



Dmanisi hominin fossils and the problem of multiple species in the early *Homo* genus

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Five skulls were found in Dmanisi, Georgia. D4500 (Skull 5), dated to 1.8 million years ago, is the most complete fossil associated with occupation contexts of the early Pleistocene. Its discovery has highlighted the debate concerning the plurality of species, not just at the beginning of the Homo genus, but for much of its evolution. The Skull 5 fossil presents a mixture of primitive and derived characteristics associated with Homo erectus and Homo habilis sensu lato. Based on data derived from the five Dmanisi skulls, we consider the hypothesis of a single evolving lineage of early Homo as a mode to explain the great range of variation of the Dmanisi fossils. Our work consists of evaluating the hypothesis that there was one unique species in the early Homo genus, Homo erectus sensu lato, through calculating the coefficient of variation, estimated from reference literature and the Dmanisi skulls. Our results do not suggest that all fossils of the early Homo genus represent a single species.

Introduction

The debate concerning the taxonomic diversity of the early *Homo* group is traditionally focused on African specimens. However, this debate has been intensified by the recent discovery of a number of well-preserved fossil skulls at the Early Pleistocene Georgian site of Dmanisi, in western Asia (Jiménez-Arenas, Palmqvist, & Pérez-Claros, 2011). This site, chronologically situated between 1.85 and 1.77 million years ago (Ma), has so far yielded five hominin fossils. Together with other archaeological and paleontological remains, these have become crucial for understanding patterns of variation, biogeography, and evolution within early *Homo*, a hominin group that arose in Africa between 2.5 and 1.5 Ma. In light of this discovery, we will discuss whether the Dmanisi fossils and other assigned *Homo* species belong to one unique evolved lineage within the *Homo* genus, or if they represent a variety of species that could have existed during this period.

The *Homo* fossils from Dmanisi fall within the *H. erectus* standard, as their features generally correspond to that species (Gabunia et al., 2000; Lordkipanidze et al., 2005, 2006; Rightmire, Lordkipanidze, & Vekua, 2006; Vekua et al., 2002). Cranial capacities range from 600 to 775cm³, and post-cranial skeletal elements present plesiomorphic features including a more medial orientation of the foot in relation to modern humans, the absence of humeral torsion, a small body size, and a low encephalization quotientation (Lordkipanidze et al., 2013).

All Dmanisi fossils are important for understanding the emergence and development of the *Homo* genus. However, the cranium D4500 and its mandible D2600, also known as Skull 5, are especially significant for considering such a group as a single evolving lineage (Lordkipanidze et al., 2013). This cranium is smaller than the other Dmanisi *Homo* fossils, and dates to 1.85 Ma. Thus, the Dmanisi fossils satisfy a model in which brain size increases overtime within the taxa. Skull 5 is also important because it is the best-preserved adult hominid skull

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from the early Pleistocene in the world. The fossil presents a mix of primitive characteristics in jaw morphology and a small cranial capacity, as well as some derived and primitive postcranial features related both to contemporary fossils from Africa and *Homo erectus* from East Asia (Lordkipanidze et al., 2013, p. 326).

The Endocranial Volume (ECV) of Skull 5 is 546 cm³, making it the smallest of the Dmanisi skulls. When compared to the *Homo habilis* hypodigm, Skull 5 is at the lower end of the range of variation – the smallest is KNM-ER 1813 with 510 cm³, and the biggest is KNM-ER 1470 with 752cm³ (Conroy et al., 1998). Another peculiarity of Skull 5 is the orientation and position of the face and mandible relative to the braincase. Facial orientation indicates that the normal range of variation for early *Homo* includes extremely prognathic and robust individuals.

Through geometric morphometrics, used to quantify the shape variation of Skull 5 and the other four Dmanisi specimens, researchers have discovered that cranial shape variation within early *Homo* paleodemes was similar in pattern and range to that seen within modern *Pan* and *Homo sapiens* demes (Lordkipanidze et al., 2013, p. 330). Thus, the question has been raised: could variation in cranial nonmetric features reflect intrademic morphological variation instead of species diversity? The perspective of the Dmanisi research team has led them to support the hypothesis of a single evolving lineage as a possible explanatory model used to conceive the variability of early *Homo*. This is not, however, the only explanation for the morphological variability of early *Homo* fossil remains.

There are two different ways of interpreting variability in hominins. One hypothesis considers variability in morphometric characters, including brain size, as a reflection of primate species' adaptation under different environment conditions. Thus, variability would be a sign of taxonomic diversity (Chamberlain & Wood, 1987; Wood & Collard, 1999a; Wood & Richmond, 2000). The other explanatory view, held by the Dmanisi team, supports variability in hominins within a single, gradually-evolving lineage containing only one species at each point in time. In this view, brain and

body size are correlated through time over the last 5 million years (Henneberg, 1995, 1997; Henneberg & de Miguel, 2004). These two divergent hypotheses are the main point of our discussion; we intend to investigate whether size variation of early *Homo* corresponds to a standard related to one unique species or a group of multiple species.

Regarding the first appearance of *Homo* in Africa, the literature is split between those who suggest a single species, *Homo habilis* (Howells, 1978, 1989; Jiménez-Arenas, Palmqist, & Pérez-Claros, 2007; Lee & Wolpoff, 2005; Miller, 1991, 2000), and those who advocate for two separate species, *Homo habilis sensu stricto* and *Homo rudolfensis* (Chamberlain & Wood 1987; Donnelly, 1996; Lieberman, Pielbeam, & Wood, 1988; Lieberman, Wood, & Pilbeam, 1996; Stringer, 1986; Wood, 1992, 1993, 1994; Wood & Collard, 1999a). The main reason for the two variant explanations relates to differences between fossils KNM-ER 1813 and ER 1470. Differences in size were explained as the result of sexual dimorphism, in which the two fossils represent one male and one female of the same species (Lee & Wolpoff, 2005; Miller, 1991; Tobias 1991). However, morphological and metric evidence also suggests it is unlikely that the two fossils belong to the same species, unless they present a sexual dimorphism pattern quite different from that of higher primates (Lieberman et al., 1988; Rightmire, 1993; Stringer, 1986).

