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Revisiting the cranial variability of the Dmanisi hominins

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ABSTRACT: The Dmanisi specimens represent the most diverse contemporaneous hominin fossils found at one single site and are key in understanding the first out -of- Africa dispersal and the origins of *Homo erectus*. Due to these reasons, they have]e been the focus of many studies in paleoanthropology in the last 30 years. However, there has not been any consensus on how to classify these fossils, nor has it been clarified how many species were co-living at that site. In this article, we aim to revisit the subject and contribute further to the discussion.

KEY WORDS: *Homo erectus, Homo georgicus, Homo caucasi*, paleoanthropology.

Original article

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Introduction

The Dmanisi site in Georgia is one of the oldest hominin sites outside of Africa (Garcia et al. 2010; Zhu et al. 2018). Located near the village of Patara Dmanisi, at an altitude of 915 m, the site is located on a basaltic spur formed at the confluence of the Pinezaouri and the Mashavera rivers. The fossiliferous deposits consist of sedimentary layers deposited on top of a volcanic basalt layer. The lowest layer in the site, which contains tools, faunal remains and human bones, was dated by several methods and recently has been contextualized by $^{40}Ar/^{39}Ar$ geochronological dating to the age of 1.81 ± 0.03 Ma (Garcia et al. 2010). Excavations of the fossiliferous strata in the site have provided five crania and four mandibles of hominins (Gabunia et al. 2000; Vekua et al. 2002; Lordkipanidze et al. 2006, 2013), which have been intensely discussed, given the importance of these fossils to the understanding of the early dispersal of *Homo* out of Africa. The site also has generated well-preserved non-hominin fauna fossils and thousands of Oldowan artifacts (Vekua et al. 2002; Mgladze et al. 2011; Lordkipanidze 2017).

The first hominin fossil (the D211 mandible) was unearthed in 1991 (Vekua and Lordkipanidze 2010). Its associated cranium, D2282, was found in 1999. The skull composed by D211and D2282 probably belonged to a young female adult, and its gracile size is accentuated by its 680cc endocranial volume (Gabunia et al. 2002). The second cranium, D2280, was also found in 1999. It has no associated mandible and is considered to be a male, with an endocranial volume of 775cc.

In 2000, the D2600 mandible was discovered (Vekua et al. 2002), but its associated cranium, D4500, was only found in 2005 (Lordkipanidze et al. 2013). This specimen is currently the earliest complete hominin skull ever found (Lordkipanidze et al. 2013), and presents an endocranial volume of 546cc, the smallest of the Dmanisi hominins. However, the robustness of the cranium and the mandible make it the largest skull on the site.

The D2700 cranium and its associated mandible D2735 (Vekua et al. 2002) were recovered in 2001. This skull, which presents an endocranial volume of 600cc, is considered to be from a subadult since its third molar is only partially erupted (Vekua et al. 2002).

The last skull, composed of the D3444 cranium, found in 2002, and its associated jaw, D3900, discovered in 2003 (Lordkipanidze et al. 2005; Lordkipanidze et al. 2006), is thought to have belonged to an older male, since its mandible and maxilla present no teeth (Lordkipanidze 2017). This individual, who presents an endocranial volume of 650cc (Lordkipanidze et al. 2006), possibly survived years without teeth before dying, suggesting that his group helped him with basic daily activities, such as food processing and eating (Lordkipanidze et al. 2005).

Since this sample is very diverse, not only in its endocranial volume but also in morphological features, this set of specimens has been classified in multiple ways. Even though it is clear that the fossils present a suite of characters typical of *Homo*, the number of species and which species are represented by the specimens are heated topics of debate (Rightmire et al. 2017).

Some claim that only one species is represented by the fossils: *Homo erectus* (Vekua et al. 2002; Ferring et al. 2011), or a species more closely related to *Homo habilis* (Lordkipnidze et al. 2007). Others, such as Rosas and Bermúdez de

Castro (1998), propose new taxonomic categories, classifying the specimens as *Homo sp. indet. (aff. ergaster)*. Similarly, Lordkipnidze et al. (2013) suggested the remains are part of a sub-subspecies unprecedentedly called *H. erectus ergaster georgicus*.

