in common with this small group. Libakos (close in age to Gerakarou) is close to the 2.0–1.6 Ma localities of Italy (Casa Frata, Olivola, and Poggio Rosso). The last cluster groups different localities across Eurasia, including Dmanisi. Interestingly, Dmanisi clusters together with the late Early Pleistocene localities of central and southern Europe, represented by Apollonia 1 and Venta Micena, Pirro Nord, and Untermassfeld. This result was also confirmed by the classification yielded by the ANN-based log-linear regression, which considered the genera composition of Dmanisi closer to the late Early Pleistocene of Europe (Fig. 1; Table 3), and upholds the interpretation made by previous authors (Martínez-Navarro and Palmqvist, 1995; Lordkipanidze et al., 2007; Rook and Martínez-Navarro, 2010; Agustí and Lordkipanidze, 2011; Cappellini et al., 2019; Krijgsman et al., 2019), who highlighted the Dmanisi faunal turnover that characterized the European late Villafranchian localities. Older western Eurasian sites such as Olivola or Poggio Rosso are all located in the opposite subgroup, probably due to the persistence of genera typical of the Middle Villafranchian (e.g., *Anancus*, *Chasmaporthetes*, *Leptobos*) and the absence of other taxa that would arrive shortly later.

#### 4.2. Palaeoecological and paleoenvironmental interpretations

The combination of environmental characteristics/preferences from vertebrate taxa recovered and the topographic architecture of the Dmanisi area allows us to make inferences about the composition of the surrounding paleolandscape at Dmanisi. The micro-mammal association is dominated by taxa adapted to steppe and dry environments (e.g., the hamsters *Cricetulus* and *Allocrietus* or the gerbil *Parameriones*). Indeed, taxa generally associated with water sources, such as rivers, lakes, etc. (i.e., *Miomys*), are less frequent in the assemblage. Similarly are those of woodland environments (i.e., *Apodemus*; Cappellini et al., 2019). The Dmanisi large fauna supports this interpretation, suggesting a landscape characterized by a mosaic of habitats, different in humidity and vegetation. The immediate vicinity of the fossil site was probably characterized by more or less dense deciduous forests (Messenger et al., 2010a). This interpretation is supported by the frequency and abundance of different cervids, that is, *Cervalces*, *Arvernoceros*, *Praemegaceros*, *Pseudodama*. These wooded plain areas probably graded into flanking slopes with shrub vegetation of varying densities, turning into dry meadows in the southernly exposed areas with more intense insolation. Indeed, pollen and phytolith analyses revealed an important fraction of vegetation of open areas (Messenger et al., 2010a, b). At a larger scale, the region was marked by drier areas, probably of open wooded savannah and grassland and by mountainous to semiarid rocky terrains, with volcanic outcrops of Mashavera Basalts of the near magmatic activity (Lordkipanidze et al., 2007; Ferring et al., 2011). Some studies also showed that the sequence of Dmanisi, although concentrated in a short time span, experienced an increase of aridity in the midpart of the succession, a time contemporaneous to the occupation of *Homo* in the region (Messenger et al., 2010a, b).

Paleotemperature and paleoprecipitation data can be inferred from certain taxa (e.g., *Testudo graeca*, herpetofauna in general, and *Hystrix refossa*; Lordkipanidze et al., 2007; Blain et al., 2014). The analysis of the herpetological taxa recovered at Dmanisi suggests a warmer (especially in summer) and drier climate than that present today (Blain et al., 2014). Climate should have been very similar to the Mediterranean one with ample delta temperature between winter and summer times. Precipitation should have been discontinuous and reduced throughout the year. The herpetofauna also informs us about the landscape around Dmanisi. Arid habitats, steppe-like or semidesertic, alternated to open Mediterranean forests, possibly characterized by patches of stony or rocky substrates (Blain et al., 2014). This agrees with the occurrence of some taxa, for example, the particularly abundant *G. meneghinii sickenbergii* (Bukhsianidze and Vekua, 2006) and the Western Caucasian tur-like species *Capra dalii*, which probably preferred such terrains and mountainous areas (Bukhsianidze and Vekua, 2006). Water bodies could have been present but probably with reduced extension or ephemeral (Blain et al., 2014). Significant increase in aridity is also marked by other proxies (pollen spectra, phytoliths; Messenger et al., 2010b) that record grass water stress in the sequence of Dmanisi. This could explain the absence at Dmanisi of hippopotamuses that characterized the Early Pleistocene faunal assemblages of Africa, the Levant, and the Western Eurasia since the late Villafranchian (Martínez-Navarro, 2004; Pandolfi and Petronio, 2015; Martínez-Navarro et al., in press). Steppe-like conditions alternating with open forests are also suggested by the presence of *Stephanorhinus* ex gr. *etruscus-hundsheimensis* (Pandolfi et al., 2021) and with the horse sample represented by the slender *E. altidens* and the larger European *E. stenonis* (Bernor et al., 2019; Bernor et al., 2021). Saarinen et al. (2021) have documented that *E. altidens*, constituting 80% of the Dmanisi *Equus* sample, was highly cursorial and adapted to open country environments and a grazing feeding strategy. *E. stenonis* was larger