In addition, there are several divergent considerations regarding the first *Homo* in Africa (1.75 Ma), *Homo erectus*. A number of researchers support the multiple taxa hypothesis by acknowledging a distinction between *H. ergaster* and *H. erectus sensu stricto* (Clarke, 2000; Stringer, 1989; Wood & Richmond, 2000), and some of them even suggest that *H. ergaster* should be split into several taxa (Schwartz & Tattersall, 1999; Tattersall, 2007). Finally, advocates of the single taxon solution suggest that both *H. erectus sensu stricto* and *H. ergaster* should be grouped within *H. erectus* (Antón, 2003; Kramer, 1993; Rightmire, 2008; Turner & Chamberlain, 1989), a taxon that could encompass the paleodeme from Dmanisi given the combination of primitive and advanced craniodental traits in the sample (Rightmire et al., 2006; Rightmire & Lordkipanidze, 2010). In this last view, *H. erectus* and *H. sapiens* represent a single evolving

lineage originating via a cladogenetic event about 2 Ma (Tobias, 1995; Wolpoff, 1999; Wolpoff, Thorne, Jelinek, & Yinyun, 1994). This hypothesis recognizes regional morphs in the hypodigm; however, these distinctions are not considered indicative of a separate species designation, because *H. erectus* is defined relative to *H. sapiens* only on the basis of plesiomorphic characters of all *Homo* fossils, from about 1.8 Ma to present.

An alternative view recognizes *H. erectus* as a widely dispersed, polytypic species (*sensu lato*) distinct from *H. sapiens*. In this view, *H. erectus* also exhibits geographic and temporal variation (Howells, 1978; Rightmire, 1993). Characteristics that are often used to differentiate Asian and African fossils do not justify a specific status for these regional morphs, and therefore cannot be used to distinguish taxa (Bräuer, 1994; Kennedy, 1991; Rightmire, 1979; Turner & Chamberlain, 1989).

In general, the variation problem associated with *Homo* fossils from the Pliocene and early Pleistocene is related to a more general paleontological problem: the recognition of paleospecies. Differentiating anatomically defined fossil species usually involves identifying morphological differences as well as recognizing similarities between two fossils consistent within a single species (Groves, 1997; McHenry, 1994; Varela, Lobo, & Hortal, 2011). However, if a species is examined from a broad biological perspective, analysis cannot only consider morphometric features; genetic analysis is equally important.

Genetic interactions occur through evolution, and the study of genetics has revealed interbreeding between *Homo neanderthalensis* and *Homo sapiens* (Green et al., 2010; Zilhão & Trinkaus, 2002), the diversity and hybridization of closely related primates such as *Pan troglodytes* and *Pan paniscus* (Arnold & Meyer, 2006; Groeneveld, Atencia, Garriga, & Vigilant, 2012), and the identification of human genomes more closely related to the bonobo or chimpanzee genomes than they are to one another (Prüfer et al., 2012). This information, however, is difficult to access from the ancient fossils of *Homo erectus* that are available for study.

Although genetics can provide different conclusions than paleontology, both are important for understanding evolutionary biology. While the first field defines a species as a group of organisms wherein two hybrids are able to generate fertile offspring, paleontology defines a species as a group of fossils with morphological traits that can be used to distinguish one group from another (Henneberg, 1997, p. 22). Such morphological traits may be able to distinguish one species from another, but this does not mean that two different paleontological species are genetically different, or that they could not reproduce. This indicates that the paleontological perspective does not have the same precision as genetics for distinguishing biological species. However, even with these limitations, it is possible to obtain satisfactory results in paleontology by using quantitative methods.

One statistical method commonly employed in the study of hominid paleospecies is the calculation of coefficients of variation (CV), which express the percentage of the standard deviation relative to the mean of certain samples or populations. This statistical test is used to examine whether a species of extant humans or other mammals differ significantly in order to determine if there is more than one species present in an archaeological sample (Cope & Lacy, 1992, 1995). Thus, it can be used to compare hominid samples to determine if a group can be labeled as a single species (Moggi-Cecchi, 2003).

CVs are commonly applied to analyses of the cranial variability of early *Homo*, to explore the development of intelligence within the genus (Henneberg, 1997), and are used to make inferences about the taxonomic affinities of the first human-dispersed population from Africa (Jiménez-Arenas et al., 2011). In addition, skeletal phenotypic plasticity may lead to morphological differences between individuals that can complicate the species identification process. Thus, CVs based on skeletal morphological traits can identify the range of variation one would expect in an extant hominid species, and thus provide insight when trying to assign hominin fossils to a species (Collard & Lycett, 2009). CV values can also be used to indicate levels of sexual dimorphism in extinct hominid species in comparison to extant species. CVs were

used to identify the higher levels of sexual dimorphism in *Australopithecus afarensis* compared to modern humans (Reno, Mccollum, Meindl, & Lovejoy, 2010).

In general, if CV values for all crania from a sample are similar, the sample may be hypothesized to represent a single species, or a 'taxon' with a narrowly defined brain size. On the other hand, variable CVs may indicate the existence of multiple species within a sample. Henneberg (1990, 1997) found a CV of 11.6 for the endocranial volume of *Homo sapiens* based upon a vast dataset. This is similar to the CV value previously published for a smaller sample (Holloway, 1980), although the published data for large and combined-sex samples of extant hominoids have already indicated that the CV of endocranial volume (ECV) is often larger than 10, with a range of 12.6-14.9 for modern humans (N = 1000, males only) (Tobias, 1971).

This study considers whether the endocranial size variation of early *Homo* reflects variation related to one unique species or to multiple species. We calculate CVs based on early *Homo* ECV values, and investigate if and how CVs change when early *Homo* specimens are separated into species groups versus when specimens are placed into temporal groups regardless of species attribution. Therefore, we investigate the hypothesis of a single evolving lineage of early *Homo*. The Dmanisi fossils are crucial evidence for this study, due to their similar temporal range but different geographic origin from that of early *Homo* in Africa.

Based on the assumption that increasing brain size in the *Homo* genus lineage is a function of time (Henneberg, 1997; Henneberg & de Miguel 2004; Van Arsdale & Wolpoff, 2012), we will thus investigate:

- a) Whether the variation in endocranial volume present in early *Homo* reflects intraspecific variation at the population level or true taxonomic species diversity,
- b) Whether CV changes when species are considered within similar and related time periods, and,
- c) Whether the Dmanisi fossils closely align with *H erectus*, the species to

which they have been morphologically assigned.