It is important to note that some studies that conclude that there is only one paleodeme represented in Dmanisi do not exclude peremptorily the possibility of multiple species being represented in the sample (Rightmire et al. 2018). Skinner et al. (2006) and Neves and Bernardo (2011), for instance, called attention to the fact that the Dmanisi sample presents more variation than ever seen in the hominin or ape lineages. Schwartz et al. (2014) suggested the specimens represent four different species, with D2600 mandible being the holotype of *Homo georgicus*. Scardia et al. (2020) also suggested that there are two different species on the site, naming D4500 as *Homo georgicus* and the other four skulls as "another species, which is not *H. erectus*" (p. 3). This naming convention follows what was first suggested by Gabunia et al. (2002), who discovered the D2600 mandible and suggested that it should be classified as *Homo georgicus*. Finally, Martinon-Torrez et al. (2008) suggested the possibility of the presence of two paleodemes at the site but does not define species names for them.

In this study, we aim to contribute further to the discussion about Dmanisi's craniomorphological diversity. To do so, we analyzed the five fossils through Discriminant Function Analyses based on size and shape and only shape information. Finally, we compared the distribution of the Georgian specimens in the morphospace with the distribution of other Plio-pleistocene hominin species.

Material and methods

This study is based on the contextualization of the Dmanisi fossils within the craniofacial morphospace defined by a comparative dataset of 87 linear craniometric dimensions of 267 specimens of Plio-Pleistocene hominins. The composition of the original database is detailed in Table 1. Given the expressive number of missing values in the database, we reduced the number of variables and specimens to be able to reconstruct the morphological diversity of hominins. This reduced database was used in our analyzes and comprises 23 craniometric variables of 121 specimens representing the following species: *P. boisei*, *P. aethiopicus*, *A. sediba*, *A. africanus*, *A. afarensis*, *H. rudolfensis*, *H. habilis*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*. Table 2 details information about the specimens kept in the analyses. The final database includes variables represented in at least 70% of the specimens and specimens with at least 50% of the variables. Of the Dmanisi fossils, D3444 was not included, since we were unable to find enough craniometric data in the literature.

Before analyses, missing values were estimated using multiple linear regressions (see Hubbe et al. 2011). Analyses were done on the original data (size and shape), and on data with the effect of size corrected (shape alone). Size correction was achieved by dividing each measurement by the geometric mean of the individual (Darroch and Mosiman 1985). Morphological affinities of the Dmanisi specimens were assessed using Linear Discriminant Functions (LDA). The LDA functions were calculated for all the species in the data, excluding the Dmanisi specimens, which identify the axes of variance that most discriminate the species represented in the comparative data. The Dmanisi specimens were then transformed to the coordinates of the first and second linear discriminant functions and the values of all the specimens in the data were plotted, allowing us to explore the morphological affinities of the Dmanisi remains without having to assume any a priori species for them. All analyses were done in R (R Core Team 2023), complemented by packages MASS (Venables and Ripley 2002), ggplot2 (Wickham 2016), and ggrepel (Slowikowski 2023).