and would likely have had a mixed feeder strategy. This sympatric horse distribution pattern shown by the Dmanisi sample is recognized also in the European samples, which share common faunal elements with Dmanisi, such as Venta Micena and Pirro Nord, although in the latter site the large horse is represented by *Equus suessenbornensis* and not by *E. stenonis* (Alberdi and Palombo, 2013). Furthermore, Eisenmann (1985, 1986) and Alberdi et al. (1998) also noted that medium- to small-sized horses with slender postcranial elements (such as metapodials and phalanges) are common in open-dry-arid environments (both in the fossil record and in the extant species). This pattern is shown in the Early Pleistocene of North Africa (Ain Boucherit and Ain Hanech) and in the European late Early Pleistocene localities (Pirro Nord and Venta Micena), where *E. altidens* also occurs.

In general, all the evidence from Dmanisi supports the interpretation of the patchy environments of both deciduous forests and open areas, with relatively dry climate, warmer, and drier than today and similar to the present Mediterranean type. Such a variety of environments and resulting resources, within close proximity to the site of Dmanisi, surely attracted herbivores, carnivores, and *Homo* (Tappen et al., 2007).

#### 4.3. The Dmanisi fauna in the framework of the late Early Pleistocene communities

Our comprehensive study of the Dmanisi large mammal assemblage has revealed some important insights into the European peri-Olduvai Bed I and II faunas. As reported in several studies included in the present volume (Bernor et al., 2001; Pandolfi et al., 2021; Bartolini-Lucenti et al., 2022) and in the GFRI and the classification algorithms provided herein, Dmanisi shows similarities in genera composition with the European late Villafranchian faunas of Venta Micena and Apollonia 1, as well as Pirro Nord and Untermaassfeld. Nevertheless, the significance of Dmanisi's large mammal faunas deserves some more discussion, to better appreciate its paleobiogeographic importance. The fauna is dominated by Asian elements with also some relevant African ones (Table 1), which are well documented in the younger localities close in age to Dmanisi. Apart from the occurrence of the genus *Homo* (Gabunia et al., 2000; Lordkipanidze et al., 2007, 2013; Rightmire et al., 2017, 2019), another African element is the saber-toothed cat *M. whitei*. Among equids, *E. stenonis* is related to European assemblages of this species which, in turn were likely derived from earlier and more primitive European *Equus livenzovensis* (Alberdi et al., 1998; Bernor et al., 2019; Bernor et al., 2021; Cirilli et al., 2021a, b, c). The earliest occurrence of *E. altidens* is from Dmanisi (1.85 Ma; Bernor et al., 2021). *E. altidens* occurs slightly later in Germany, Italy, and Spain (Alberdi and Palombo, 2013; Palombo and Alberdi, 2017). Its geographic origin is currently a matter of debate. Alberdi et al. (1998) correctly recognized that *E. altidens* is a stenonine horse and derived from a species of this clade. Guerrero-Alba and Palmqvist (1997) posed a North African origin of *E. altidens* based on its similarity to Early Pleistocene species *Equus numidicus* and the extant *Equus grevyi* both with elongate third metapodials. Bernor et al., 2021 posed an alternative hypothesis that *E. altidens* evolved from a stenonine horse in West Asia wherein seasonal dry environments likely arose before those in Europe. *E. altidens* demonstrates a zoogeographic connection between West Asia, Europe, and likely North Africa around 2.0 Ma. As reported earlier, the medium- to small-sized horses are associated with open and arid environments (Saarinen et al., 2021).

The first dispersal of genus *Homo* representatives out of Africa was associated with the Plio-Pleistocene global trend of increased seasonality accompanied by cooling and increased aridity (Shackleton et al., 1984; Bobe et al., 2002; deMenocal, 2004;

Mosbrugger et al., 2005). The change of closed mesic woodlands by progressive opening of grasslands in East Africa (the so-called ‘Savannahstan’; Hughes et al., 2008; Belmaker, 2010; Dennell, 2010; Lahr, 2010) expanded towards Southeast Asia around ca. 1.8 Ma and created suitable corridor for dispersal of fauna (Dennell, 2010; Cerling et al., 2011; Carotenuto et al., 2016a). The faunal records from Dmanisi suggests that the earliest Plio-Pleistocene ‘Out-of-Africa’ does not include only the genus *Homo* but might have involved other taxa in a faunal exchange between Africa and Eurasia.