Materials and Methods

In this study, the endocranial volumes of various samples of hominids were obtained in order to compare their CVs. For this purpose, data were selected from collections of *Australopithecus africanus*, *Paranthropus boisei*, *Homo habilis*, *Homo ergaster*, the Dmanisi fossils, *Homo erectus*, *Homo neanderthalensis*, *Pan troglodytes* and *Homo sapiens*. Data concerning the ECV of fossils come from studies undertaken by Arif, Baba, Suparka, Zaim, and Setoguchi (2001), Baba et al. (2003), Balter (2009), Broadfield and Yuan (2004), Brown, Walker, Ward, and Leakey (1993), Chiu, Ku, Chang, and Chang (1973), Conroy et al. (1998), Gilbert and Asfaw (2009), Harvati, Stringer, and Karkanas (2011), Hawks and Wolpoff (2001), Holloway (1980, 1981, 1983); Macchiarelli et al. (2004), Lee and Wolpoff (2003), Lordkipanidze et al. (2006, 2013), Márquez, Mowbray, Sawyer, Jacob, and Silvers (2001), Rak, Kimbel, and Hovers (1994), Rightmire (1985, 1993), Rightmire et al. (2006), Spoor et al. (2007), Steward (1977), Tobias (1971), Trinkaus (1985), and Woo and Chao (1959). ECV data on *Pan troglodytes* are from Booth (2010), and data for *Homo sapiens* are taken from Henneberg (1997). Data are summarized in Table 1, which contains the name, geographic origin, and chronological band of each species. Individual information for each fossil is presented in the Supplementary Information at the end of this paper. Before presenting our results, it is important to review information concerning the chosen species to identify the main relationships between samples.

Species groups

Early *Homo* can be distinguished from *Australopithecus* primarily due to *Homo*'s large brain size, which ranges from 600 to 700 cm³, and total bipedalism (Cela-Conde & Ayala 2007). In addition, early *Homo* shows greater rounding of the skull, a reduced jaw and zygomatic maxillofacial area, a large supra-orbital area, a facial profile more rectilinear than projecting forward, a rounded dental arch with small canines, and no sagittal crest (Rightmire, 1993).

Table 1. Summarized information for each species.

Species	Number	Geographic Distribution	Chronology (Ma)
<i>Australopithecus africanus</i>	8	Africa	2.7 – 2
<i>Paranthropus boisei</i>	10	Africa	2.4 – 1.41
Early <i>Homo</i>	9	Africa	1.9 – 1.6
<i>Homo ergaster</i>	8	Africa	1.78 – 0.75
<i>Homo erectus</i> (Dmanisi)	5	Asia	1.8 – 1.78
<i>Homo erectus</i>	27	Asia	1.3 – 0.07
<i>Homo neanderthalensis</i>	25	Eurasia	0.1 – 0.02
<i>Pan troglodytes</i>	18	Africa	Current
<i>Homo sapiens</i>	10000	All continents	Current

The chronology (Ma) is in million of years. ‘Earlier *Homo*’ refers to the first *Homo* representative species in Africa – *Homo habilis* (sensu lato) and *Homo rudolfensis*. ‘Eurasia’ refers to Neanderthal fossils that have come from the European and Asian continents, which indicate a big variability due geographical distance.

The hypodigm of *Homo habilis sensu lato* is variable in size. This variation is so pronounced that the dataset was divided into two sub-groups (Chamberlain & Wood, 1987; Groves, 1997; Lieberman et al., 1988, 1996; Rightmire, 1993; Stringer, 1986; Wood, 1993). Whereas *Homo rudolfensis*, represented by KNM-ER 1470, has the largest brain (750 cm³), a broad and flat face, big teeth (Wood, 1992), lower prognathism, and a reduced supraorbital torus (Rightmire, 1993), the other taxon, *Homo habilis sensu stricto*, has a smaller brain, shorter face and smaller teeth than *Homo rudolfensis*. In the case of KNM-ER 1813, brain size is 510 cm³. Our analysis considers the *sensu lato* of *Homo habilis* because the high degree of variability, if compared with species *sensu stricto*, contributes to discussions of whether variable groups must be divided into many species or maybe conceived of as one species with intraspecies variation.

Studies regarding *Homo erectus* and *Homo ergaster* recognize that Asian *H. erectus* is the

more derived of the geographic samples (Antón, 2003, p. 154). Discussions concerning variability note that cranial superstructures, such as the metopic and sagittal keels and supraorbital tori, are more robust in *Homo ergaster* (Gabunia et al., 2000). *Homo ergaster* also has thicker cranial vaults and low, highly angulated crania. These features are autapomorphies and allow for differentiation between Asian *H. erectus* and early African forms of *H. ergaster* (Wood & Collard, 1999b).

Other skeletal features also differ between African and Asian specimens of *Homo erectus*. Cranial vaults are more pear-shaped when viewed from above in Asian specimens (Antón, 2003, p. 146). In addition, Asian temporal lines are highly divergent from one another as they proceed posteriorly, whereas in African specimens these lines remain parallel to one another and higher on the vault. The structure of the glenoid fossa is more mediolaterally elongated and foreshortened anteroposteriorly in African than in Asian forms

(Picq, 1990). The supraorbital tori are more massive, on average, in Asia than in Africa, although both African and Indonesian samples exhibit large ranges of size variation (Antón, 2003). In addition, Asian *Homo erectus* faces are more massive than their existing early African and Georgian counterparts, and are likely more prognathic (Wolpoff, 1999). The Dmanisi group exhibits similarities to eastern African fossils attributed to *Homo ergaster* and *Homo erectus*, although Skull 5 has a morphological affinity with early representatives of *Homo* in eastern Africa, relative to *Homo habilis* and *Homo rudolfensis* (Lordkipanidze et al., 2013, p. 328).

Coefficient of Variation

Variation within samples was examined using the coefficient of variation, also known as the measure of relative variability. CV is calculated by dividing the sample's standard deviation (SD) by the mean: $CV = (SD / \text{mean}) \times 100$. Comparisons between potential groupings were made by calculating the CV for each group. CV was calculated two different ways in order to observe the influence of the smallest values as an indicator identifying one unique group.

First, CVs were obtained for groups formed by a single species as well as larger groups formed by the sum of two or more species. As we differentiated groups in which Dmanisi is found, we considered sets formed by *H.ergaster* + Dmanisi, *H.erectus* + Dmanisi, earlier *Homo* + Dmanisi, and earlier *Homo* + *H.ergaster* + Dmanisi (respectively Groups 8, 9, 13 and 12 – see Table 2). However, since our goal was to study how groups without the Dmanisi sample behaved when associated, we also considered groups with *H.ergaster* + *H.erectus* and earlier *Homo* + *H.ergaster* (Groups 7, 11 – see Table 2).