Table 1. Species included in the original databank

Species	N	Source
Homo sp. (Dmanisi)	4	Wood (1991), Laird et al. (2017), Rightmire et al. (2017), Ni et al. (2021)
S. tchadensis	1	Zollikofer et al. (2005)
A. afarensis	16	Wood (1991), Kimbel et al. (2004)
A. africanus	17	Wood (1991), Laird et al. (2017)
A. sediba	1	Berger et al. (2010), Laird et al. (2017)
P. aethiopicus	2	Berger et al. (2010), Kimbel et al. (2004), Wood (1991)
P. boisei	8	Wood (1991)
P. robustus	11	Wood (1991), Laird et al. (2017)
H. habilis	9	Wood (1991), Laird et al. (2017)
H. erectus	53	Wood (1991), Rightmire (1996), Laird et al. (2017), Ni et al. (2021), Rightmire et al. (2017), Kaifu et al. (2008), Weidenreich (1943), Rightmire (1990), Stringer cranial data
H. heidelbergensis	27	Ni et al. (2021), Stringer cranial data, Laird et al. (2017), Rightmire (1996), Guipert et al. (2014) , Stringer et al. (1979), Arsuaga et al. (1997) , Howell (1960), Rak et al. (2021), Young (1938), Marston (1937)
H. floresiensis	1	Kaifu et al. (2011)
H. antecessor	1	Arsuaga et al. (1999)
H. naledi	3	Laird et al. (2017)
H. neanderthalensis	27	Ni et al. (2021), Stringer cranial data, Howell (1960), Martin and Saller (1957), Guipert et al. (2014), Guipert (2010), Sergi (1991)
H. sapiens	21	Ni et al. (2021), Stringer cranial data
H. longi	1	Ni et al. (2021)

Table 2. Species and specimens included in this study

Species	N	Specimens	Source
Homo sp. (Dmanisi)	4	D2280, D2282, D2700, D4500.	Wood (1991), Laird et al. (2017), Rightmire et al. (2017), Ni et al. (2021)
Au. afarensis	1	A.L. 444-2.	Wood (1991)
Au. africanus	2	Sts 5, Sts 71.	Wood (1991)

Species	N	Specimens	Source
Au. sediba	1	MH1	Berger et al. (2010), Laird et al. (2017)
P. aethiopicus	1	KNM-WT 17000.	Wood (1991), Berger et al. (2010)
P. boisei	4	KNM-ER 406, KNM-ER 407, KNM-ER 732, OH 5.	Wood (1991)
H. habilis	3	KNM-ER 1805, KNM-ER 1813, OH 24.	Wood (1991), Ni et al. (2021)
H. rudolfensis	1	KNM-ER 1470.	Wood (1991)
H. erectus	15	Hexian, KNM-ER 3733, KNM-ER 3883, KNM-WT 15000, Nanjing 1, Ngandong 7, Ngandong 11, Ngandong 12, OH 9, Sambungmacan 1, Sambungmacan 3, Sangiran 2, Sangiran 17, Zhoukoudien X, Zhoukoudien XI.	Wood (1991), Weidenreich (1943), Rightmire (1990), Kaifu et al. (2008), Ni et al. (2021), Stringer personal data
H. heidelbergensis	13	Arago, Broken Hill, Bodo, Ceprano, Dali, Kabwe, Petralona, Sima de los Huesos 4, Sima de los Huesos 5, Sima de los Huesos 6, Steinheim, Narmada, Jinniushan.	Stringer et al. (1979), Wood (1991), Rightmire (1996), Arsuaga et al. (1997), Lubsen e Corrucini (2011), Guipert et al. (2014), Rightmire et al. (2017), Ni et al. (2021), Stringer personal data
H. neanderthalensis	14	Amud 1, Forbes Quarry, Gibraltar 1, Guattari 1, La Chapelle-Aux-Saints, La Ferrassie 1, Saccopastori 1, Saccopastori 2, Shanidar 1, Shanidar 5, Spy 1, Spy 2, Saint Cesaire, Tabun.	Stringer et al. (1979), Guipert et al. (2014), Ni et al. (2021), Stringer personal data
H. sapiens	62	Arene Candide 1, Arene Candide 4, Arene Candide 5, Afalou 9, Afalou 10, Afalou 29, Afalou 32, Brno3, Chancelade, Cohuna, Cro-Magnon 1, Cro-Magnon 2, Dolní Vestonice 3, Elyie Springs, Eroel 2, Fish Hoek, Gough 1, Gramat, Grotte des Enfant 6, Hayonim, Hohlenstein I, Hohlenstein 2, Hotu, Jebel Irhoud 1, Jebel Irhoud 2, Kafi, Kanalda, Keilor, Kostenki14, Ks 1, L Nitch, Liujiang, Minat 1, Mladec 1, Mladec 5, Nahal E, Nahal Oren, Oberkassel M, Oberkassel F, Omo 2, Ona1938, Ona1933, Ortucchio 1, Pataud 2, Paviland 1, Predmostí 3, Predmostí 4, Qfzeh 6, Qfzeh 9, Skull 5, Skull 9, Taforalt XI, Taforalt 17, Teodoro 3, Teviec I, Teviec 11, Upper Cave 101, Upper Cave 103, Wadjak 1, Ndutu, LH 18, Oase.	Ni et al. (2021), Stringer personal data

