Does Early *Homo* Dental Size Variation Follow a Neutral Pattern of Divergence?

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ABSTRACT

The fragmentary early *Homo* fossil record represents a temporally expansive and complex lineage that is morphologically and geographically diverse. This large amount of variation, which also captures the transition period from *Australopithecus* to *Homo,* has been the focus of a number of studies that have attempted to tease apart taxonomic relationships among specimens, however, results have been ambiguous. More recently, several craniomandibular studies have focused instead on reconstructing the evolutionary processes that produced this diversity, showing that some of it may be consistent with non-adaptive evolutionary processes, providing an added level of complexity to how our lineage evolved and diversified. Here, we add to this body of work by applying methods developed from evolutionary quantitative genetics to assess whether genetic drift or natural selection was responsible for the observed diversification in early *Homo* tooth size variation. Utilizing previously published standard dental measurements of *Homo* fossil specimens dated between 2.8 and 1.5 million years (Ma), we found that mandibular dental size variation does not deviate from a model of genetic drift across regions (southern Africa, southeastern Africa, eastern Africa, northeastern Africa, Dmanisi), or across time periods (2.8–2.3 Ma, 2.29–1.8 Ma, 1.79–1.5 Ma). In contrast, the null hypothesis of genetic drift was rejected for maxillary dentition, specifically between some of the earliest *Homo* specimens and later *Homo*, and comparisons involving the Dmanisi hominins. The latter could illustrate that adaptation, probably dietary, was an important factor in the earliest migrations of *Homo* out of Africa, and the former could indicate an interesting pattern of selection between time periods in early *Homo*, possibly representative of different species. Finally, the contrasting pattern seen between mandibular and maxillary dentition is consistent with studies indicating that morphological integration is stronger in mandibular dentition, and thus a potential constraint on the effect of diversifying selection.

INTRODUCTION

The emergence of the genus *Homo* is an important stage in human evolution, however, the actual transition from *Australopithecus* to *Homo* was not necessarily marked by distinct morphological and technological transformations (Kimbel and Villmoare 2016; Schroeder 2021). Instead, this transition period, between 2 and 3 million years ago (Ma), is represented by a sparse fossil record, an overlap of morphological and technological traits across time and space, and a lack of consensus regarding what constitutes an affiliation with *Homo* (Kimbel and Villmoare 2016; Schroeder 2021). A number of previous studies have focused on either identifying the most likely ancestor of *Homo* and in turn the most likely region for the emergence of the genus (Antón et al. 2014; Dunsworth 2010; Wood 1992), or differentiating between inter- and intra-specific variation in early *Homo* to delineate taxonomic relationships among species and genera (Kramer et al. 1995; Lieberman et al. 1996; Miller 1991, 2000). However, these studies have not had much success. This is because although this transitional fossil record is sparse, it is also diverse and therefore poses a difficulty for taxonomic classification, leading to complex questions about how this diversity came about.

Morphological variation within and between hominin groups is the result of a deep evolutionary history, a combination of evolutionary processes, and a multitude of ecological factors (e.g., Ackermann and Smith 2007; Faith et al. 2021; Foley 2016; Lynch and Walsh 1998; McKee 2017; Potts and Faith 2015; Sponheimer et al. 2013; Stanley 1992). Most traditional explanations for the cause of variation in early

Homo have focused on adaptive evolutionary scenarios, specifically on directional selection influencing a given trait (see review in Tattersall 2021). For example, morphological changes during the transition to *Homo* have been described as an adaptive response to environmental changes in Africa ca. 2.5 Ma (Bobe and Behrensmeyer 2004; Reed 1997; Stanley 1992; Vrba 1985, 1995, 1996). However, recent work has pointed to non-adaptive processes, such as genetic drift, as a potential player during the emergence and evolution of the genus *Homo* (Ackermann and Cheverud 2004; Schroeder and Ackermann 2017; Schroeder et al. 2014; Weaver et al. 2007). Recent isotopic studies have also indicated that the earliest *Homo* specimen, the Ledi-Geraru mandible LD 350-1 (assigned to *Homo* based on dental and mandibular morphology; Villmoare et al. 2015) did not differ dietarily from *Australopithecus*, underscoring the potential of non-adaptive processes during the early diversification of the genus, at least as it pertains to diet (Patterson et al. 2019; Robinson et al. 2017). Furthermore, the wide range of brain sizes within early *Homo* (Spoor et al. 2015) challenges the linear notion of the emergence of *Homo*-like morphology (e.g., Walker and Leakey 1978 and Tattersall and Eldredge 1977, as described in Kimbel and Villmoare 2016). Collectively, the studies mentioned above support the idea that the emergence and evolution of *Homo* could be characterized by multiple lineages reflecting evolutionary innovation (Antón et al. 2014). In such a scenario, *Homo*-like morphology could have evolved multiple times, in different regions or at different times, as a result of varying evolutionary processes acting within the context of habitat instability and fragmentation (Antón et al. 2014). This possibility has important implications for debates about the most likely ancestor of the genus *Homo* (e.g., Asfaw et al. 1999; Berger 2012; de Ruiter et al. 2017; Kimbel and Rak 2017), leaving these debates somewhat obsolete.

The insights from the studies outlined in the previous paragraph have moved the needle toward a better understanding of the evolutionary processes underlying cranial and mandibular variation in early *Homo*, but dental remains have been somewhat overlooked. In mammals, teeth are the most commonly preserved element in the fossil record due to their density (Briggs 2003). In addition, teeth have complex and sometimes rapidly evolving phenotypes, which allows for taxonomic identification (Polly 2016). Teeth are also an important proxy for genetic information and dietary function in the deep past (e.g., Meloro and Raia 2010; Santana et al. 2011; Selig et al. 2019; Szuma 2007; Ungar and Hlusko 2016), and have been used previously to estimate rates and modes of evolution (Gingerich 2009; Gómez-Robles 2019; Gómez-Robles et al. 2017). Many dental traits, including certain linear measurements, have been shown to be heritable and therefore they can be used successfully to understand the evolution of morphological variation over time (Hlusko et al. 2016). Standard dental metrics of tooth size can be useful for differentiating between hominin groups (e.g., Suwa et al. 1996; Wood 1981), and have been used in studies of sexual dimorphism across primate evolution (e.g., Plavcan 2001) and to infer hom-

inin diet (Ungar 2012; Ungar et al. 2006). In addition, the internal structure of the teeth has been shown to be taxonomically informative, and relevant here, a recent study by Zanolli and colleagues (2022) argues that a number of southern African early *Homo* dental remains belong to either *Paranthropus* or *Australopithecus* based on this type of data. Taken together, these studies highlight the importance of dental data in paleoanthropological research, but also the potential for further investigation of evolutionary processes. Although early work by Brace (1963, 1964) did attempt to explain some of the large-scale morphological dental changes in the hominin fossil record, i.e., structural reduction of dentition, by proposing the Probable Mutation Effect hypothesis, which links overall size reduction with a loosening of selective pressures and random mutation, this hypothesis is not easily testable (as discussed in Holloway 1966).

Here, we apply statistical tests developed from evolutionary quantitative genetics (Lande 1979) to determine the extent to which genetic drift and/or natural selection can explain the diverse dental size variation in early *Homo*, with genetic drift as the null hypothesis. A rejection of the null hypothesis indicates that dental size morphology is either more or less variable for divergence to have occurred through random or neutral forces alone, thus pointing to the role of natural selection. The goal of this study is to elucidate the evolutionary processes underlying dental size variability in early *Homo*. This information may provide further understanding of potential adaptive scenarios during the emergence of our genus. We compare specimens across different time periods, and geographic regions. Based on a previous study of cranial and mandibular variation in the genus *Homo*, we expect to find a rejection of the null hypothesis of genetic drift across different geographic regions and temporal periods, reflecting a difference in environmental conditions and potentially diet (Schroeder and Ackermann 2017).

MATERIALS

EARLY *HOMO* SAMPLE
Standard metric data of permanent mandibular and maxillary dentition of early *Homo* specimens were collected from the published literature (Blumenschine 2003; Bromage et al. 1995; Clarke et al. 1970; Curnoe and Tobias 2006; Gabunia and Vekua 1995; Grine 1993, 2005; Grine et al. 2019; Keyser 2000; Kimbel et al. 1997; Leakey et al. 1978; Moggi-Cecchi et al. 2006; Prat 2005; Rightmire et al. 2006; Tobias 1991; Wood 1991). We define early *Homo* as individuals dated to approximately 1.5 Ma and older, which includes specimens that have been referred to as *Homo rudolfensis*, *Homo habilis*, *Homo erectus*, and *Homo* sp. The complete dataset is comprised of 99 early *Homo* fossil specimens from the following sites: Sterkfontein and Swartkrans (StW, SK, southern Africa); Koobi Fora and Olduvai Gorge (KNM-ER, OH, eastern Africa); Uraha (UR, southeastern Africa); Hadar, Ledi-Geraru, and Omo (AL, L, LD, Omo, northeastern Africa); and Dmanisi, Georgia (D). These specimens are listed in
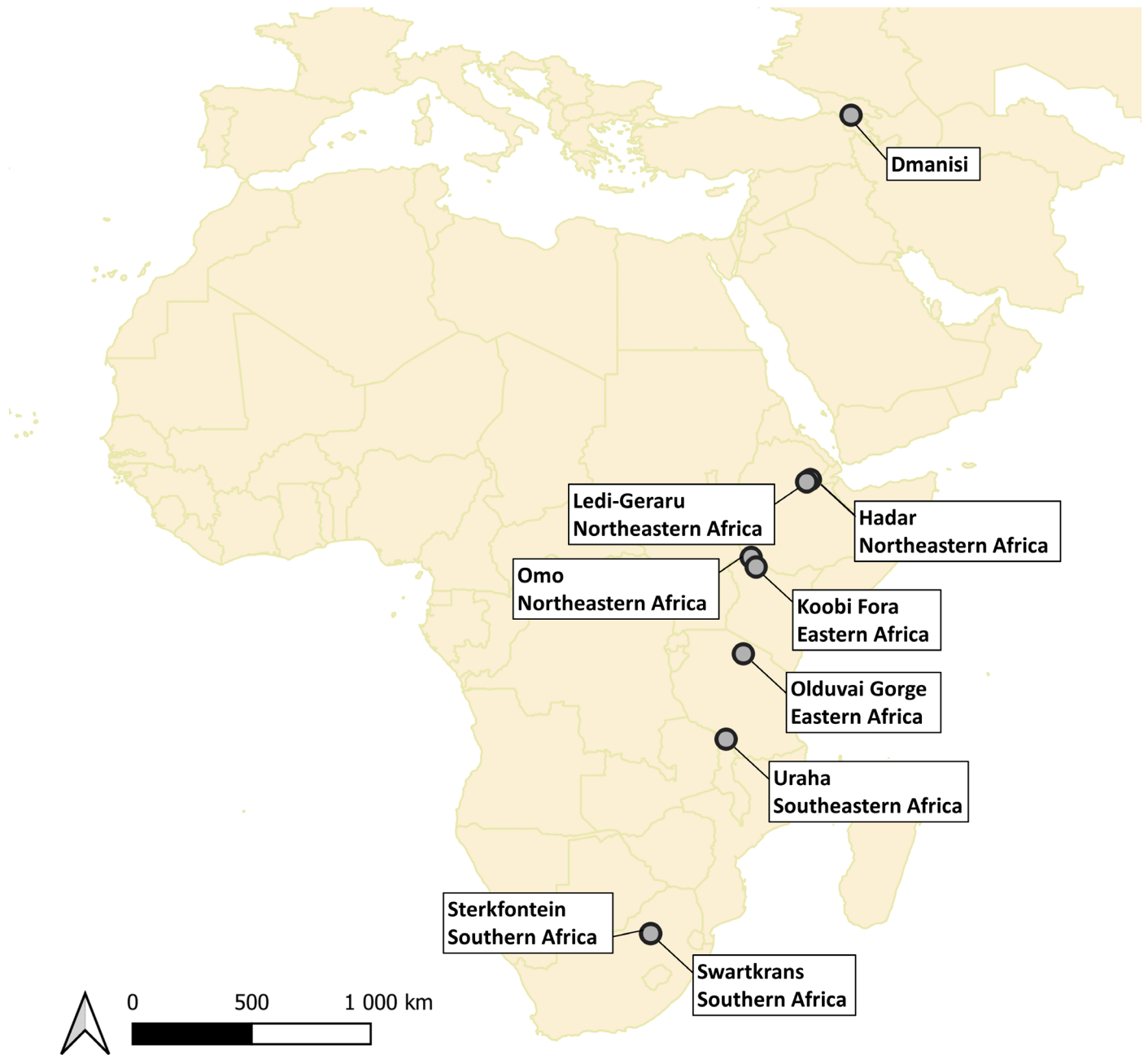
Figure 1. Map of specimen localities, including the geographic region of the localities utilized in this study (map created with QGIS).

Supplementary Material Table S1, together with their dates and geographic region. Specimens for which taxon identification has been questioned by Zanolli et al. (2022) are also indicated. A map of localities and geographic region is provided in Figure 1.

Two standard tooth measurements, buccolingual (BL) and mesiodistal (MD) maximum crown length, were collected from the literature. The literature is varied in its application of interstitial wear correction, but if a correction was made, then this estimated measurement was used. When applicable, data obtained from the left and right antimeres were averaged.

EXTANT HOMINOID SAMPLE

The comparative dental data comprises two extant hominoids: *Homo sapiens* and *Pan troglodytes*. The dataset includes both BL and MD maximum crown length measurements of the right dentition for all teeth. Buccolingual measurements of the mandibular molars can be collected either at the trigonid or the talonid. As some measurements in the published early *Homo* literature do not include this detail, the measurement that best reflects the maximum BL dimension, the trigonid, was used for this study. For each subset, individuals with missing data were excluded.