The CV of the set *Homo* lineage, presented as Group 10 (Table 2), is consistent with the hypothesis proposed by the Dmanisi research team. According to this hypothesis, the *Homo* population from Dmanisi likely originated from an Early Pleistocene expansion of the *H. erectus* lineage from Africa toward Asia (Lordkipanidze et al., 2013, p.330). Thus, we considered all fossil representatives of *Homo ergaster*, Dmanisi, and *Homo erectus* from Asia. These groupings do not depend on delimited ranges of time. The main objective is to identify which groups have

the greatest CVs, considering those comprised of only one species, as well as those comprised of two or more species, and those that are usually placed in an extensive geographic and temporal range, as is the case for the *H.ergaster* + *H.erectus* and *Homo* lineages (Table 2).

In the second step, CVs were estimated for all species as ordered by specific chronological ranges, regardless of the origin of each species. We considered the temporal range between 2.0 and 1.5 Ma as appropriate for ordering the main data collected from the bibliography, because this range covers the period during which *Homo habilis*, *Homo erectus* from Dmanisi, and *H.ergaster* must have coexisted.

We have not stipulated any specific value of CV for ECV to establish definitively the boundary for when one *Homo* group consists of more than one species. Instead, we have chosen the CV value of 15.2% used by Henneberg (1995) as a way to distinguish between species. This method was applied by Cope and Lacy (1992) to test deviations in the CVs of various grouped cranial capacities observed in modern humans. We have considered all values of CV for ECV exceeding 15.2 to indicate the presence of multiple species within the sample analyzed.

Results

We obtained two types of results. When all data are grouped by acknowledged taxon, such as *Australopithecus africanus*, *Paranthropus boisei*, *Homo erectus* (Asia), Dmanisi fossils, *Homo neanderthalensis*, *Pan troglodytes* and *Homo sapiens*, CVs are usually below 15.2 (Blue lines – Figure 1). However, when more than one taxon is clustered, CVs over 15.2 are observed, which indicates the existence of multiple species (Black lines – Figure 1). This result was expected since multiple species were grouped. There are, however, groups formed by two species in which the CV is below 15.2, indicating that they could be grouped as one unique species, like *H.ergaster* and *H.erectus* (14.9 – Table 1).

The CV of the *Homo* lineage is 19 – approximately 4 units larger than the maximum accepted value to consider the sample as a single species (Group 10 – Table 2). The sets formed by *H.ergaster* + Dmanisi, *H.erectus* + Dmanisi, *Homo* lineage, and earlier *Homo*

Table 2. Values of CV for each group.

Groups	Species	Average ECV (cm ³)	D	V
1	<i>Australopithecus africanus</i> (n=8)	462.6	50.9	11.0
2	<i>Paranthropus boisei</i> (n=10)	498.0	27.2	5.4
3	Earlier <i>Homo</i> (n=9)	666.3	98.4	14.7
4	<i>Homo ergaster</i> (n=8)	854.2	166.4	15.0
5	<i>Homo erectus</i> (Dmanisi) (n=5)	644.4	84.7	13.1
6	<i>Homo erectus</i> (Asia) (n=27)	1009.4	133.0	13.1
7	<i>Homo ergaster</i> + <i>H.erectus</i> (n=35)	973.9	145.9	14.9
8	<i>H.ergaster</i> + <i>Dmanisi</i> (n=13)	773.5	152.6	19.7
9	<i>H.erectus</i> + <i>Dmanisi</i> (n=32)	952.4	184.1	19.3
10	<i>Homo lineage</i> (n=39)	932.7	177.4	19.0
11	Earlier <i>Homo</i> + <i>Homo ergaster</i> (17)	754.7	146.3	19.3
12	Earlier <i>Homo</i> + <i>H.ergaster</i> + Dmanisi (n=22)	729.7	141.1	19.3
13	Earlier <i>Homo</i> + Dmanisi (n=14)	658.5	91.0	13.8
14	<i>Homo neanderthalensis</i> (n=25)	1412.9	180.7	12.8
15	<i>Pan troglodytes</i> (n=18)	367.7	19.8	5.38
16	<i>Homo sapiens</i> (n=10000)	1349.3	157.0	11.6

We use ‘groups’ instead of ‘species’ because some groups may be considered to be one single evolving lineage. The Earlier *Homo* (3) is comprised of *Homo habilis sensu stricto* and *Homo rudolfensis*. In the case of the *Homo lineage* (10), we have considered all fossils representative of *Homo ergaster*, Dmanisi and *Homo erectus* from Asia. The biggest *Australopithecus* hypodigm (afarensis) was not considered due to the small number of data able to provide endocranial volumes (Holloway et al., 2004).

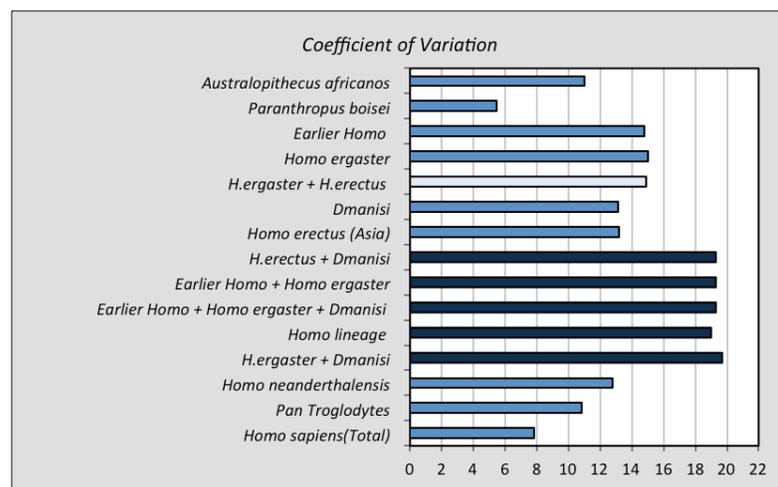


Figure 1. Comparison of the coefficients of variation for endocranial variation of series of hominin data.

The blue lines correspond to groups of a single species in which CV is below 15.2. The black lines are the groups with CV above 15.2 and the light blue line is related to the group formed by two species with the CV below 15.2.

+ *H.ergaster* + Dmanisi have CVs greater than 15.2 (Groups 8, 9, 10, and 12 – Table 2). Nevertheless, Group 13, formed by earlier *Homo* + Dmanisi, has a CV of 13.8. We also investigated how groups without the Dmanisi sample behaved when amalgamated together, by grouping *H. erectus* + *H.ergaster* as well as earlier *Homo* + *H.ergaster* (Groups 7 and 11 – Table 2). CV values for both sets indicated that they were comprised of multiple species, since the CV in each case exceeded the maximum value for a single species.