Results

Figure 1 presents the distribution of individuals and species when size and shape are taken into consideration. As can be seen, two main groups are formed in the morphospace: the left upper quadrant of the graph is occupied by *P. boisei*, *P. aethiopicus*, *A. sediba*, *A. africanus*, *A. afarensis*, *H. rudolfensis*, and *H. habilis*. The right lower quadrant of the graph is occupied by *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*. The material from Dmanisi occupies an intermediate position between these two main groups. D4500 lies within the distribution of *P. boisei*. D2700 lies within the distribution of *H. habilis*, while D2280 and D2282 approach the distribution of *H. erectus*. Table 3 shows the correlation between each linear discriminant function and the original variables in the analysis, which facilitates the interpretation of the morphological differences observed in the data. The first discriminant function is strongly correlated with measurements associated with neurocranium height (basion-bregma distance), breadth (minimum frontal breadth, maximum parietal breadth), and length (glabella-bregma chord, parietal sagittal length chord, occipital sagittal length chord), showing smaller individuals on the left side of the plot and larger individuals on the right. The separation of the Dmanisi specimens on this axis then follows closely their reported braincase sizes. The second discriminant function does not have strong correlations with variables, but moderate negative correlations are observed with occipital breadth (biasterionic breadth chord) and upper facial and nasal breadths (superior facial breadth, maximum nasal width). Therefore, in this axis, specimens with narrower faces, noses, and occipitals tend to occupy a higher position.

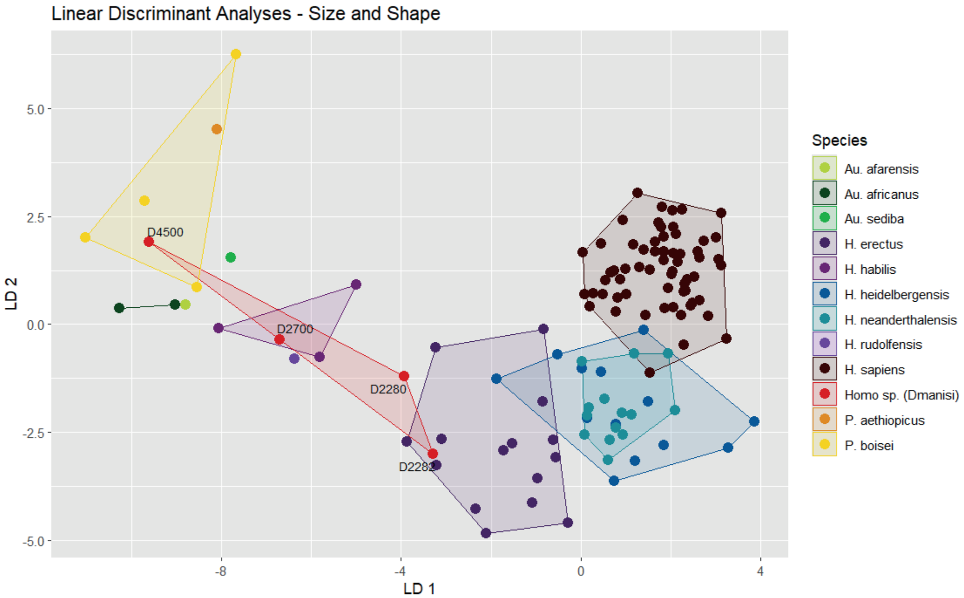

Fig. 1. Morphological affinities of hominin species based on the coordinates of the first two Linear Discriminant Functions (LDF), using size and shape information