The modern samples are comprised of roughly equal

numbers of males and females. The *Homo sapiens* sample consists of 112 individuals (n=56 females, n=56 males) from the Raymond Dart Collection housed in the Department of Anatomical Sciences at the University of the Witwatersrand (South Africa). Approval was provided by the curator, B. Billings. The *Pan troglodytes* sample is part of the Hamann-Todd non-human primate collection housed at the Cleveland Museum of Natural History (USA) and comprises 81 individuals (n=49 females, n=32 males). All data were collected by LS using Mitutoyo digital sliding dental calipers following Plavcan (1990). Individuals with minimal dental wear were prioritized.

METHODS

PRINCIPAL COMPONENT ANALYSIS

A principal component analysis (PCA) was performed on the covariance matrices of each of the trait subsets (Table 1). Principal component plots of principal component (PC) 1 and PC2 were used to visualize the similarities and differences between hominin specimens in the context of the variation of our extant samples. As the regression tests that follow are based on principal components, we also use these PCA visualizations as a way to determine whether the dental traits we use are taxonomically diagnostic, that is, whether they can differentiate between groups, and whether the variation in our early *Homo* samples is comparable to what is seen in *Homo sapiens* and *Pan troglodytes*. These analyses were performed in PAST v4.11 (Hammer et al. 2001).

TESTING THE NULL HYPOTHESIS OF GENETIC DRIFT

According to Lande (1979), the neutral model of evolution for diverging populations is given by the equation: $B_t = G(t/N_e)$, whereby B_t is the expected between population variance/covariance (V/CV) matrix, G is the additive genetic V/CV matrix, t is the number of generations since divergence, and N_e is the effective population size. G-matrices are unattainable for fossil taxa, therefore, we use the phenotypic V/CV matrix as a substitute (P-matrix). The P-matrix has been found by Cheverud (1988) and others (e.g., Sodini et al. 2018) to be highly correlated with the G-matrix (~0.81) for large sample sizes (n>40), which has allowed for this substitution to be used in similar studies (e.g., Ackermann and Cheverud 2004; Marriog and Cheverud 2004; Schroeder and Ackermann 2017). The relationship therefore becomes $B_t = P(t/N_e)$. Following Ackermann and Cheverud (2002), we assess the between- and within-group phenotypic variation among early *Homo* specimens using a regression test based on the theory that if genetic drift is responsible for the size variation observed within early *Homo* dentition, a proportional relationship should exist for the pattern of between-group variation and within-group variation ($B_t \propto P$). In this particular use of the equation, t/N_e is treated as a constant.

Due to the small sample size of our fossil groups, the P-matrix could not be accurately estimated and therefore we use two extant species as models of within-group variation, namely *Homo sapiens* and *Pan troglodytes*. This is because although the pattern of within-group variation in the skull is similar across hominoids with different evolutionary histories (Ackermann 2002; Jung et al. 2023), we do not have a good grasp of the extent of hominin within-group variation, especially given the wide temporal variation. Therefore, using two model species with a ~7 Ma or older divergence date (Langergraber et al. 2012) represented by two relatively different V/CV matrices allows for a more conservative interpretation of the results. In addition, sexual dimorphism in each model species is accounted for by utilizing the residual covariance matrix from a MANOVA as our P-matrix, with sex as the independent variable.

To perform the regression test, first P is decomposed into its principal components. Next, B_t is calculated by finding the diagonal variance of the matrix generated from the product of the principal components of P (eigenvectors) and the group means of the fossil groups/individuals being compared. This comparison can be pairwise comparisons across two groups, or comparisons across multiple groups. Finally, Bt is logged and regressed on the log-transformed eigenvalues of P. If groups have diversified through genetic drift, then the regression slope will not be distinguishable from a slope of 1.0 at a predetermined significance level. A non-proportional relationship or rejection of the null hypothesis of genetic drift indicates greater than expected variability under a neutral model, therefore indicating that natural selection may have been at work. Multiple studies have shown the ability of this test to distinguish between genetic drift and selection in both fossil and extant groups (e.g., Ackermann and Cheverud 2004; Assis et al. 2017; Machado et al. 2022; Marroig and Cheverud 2004; Ponce de León et al. 2018; Schroeder and Ackermann 2017, 2023; Schroeder et al. 2014, 2022; Smith 2011; Tran and Schroeder 2021; Weaver et al. 2007).

Another aspect of this method that can be utilized to further assess the pattern of between and within-group variation is to consider the magnitude of the slope. Slopes larger than 1.0 indicate that there is more between-group variation in the major PCs than expected under a model of drift, whereas slopes smaller than 1.0 indicate that there is less than expected between-group variation in the major PCs. The latter can be indicative of stabilizing selection, and the former can signify diversifying selection (Ackermann and Cheverud 2002).

It is important to note that a failure to reject the null hypothesis is not the same as accepting the null hypothesis of genetic drift, nor does it completely remove the possibility that non-random processes were acting. Rather, it indicates that the effect of these processes is so small, they cannot be distinguished from divergence due to drift. In addition, the structure of the test makes it difficult to reject the null hypothesis when few traits are being compared. For this reason, any significant deviation from a slope of 1.0 will likely indicate that selection has occurred. We take this high false negative rate into account by assessing significance of our regression tests at an alpha level of 0.05 but also indicate

TABLE 1. LIST OF FOSSIL SPECIMENS AND TRAITS IN EACH SUBSET[a].

	Fossils	Geographic regions represented	Traits
Subset 1	SK 15, SK 45, SK 843t, D211, D2735, UR 501, Omo 74-18, KNM-ER 1506, KNM-ER 1802, KNM-ER 3734, KNM-ER 806, KNM-ER 992, OH 13, OH 16, OH 37, OH 7, KNM-ER 992, KNM-ER 60000, KNM-WT 15000, KNM-ER 64060 (n=20)	Southern Africa, Dmanisi, Northeastern Africa, Eastern Africa, Southeastern Africa	M_1 MD, M_2 MD, M_1 BL, M_2 BL (k=4)
Subset 2	SK 27, D2700, L894-1, KNM-ER 1590, KNM-ER 1805, KNM-ER 1813, A.L. 666-1, OH 13, OH 16, OH 24, OH 39, OH 65 (n=12)	Southern Africa, Dmanisi, Northeastern Africa, Eastern Africa	P^3 MD, M^1 MD, M^2 MD, P^3 BL, M^1 BL, M^2 BL (k=6)
Subset 3	SK 27, StW 151, StW 75-79, D2700, KNM-ER 1805, KNM-ER 1813, A.L. 666-1, OH 16, OH 39, OH 65 (n=10)	Southern Africa, Dmanisi, Northeastern Africa, Eastern Africa	I^2 MD, C^1 MD, P^3 MD, I^2 BL, C^1 BL (k=5)
Subset 4	D2700, KNM-ER 1590, KNM-ER 1805, KNM-ER 1813, A.L.666-1, OH 16, OH 39, OH 65 (n=8)	Southern Africa, Dmanisi, Northeastern Africa, Eastern Africa	C^1 MD, P^3 MD, P^4 MD, M^1 MD, M^2 MD, C^1 BL, P^3 BL, P^4 BL, M^1 BL, M^2 BL (k=10)
Subset 5	StW 151, D2735, D211, UR 501, Omo 75-14a, KNM-ER 1802, KNM-ER 3734, OH 13, OH 16, OH 7, KNM-ER 992, KNM-ER 60000, KNM-WT 15000, KNM-ER 64060 (n=14)	Southern Africa, Dmanisi, Northeastern Africa, Eastern Africa, Southeastern Africa	P_3 MD, P_4 MD, M_1 MD, P_3 BL, P_4 BL, M_1 BL (k=6)
Subset 6	StW 53, D2700, L894-1, KNM-ER 1506, KNM-ER 1590, KNM-ER 1805, KNM-ER 1813, A.L. 666-1, OH 13, OH 16, OH 24, OH 39, OH 65 (n=13)	Southern Africa, Dmanisi, Northeastern Africa, Eastern Africa	P^3 MD, P^4 MD, P^3 BL, P^4 BL (k=4)
Subset 7	StW 19b, StW 53, D2700, L894-1, KNM-ER 1805, KNM-ER 1813, KNM-ER 62000, OH 13, OH 16, OH 24, OH 65 (n=11)	Southern Africa, Dmanisi, Northeastern Africa, Eastern Africa	M^2 MD, M^3 MD, M^2 BL, M^3 BL (k=4)
Subset 8	D2735, KNM-ER 64060, KNM-ER 992, KNM-WT 15000, LD350-1, OH 7, StW 151 (n=7)	Southern Africa, Eastern Africa, Dmanisi, Northeastern Africa	I_2 MD, C_1 MD, P_3 MD, P_4 MD, I_2 BL, P_3 BL, P_4 BL (k=7)

[a]n = the number of specimens in each subset; k = the number of traits in each subset.

where p-values are close to significant (0.05>p< 0.1). While lowering the alpha value does not exactly offset this high false negative rate, it does provide a way to assess the pattern of results (as reflected by the regression tests and their plots) against a more reasonable benchmark given the test's low power. All regression tests were performed in R version 4.1.3 using the DriftTest function in the package 'EvolQG' v. 0.2-9 (Melo et al. 2016).

ANALYSIS PLAN

Due to the incompleteness of the early *Homo* dental data, not all specimens share the same traits (i.e., MD or BL lengths of certain teeth). As a result, multiple trait subsets were constructed to maximize the number of specimens in some and maximize the number of shared traits in others, and to include as many fossils specimens as possible from various sites to account for geographic variation. This re-

sulted in eight trait subsets, as shown in Table 1. The table provides information about the number of traits, which traits these are, and number of individuals in each subset. In subsequent analyses, each subset was analyzed separately.

For the analyses of these eight subsets, we focused on comparing early *Homo* specimens across geographic regions, and through time. The first set of analyses compared specimens in each subset grouped according to their respective geographic regions (number of regions range from 4 to 5 per subset), with the aim of determining whether genetic drift could explain the differences in dental size variation among eastern African, southern African, southeastern African, northeastern African, and Georgian early *Homo* specimens. The second set of analyses compared specimens grouped according to geological age. Specimens were divided into those between 2.8 and 2.3 Ma (designated 'earliest *Homo*'), those between 2.29 and 1.8 Ma (designated 'early *Homo*'), and those younger than 1.79 Ma (designated as 'later *Homo*'), resulting in three temporal groups. These date ranges were chosen as they mark major environmental changes documented in various climatic, isotopic, sedimentary, and vegetation records, which have been proposed as important influences for the evolution of our genus (Dupont et al. 2005; Pickering et al. 2019; Potts 2012; Potts and Faith 2015; Schroeder 2021; Trauth et al. 2005). If drift is rejected, we also performed more detailed pairwise analyses between regions and between time periods to further understand the adaptive scenarios that could potentially be at play. Finally, we reran all regional analyses with an updated southern African early *Homo* dataset based on the findings of Zanolli et al. (2022) to determine if the exclusion of specimens identified in their study as not belonging to the genus *Homo* would affect our results.

RESULTS

PRINCIPAL COMPONENT ANALYSES
Figure 2 presents the PC plots (of PC1 and PC2) for each trait subset described in Table 1, and PC loadings are given in Supplementary Material Table S2. The first two PCs explain between 86% and 93% of the variation between specimens across the eight subsets. In most plots, group separation occurs along PC1, with some overlap, but analyses 4, 5, and 8 display complete separation between groups (see Figure 2D, E, H). These analyses also have more traits than the first set (between 6 and 10 traits each), indicating that more traits are useful for taxonomic separation.

In trait subset 1, a mandibular subset with the largest number of fossils, the early *Homo* sample displays greater variability than both the *Pan troglodytes* and *Homo sapiens* groups, indicating taxonomic diversity within this group (see Figure 2A). There is overlap between southern and eastern African early *Homo* specimens, however, the specimen from northeastern Africa (Omo 74-18) falls outside of these convex hulls. UR 501 from southeastern Africa is another early *Homo* specimen that separates from the rest. In subset 2, a maxillary subset, there is separation of

early *Homo* from the comparative groups (see Figure 2B), with most specimens falling within a convex hull denoting eastern African specimens, and no obvious separation between specimens from different time periods. The two specimens that fall slightly outside of the early *Homo* group are SK 27 from southern Africa and L894-1 from northeastern Africa. Subset 3, a maxillary subset, shows overlap between the early *Homo* group and both *Pan troglodytes* and *Homo sapiens* (see Figure 2C). Dmanisi specimen D2700, and northeastern Africa specimen A.L. 666-1, fall outside of the eastern and southern Africa convex hulls, however, subset 3 may not reflect the extent of variability of these groups due to its smaller sample size. Subsets 4 and 5 produce complete separation between groups (see Figure 2D, E). In subset 4, a maxillary subset, D2700 falls outside of the early *Homo* convex hull, and in subset 5, a mandibular analysis, Omo 74-18, D2735, and UR 501 fall outside of the convex hull representing eastern African early *Homo* variability. At 2.5 Ma, the UR 501 mandible is one of the earliest *Homo* specimens. Maxillary subsets 6 and 7 show overlap between some comparative groups (see Figure 2F, G). The early *Homo* group is differentiated from *Pan troglodytes* and *Homo sapiens* along PC1. Two southern African specimens, Stw 53 and Stw 19b fall outside of the eastern African early *Homo* convex hull in subset 6 and 7 respectively. Both of these specimens have been reassigned to *Australopithecus* in Zanolli et al. (2022). In addition, no differentiation across time periods in the PCA plots of subsets 6 and 7 is easily discernible. Finally, due to the small number of specimens in subset 8, the convex hull most likely does not capture the full extent of variation of the early *Homo* group (see Figure 2H). However, we note that LD350-1, the earliest *Homo* specimen to date, falls far outside of the early *Homo* convex hull, at both positive extremes of PC1 and PC2.