When we order the hominid ECV data by specific different species, such as *Homo habilis sensu lato*, *Homo ergaster* and Dmanisi fossils (Table 3). These results support the hypothesis that hominin brain growth is a function of time (Henneberg, 1997, 2005; Van Arsdale & Wolpoff, 2012), in the *Homo* species. In this case, instead of integrating all fossils corresponding to certain taxa, we chose a set of fossils that fall within the temporal range between 2.0 and 1.5 Ma. Following Figure 2, endocranial volume is strongly correlated with time, with an increase in the more recent fossils ($r^2 = 0.69$).

Within the period from 2.0 to 1.5 Ma, CV values are close to the limit for considering each group as representing a single species. We observed a pattern of diminishing CVs of ECV: the smaller the number of grouped species, the lower the CV will be. That is, group 1 > group 2 > group 3 > group 4. Thus, Group 1 – formed by *Paranthropus boisei* + *Homo habilis sensu lato* + *Homo ergaster* + the Dmanisi fossils – has a CV of 20, greater than Group 4, formed only by *Homo habilis sensu lato* + the Dmanisi fossils, which has a CV of 13.8. Group 4 is the only group with a value that can be considered to indicate the presence of only one species. However, this relation was not observed in the group formed by *Homo habilis sensu lato* + *Homo ergaster*, or in the Dmanisi + *Homo ergaster* group. The two African species (*H. habilis* and *H. ergaster*) would have lived in the same chronological context, between 2.0 and 1.5 Ma, but the CV value of 16.2 indicates that a single species is improbable. Similarly, the *Homo ergaster* + Dmanisi sample group has a value of 16.7. These results show that *Homo ergaster* cannot be grouped with other contemporary species. Finally, the Dmanisi sample cannot be added to *Homo*

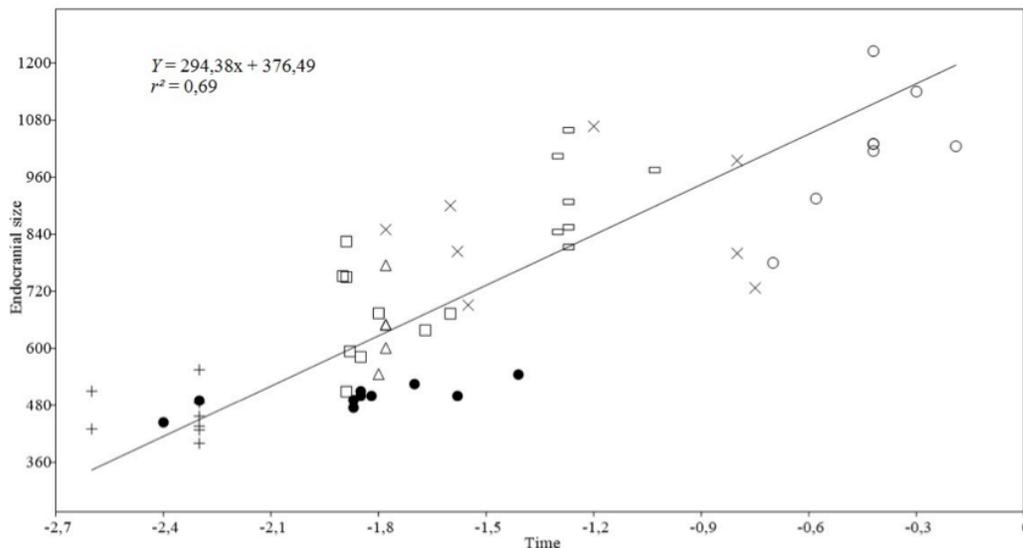


Figure 2. Endocranial volume of hominin fossils distributed through time

In this figure, *Australopithecus africanus* (crosses), *Paranthropus boisei* (filled circle), *Homo habilis sensu lato* (square), *Homo ergaster* (X), *Homo erectus* – Georgia (triangle), *Homo erectus* – Indonesia (rectangle), *Homo erectus* – China (empty circle).

The Endocranial size (in cm^3) is a function of time for 37 specimens of Pleistocene *Homo*. *H. neanderthalensis*, *H. sapiens* and *Pan troglodytes* are not shown. The time scale is reversed, so that the negative sign represents movement back in time as measured in millions of years.

erectus or *Homo ergaster*, but they can be added to early *Homo*. Therefore, the Dmanisi *Homo* specimens are not closely aligned with *H. erectus*, the species to which the Dmanisi research team has morphologically assigned them.

Discussion

The Dmanisi research team explains morphological diversity at the beginning of the *Homo* genus, in which the Georgian *Homo* fossils are included, as a probable reflection of variation between demes of a single evolving lineage – in this case, *Homo erectus* (Lordkipanidze et al., 2013, p. 330). The hypothesis of multiple independent lineages (paleospecies) is considered to be less likely, especially in the absence of empirical evidence for adaptation to separate ecological niches. Based on the methods we have used here, there is a possibility that this assumption could be supported. However, this must be accomplished by arranging the data according to specific ranges of time, instead of grouping all fossils in accordance with acknowledged species designations regardless of geographic and temporal range. In this case, data concerning the endocranial volume of *Homo habilis sensu lato*, or earlier *Homo*, could be added to the Dmanisi fossils to treat the size variation in endocranial volume as evidence to classify them as a unique group. However, a union between *Homo ergaster* specimens dated to between 2.0 and 1.5 Ma, early *Homo*, and the Dmanisi samples is not possible, which supports the multiple lineage hypothesis for early *Homo*.

When groups of all species are structured by type, we can observe greater values of CV for ECV than when they are ordered by time. In general, CV values are approximately the same (19), varying slightly between the groups, and are about 4 units larger than the maximum accepted value to distinguish a single species. The group formed by data from all *Homo ergaster* and *Homo habilis sensu lato* specimens (Group 11 – Table 2) has a sufficiently large CV value to exclude the possibility that this group contained only one species (19.3). The group formed by these last fossils in addition to the Dmanisi skulls (Group 12 – Table 2) has a similar value. Finally, the CV of the *Homo* lineage group is also 19 (Group 10 - Table 2).