Table 3. Correlations between the original variables and the linear discriminant functions calculated in the size and shape, and shape only analyses*

Measurement	LD1	LD2	LD1	LD2
Basion bregma	0.751	0.253	0.491	0.467
Basion nasion	0.146	-0.244	-0.490	0.140
Mastoid length	-0.076	0.251	-0.319	0.393
Minimum frontal breadth	0.793	-0.281	0.774	-0.108

Measurement	LD1	LD2	LD1	LD2
Maximum parietal breadth	0.808	-0.375	0.786	-0.230
Biporionic breadth	0.407	-0.264	0.044	0.014
Supramastoid breadth	0.488	-0.467	-0.022	-0.206
Glabella bregma chord	0.701	-0.157	0.494	0.143
Parietal sagittal length chord	0.824	0.421	0.628	0.655
Lambda inion chord	0.627	-0.055	0.438	0.165
Occipital sagittal length chord	0.836	0.295	0.638	0.489
Biasterionic breadth chord	0.587	-0.535	0.376	-0.414
Superior facial height	-0.441	-0.324	-0.755	-0.167
Superior facial length	-0.157	-0.289	-0.540	-0.027
Superior facial breadth	0.145	-0.499	-0.379	-0.345
Biorbital breadth	0.496	-0.445	0.174	-0.306
Bimaxillary breadth	-0.216	-0.343	-0.730	-0.078
Orbital breadth	0.518	-0.203	0.229	0.076
Orbital height	-0.102	-0.447	-0.580	-0.211
Vertical thickness of supraorbital torus	0.080	-0.456	-0.077	-0.386
Maximum nasal width	0.020	-0.513	-0.315	-0.382
Nasal height	-0.031	-0.348	-0.445	-0.161
Maxillo alveolar breadth	-0.337	-0.248	-0.788	0.013

Figure 2 depicts the distribution of individuals and species when only shape information is taken into consideration. The australopithecines *(P. aethiopicus, P. boisei*, *A. africanus*, *A. afarensis* and *A. sediba*) occupy the left side of the morphospace, while the right half is occupied only by species of the genus *Homo* (*H. rudolfensis*, *H. habilis*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*). The relative position of the Dmanisi specimens is very similar to the previous analysis, occupying an intermediate space between these two groups. D4500 appears close to the distribution of *P. boisei*, D2700 lies very near to the distribution of *H. habilis*, while D2280 and D2282 are completely integrated within the distribution of *H. erectus*. Table 3 shows the correlations between these linear discriminant functions and the original size- corrected variables. The first discriminant function shows high positive correlation with relative cranial breadth (minimum frontal breadth, maximum parietal breadth) and high negative correlations with superior facial height and breadth (superior facial height, and bimaxillary breadth). As these variables are size corrected, the specimens to the left of the plot show relatively wider neurocrania and shorter and narrower faces, which supports that the differentiation observed among the Dmanisi specimens in the previous analysis is not only a reflection of their distinct sizes. As with

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* In the spirit of the academic freedom the Editors recognize the right of the Authors to express their opinions and conclusions, irrespective of the opinions of the Editors.

the previous analysis, the second discriminant function does not show any particularly high correlations with the original size corrected data, but it shows moderate positive correlations with posterior neurocranium length (parietal sagittal length chord, and occipital sagittal length chord).