REGRESSION ANALYSES BY REGION
The results of logged between-group (y-axis) regressed on logged within-group variation (x-axis) across early *Homo* dentition grouped by geographic region for the eight subsets are summarized in Table 2. The results indicate that in approximately 75% of all analyses performed using both comparative V/CV matrices (human and chimpanzee), the null hypothesis of genetic drift could not be rejected (at a 0.1 significance level). This is apparent in subsets 1, 3, 5, 6, and 8 (see Table 2). These results suggest that differences in the pattern of covariance for dental size as measured by the traits in these subsets (see Table 1) are negligible regardless of regional diversity.

In the remaining 25% of cases, rejections are detected in subsets 2, 4, and 7, which are all analyses of maxillary dental data. Those designated with 'possibly' are representative of p-values between 0.05 and 0.10. For subset 2, a possible rejection of the null hypothesis is apparent within the early *Homo* sample using a *Pan troglodytes* V/CV matrix (see Table 2). For subset 4, a rejection of the null hypothesis of genetic drift is present within early *Homo* using both *Homo sapiens* and *Pan troglodytes* V/CV matrices. For subset 7, a possible rejection of the null hypothesis of genetic
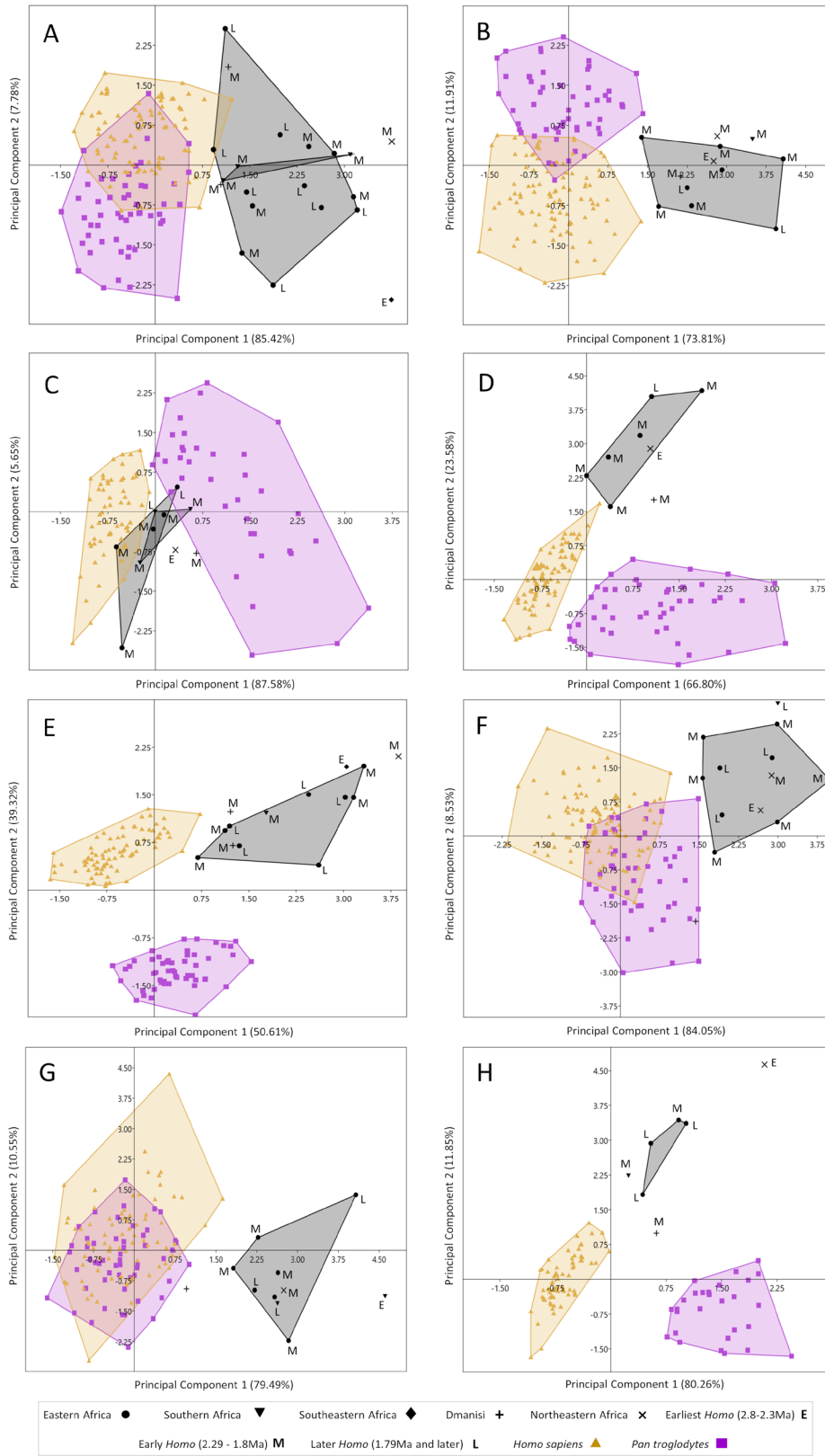
Figure 2. Principal component plots for each subset. Symbol legend is provided below the figure. Convex hulls are drawn to indicate the species distributions of Homo sapiens *and* Pan troglodytes *(orange and purple, respectively), as well as various regions in the early* Homo *group (grey, differentiated by symbols). Specimens in the early* Homo *group are also labelled according to time period. Early* Homo *specimens in each subset are described in Table 1. A) Subset 1; B) Subset 2; C) Subset 3; D) Subset 4; E) Subset 5; F) Subset 6; G) Subset 7; H) Subset 8.*

TABLE 2. RESULTS OF REGRESSION ANALYSES OF BETWEEN- VERSUS WITHIN-GROUP VARIANCE ACROSS REGIONS AS A TEST OF THE NULL HYPOTHESIS OF GENETIC DRIFT[a].

Subset	Extant Model	Rejection of Genetic Drift?[b]	Slope	95% Slope Confidence Interval		R^2	*t*-stat	*p*-value
Subset 1 (Mandibular)	*Homo sapiens*	No	1.25	-0.26	2.76	0.86	0.71	0.55
	Pan troglodytes	No	1.70	0.54	2.86	0.95	2.60	0.12
Subset 2 (Maxillary)	*Homo sapiens*	No	0.80	0.20	1.40	0.77	0.92	0.41
	Pan troglodytes	Possibly	0.34	-0.47	1.14	0.25	2.29	**0.08**
Subset 3 (Maxillary)	*Homo sapiens*	No	0.86	-0.47	2.19	0.59	0.33	0.77
	Pan troglodytes	No	1.09	0.32	1.86	0.87	0.37	0.74
Subset 4 (Maxillary)	*Homo sapiens*	Yes	0.23	-0.32	0.79	0.10	3.19	**0.01**
	Pan troglodytes	Yes	0.40	-0.14	0.95	0.27	2.53	**0.04**
Subset 5 (Mandibular)	*Homo sapiens*	No	1.16	0.29	2.03	0.77	0.50	0.64
	Pan troglodytes	No	1.11	-0.90	3.12	0.37	0.15	0.89
Subset 6 (Maxillary)	*Homo sapiens*	No	0.41	-1.32	2.15	0.34	1.46	0.28
	Pan troglodytes	No	1.21	-1.81	4.24	0.60	0.30	0.79
Subset 7 (Maxillary)	*Homo sapiens*	No	1.63	0.59	2.68	0.96	2.61	0.12
	Pan troglodytes	Possibly	1.87	0.81	2.94	0.97	3.52	**0.07**
Subset 8 (Mandibular)	*Homo sapiens*	No	1.14	0.38	1.89	0.75	0.46	0.66
	Pan troglodytes	No	0.99	-0.26	2.24	0.45	0.01	0.99

[a]Significant *p*-values at an alpha level of 0.1 are shown in bold.
[b]Analyses designated as 'yes' are representative of *p*-values less than 0.05 and those designated as 'possibly' are representative of *p*-values between 0.05 and 0.10.

drift is present within early *Homo* using a *Pan troglodytes* V/CV matrix. The slope for analyses 2 and 4 is <1.0, and the examination of the regression plots indicates that there is less between-group variation (y-axis) than within-group variation (x-axis) in the first few PCs and more in the lesser PCs, where numbers on the figures represent the numbers of these PCs (Figure 3A, B, C). This may point to the action of stabilizing selection on the major PCs. In contrast, the slope for subset 7 is >1.0, which indicates more between-group variation in the first few PCs and less in the minor PCs (Figure 3D), pointing to diversifying selection on the major PCs. All other regression plots can be found in Supplementary Material Figure S1.

When these analyses were conducted on an updated southern African early *Homo* sample (in accordance with Zanolli et al. 2022), we find minimal differences between regression results (see Table 2 compared to Supplementary Material Table S3), and therefore, to maximize sample size, no further analyses based on this updated dataset were conducted.

REGRESSION ANALYSES BY TIME PERIOD
Table 3 summarizes the results of logged between-group regressed on logged within-group variation across early *Homo* dentition when the data are separated according to time period for the eight subsets. The results indicate that in approximately 81% of all analyses using both comparative V/CV matrices, the null hypothesis of genetic drift cannot be rejected (at a 0.10 alpha level). This is apparent in maxillary analyses 1, 3, 4, 5, 6, and 8 (see Table 3). In the remaining 19% of cases, drift is rejected at a 0.10 alpha level in analyses 2 and 7. For subset 2, a rejection of the null hypothesis is present within early *Homo* using both *Homo sapiens* and *Pan troglodytes* V/CV matrices. For subset 7, a possible rejection is detected using only the *Pan troglodytes* V/CV matrix. The slope for all analyses that produced rejections of the null hypothesis of genetic drift is greater than 1.0, indicating more between-group variation in the first few PCs and less than expected in the minor PCs, and possibly pointing to diversifying selection (Figure 4A, B, C). All other regression plots can be found in Supplementary Material Figure S2.
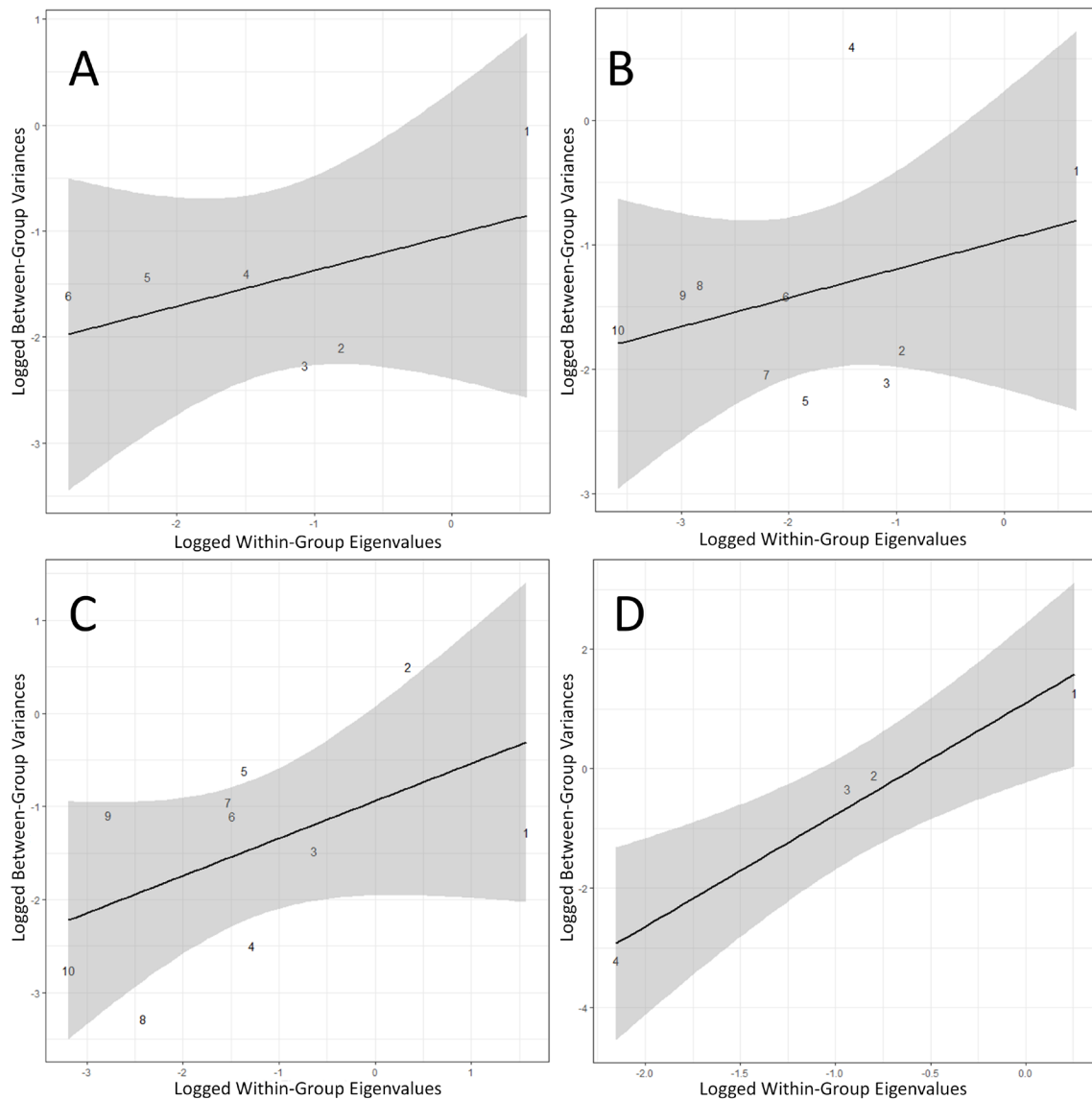
*Figure 3. Regression plots of between versus within-group variance for **regional** analyses for which the null hypothesis of genetic drift was rejected (indicated in Table 2). Regression points (x, y) are labelled as numbers, which refers to principal component numbers. Within-group variance (logged eigenvalues) is on the x-axis, and between-group variance (variance along the diagonal of the product of group means and eigenvectors) is on the y-axis. 95% confidence intervals are shown. A) Subset 2 – Pan troglodytes V/CV model; B) Subset 4 – Homo sapiens V/CV model; C) Subset 4 – Pan troglodytes V/CV model; D) Subset 7 – Pan troglodytes V/CV model.*