It is important to emphasize that data for each of these species have been collected from large and diverse contexts, as presented in the “species groups” (see Materials and Methods), and that this may have contributed to high CV values. According to Miller (1991), some characteristics, such as sexual dimorphism and the geographical and chronological ranges included, can influence the CV results. We did not consider sexual dimorphism in our analysis because of the unknown sex of the most of the fossils, although many authors indicate a more accentuated sexual dimorphism in *Homo* species from the Plio-pleistocene than in *Homo* species from the middle and late Pleistocene (Frayer & Wolpoff, 1985; McHenry, 1996; Tobias, 1991). A high variation of sexual dimorphism correlates with a high variation of size in primate species, because males are usually larger and more robust than females. Thus, the high variation values of *Homo* species may be related to species with accentuated dimorphism instead of a dataset comprised of two or more different species.

Although we did not consider sexual dimorphism, we did not observe CVs high enough to distinguish two species in groups such as *Homo habilis sensu lato*, which have been hypothesized to have had accentuated dimorphism (Lee & Wolpoff, 2005; Miller, 1991; Tobias 1991). Apart from sex-related differences, geographic and temporal factors could be posited as possible causes for high CV values. However, large ranges are not necessarily a determining factor for variability when CVs for ECV are being compared. For instance, temporal data indicate that *Homo ergaster* would have existed for more than 1 million years (ranging from 1.78 Ma for KNM ER 3733 to 0.75 Ma for OH 12 – see Supplementary Information). However, even though the CV for this group is greater than those of other species (15), this value indicates the presence of one unique species (Table 2). The Dmanisi *Homo* specimens, on the other hand, come from western Asia and are therefore distinguishable from the first African *Homo* based on geographic context. They can be associated with the first African *Homo* temporally, specifically *Homo habilis sensu lato*, since the CV for this grouping is 13.8 (Group 4 – Table 3). Despite the fact that *Homo habilis sensu lato* and the first members of *Homo ergaster* lived in the same region at the same time, they cannot be considered as a unique group simply due to such

overlap, since the CV value for this group is 16.2 (Group 3 – Table 3).

It seems that the group formed by *Homo habilis sensu lato*, *Homo ergaster*, and Dmanisi (Group 11 – Table 2) has a CV value too high to support the hypothesis that this grouping represents only one unique species (19.3). Nevertheless, the CV value for such a group is lower (15.8 – Table 3, Group 2) if only the representative fossils situated between 2.0 and 1.5 Ma are considered. This can be partially explained by the size of the sample; larger samples tend to have lower coefficients of variation than smaller samples, because a higher number of individuals usually decreases the standard deviation, and thus the CV.

When the dataset is ordered according to the time range of 2.0 to 1.5 Ma, it is possible to consider endocranial variation of the group comprised of the Dmanisi fossils and *Homo habilis sensu lato* as one unique species because the CV (13.8) is lower than the value expected for a group containing multiple species (15.2). However, when *Homo ergaster* is included in the dataset, the value changes considerably, as seen for Groups 2 and 3 (Table 3). This increased CV exceeds the maximum value acceptable for a group comprised of one unique species. This indicates how different *Homo ergaster* is in relation to *Homo habilis sensu lato* as well as to the Dmanisi representatives. Due to the fact that *Homo ergaster* existed at the same time as Dmanisi, but presents a CV too large to indicate one unique species, they can be interpreted as different species instead of as one unique group. This supports the hypothesis presented by authors describing KNM ER 42700, discovered in 2000 (Spoor et al., 2007). The distinction between *H. erectus* and *H. habilis* taxa, independent of overall cranial size, suggests evolution in two directions.

When all specimens present within the chronological range of 2.0 to 1.5 Ma are grouped, the CV (20) is bigger than that expected for a group comprised of one unique species (Group 1 – Table 3). This CV value is greater than that estimated for Group 2 (15.8), which is comprised only of fossils of the *Homo* genus dated to this same temporal period. This comparison is important because it indicates an association between genus and CV. In this case, a set formed of *Homo* and *Paranthropus boisei* fossils

from 2.0 to 1.5 Ma is different from a group comprised only of *Homo* specimens dated to the same period.

Although it is possible to recognize the influence of space and time on variation within a deme, it is important to assume that there is a relationship between great ranges of time and space and high levels of CV for all cases described. For instance, the large geographical zone from which Neanderthal fossils were collected (from Gibraltar, south of Spain, to Israel) may contribute to the group's CV (12.8). According to previous studies, cranial capacity of the Neanderthal group increases significantly within the European sample without a significant change in variability (Hawks & Wolpoff, 2001, pp. 1481-1482). Due to this increase, the Würm Neanderthals demonstrate a deviation from the overall non-European mean, wherein cranial capacity increases over time (Ruff, Trinkaus, & Holliday, 1997). However, this variation does not necessarily divide the Neanderthal group in two because the value is below the maximum accepted for considering multiple species. Nevertheless, early *Homo* represents a different situation. Even having cohabitated in the same spatial context during the chronological band of 2.0 to 1.5 Ma, *Homo habilis sensu lato* and *Homo ergaster* present a CV value too high to consider the two species as one (Group 3 – Table 3). Furthermore, it is possible to consider one unique group comprised of *Homo habilis sensu lato* and the Dmanisi fossils, even taking into account their different geographical origins (Group 4 – Table 3). Such an association suggests a very old origin for the Georgian *Homo* species, perhaps as a direct derivative of the first *Homo* in Africa.

Table 3. *Homo* fossil data ordered by groups and chronology

Group 1	ECV ³	Time (Ma)
KNM ER 13750 <i>P. boisei</i>	475	1.87
KNM ER 23000	491	1.87
OH 5	500	1.85
KNM ER 407	510	1.85
KNM WT 17400	500	1.82
KNM ER 406	525	1.7
KNM ER 732	500	1.58
KNM ER 1470* <i>H. habilis</i>	752	1.9
KNM ER 1813	509	1.89
KNM ER 1590*	825	1.89
KNM ER 3732*	750	1.89
OH 24	594	1.88
OH 7	674	1.8
KNM ER 1805	582	1.85
OH 16	638	1.67
OH 13	673	1.6
Dmanisi 2280 Dmanisi	775	1.78
Dmanisi 2282	650	1.78
Dmanisi 2700	601	1.78
Dmanisi 3444	650	1.78
Dmanisi 4500	546	1.8
KNM ER 3733 <i>H. ergaster</i>	850	1.78
KNM WT 15000	900	1.6
KNM ER 3883	804	1.58
KNM ER 42700	691	1.55
Average	638.6	
SD	127.8	
CV	20.0	