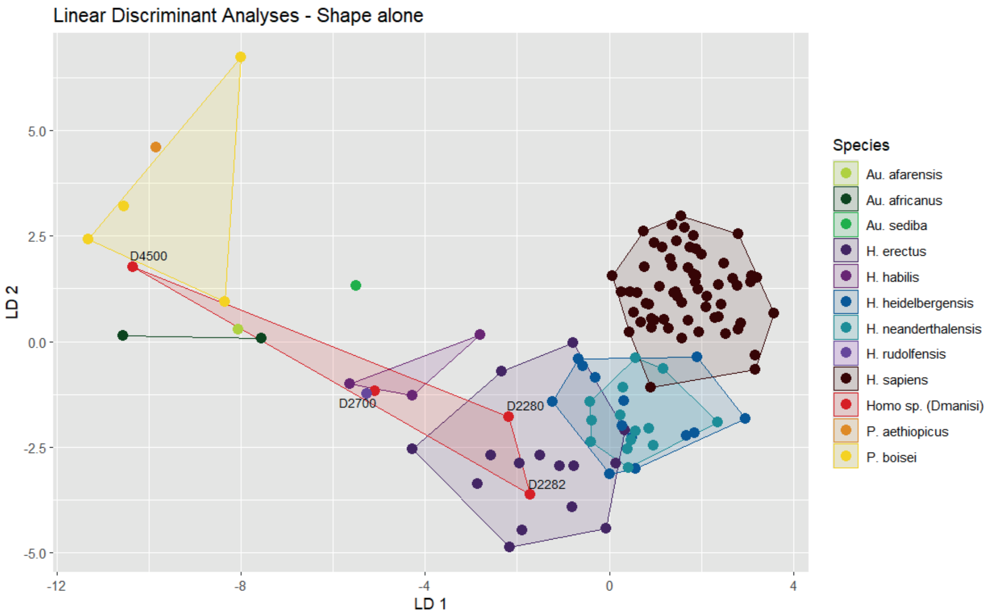

Fig. 2. Morphological affinities of hominin species based on the coordinates of the first two Linear Discriminant Functions (LDF), using only shape information

Discussion and conclusions

Our results illustrate the magnitude of the variation observed among the Dmanisi specimens when they are placed within the context of the morphological variation of hominins. The four crania show morphological affinities that spread across the observed variation that separates two different hominin genera (*Paranthropus*, and *Homo*) and three different species (*Paranthropus boisei, Homo habilis* and *Homo erectus*). This high level of variance is particularly striking when we take into consideration that the fossils were retrieved from the same site and present very close ages (1.81 ± 0.03 Ma; Garcia et al. 2010, Ferring et al. 2011). No other species included in our analysis share these same characteristics, which further accentuates the relative morphological variance among the Dmanisi fossils.

Our results are in agreement with several previous analyses. Skinner et al. (2006), who analyzed the mandibular size and shape of the Georgian specimens, emphasized that the variation of the Dmanisi individuals does not resemble that of any living species. Neves and Bernardo (2011) stated that the "Georgian specimens constitute the most variable regional sample of Early *Homo*" (p. 109). Their analyses were based on Principal Components applied to a dataset of 17 Plio-pleistocene mandibles, including *Homo antecessor*, *Homo ergaster*, *Homo erectus*, *Homo habilis*, *Homo rudolfensis*, and three Georgian mandibles (D211, D2600, and D2735). Scardia et al. (2020) claimed that Skull 5 (D4500 and D2600) is completely different from the other four skulls found at Dmanisi. Their results are replicated in our analyses, which show that D4500, the smallest of the Dmanisi fossils, shows higher affinities with *Paranthropus* than with *Homo*, and has the most distinct position of all the Dmanisi specimens. Accordingly, the authors suggest that there are two species at the site: *Homo georgicus*, represented by Skull 5, and another non-*erectus* species, represented by the remaining specimens. Lordkipanidze et al. (2013) claimed that Dmanisi's variation can be explained by sexual dimorphism and the biological age of the individuals, defining the smaller skulls as female and/or subadult and the larger skulls as male adults. Similarly, Rightmire et al. (2018) stated that the variation among the Dmanisi group is not extraordinary, and could be well explained by sexual dimorphism, since Skull 5 "shares with the four other Dmanisi individuals a total morphological pattern" (p. 490). Surprisingly, the authors affirm in the same study that "patterning of sex dimorphism at Dmanisi may differ from that in extant apes, living humans, and mid Pleistocene hominins" (p. 492). Although this view of taxa homogeneity is supported by Zollikofer et al. (2014), the hypothesis of sexual dimorphism explaining the variance seen in Dmanisi is not strongly supported by our analyses, since the affinity of D4500 with *Paranthropus* would presume a level of sexual dimorphism unseen among the hominins included in our dataset. While it is not impossible that the species could show more dimorphism than observed among early *Homo*, this would go against the general trend of reduced dimorphism seen in the *Homo erectus*, and we argue this is not a parsimonious explanation for the variance observed.