REGIONAL AND TEMPORAL PAIRWISE REGRESSION ANALYSES

To better understand the potential driving factors within the subsets that produced a rejection of the null hypothesis of genetic drift, we conducted a series of pairwise comparisons, first between geographic regions, and then time periods. For the regional groups, some of which were also separated by time period within region, pairwise regression analyses of between- versus within-group variance were performed on subsets 2, 4, and 7 (Table 4). In subset 2, there was a rejection of the null hypothesis of genetic drift between dentition from northeastern Africa and eastern Africa (p<0.05), and a possible rejection between the earliest *Homo* and later *Homo* in eastern Africa (p<0.10). In sub-

set 4, there was a rejection of the null hypothesis between the Dmanisi hominins and early *Homo* from eastern Africa (p<0.05). In subset 7, there were possible rejections of the null hypothesis of genetic drift (p<0.10) between the Dmanisi hominins and early *Homo* from eastern Africa, between Dmanisi and northeastern Africa, and northeastern Africa and eastern Africa. Finally, there a was a rejection of the null hypothesis of genetic drift between the earliest *Homo* and later *Homo* in southern Africa (p<0.05).

The pairwise regression analyses results within time periods were performed on subsets 2 and 7 (Table 5). As a reminder, specimens were divided into those between 2.8 and 2.3 Ma (designated 'earliest *Homo*'), those between 2.29 and 1.8 Ma (designated 'early *Homo*'), and those younger

TABLE 3. RESULTS OF REGRESSION ANALYSES OF BETWEEN- VERSUS WITHIN-GROUP VARIANCE ACROSS TIME PERIODS AS A TEST OF THE NULL HYPOTHESIS OF GENETIC DRIFT[a].

Subset	Extant Model	Rejection of Genetic Drift?[b]	Slope	95% Slope Confidence Interval		R²	t-stat	*p*-value
Subset 1 (Mandibular)	*Homo sapiens*	No	1.37	-1.60	4.35	0.66	0.54	0.64
	Pan troglodytes	No	1.96	-1.61	5.52	0.74	1.16	0.37
Subset 2 (Maxillary)	*Homo sapiens*	Yes	-0.11	-0.85	0.63	0.04	4.15	**0.01**
	Pan troglodytes	Yes	0.00	-0.88	0.89	0.00	3.14	**0.03**
Subset 3 (Maxillary)	*Homo sapiens*	No	0.51	-0.92	1.93	0.30	1.10	0.35
	Pan troglodytes	No	0.70	0.05	1.35	0.80	1.45	0.24
Subset 4 (Maxillary)	*Homo sapiens*	No	0.97	-0.20	2.13	0.31	0.07	0.95
	Pan troglodytes	No	0.49	-0.53	1.51	0.13	1.15	0.28
Subset 5 (Mandibular)	*Homo sapiens*	No	1.76	0.62	2.90	0.82	1.84	0.14
	Pan troglodytes	No	0.98	-2.31	4.27	0.15	0.02	0.99
Subset 6 (Maxillary)	*Homo sapiens*	No	1.61	-3.24	6.46	0.51	0.54	0.64
	Pan troglodytes	No	0.61	-1.37	2.59	0.46	0.86	0.48
Subset 7 (Maxillary)	*Homo sapiens*	No	1.57	-0.75	3.89	0.81	1.06	0.40
	Pan troglodytes	Yes	1.69	1.30	2.07	0.99	7.57	**0.02**
Subset 8 (Mandibular)	*Homo sapiens*	No	1.00	-1.72	3.72	0.15	0.00	1.00
	Pan troglodytes	No	1.17	0.22	2.12	0.67	0.47	0.66

[a]Significant *p*-values at an alpha level of 0.1 are shown in bold.
[b]Analyses designated as 'yes' are representative of *p*-values less than 0.05 and those designated as 'possibly' are representative of *p*-values between 0.05 and 0.10.

than 1.79 Ma (designated as 'later *Homo*'). In subset 2, there were rejections of the null hypothesis detected between the earliest *Homo* and early *Homo*, and between the earliest *Homo* and later *Homo* (p<0.05). In subset 7, there were potential rejections of the null hypothesis of genetic drift between the earliest *Homo* and early *Homo*, and between early *Homo* and later *Homo* (p<0.10).

DISCUSSION

The main aim of this study was to determine if genetic drift or natural selection was responsible for the observed diversification in early *Homo* tooth size. In the majority of analyses, we could not reject the null hypothesis of genetic drift. While it is difficult to reject a model of genetic drift when the number of traits is small, this result indicates that dental size variation between most fossils grouped according to time and geography is proportional to that seen within groups. Similar to previous craniomandibular studies (Schroeder and Ackermann 2017; Schroeder et al. 2014), the results reported here point to the potential importance of non-adaptive processes during the evolution of *Homo*.

In the cases where the null hypothesis of genetic drift was rejected or 'possibly' rejected, natural selection may have had a role in the divergence of groups within the

early *Homo* hypodigm. Firstly, analyses conducted across different regions yielded rejections or 'possible' rejections of the null hypothesis of genetic drift in maxillary subsets 2, 4, and 7, and analyses across different time periods (2.8 and 2.3 Ma, 2.29 and 1.8 Ma, younger than 1.79 Ma) yielded rejections or 'possible' rejections of the null hypothesis in maxillary subsets 2 and 7 (see Tables 2 and 3). Subset 2 in both the regional and temporal analysis, and subset 4 in the regional analysis produced slopes below 1.0, demonstrating less between-group variation or more within-group variation than expected under a neutral model, which may reflect stabilizing selection in the major PCs. Subset 7 in both the regional and temporal analysis produced a slope greater than 1.0 indicating more between-group variation than expected under conditions of neutrality, which may reflect diversifying selection in the major PCs. Noteworthy is that more rejections of the null hypothesis of genetic drift were detected across regions than time periods (see Table 2 versus Table 3), indicating that for some cases, ecological changes due to climate shifts over the time range analyzed here may not have produced a strong selective response in dental size variation. This result supports our prediction of finding a rejection of the null hypothesis across different geographic regions, which may reflect a difference in base-
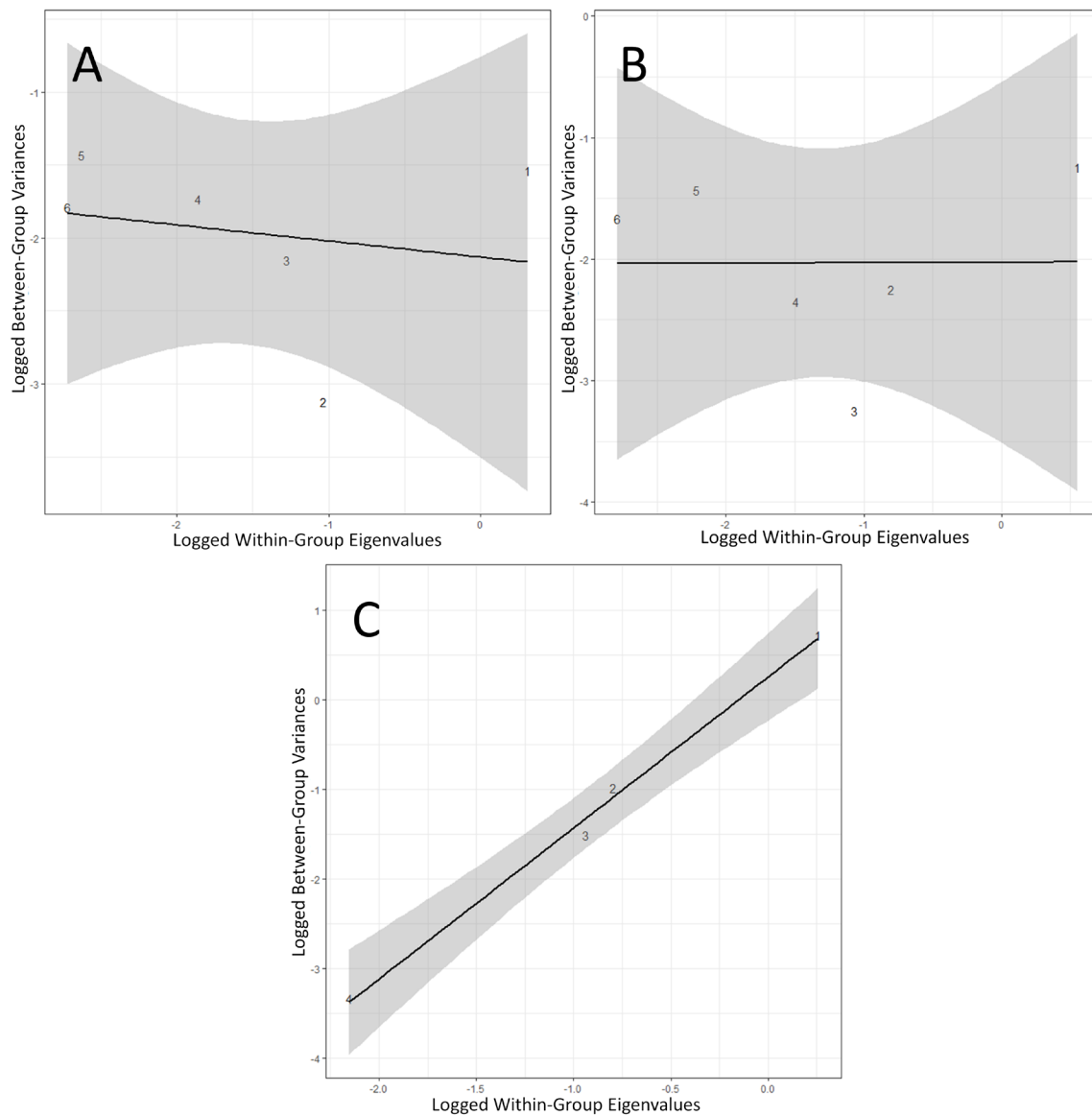
*Figure 4. Regression plots of between versus within-group variance for **temporal** analyses for which the null hypothesis of genetic drift was rejected (indicated in Table 3). Regression points (x, y) are labelled as numbers, which refers to principal component numbers. Within-group variance (logged eigenvalues) is on the x-axis, and between-group variance (variance along the diagonal of the product of group means and eigenvectors) is on the y-axis. 95% confidence intervals are shown. A) Subset 2 – Homo sapiens V/CV model; B) Subset 2 – Pan troglodytes V/CV model; C) Subset 7 – Pan troglodytes V/CV model.*

line environmental conditions. Another important point is that two models for V/CV estimation were utilized in this study, *P. troglodytes* and *H. sapiens*, to account for our lack of understanding of variation in fossil groups. This decision sometimes led to differential results in the regression tests, which is a direct reflection of the difference between the pattern of variation represented by these estimated V/CV matrices, so analyses with consistent results using both models could be considered more robust. However, as mentioned above, these regression tests have high false negative rates, so when there is some evidence of a deviation from a slope of 1.0, this is most likely to indicate an inconsistency with the neutral model of evolution.

More detailed pairwise analyses provided further insight into these rejections (see Tables 4 and 5). The null hypothesis of genetic drift was rejected (at an alpha level of 0.10) between the earliest *Homo* and other *Homo* specimens in maxillary subset 2, and the earliest *Homo* compared to early-mid geologically aged *Homo* specimens as well as early-mid *Homo* compared to later *Homo* in maxillary subset 7 (see Table 5). Pairwise analyses of regional groups (see Table 4) showed that the rejections of the null hypothesis in subset 2 across both regional and temporal analyses are driven by comparisons with A.L. 666-1—a maxilla from northeastern Africa dated to 2.33 Ma and the only specimen included in the 'earliest *Homo*' grouping in this analysis—

TABLE 4. PAIRWISE REGRESSION TEST RESULTS FOR REJECTIONS OF DRIFT IDENTIFIED IN TABLE 2 (regional analyses)[a].