Group 2	ECV ³	Time (Ma)
KNM ER 1470* <i>H. habilis</i>	752	1.9
KNM ER 1813	509	1.89
KNM ER 1590*	825	1.89
KNM ER 3732*	750	1.89
OH 24	594	1.88
OH 7	674	1.8
KNM ER 1805	582	1.85
OH 16	638	1.67
OH 13	673	1.6
Dmanisi 2280 Dmanisi	775	1.78
Dmanisi 2282	650	1.78
Dmanisi 2700	601	1.78
Dmanisi 3444	650	1.78
Dmanisi 4500	546	1.8
KNM ER 3733 <i>H. ergaster</i>	850	1.78
KNM WT 15000	900	1.6
KNM ER 3883	804	1.58
KNM ER 42700	691	1.55
Average	692.4	
SD	109.6	
CV	15.8	

In these charts 'ECV' is the 'endocranial capacity' in cm³, 'SD' is the 'standard deviation' and 'CV' is the 'coefficient of variation'. '*' indicate the bigger Earlier *Homo* specimens, also named *Homo rudolfensis*. All groups are inserted in the period between 2.0 – 1.5 Ma. Group 1 is formed by *Paranthropus boisei*, *Homo habilis sensu lato*, *Homo ergaster* and the *Homo* fossils from Dmanisi. Group 2 is formed by *Homo habilis sensu lato*, *Homo ergaster* and the *Homo* fossils from Dmanisi. Group 3 is formed by *Homo habilis sensu lato* and the *Homo ergaster*. Group 4 is formed by *H. habilis sensu lato* and the *Homo* fossils from Dmanisi.

Group 3	ECV ³	Time (Ma)
KNM ER 1470* <i>H. habilis</i>	752	1.9
KNM ER 1813	509	1.89
KNM ER 1590*	825	1.89
KNM ER 3732*	750	1.89
OH 24	594	1.88
OH 7	674	1.8
KNM ER 1805	582	1.85
OH 16	638	1.67
OH 13	673	1.6
KNM ER 3733 <i>H. ergaster</i>	850	1.78
KNM WT 15000	900	1.6
KNM ER 3883	804	1.58
KNM ER 42700	691	1.55
<i>Average</i>	710.9	
<i>SD</i>	115.3	
<i>CV</i>	16.2	

Group 5	ECV ³	Time (Ma)
KNM ER 3733 <i>H. ergaster</i>	850	1.78
KNM WT 15000	900	1.6
KNM ER 3883	804	1.58
KNM ER 42700	691	1.55
Dmanisi 2280 Dmanisi	775	1.78
Dmanisi 2282	650	1.78
Dmanisi 2700	601	1.78
Dmanisi 3444	650	1.78
Dmanisi 4500	546	1.8
<i>Average</i>	718.5	
<i>SD</i>	119.6	
<i>CV</i>	16.6	

Group 4	ECV ³	Time (Ma)
KNM ER 1470* <i>H. habilis</i>	752	1.9
KNM ER 1813	509	1.89
KNM ER 1590*	825	1.89
KNM ER 3732*	750	1.89
OH 24	594	1.88
OH 7	674	1.8
KNM ER 1805	582	1.85
OH 16	638	1.67
OH 13	673	1.6
Dmanisi 2280 Dmanisi	775	1.78
Dmanisi 2282	650	1.78
Dmanisi 2700	601	1.78
Dmanisi 3444	650	1.78
Dmanisi 4500	546	1.8
<i>Average</i>	658.5	
<i>SD</i>	91.4	
<i>CV</i>	13.8	

Conclusion

Analysis of the ECV through CV values reaffirms the hypothesis of a single lineage in hominin evolution, but closer correspondence of the Dmanisi fossils to *Homo habilis sensu lato* than to *Homo ergaster* and Asian fossils implies that further research is still necessary in this area. It would be useful to investigate why a single lineage hypothesis should be linked to *Homo erectus*, since it also appears possible to justify such a lineage closer to early *Homo* in Africa. Our study provides incomplete results because it focuses only on cranial size, which is only one part of the larger body of information related to the definition of paleospecies. Further research that incorporates other dimensions of the problem of defining species, such as the comparison of post-cranial anatomy between species and morphological analysis through new methods, is required. Our results clarify the discussion of the position of the Dmanisi fossils in a specific "taxon" and its replication within the models of explanation for the evolution of the *Homo* genus, considering the important question relating to the presence of multiple or single species at the beginning of this genus.

More than just providing a means for testing the hypothesis of whether or not the high level of

variation within the *Homo* genus is interpreted as evidence for one unique species, the results of this study suggest that time is an important factor to consider when defining specific taxa. Short periods of time may reduce the number of taxa in the *Homo* genus, but there is insufficient evidence to suggest the presence of one unique taxon during the period of early *Homo*. Therefore, the continued possibility of multiple lineages within early *Homo* is reiterated.

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Supplementary Information

Species	CC cm ³	Chronology (Ma)	Source
<i>Australopithecus africanus</i>			
MLD 1	510	2.6-2.7	Holloway <i>et al.</i> (2004)
MLD 37/38	430	2.6-2.7	Holloway <i>et al.</i> (2004)
STs 5	485	2.0-2.7	Holloway <i>et al.</i> (2004)
STs 19/58	436	2.0-2.7	Holloway <i>et al.</i> (2004)
STs 60	400	2.0-2.7	Holloway <i>et al.</i> (2004)
STs 71	428	2.0-2.7	Holloway <i>et al.</i> (2004)
STw 505	555	2.0-2.7	Holloway <i>et al.</i> (2004)
Type 2	457	2.0-2.7	Holloway <i>et al.</i> (2004)
<i>Paranthropus boisei</i>			
Omo L388y-6	444	2.4	Holloway <i>et al.</i> (2004)
Omo 323-896	490	2.3	Brown <i>et al.</i> (1993)
KNM ER 13750	475	1.87	Holloway <i>et al.</i> (2004)
KNM ER 23000	491	1.87	Brown <i>et al.</i> (1993)
OH 5	500	1.85	Holloway <i>et al.</i> (2004)
KNM ER 407	510	1.85	Holloway <i>et al.</i> (2004)
KNM WT 17400	500	1.82	Brown <i>et al.</i> (1993)
KNM ER 406	525	1.7	Holloway <i>et al.</i> (2004)
KNM ER 732	500	1.56-1.6	Holloway <i>et al.</i> (2004)
KGA 10-525	545	1.41	Holloway <i>et al.</i> (2004)
<i>Homo habilis sensu lato</i>			
KNM ER 1470*	752	1.9	Holloway <i>et al.</i> (2004)
KNM ER 1813	509	1.88-1.9	Conroy <i>et al.</i> (1998)
KNM ER 1590*	825	1.88-1.9	Holloway <i>et al.</i> (2004)
KNM ER 3732*	750	1.88-1.9	Holloway <i>et al.</i> (2004)
OH 24	594	1.88	Tobias (1971)
OH 7	674	1.8	Tobias (1971)
KNM ER 1805	582	1.85	Conroy <i>et al.</i> (1998)
OH 16	638	1.67	Tobias (1971)
OH 13	673	1.6	Tobias (1971)