Ultimately, our study shows that the variability displayed by the Georgian fossils is not found in any other Plio-Pleistocene hominin, even when analyzing *Homo erectus* and *Homo sapiens*, which have the largest number of specimens of all hominins included in our study. Once more, this level of variance is particularly noteworthy when we consider that *H. erectus* spans more than 1.7 million years and shows a much more stable morphological pattern than the one observed in Dmanisi.

It is important to note that defining what species are present at Dmanisi is another difficult task. Many authors argue that the Georgian specimens are a transitory clade between *H. habilis* and *H. erectus*. As stated by Rightmire et al. (2018) "the Caucasus hominins share features with African *H. habilis* but had not yet evolved a full suite of characters diagnostic for later *H. erectus*" (p. 492). The answer to this question also affects another important discussion, which is defining what species first left Africa. Vekua et al. (2002), for instance, argued that the first humans to leave Africa were similar to *H. habilis*, and had not yet developed the full *H. erectus* suite. Other authors (e.g., Ferring et al. 2011 and Scardia et al. 2020) believe that an early *Homo* species first differentiated in Africa, left the African continent, gave rise to the Georgian fossils, and then returned to Africa as *H. erectus*. Our results show that with the exception of D4500, the Dmanisi specimens present a transitory morphology between *H. habilis* and *H. erectus*, concurring with Ferring et al. (2011) and Scardia et al. (2020) that a transitory species evolved into *H. erectus* in Dmanisi, then returned to Africa.

Even though we tend to avoid "species inflation", when, for example, "subspecies are raised to species'' (Isaac et al. 2004; p. 464), we concur with the statement of Schwartz et al. (2014) that ignoring Skull 5's "distinct identity is effectively to deny the utility of morphology in systematics" (p. 360). In this respect, we suggest classifying D4500 as *Homo georgicus*, taking into account the precedence of Gaburnia et al. (2002), and the remaining skulls as *Homo caucasi*, an intermediary species between *Homo habilis* and *Homo erectus*, taking into account our results and the observations above. However, we feel at odds to classify a hominin specimen (in this case D4500) that display s only 546 cm^3 of cranial capacity and a large dentognathic apparatus in the genus *Homo*. Irrespective of their taxonomic classification, it is important to emphasize that these fossils cannot be easily grouped into a single paleodeme, unless extreme levels of sexual dimorphism for hominins are considered possible. As such, while the discussion about their taxonomic classification continues, we suggest that these species should not be grouped a priori into one single paleodeme, especially when D4500 is considered. The distinct characteristics of the latter can be more informative to general discussions about the trends of evolution in *Homo* when it is not integrated and subsumed into the variation of the remainder hominins from Dmanisi.

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Conflict of interests

The authors declare that there is no conflict of interest that could be perceived as prejudicial to the impartiality of the reported research.

Authors' contribution

WA conceived the study; WA and MS designed the study; LV and MS compiled the data used for the study; MH and MS conducted the experiments; WA, LV, MH and MS analyzed the data; WA, LV, MH and MS wrote the manuscript.

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