Pairwise comparison	Extant model	Rejection of Genetic Drift?[b]	Slope	95% Slope Confidence Interval		R²	t-stat	*p*-value
Subset 2								
Eastern Africa - Southern Africa	*Homo sapiens*	No	1.05	0.19	1.91	0.74	0.16	0.88
	Pan troglodytes	No	0.02	0.00	-2.53	0.00	1.07	0.34
Southern Africa - Dmanisi	*Homo sapiens*	No	1.47	-0.07	3.02	0.64	0.85	0.44
	Pan troglodytes	No	0.87	0.22	-1.43	0.22	0.16	0.88
Dmanisi - Eastern Africa	*Homo sapiens*	No	0.76	-1.49	3.00	0.18	0.30	0.78
	Pan troglodytes	No	0.83	0.19	-1.56	0.19	0.20	0.85
Northeastern Africa - Dmanisi	*Homo sapiens*	No	0.76	-1.64	3.16	0.16	0.27	0.80
	Pan troglodytes	No	0.70	0.28	-0.85	0.28	0.54	0.62
Northeastern Africa - Eastern Africa	*Homo sapiens*	Yes	-0.29	-1.54	0.96	0.09	2.86	**0.05**
	Pan troglodytes	No	-1.20	0.18	-4.73	0.18	1.74	0.16
Northeastern Africa - Southern Africa	*Homo sapiens*	No	2.69	-1.87	7.26	0.40	1.03	0.36
	Pan troglodytes	No	0.37	0.04	-2.01	0.04	0.74	0.50
Early *Homo* - Later *Homo* in Eastern Africa	*Homo sapiens*	Possibly	0.34	0.24	-0.50	0.24	2.19	**0.09**
	Pan troglodytes	No	0.80	0.32	-0.81	0.32	0.34	0.75
Subset 4								
Dmanisi - Eastern Africa	*Homo sapiens*	Yes	0.03	-0.92	0.97	0.00	2.37	**0.05**
	Pan troglodytes	No	0.85	-0.23	1.92	0.29	0.33	0.75
Northeastern Africa - Dmanisi	*Homo sapiens*	No	0.34	-1.17	1.84	0.03	1.02	0.34
	Pan troglodytes	No	0.15	-0.98	1.28	0.01	1.74	0.12
Northeastern Africa - Eastern Africa	*Homo sapiens*	No	1.09	0.03	2.15	0.41	0.19	0.85
	Pan troglodytes	No	0.12	-1.21	1.45	0.01	1.53	0.17
Early *Homo* - Later *Homo* in Eastern Africa	*Homo sapiens*	No	1.15	-0.39	2.70	0.27	0.23	0.82
	Pan troglodytes	No	0.75	-0.24	1.73	0.28	0.59	0.57
Subset 7								
Eastern Africa - Southern Africa	*Homo sapiens*	No	1.52	-0.72	3.76	0.81	1.00	0.42
	Pan troglodytes	No	2.88	-1.42	7.18	0.81	1.88	0.20
Southern Africa - Dmanisi	*Homo sapiens*	No	1.68	0.24	3.12	0.93	2.04	0.18
	Pan troglodytes	No	2.74	0.05	5.43	0.91	2.78	0.11
Dmanisi - Eastern Africa	*Homo sapiens*	No	1.81	-0.94	4.55	0.80	1.27	0.33
	Pan troglodytes	Possibly	2.67	0.68	4.67	0.94	3.61	**0.07**
Northeastern Africa - Dmanisi	*Homo sapiens*	No	2.31	-0.17	4.79	0.89	2.26	0.15
	Pan troglodytes	Possibly	2.94	0.41	5.48	0.93	3.30	**0.08**

TABLE 4. PAIRWISE REGRESSION TEST RESULTS FOR REJECTIONS OF DRIFT IDENTIFIED IN TABLE 2 (regional analyses)[a] (continued).

Pairwise comparison	Extant model	Rejection of Genetic Drift?[b]	Slope	95% Slope Confidence Interval		R²	t-stat	*p*-value
Subset 7								
Northeastern Africa - Eastern Africa	*Homo sapiens*	Possibly	-0.55	-2.20	1.10	0.51	4.05	**0.06**
	Pan troglodytes	No	-0.28	-4.32	3.76	0.04	1.36	0.31
Northeastern Africa - Southern Africa	*Homo sapiens*	No	1.07	-0.17	2.31	0.87	0.24	0.83
	Pan troglodytes	No	1.41	0.36	2.47	0.94	1.68	0.23
Early *Homo* - Later *Homo* in Eastern Africa	*Homo sapiens*	No	4.75	-3.77	13.27	0.74	1.89	0.20
	Pan troglodytes	No	1.69	0.60	2.78	0.96	2.71	0.11
Earliest *Homo* - Later *Homo* in Southern Africa	*Homo sapiens*	Yes	2.60	1.87	3.34	0.99	9.38	**0.01**
	Pan troglodytes	No	1.99	0.86	3.12	0.97	3.78	0.06

[a]Significant *p*-values at an alpha level of 0.1 are shown in bold.
[b]Analyses designated as 'yes' are representative of *p*-values less than 0.05 and those designated as 'possibly' are representative of *p*-values between 0.05 and 0.10.

as well as dental size variability across time in eastern Africa (see Table 1 for specimens included in this analysis). In terms of the underlying cause of morphological variability in eastern Africa, a previous paleoclimatic study suggested that this was indicative of an adaptive signal (Potts and Faith 2015). This suggestion is comparable to our finding of adaptive divergence in dental traits within eastern Africa between 2.3–1.5 Ma (during a period of high climatic variability), and may possibly be reflecting taxonomic diversity within this group (e.g., *Homo habilis* and *Homo rudolfensis*). In maxillary subset 4, we rejected the null hypothesis of genetic drift (at a 0.10 alpha level) between dentition from Dmanisi and eastern African early *Homo* specimens. This result mirrors that of a previous craniomandibular study (Schroeder and Ackermann 2017), possibly reflecting adaptive divergence as hominins moved out of Africa and into different habitats and climates. The rejections of the null hypothesis (at an alpha level of 0.10) detected in subset 7 in both the regional and temporal analyses are driven by the comparisons of StW 19b and StW 53, specimens from Sterkfontein that may be represented by some time depth and the only southern African specimens in this analysis. Both of these specimens have recently been reassigned to *Australopithecus* by Zanolli et al. (2022) based on the dentine surface of their teeth, which adds an interesting possibility that perhaps these two specimens are adaptively different; an inference that would support Zanolli et al.'s (2022) between-group principal component analyses showing that Stw 53 groups separately from Stw 19b. The PCA plots in Figure 2 generally agree with these results in that they highlight the differentiation between specimens mentioned above (e.g., Dmanisi) and other early *Homo* groups. Two additional notable results from the PCAs are firstly that the size of the early *Homo* convex hulls in some analyses are larger than the convex hulls of the comparative species (*H. sapiens* and *P. troglodytes*) indicating a larger amount of variation (i.e., see Figure 2A, E), and then, secondly, that there is a large separation between the earliest *Homo* specimen, LD 350-1, and other specimens in Figure 2H. These findings could signify taxonomic diversity within the hypodigm. However, importantly, for LD 350-1, if this result is indicative of taxonomic differentiation, it is not driven by adaptive divergence.

An interesting finding in our analyses is the difference in results in maxillary and mandibular dentition; the null hypothesis was only rejected for maxillary teeth. When considering the pattern of the slopes (above or below 1.0), it appears that most mandibular analyses produce slopes above 1.0 (5/6 in Table 1 and 4/6 in Table 2), and most maxillary analyses produce slopes below 1.0 (6/10 in both Table 1 and 2). This pattern suggests more stabilizing selection in maxillary dentition, however, the slopes associated with rejections of the null hypothesis of genetic drift are both below and above 1.0.

Another possibility is to interpret the difference in results between maxillary and mandibular dentition through a morphological integration lens. Morphological integration refers to the coordination/covariation of phenotypic traits due to functional, developmental, or genetic factors (Hallgrímsson et al. 2009; Olson and Miller 1958), leading

**TABLE 5. PAIRWISE REGRESSION TEST RESULTS FOR REJECTIONS OF DRIFT
IDENTIFIED IN TABLE 3 (temporal analyses)[a].**

Pairwise comparison	Extant model	Rejection of Genetic Drift? [b]	Slope	95% Slope Confidence Interval		R²	t-stat	*p*-value
Subset 2								
Earliest *Homo* - Early *Homo*	*Homo sapiens*	No	-0.72	-3.68	2.24	0.10	1.62	0.18
	Pan troglodytes	Yes	-0.44	-1.37	0.49	0.30	4.29	**0.01**
Earliest *Homo* - Later *Homo*	*Homo sapiens*	Yes	-0.23	-1.41	0.94	0.07	2.91	**0.04**
	Pan troglodytes	Yes	-0.06	-0.98	0.86	0.01	3.19	**0.03**
Early *Homo* - Later *Homo*	*Homo sapiens*	No	0.16	-1.38	1.69	0.02	1.52	0.20
	Pan troglodytes	No	0.31	-1.45	2.08	0.06	1.08	0.34
Subset 7								
Earliest *Homo* - Early *Homo*	*Homo sapiens*	Possibly	0.19	-0.89	1.27	0.22	3.23	**0.08**
	Pan troglodytes	No	0.73	-2.13	3.58	0.37	0.41	0.72
Earliest *Homo* - Later *Homo*	*Homo sapiens*	No	1.79	-0.94	4.53	0.80	1.25	0.34
	Pan troglodytes	No	1.40	-1.26	4.05	0.72	0.64	0.59
Early *Homo* - Later *Homo*	*Homo sapiens*	No	2.57	-1.70	6.84	0.77	1.58	0.25
	Pan troglodytes	Possibly	2.65	0.20	5.09	0.92	2.90	**0.10**

[a]Significant *p*-values at an alpha level of 0.1 are shown in bold.
[b]Analyses designated as 'yes' are representative of *p*-values less than 0.05 and those designated as 'possibly' are representative of *p*-values between 0.05 and 0.10.

to potential coevolution of traits (Cheverud 1996). Modularity refers to instances where a subset of traits is highly integrated with one another to the exclusion of other traits (Hallgrímsson et al. 2009). The effect of these two factors on the evolution of morphology relates to the ability of a population to respond to natural selection, as highly integrated traits would be more constrained to evolve in certain directions than weakly integrated traits that could evolve in any direction (Hallgrímsson et al. 2009; Hansen and Houle 2008). A geometric morphometric shape study by Gómez-Robles and Polly (2012) of hominin teeth found that while all dentition is strongly integrated, when looking at each arcade separately there is weaker morphological integration between postcanine maxillary dentition compared to postcanine mandibular dentition. This evolutionary dynamic is also seen in studies of pleiotropic effects on dentition, which have indicated incomplete pleiotropy in maxillary teeth, reflected in weaker genetic correlations between teeth, compared to the mandibular arcade (Hlusko 2004). Gómez-Robles and Polly (2012) describe their results as

reflective of lower dentition being more tightly integrated as a whole due to the evolutionary constraint imposed by relatively evolutionarily stable mandibular morphology in hominids (Polanski 2011), whereas the upper dentition is less integrated as a whole, which could be linked to more variable patterns of integration in the cranium and face of hominids (Polanski and Franciscus 2006), meaning that the upper dentition can more freely respond to selective pressures (Gómez-Robles and Polly 2012). In our study, the finding that rejections of the null hypothesis of genetic drift are limited to maxillary dentition is consistent with this reasoning in Gómez-Robles and Polly (2012), and although we focus on dental size variation here, our results may be reflecting the possibility that strong selective responses are more likely to be detected in maxillary dentition as these teeth are less integrated.

Overall, our results indicate that the null hypothesis of genetic drift could not be rejected in the majority of comparisons. For the cases that are not consistent with the neutral model of evolution, adaptive diversification in the den-

tition within early *Homo* (Ungar 2012) may be a result of environmental changes (Bobe and Behrensmeyer 2004; Cerling 1992; Reed 1997; Stanley 1992; Vrba 1985, 1995, 1996), environmental variability (Potts 1998; Schroeder 2021), dietary changes (e.g., Ungar 2012) and/or shifts to new foraging strategies (Braun et al. 2010; Ferraro et al. 2013; Lepre et al. 2011; Potts 2012; Stanley 1992). While we do not find strong adaptive signals in the teeth to support Vrba's (1985) Turnover Pulse Hypothesis for adaptive changes occurring between 2.7 and 2.5 Ma, results of subset 2 do support models of adaptive responses to climatic variability in eastern Africa after 2.3 Ma (e.g., Potts and Faith 2015). The lack of adaptive signals do, however, corroborate results of recent stable isotope analyses, which indicate that the diet of the earliest *Homo* specimen, L.D. 350-1 was similar to that of *Australopithecus*, despite changing environments (Patterson et al. 2019; Robinson et al. 2017).

Although the findings of our study mirror those of previous studies of the genus *Homo* that have indicated a mixture of non-adaptive and adaptive processes at play (e.g., Baab 2018, 2021; Diniz-Filho and Raia 2017; Gómez-Robles et al. 2017; Schroeder and Ackermann 2017; Schroeder et al. 2014; Weaver et al. 2007), and expand the assessment of evolutionary processes in the hominin fossil record by analyzing dental metrics, there are inherent methodological problems that need to be stated.

As with most research of hominin fossil data, the sample sizes are small. For dental remains, the sample size issue is exacerbated by the majority being represented by isolated teeth, which may lead to a misrepresentation of variation in the early *Homo* hypodigm (as discussed above). As a result, this limits the number of analyses that can be performed, and decisions must be made whether to maximize the number of specimens or the number of variables for each subset. In addition, a recent study by Rathmann et al. (2023) shows that when assessing patterns of neutral variation in humans, non-metric dental data outperforms standard dental metrics. Therefore, a future study should incorporate additional data types (non-metric, shape, etc.) to fully assess the null hypothesis of genetic drift underlying dental evolution in the genus *Homo*. Finally, the early *Homo* dataset used in this study is collated from the published literature, meaning that inter-observer error in how teeth are measured could bias these measurements. It is not possible to quantify the inter-observer error rate but given the early *Homo* convex hulls depicted in Figure 2, which is comparable to the variability in our comparative species, we believe that this rate is not particularly high.