Species	CC cm ³	Chronology (Ma)	Source
<i>Homo ergaster</i>			
KNM ER 3733	850	1.78	Holloway (1983)
KNM WT 15000	900	1.6	Holloway (1983)
KNM ER 3883	804	1.58	Holloway (1983)
KNM ER 42700	691	1.55	Spoor <i>et al.</i> (2007)
OH 9	1067	1.2	Holloway (1983)
Daka (Bou-VP-2/66)	995	0.78-1	Gilbert & Asfaw(2009)
Buia (UA 31)	800	0.78-1	Macchiarelli <i>et al.</i> (2004)
OH 12	727	0.75	Holloway (1983)
Georgia			
Dmanisi 2280	775	1.78	Rightmire <i>et al.</i> (2006)
Dmanisi 2282	650	1.78	Rightmire <i>et al.</i> (2006)
Dmanisi 2700	601	1.78	Rightmire <i>et al.</i> (2006)
Dmanisi 3444	650	1.78	Lordkipanidze <i>et al.</i> (2006)
Dmanisi 4500	546	1.8	Lordkipanidze <i>et al.</i> (2013)
<i>Homo erectus</i> – Indonesia			
Ngawi 1	1000	?	
Sangiran 17	1004	1.3	Holloway <i>et al.</i> (2004)
Sangiran IX	845	1.3	Coqueugniot <i>et al.</i> (2004)
Sangiran 2	813	1.27	Holloway <i>et al.</i> (2004)
Sangiran 4	908	1.27	Holloway <i>et al.</i> (2004)
Sangiran 10	855	1.27	Holloway <i>et al.</i> (2004)
Sangiran 12	1059	1.27	Holloway <i>et al.</i> (2004)
Sangiran 3	975	1.03	Holloway <i>et al.</i> (2004)
Trinil 2	940	0.7-1.0	Holloway <i>et al.</i> (2004)
Ngandong 6 (Solo 5)	1251	> 0.5	Holloway (1980, 1981)
Ngandong 7 (Solo 6)	1013	> 0.5	Holloway (1980, 1981)
Ngandong 10 (Solo 9)	1135	> 0.5	Holloway (1980, 1981)
Ngandong 11 (Solo 10)	1231	> 0.5	Holloway (1980, 1981)
Ngandong 12 (Solo 11)	1090	> 0.5	Holloway (1980, 1981)
Sambungmacan 1	1100	> 0.09	Baba <i>et al.</i> (2003)
Sambungmacan 3	917	> 0.09	Márquez <i>et al.</i> (2001)
Sambungmacan 4	1006	> 0.09	Baba <i>et al.</i> (2003)
Ngandong 1 (Solo 1)	1172	0.05-0.1	Holloway (1980; 1981)

Species	CC cm ³	Chronology (Ma)	Source
<i>Homo erectus</i> – China			
Gongwang 1	780	0.7	Lee <i>et al.</i> (2003)
Zhoukoudian 3 / E1	915	0.58	Chiu <i>et al.</i> (1973)
Lantian	780	0.53-1	Woo (1965)
Zhoukoudian 2 / D1	1030	0.42	Chiu <i>et al.</i> (1973)
Zhoukoudian 10 / L1	1225	0.42	Rightmire (1985)
Zhoukoudian 11 / L2	1015	0.42	Rightmire (1985)
Zhoukoudian 12 / L3	1030	0.42	Rightmire (1985)
Zhoukoudian 5	1140	0.3	Rightmire (1985)
Hexian 1	1025	0.19	Rightmire (1993)
<i>Homo neanderthalensis</i>			
Apidima 2	1454	0.1-0.3	Harvati <i>et al.</i> (2011)
Spy 1	1305	0.1	Lee <i>et al.</i> (2003)
Spy 2	1553	0.1	Lee <i>et al.</i> (2003)
Tabun 1	1271	0.1	Lee <i>et al.</i> (2003)
Saccopastore 1	1258	0.1	Lee <i>et al.</i> (2003)
Saccopastore 2	1300	0.1	Lee <i>et al.</i> (2003)
Amud 1	1750	0.05-0.07	Rak <i>et al.</i> (1994)
Kaprina 3	1200	0.04-0.1	Hawks <i>et al.</i> (2001)
Biache	1200	0.04-0.1	Hawks <i>et al.</i> (2001)
Gánovce	1320	0.04-0.1	Hawks <i>et al.</i> (2001)
Fontéchevade	1350	0.04-0.1	Hawks <i>et al.</i> (2001)
La Chaise (Suard) 1	1065	0.04-0.1	Hawks <i>et al.</i> (2001)
Shanidar 1	1600	0.06-0.08	Steward (1977)
Chapelle-aus-Saints	1625	0.06	Trinkaus (1985)
La Ferrassie 1	1681	0.05	Lee <i>et al.</i> (2003)
Le Moustier 1	1564	0.05	Lee <i>et al.</i> (2003)
Monte Circeo 1	1551	0.05	Schwartz & Tattersall (1996)
Teshik-Tash	1578	0.05	Lee <i>et al.</i> (2003)
Forbes Quarry	1270	0.05	Lee <i>et al.</i> (2003)
Guattari	1550	0.05	Lee <i>et al.</i> (2003)
La Quina 5	1367	0.05	Lee <i>et al.</i> (2003)
La Quina 18	1260	0.05	Lee <i>et al.</i> (2003)
Neandertal	1525	0.05	Lee <i>et al.</i> (2003)
Gibraltar 1	1200	0.03-0.04	Balter (2012)
Feldhofer	1525	0.02-0.04	Hawks <i>et al.</i> (2001)

Species	CC cm ³	Chronology (Ma)	Source
<i>Pan troglodytes</i>			
Specimen 1	364	Contemporary	Booth (2010)
Specimen 2	378		
Specimen 3	368		
Specimen 4	376		
Specimen 5	375		
Specimen 6	374		
Specimen 7	376		
Specimen 8	404		
Specimen 9	345		
Specimen 10	361		
Specimen 11	386		
Specimen 12	381		
Specimen 13	355		
Specimen 14	393		
Specimen 15	360		
Specimen 16	344		
Specimen 17	360		
Specimen 18	218		