Several authors have recognized the Levantine Corridor as the most likely dispersal route to the arrival in the Caucasus (Martínez-Navarro 2004, 2010), by fossil and archaeological evidence. Indeed, in this area, many localities show a mixed mammal assemblage of Eurasian and African elements. Among these, the best-known locality is Ubeidiya, whose faunal list includes the African species *Kolpochoerus olduvaiensis*, *Megantereon* cf. *M. whitei*, *Pelorovis oldowayensis*, *Equus* cf. *Equus tabeti*, and the genera *Theropithecus*, *Hippopotamus*, *Oryx*, and *Homo*, combined with several other Eurasian species (Belmaker, 2010). Although younger than Dmanisi, Ubeidiya confirms the role of the Levantine Corridor, and the Pontocaspian region in general as a principal crossroad for the faunal exchange between Eurasia and Africa, including for the genus *Homo* (as also pointed out by Krijgsman et al., 2019). The occurrence of the slender-limbed *Equus* cf. *E. tabeti* in Ubeidiya confirms the presence of prevailing open and arid environment, as hypothesized for Dmanisi, and as reported in the Early Pleistocene North African paleoanthropological localities of Aïn Boucherit (2.4–1.9 Ma), Aïn Hanech (1.9–1.7 Ma), and Tighennif (ca 1.0 Ma) where *E. numidicus*, *E. tabeti*, and *Equus mauritanicus* co-occur, respectively (Eisenmann, 1980; Geraads et al., 1986; Sahnouni et al., 2018). Furthermore, the first occurrences in the Dmanisi faunal assemblage of *Canis borjgali*, *Canis (Xenocyon) lycaonoides*, *Soergelia minor*, *Praemegaceros obscurus*, *Bison georgicus*, and *E. altidens* represent the oldest source for the European post Olduvai event faunas. Indeed, after their first appearance in Dmanisi, these taxa are found to be widespread in Europe in the late Early Pleistocene localities younger in age than Dmanisi, as Apollonia 1 in the Mygdonia Basin, Selvella and Pirro Nord in Italy, and Barranco León and Venta Micena in Spain. The presence of these taxa in Central Europe is confirmed also by the fossil evidence of the Epivillafranchian localities, such as Untermassfeld (Germany). The arrival of these taxa marks the disappearance of older, more primitive species, such as *Pliocrocuta perrieri*, *Megantereon cultridens*, *Chasmaporthetes lunensis*, *Canis arnensis*, *Canis (Xenocyon) falconeri*, *Gazella borbonica*, *Gazellospira torticornis*, *Leptobos etruscus*, and *Equus senzepsensis* and *Equus stehlini* from western Eurasian localities (Rook and Martínez-Navarro, 2010).

## 5. Conclusions

The large mammal fossil record from Dmanisi is well suited for a comprehensive zoogeographic analysis comparing a broad suite of Eurasian and African Pleistocene localities. Dmanisi was geographically positioned as a key biogeographic crossroads, acting as a gateway for taxa westward dispersal events from Asia to Europe as well as on South-North/North-South corridors (Africa–Europe/Europe–Africa). During Pliocene and Pleistocene times, many species expanded their geographic ranges at the interregional to intercontinental scales. This was particularly apparent when glacial pulses occurred around the Plio-Pleistocene boundary. The faunal affinities revealed by the GFRIs, and by the closeness index discussed here, support the biogeographic connection with Eurasian localities already noted by abundant literature on the site. This is particularly evident with younger European sites, evidence

of the westward expansion of certain taxa from their Asian origin (e.g., for Canidae, refer to the study by Bartolini-Lucenti et al., 2020, 2021). Roaming through the grassland biome extended from east Africa throughout Eurasia, other taxa, including hominids, reached the Palearctic region. The Pontocaspian region, which includes Dmanisi, offers extensive records of this dispersion. Moreover, the Early Pleistocene glacial pulses were likely a key factor of large mammal dispersal, while, in addition, the occurrence of a few taxa (*Struthio dmanisensis*, *Palaeotragus* cf. *priasovicus*) represent a case of long-term survivors that evidently continued to exist from older faunal complexes. The Caucasus was likely a biogeographic refugium in the late Neogene and Pleistocene (known in literature as ‘Colchic refugium’).

## Declaration of competing interest

There is no conflict of interest.

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## Supplementary Online Material

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