CONCLUSION

Traditionally, morphological change and variability in human evolution has been attributed to adaptive divergence within and between groups. This study supports the alternative proposal that random change also played a role in the diversification of early *Homo* (Ackermann and Cheverud 2004; Schroeder et al. 2014; Weaver et al. 2007). Specifically, our results indicate that mandibular dental size variation does not deviate from a model of genetic drift

across regions nor time period. For analyses where the null hypothesis of genetic drift was rejected, which are limited to the maxillary dentition, we find that these rejections support previous adaptive hypotheses related to climatic oscillations between 2 and 3 Ma, as well as the differentiation of the Dmanisi hominins as they moved out of Africa. Although the widespread non-rejection of genetic drift in mandibular dentition may point to the stronger action of genetic drift acting on small populations in isolation, it may also be a statistical artifact reflecting the high false negative rate of our tests due to the low number of traits being compared. However, it is also possible that as early *Homo* emerged and evolved alongside the proliferation of stone tools, hominins were increasingly reliant on cultural adaptations as opposed to biological adaptations to manage environmental changes (Ackermann and Cheverud 2004; Lynch 1990; Schroeder et al. 2014). The contrasting patterns between the maxillary and mandibular results could reflect previous findings that identified stronger morphological integration in mandibular dentition (Gómez-Robles and Polly 2012), indicating a potential constraint on the response to diversifying selection. Overall, this study highlights the potential of assessing evolutionary processes using a quantitative genetics approach for testing adaptive hypotheses in human evolution.

DATA AVAILABILITY STATEMENT

All hominin data are available from the published literature. A reference list is given in the Supplementary Material. Human dental measurements are available upon request from the curating institution in accordance with their policies on the distribution of data to for third-party use.

REFERENCES

Ackermann, R.R., 2002. Patterns of covariation in the hominoid craniofacial skeleton: implications for paleoanthropological models. J. Hum. Evol. 43, 167–187.

Ackermann, R.R., Smith, R.J., 2007. The macroevolution of our ancient lineage: what we know (or think we know) about early hominin diversity. Evol. Biol. 34, 72–85.

Ackermann, R.R., Cheverud, J.M., 2002. Discerning evolutionary processes in patterns of tamarin (genus *Saguinus*) craniofacial variation. Am. J. Phys. Anthropol. 117, 260–271.

Ackermann, R.R., Cheverud, J.M., 2004. Detecting genetic drift versus selection in human evolution. Proc. Nat. Acad. Sci. U.S.A. 101, 17946–17951.

Antón, S.C., Potts, R., Aiello, L.C., 2014. Evolution of early *Homo*: an integrated biological perspective. Science 345, 1236828.

Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., Suwa, G., 1999. *Australopithecus garhi*: a new species of early hominid from Ethiopia. Science 284(5414), 629–635.

Assis, A.P.A., Rossoni, D.M., Patton, J.L., Marroig, G., 2017. Evolutionary processes and its environmental correlates in the cranial morphology of western chipmunks (*Tamias*). Evolution 71, 595e609.

Baab, K.L., 2021. Reconstructing cranial evolution in an extinct hominin. Proc. Royal Soc. B 288(1943), 20202604.

Baab, K.L., 2018. Evolvability and craniofacial diversification in genus *Homo*. Evolution 72(12), 2781–2791.

Berger, L., 2012. *Australopithecus sediba* and the earliest origins of the genus *Homo*. J. Anthropol. Sci. 90, 117-131.

Berger, L.R., Hawks, J., de Ruiter, D.J., Churchill, S.E., Schmid, P., Delezene, L.K., Kivell, T.L., Garvin, H.M., Williams, S.A., DeSilva, J.M., Skinner, M.M., Musiba, C.M., Cameron, N., Holliday, T.W., Harcourt-Smith, W., Ackermann, R.R., Bastir, M., Bogin, B., Bolter, D., Brophy, J., Cofran, Z.D., Congdon, K.A., Deane, A.S., Dembo, M., Drapeau, M., Elliott, M.C., Feuerriegel, E.M., Garcia-Martinez, D., Green, D.J., Gurtov, A., Irish, J.D., Kruger, A., Laird, M.F., Marchi, D., Meyer, M.R., Nalla, S., Negash, E.W., Orr, C.M., Radovcic, D., Schroeder, L., Scott, J.E., Throckmorton, Z., Tocheri, M.W., VanSickle, C., Walker, C.S., Wei, P., Zipfel, B., 2015. *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. eLife 4, e09560.

Bilsborough, A., 1969. Rates of evolutionary change in the hominid dentition. Nature 223(5202), 146–149.

Blumenschine, R.J., 2003. Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. Science 299, 1217–1221.

Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 399-420.

Brace, C.L., 1963. Structural reduction in evolution. Am. Nat. 97, 39–49.

Brace, C.L., 1964. The probable mutation effect. Am. Nat. 98, 453–455.

Braun, D.R., Harris, J.W.K., Levin, N.E., McCoy, J.T., Herries, A.I.R., Bamford, M.K., Bishop, L.C., Richmond, B.G., Kibunjia, M., 2010. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. Proc. Nat. Acad. Sci. U.S.A. 107, 10002-10007.

Briggs, D.E.G., 2003. The role of decay and mineralization in the preservation of soft-bodied fossils. Annu. Rev. Earth Planet. Sci. 31, 275–301.

Bromage, T.G., Schrenk, F., Zonneveld, F.W., 1995. Paleoanthropology of the Malawi Rift: an early hominid mandible from the Chiwondo Beds, northern Malawi. J. Hum. Evol. 28, 71-108.

Brown, B., Walker, A., 1993. The Dentition. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge MA, pp. 161–192.

Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., Wayhu Saptomo, E., Awe Due, R., 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature 431(7012), 1055–1061.

Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. Global Planet. Change 5, 241–247.

Cheverud, J.M., 1988. A comparison of genetic and phenotypic correlations. Evolution 42, 958–968.

Cheverud, J.M., 1996. Developmental integration and the evolution of pleiotropy. Am. Zool. 36, 44–50.

Clarke, R.J., Howell, F.C., Brain, C.K., 1970. More evidence of an advanced hominid at Swartkrans. Nature 225, 1219–1222.

Curnoe, D., Tobiás, P.V., 2006. Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. J. Hum. Evol. 50, 36-77.

de Ruiter, D.J., Churchill, S.E., Hawks, J., Berger, L.R., 2017. Late australopiths and the emergence of *Homo*. Annu. Rev. Anthropol. 46, 99–115.

deMenocal, P.B., 1995. Plio-Pleistocene African climate and the paleoenvironment of human evolution. Science 270, 53–59.

Diniz-Filho, J.A.F. and Raia, P., 2017. Island Rule, quantitative genetics and brain–body size evolution in *Homo floresiensis*. Proc. Royal Soc. B 284(1857), 20171065.

Dunsworth, H.M., 2010. Origin of the genus *Homo*. Evol. Educ. Outreach 3(3), 353–366.

Dupont, L.M., Donner, B., Vidal, L., Pérez, E.M., Wefer, G., 2005. Linking desert evolution and coastal upwelling: Pliocene climate change in Namibia. Geology 33, 461–464.

Faith, J.T., Du, A., Behrensmeyer, A.K., Davies, B., Patterson, D.B., Rowan, J., Wood, B., 2021. Rethinking the ecological drivers of hominin evolution. Trends Ecol. Evol. 36(9), 797–807.

Ferraro, J. V., Plummer, T.W., Pobiner, B.L., Oliver, J.S., Bishop, L.C., Braun, D.R., Ditchfield, P.W., Seaman, J.W., Binetti, K.M., Seaman, J.W., Hertel, F., Potts, R., 2013. Earliest archaeological evidence of persistent hominin carnivory. PLoS One 8, e62174.

Foley, R.A., 2016. Mosaic evolution and the pattern of transitions in the hominin lineage. Phil. Trans. R. Soc. B 371(1698), 20150244.

Gabunia, L., Vekua, A., 1995. A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. Nature 373(6514), 509–512.

Gingerich, P.D., 2009. Rates of evolution. Annu. Rev. Ecol. Evol. Syst. 40, 657–675.

Gómez-Robles, A., 2019. Dental evolutionary rates and its

implications for the Neanderthal–modern human divergence. Sci. Adv. 5(5), eaaw1268.

Gómez-Robles, A., Smaers, J.B., Holloway, R.L., Polly, P.D. and Wood, B.A., 2017. Brain enlargement and dental reduction were not linked in hominin evolution. Proc. Nat. Acad. Sci. U.S.A. 114(3), 468–473.

Gomez-Robles, A. and Polly, P.D., 2012. Morphological integration in the hominin dentition: evolutionary, developmental, and functional factors. Evolution 66(4), 1024–1043.

Grine, F.E., 1993. Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans formation. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 75–116.

Grine, F.E., 2005. Early *Homo* at Swartkrans, South Africa: a review of the evidence and an evaluation of recently proposed morphs. S. Afr. J. Sci. 101, 43–52.

Grine, F.E., Leakey, M.G., Gathago, P.N., Brown, F.H., Mongle, C.S., Yang, D., Jungers, W.L., Leakey, L.N., 2019. Complete permanent mandibular dentition of early *Homo* from the upper Burgi Member of the Koobi Fora Formation, Ileret, Kenya. J. Hum. Evol. 131, 152–175.

Hallgrímsson, B., Jamniczky, H., Young, N.M., Rolian, C., Parsons, T.E., Boughner, J.C. and Marcucio, R.S., 2009. Deciphering the palimpsest: studying the relationship between morphological integration and phenotypic covariation. Evol. Biol. 36, 355–376.

Hammer, Ø., Harper, D.A. and Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4(1), 9.

Hansen, T.F., Houle, D., 2008. Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21, 1201–1219.

Hlusko, L.J., 2004. Integrating the genotype and phenotype in hominid paleontology. Proc. Nat. Acad. Sci. U.S.A. 101, 2653–2657.

Hlusko, L.J., 2016. Elucidating the evolution of hominid dentition in the age of phenomics, modularity, and quantitative genetics. Ann. Anat.-Anat. Anz. 203, 3–11.

Hlusko, L.J., Schmitt, C.A., Monson, T.A., Brasil, M.F., Mahaney, M.C., 2016. The integration of quantitative genetics, paleontology, and neontology reveals genetic underpinnings of primate dental evolution. Proc. Nat. Acad. Sci. U.S.A. 113, 9262–9267.

Holloway, R.L., 1966. Structural reduction through the "probable mutation effect". A critique with questions regarding human evolution. Am. J. Phys. Anthropol. 25, 7–11.

Jung, H., Strait, D., Rolian, C. and Baab, K.L., 2023. Functional morphological integration related to feeding biomechanics in the hominine skull. J. Hum. Evol. 182, 103401.

Keyser, A.W., 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. S. Afr. J. Sci. 96(4), 189–193.

Kimbel, W.H., Delezene, L.K., 2009. "Lucy" redux: A re-

view of research on *Australopithecus afarensis*. Am. J. Phys. Anthropol. 140(S49), 2–48.

Kimbel, W.H., Rak, Y., 2017. *Australopithecus sediba* and the emergence of *Homo*: questionable evidence from the cranium of the juvenile holotype MH 1. J. Hum. Evol. 107, 94–106.

Kimbel, W.H., Johanson, D.C., Rak, Y., 1997. Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. Am. J. Phys. Anthropol. 103, 235–262.

Kimbel, W.H., Rak, Y., Johanson, D.C., 2004. The Skull of *Australopithecus afarensis*. Oxford University Press, Oxford.

Kimbel, W.H., Villmoare, B., 2016. From *Australopithecus* to *Homo*: the transition that wasn't. Phil. Trans. R. Soc. B 371(1698), 20150248.

Klingenberg, C.P., 2008. Morphological integration and developmental modularity. Annu. Rev. Ecol. Evol. Syst. 39, 115–132.

Kramer, A., Donnelly, S.M., Kidder, J.H., Ousley, S.D., Olah, S.M., 1995. Craniometric variation in large-bodied hominoids: testing the single-species hypothesis for *Homo habilis*. J. Hum. Evol. 29, 443–462.

Lande, R., 1979. Quantitative genetic analysis of multivariate evolution applied to brain:body size allometry. Evolution 33, 402–416.

Langergraber, K.E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., Inoue-Muruyama, M., Mitani, J.C., Muller, M.N. and Robbins, M.M., 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. Proc. Nat. Acad. Sci. U.S.A. 109(39), 15716–15721.

Leakey, M.G., Spoor, F., Dean, M.C., Feibel, C.S., Antón, S.C., Kiarie, C., Leakey, L.N., 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. Nature 488(7410), 201–204.

Leakey, R.E, Leakey, M.G., Behrensmeyer, A.K., 1978. The Hominid Catalogue. In: Leakey, M.G., Leakey, R.E. (Eds.), Koobi Fora Research Project Vol. 1. Clarendon Press, Oxford, pp. 86–182.

Lepre, C.J., Roche, H., Kent, D. V., Harmand, S., Quinn, R.L., Brugal, J.P., Texier, P.J., Lenoble, A., Feibel, C.S., 2011. An earlier origin for the Acheulian. Nature 477, 82–85.

Lieberman, D.E., Wood, B.A., Pilbeam, D.R., 1996. Homoplasy and early *Homo*: an analysis of the evolutionary relationships of *H. habilis* sensu stricto and *H. rudolfensis*. J. Hum. Evol. 30, 97–120.

Lynch, M., 1990. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. Am. Nat. 136, 727–741.

Lynch, M., Walsh, B., 1998. Genetics and Analysis of Quantitative Traits. Sinauer, Sunderland, MA.

Machado, F.A., Marroig, G., Hubbe, A., 2022. The pre-eminent role of directional selection in generating extreme morphological change in glyptodonts (Cingulata; Xenarthra). Proc. R. Soc. B 289, 20212521.

Marroig, G., Cheverud, J.M., 2004. Did natural selection or

genetic drift produce the cranial diversification of neo-tropical monkeys? Am. Nat. 163(3), 417–428.

McKee, J.K., 2017. Correlates and catalysts of hominin evolution in Africa. Theory Biosci. 136(3), 123–140.

Melo, D., Garcia, G., Hubbe, A., Assis, A.P., Marroig, G., 2016. EvolQG-An R package for evolutionary quantitative genetics. F1000Research 4(925), 925.

Meloro, C. and Raia, P., 2010. Cats and dogs down the tree: the tempo and mode of evolution in the lower carnassial of fossil and living Carnivora. Evol. Biol. 37, 177–186.

Miller, J.A., 1991. Does brain size variability provide evidence of multiple species in *Homo habilis*? Am. J. Phys. Anthropol. 84, 385–398.

Miller, J.M.A., 2000. Craniofacial variation in *Homo habilis*: an analysis of the evidence for multiple species. Am. J. Phys. Anthropol. 112, 103–128.

Moggi-Cecchi, J., Grine, F.E., Tobiás, P.V., 2006. Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966-1996 excavations): catalogue, individual associations, morphological descriptions and initial metrical analysis. J. Hum. Evol. 50, 239–328.

Olson, E.C., Miller, R.L., 1958. Morphological Integration. University of Chicago Press, Chicago.

Patterson, D.B., Braun, D.R., Allen, K., Barr, W.A., Behrensmeyer, A.K., Biernat, M., Lehmann, S.B., Maddox, T., Manthi, F.K., Merritt, S.R. and Morris, S.E., 2019. Comparative isotopic evidence from East Turkana supports a dietary shift within the genus *Homo*. Nat. Ecol. Evol. 3(7), 1048–1056.

Pickering, R., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C., Green, H.E., Paul, B., Ritzman, T., Strait, D.S., Schoville, B.J., Hancox, P.J., 2019. U–Pb-dated flowstones restrict South African early hominin record to dry climate phases. Nature 565, 226–229.

Plavcan, J.M., 1990. Sexual Dimorphism in the Dentition of Extant Anthropoid Primates. Ph.D. Dissertation. University of Michigan.

Plavcan, J.M., 2001. Sexual dimorphism in primate evolution. Am. J. Phys. Anthropol. 116, 25–53.

Polanski, J.M., 2011. Morphological integration of the modern human mandible during ontogeny. Int. J. Evol. Biol. 2011, 545879.

Polanski, J.M., Franciscus, R.G., 2006. Patterns of craniofacial integration in extant *Homo*, *Pan*, and *Gorilla*. Am. J. Phys. Anthropol. 131, 38–49.

Ponce de León, M.S., Koesbardiati, T., Weissmann, J.D., Milella, M., Reyna-Blanco, C.S., Suwa, G., Kondo, O., Malaspinas, A.-S., White, T.D., Zollikofer, C.P.E., 2018. Human bony labyrinth is an indicator of population history and dispersal from Africa. Proc. Natl. Acad. Sci. USA 115, 4128e4133.

Polly, P.D., 2016. Quantitative genetics provides predictive power for paleontological studies of morphological evolution. Proc. Nat. Acad. Sci. U.S.A. 113(33), 9142–9144.

Potts, R., 1998. Variability selection in hominid evolution. Evol. Anthropol. 7, 81–96.

Potts, R., 2012. Environmental and behavioral evidence pertaining to the evolution of early *Homo*. Curr. Anthropol. 53, S299–S317.

Potts, R., Faith, J.T., 2015. Alternating high and low climate variability: the context of natural selection and speciation in Plio-Pleistocene hominin evolution. J. Hum. Evol. 87, 5–20.

Prat, S., 2005. First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3-2.4 Myr. J. Hum. Evol. 49, 230–240.

Rathmann, H., Perretti, S., Porcu, V., Hanihara, T., Scott, G.R., Irish, J.D., Reyes-Centeno, H., Ghirotto, S. and Harvati, K., 2023. Inferring human neutral genetic variation from craniodental phenotypes. Proc. Nat. Acad. Sci. U.S.A. Nexus 2(7), pgad217.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 32, 289–322.

Rightmire, G.P., Lordkipanidze, D. and Vekua, A., 2006. Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. J. Hum. Evol. 50(2), 115–141.

Robinson, J.R., Rowan, J., Campisano, C.J., Wynn, J.G., Reed, K.E., 2017. Late Pliocene environmental change during the transition from *Australopithecus* to *Homo*. Nat. Ecol. Evol. 1(6), 1–7.

Santana, S.E., Strait, S. and Dumont, E.R., 2011. The better to eat you with: functional correlates of tooth structure in bats. Funct. Ecol. 25(4), 839–847.

Schroeder, L. and Ackermann, R.R., 2023. Moving beyond the adaptationist paradigm for human evolution, and why it matters. J. Hum. Evol. 174, 103296.

Schroeder, L., Elton, S. and Ackermann, R.R., 2022. Skull variation in Afro-Eurasian monkeys results from both adaptive and non-adaptive evolutionary processes. Sci. Rep. 12(1), 12516.

Schroeder, L., 2021. Factors shaping the evolution of early *Homo*. eLS 2, 1–8.

Schroeder, L., Ackermann, R.R., 2017. Evolutionary processes shaping diversity across the *Homo* lineage. J. Hum. Evol. 111, 1–17.

Schroeder, L., Roseman, C.C., Cheverud, J.M., Ackermann, R.R., 2014. Characterizing the evolutionary path(s) to early *Homo*. PLoS One 9, 1–20.

Selig, K.R., Sargis, E.J. and Silcox, M.T., 2019. The frugivorous insectivores? Functional morphological analysis of molar topography for inferring diet in extant treeshrews (Scandentia). J. Mammal. 100(6), 1901–1917.

Smith, H.F., 2011. The role of genetic drift in shaping modern human cranial evolution: a test using microevolutionary modeling. Int. J. Evol. Biol. 2011, 145262.

Sodini, S.M., Kemper, K.E., Wray, N.R. and Trzaskowski, M., 2018. Comparison of genotypic and phenotypic correlations: Cheverud's conjecture in humans. Genetics 209, 941–948.

Sponheimer, M., Alemseged, Z., Cerling, T.E., Grine, F.E., Kimbel, W.H., Leakey, M.G., Lee-Thorp, J.A., Manthi, F.K., Reed, K.E., Wood, B.A., Wynn, J.G., 2013. Isotopic evidence of early hominin diets. Proc. Nat. Acad. Sci.

U.S.A. 110(26), 10513–10518.

Spoor, F., Gunz, P., Neubauer, S., Stelzer, S., Scott, N., Kwekason, A., Dean, M.C., 2015. Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo*. Nature 519, 83–86.

Stanley, S.M., 1992. An ecological theory for the origin of *Homo*. Paleobiology 18(3), 237–257.

Suwa, G., White, T.D. and Howell, F.C., 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. Am. J. Phys. Anthropol. 101, 247–282.

Szuma, E., 2007. Geography of dental polymorphism in the red fox *Vulpes vulpes* and its evolutionary implications. Biol. J. Linn. Soc. 90(1), 61-84.

Tattersall, I., 2021. Natural selection as agent of evolutionary change: a view from paleoanthropology. In: Delisle, R.G. (Ed.), Natural Selection. Springer, Cham, pp. 419–439.

Tattersall, I. and Eldredge, N., 1977. Fact, theory, and fantasy in human paleontology. Am. Sci. 65(2), 204–211.

Tobias, P.V., 1991. Olduvai Gorge, Volume 4: The Skulls, Endocasts and Teeth of *Homo habilis*. Cambridge University Press, Cambridge.

Tran, C.N.H., Schroeder, L., 2021. Common evolutionary patterns in the human nasal region across a worldwide sample. Am. J. Phys. Anthropol. 176, 422–433.

Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., 2005. Late Cenozoic moisture history of East Africa. Science 309, 2051–2053.

Ungar, P.S., Hlusko, L.J., 2016. The evolutionary path of least resistance. Science 353(6294), 29–30.

Ungar, P.S., 2012. Dental evidence for the reconstruction of diet in African early *Homo*. Curr. Anthropol. 53(S6), S318–S329.

Ungar, P.S., Grine, F.E., Teaford, M.F., 2006. Diet in early *Homo*: a review of the evidence and a new model of adaptive versatility. Ann. Rev. Anthropol. 35, 209–228.

Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan, J., Braun, D.R., Arrowsmith, J.R., Reed, K.E., 2015. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science 347(6228),1352–1355.

Vrba, E.S., 1985. Ecological and adaptive changes associated with early hominid evolution. In: Delson, E. (Ed.), Ancestors: The Hard Evidence. Alan R. Liss, New York, pp. 63–71.

Vrba, E.S., 1995. On the connections between paleoclimate and evolution. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 24–45.

Vrba, E.S., 1996. Climate, heterochrony, and human evolution. J. Anthropol. Res. 52, 1–28.

Walker, A., Leakey, R.E., 1978. The hominids of east Turkana. Sci. Am. 239(2), 54–67.

Weaver, T.D., Roseman, C.C., Stringer, C.B., 2007. Were Neandertal and modern human cranial differences produced by natural selection or genetic drift? J. Hum. Evol. 53, 135–145.

Wood, B.A., 1981. Tooth size and shape and their relevance to studies of hominid evolution. Phil. Trans. R. Soc. B 292, 65–76.

Wood, B.A., 1991. Koobi Fora Research Project, Volume 4. Hominid Cranial Remains. Clarendon Press, Oxford.

Wood, B.A., 1992. Origin and evolution of the genus *Homo*. Nature 355, 783–790.

Wood, B.A., 1993. Early *Homo*: how many species? In: Kimbel, W.H., Martin, L.B., (Eds.), Species, Species Concepts, and Primate Evolution. Plenum, New York, pp. 485–522.

Wynn, J.G., 2004. Influence of Plio-Pleistocene aridification on human evolution: evidence from paleosols of the Turkana Basin, Kenya. Am. J. Phys. Anthropol. 123, 106–118.

Zanolli, C., Davies, T.W., Joannes-Boyau, R., Beaudet, A., Bruxelles, L., de Beer, F., Hoffman, J., Hublin, J.J., Jakata, K., Kgasi, L., Kullmer, O., Macchiarelli, R., Pan, L., Schrenk, F., Santos, F., Stratford, D., Tawane, M., Thackeray, F., Xing, S., Zipfel, B., Skinner, M.M., 2022. Dental data challenge the ubiquitous presence of *Homo* in the Cradle of Humankind. Proc. Nat. Acad. Sci. U.S.A. 119, 1–11.

Supplement 1: Does Early *Homo* Dental Size Variation Follow a Neutral Pattern of Divergence?

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SUPPLEMENT 1
This supplement includes: Supplementary Material Tables S1–S3, Figures S1–S2, and references.

Table S1. Early *Homo* dental specimens utilized in this study*

Specimen Number (reference for measurements in parentheses)	Geological age (Ma)	Reference for age	Region	Maxillary/ Mandibular
Hadar (Northeastern Africa)				
A.L.666-1 (Kimbel et al., 1997)	2.33	Kimbel et al., 1997	Northeastern Africa	Maxillary
Dmanisi (Georgia)				
D2700 (Rightmire et al., 2006)	1.81-1.77	Calvo-Rathert et al., 2008	Eurasia	Maxillary
D211 (Gabunia & Vekua, 1995)	1.81-1.77	Calvo-Rathert et al., 2008	Eurasia	Mandibular
D2735 (Rightmire et al., 2006)	1.81-1.77	Calvo-Rathert et al., 2008	Eurasia	Mandibular
Drimolen (Southern Africa)				
DNH 35 (Keyser, 2000)	2.04-1.95	Herries et al., 2020	Southern Africa	Mandibular
DNH 45 (Moggi-Cecchi et al., 2010)	2.04-1.95	Herries et al., 2020	Southern Africa	Maxillary
*DNH 70 (Moggi-Cecchi et al., 2010)	2.04-1.95	Herries et al., 2020	Southern Africa	Maxillary
Koobi Fora (Eastern Africa)				
KNM-ER 1462 (Leakey et al., 1978)	1.9	Joordens et al., 2013	Eastern Africa	Mandibular
KNM-ER 1480 (Leakey et al., 1978)	1.85	Joordens et al., 2013	Eastern Africa	Mandibular
KNM-ER 1482 (Leakey et al., 2012)	2.05-1.95	Joordens et al., 2013	Eastern Africa	Mandibular
KNM-ER 1502 (Leakey et al., 1978)	1.55-1.80	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 1506 (Leakey et al., 1978)	1.7	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 1507 (Wood, 1991)	1.60-1.85		Eastern Africa	Mandibular
KNM-ER 1590 (Leakey et al., 1978)	1.88-1.67	Joordens et al., 2013	Eastern Africa	Maxillary
KNM-ER 1801 (Leakey et al., 2012)	2.05-1.95	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 1802 (Bromage et al., 1995)	2.05-1.95	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 1805 (Leakey et al., 1978)	1.85-1.6	Gathago and Brown, 2006	Eastern Africa	Maxillary
KNM-ER 1813 (Leakey et al., 1978)	1.9	Gathago and Brown, 2006	Eastern Africa	Maxillary
KNM-ER 1814 (Leakey et al., 1978)	1.60-1.85	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 2597 (Wood, 1991)	1.85	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 2599 (Wood, 1991)	1.85	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 2601 (Wood, 1991)	1.9	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 3734 (Wood, 1991)	1.9-1.88	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 3953 (Wood, 1991)	1.9	Gathago and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 60000 (Leakey et al., 2012)	1.87-1.78	Leakey et al., 2012	Eastern Africa	Maxillary
KNM-ER 62000 (Leakey et al., 2012)	1.95-1.91	Leakey et al., 2012	Eastern Africa	Maxillary
KNM-ER 64060 (Grine et al., 2019)	2.02-2.03	Grine et al., 2019	Eastern Africa	Mandibular
KNM-ER 806 (Wood, 1991)	1.5	McDougall and Brown, 2006	Eastern Africa	Mandibular

KNM-ER 807 (Leakey et al., 1978)	1.6	McDougall and Brown, 2006	Eastern Africa	Maxillary
KNM-ER 808 (Leakey et al., 1978)	1.5	McDougall and Brown, 2006	Eastern Africa	Maxillary
KNM-ER 816 (Leakey et al., 1978)	1.5	McDougall and Brown, 2006	Eastern Africa	Maxillary
KNM-ER 820 (Leakey et al., 1978)	1.67	McDougall and Brown, 2006	Eastern Africa	Mandibular
KNM-ER 992 (Tobias, 1991)	1.49	McDougall and Brown, 2006	Eastern Africa	Maxillary
KNM-WT 15000 (Brown and Walker, 1993)	1.55-1.39	McDougall, 1985	Eastern Africa	Both
KNM-WT 42718 (Prat et al., 2005)	2.3-2.4	Prat et al., 2005	Eastern Africa	Mandibular
Omo Basin (Ethiopia)				
L26-1g (Wood, 1991)	2.4	Brown, 1994	Northeastern Africa	Mandibular
L28-30 (Wood, 1991)	2.35	Brown, 1994	Northeastern Africa	Mandibular
L28-31 (Wood, 1991)	2.36-2.33	Brown, 1994	Northeastern Africa	Mandibular
L398-1699 (Wood, 1991)	2.35	Brown, 1994	Northeastern Africa	Mandibular
L398-573 (Wood, 1991)	2.35	Brown, 1994	Northeastern Africa	Maxillary
L894-1 (Wood, 1991)	1.88	Brown, 1994	Northeastern Africa	Maxillary
Omo 29-43 (Wood, 1991)	2.0-2.19	Brown, 1994	Northeastern Africa	Mandibular
Omo 74-18 (Wood, 1991)	1.8	Brown, 1994	Northeastern Africa	Mandibular
Omo 75-14a (Wood, 1991)	2.31-2.12	Suwa et al., 1996	Northeastern Africa	Mandibular
Omo 75s-15 (Wood, 1991)	2.2	Brown, 1994	Northeastern Africa	Mandibular
Omo 75s-16 (Wood, 1991)	2.2	Brown, 1994	Northeastern Africa	Mandibular
Omo k7-19 (Wood, 1991)	2.0-2.19	Brown, 1994	Northeastern Africa	Mandibular
Omo SH1-17 (Wood, 1991)	2.0-2.19	Brown, 1994	Northeastern Africa	Maxillary
Omo P933-1 (Wood, 1991)	2.3	Brown, 1994	Northeastern Africa	Maxillary
Ledi-Geraru (Ethiopia)				
LD350-1 (Villmoore et al., 2015)	2.8	DiMaggio et al., 2015	Northeastern Africa	Mandibular
Olduvai Gorge				
OH 13 (Tobias, 1991)	1.65	McHenry, 2012	Eastern Africa	Both
OH 15 (Tobias, 1991)	1.65	McHenry, 2012	Eastern Africa	Maxillary
OH 16 (Tobias, 1991)	1.75	McHenry, 2012	Eastern Africa	Both
OH 21 (Tobias, 1991)	1.9	McHenry, 2012	Eastern Africa	Maxillary
OH 24 (Tobias, 1991)	1.8	McHenry, 2012	Eastern Africa	Maxillary

OH 27 (Tobias, 1991)	1.8	McHenry, 2012	Eastern Africa	Mandibular
OH 37 (Tobias, 1991)	1.65	McHenry, 2012	Eastern Africa	Mandibular
OH 39 (Tobias, 1991)	1.8	McHenry, 2012	Eastern Africa	Maxillary
OH 4 (Tobias, 1991)	1.9	McHenry, 2012	Eastern Africa	Mandibular
OH 41 (Tobias, 1991)	1.75	McHenry, 2012	Eastern Africa	Maxillary
OH 42 (Tobias, 1991)	1.6-1.79	McHenry, 2012	Eastern Africa	Maxillary
OH 44 (Tobias, 1991)	1.85	McHenry, 2012	Eastern Africa	Maxillary
OH 45 (Tobias, 1991)	1.85	McHenry, 2012	Eastern Africa	Maxillary
OH 6 (Tobias, 1991)	1.85	McHenry, 2012	Eastern Africa	Both
OH 65 (Blumenschine et al., 2003)	1.8	McHenry, 2012	Eastern Africa	Both
OH 7 (Tobias, 1991)	1.75	McHenry, 2012	Eastern Africa	Mandibular
Sterkfontein (Southern Africa)				
Se 1508 (Curnoe and Tobias, 2006)	1.7-1.4	Kuman and Clarke, 2000	Southern Africa	Maxillary
Se 1937 (Curnoe and Tobias, 2006)	1.7-1.4	Kuman and Clarke, 2000	Southern Africa	Mandibular
Se 2396 (Curnoe and Tobias, 2006)	1.7-1.4	Kuman and Clarke, 2000	Southern Africa	Maxillary
*Se 255 (Curnoe and Tobias, 2006)	1.7-1.4	Kuman and Clarke, 2000	Southern Africa	Maxillary
*StW 151 (Moggi-Cecchi et al., 2006)	2.61-2.07	Pickering and Herries, 2020	Southern Africa	Maxillary
*StW 19b (Wood, 1991)	2.61-1.4	Kuman and Clarke, 2000	Southern Africa	Maxillary
StW 33 (Curnoe and Tobias, 2006)	1.7-1.4	Kuman and Clarke, 2000	Southern Africa	Maxillary
StW 34 (Curnoe and Tobias, 2006)	2.61-1.4	Kuman and Clarke, 2000	Southern Africa	Maxillary
StW 42 (Curnoe and Tobias, 2006)	2.61-1.4	Kuman and Clarke, 2000	Southern Africa	Maxillary
*StW 53 (Curnoe and Tobias, 2006)	1.78-1.49	Herries and Shaw, 2011	Southern Africa	Both
StW 75-79 (Curnoe and Tobias, 2006)	1.78-1.49	Herries and Shaw, 2011	Southern Africa	Maxillary
StW 80 (Moggi-Cecchi et al., 2006)	1.7-1.4	Kuman and Clarke, 2000	Southern Africa	Mandibular
Swartkrans (Southern Africa)				
*SK 15 (Tobias, 1991)	1.9-2.1	Pickering et al., 2011	Southern Africa	Mandibular
SK 18a (Wood, 1991)	1.65-1.07	Pickering et al., 2011	Southern Africa	Mandibular
SK 2635 (Grine, 2005)	1.65-1.07	Pickering et al., 2011	Southern Africa	Maxillary
SK 27 (Clarke, 1977)	2.3-1.8	Pickering et al., 2011	Southern Africa	Maxillary
SK 42 (Curnoe and Tobias, 2006)	2.3-1.8	Pickering et al., 2011	Southern Africa	Maxillary
SK 45 (Tobias, 1991)	2.3-1.8	Pickering et al., 2011	Southern Africa	Mandibular
SK 68 (Wood, 1991)	2.3-1.8	Pickering et al., 2011	Southern Africa	Maxillary
SK 74b (Wood, 1991)	2.3-1.8	Pickering et al., 2011	Southern Africa	Mandibular
SK 843t (Wood, 1991)	2.3-1.8	Pickering et al., 2011	Southern Africa	Mandibular
SK 846a (Wood, 1991)	2.3-1.8	Pickering et al., 2011	Southern Africa	Mandibular
SK 847 (Clarke et al., 1970)	1.9-2.1	Pickering et al., 2011	Southern Africa	Mandibular
SKX 21204 (Grine, 1993)	2.3-1.8	Pickering et al., 2011	Southern Africa	Mandibular
SKX 2354 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Mandibular
SKX 2355 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Mandibular
SKX 257 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Mandibular
SKX 258 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Mandibular
SKX 268 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Maxillary
SKX 334 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Maxillary
SKX 339 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Maxillary
SKX 610 (Grine, 1993)	1.65-1.07	Pickering et al., 2011	Southern Africa	Maxillary
Uraha (Malawi)				
UR 501 (Bromage et al., 1995)	2.3-2.5	Bromage et al., 1995	Southeastern Africa	Mandibular

* Star indicates specimens whose membership in the genus *Homo* has been questioned by Zanolli et al., (2022)

Table S2. PC loadings for each analysis subset

Subset 1	PC 1	PC 2	PC 3	PC 4
M_1 MD	0.48	0.13	0.82	0.28
M_2 MD	0.62	-0.63	-0.10	-0.46
M_1 BL	0.39	0.76	-0.18	-0.49
M_2 BL	0.49	0.07	-0.53	0.69
Eigenvalue	5.83	0.53	0.35	0.12
% variance	85.42	7.80	5.10	1.69

Subset 2	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
P^3 MD	0.30	0.57	-0.17	0.20	0.72	0.03
M^1 MD	0.43	-0.37	-0.36	0.61	-0.13	-0.40
M^2 MD	0.49	-0.14	-0.55	-0.59	-0.07	0.28
P^3 BL	0.42	0.62	0.22	0.02	-0.62	-0.10
M^1 BL	0.31	-0.23	0.36	0.36	0.00	0.77
M^2 BL	0.46	-0.29	0.60	-0.33	0.29	-0.39
Eigenvalue	4.28	0.69	0.40	0.19	0.15	0.08
% variance	73.81	11.91	6.92	3.35	2.56	1.45

Subset 3	PC 1	PC 2	PC 3	PC 4	PC 5
I^2 MD	0.28	0.72	0.10	0.21	-0.59
C^1 MD	0.82	-0.18	-0.37	-0.40	-0.03
P^3 MD	0.16	0.15	0.81	-0.51	0.21
I^2 BL	0.28	0.40	-0.07	0.41	0.77
C^1 BL	0.38	-0.51	0.44	0.61	-0.15
Eigenvalue	12.15	0.78	0.47	0.30	0.17
% variance	87.58	5.65	3.38	2.14	1.24

Subset 4	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10
C^1 MD	0.82	-0.37	0.18	-0.15	-0.31	0.16	0.03	-0.13	0.02	0.00
P^3 MD	0.16	0.17	0.32	0.10	0.25	0.30	-0.46	0.64	0.21	-0.07
P^4 MD	0.07	0.30	0.34	0.16	-0.06	0.09	0.78	0.31	-0.09	0.21
M^1 MD	0.05	0.39	0.04	-0.51	0.31	0.48	0.06	-0.29	-0.30	-0.28
M^2 MD	0.12	0.41	0.30	-0.49	-0.07	-0.63	-0.16	-0.02	0.14	0.20
C^1 BL	0.42	-0.01	-0.56	-0.04	0.53	-0.31	0.17	0.28	-0.13	-0.01
P^3 BL	0.23	0.26	0.13	0.52	0.23	0.00	-0.27	-0.39	-0.33	0.45
P^4 BL	0.19	0.31	0.06	0.41	0.02	-0.19	0.11	-0.27	0.38	-0.66
M^1 BL	0.07	0.28	-0.41	-0.06	-0.08	0.33	0.05	-0.14	0.65	0.42
M^2 BL	0.10	0.43	-0.39	0.08	-0.63	0.03	-0.18	0.25	-0.37	-0.13
Eigenvalue	11.95	4.22	0.51	0.40	0.22	0.19	0.15	0.13	0.08	0.05
% variance	66.80	23.58	2.82	2.21	1.25	1.06	0.82	0.74	0.46	0.26

Subset 5	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
P_3 MD	0.62	-0.72	-0.05	-0.07	0.27	0.12
P_4 MD	0.43	0.10	-0.10	0.56	-0.68	0.16
M_1 MD	0.36	0.37	-0.72	-0.13	0.18	-0.41
P_3 BL	0.32	0.33	0.12	-0.70	-0.22	0.49
P_4 BL	0.38	0.17	0.65	-0.07	-0.04	-0.63
M_1 BL	0.23	0.44	0.20	0.42	0.62	0.38

Eigenvalue	4.68	3.64	0.39	0.24	0.18	0.13
% variance	50.61	39.32	4.21	2.58	1.91	1.37

Subset 6			
	PC 1	PC 2	PC 3	PC 4
P^3 MD	0.41	-0.19	0.87	-0.20
P^4 MD	0.44	0.85	0.05	0.29
P^3 BL	0.57	-0.49	-0.24	0.61
P^4 BL	0.56	-0.02	-0.43	-0.71
Eigenvalue	3.01	0.31	0.20	0.06
% variance	84.05	8.53	5.69	1.74

Subset 7			
	PC 1	PC 2	PC 3	PC 4
M^2 MD	0.47	-0.41	0.63	-0.46
M^3 MD	0.55	-0.55	-0.52	0.34
M^2 BL	0.44	0.42	0.44	0.66
M^3 BL	0.53	0.59	-0.37	-0.48
Eigenvalue	4.41	0.59	0.37	0.18
% variance	79.49	10.55	6.75	3.22

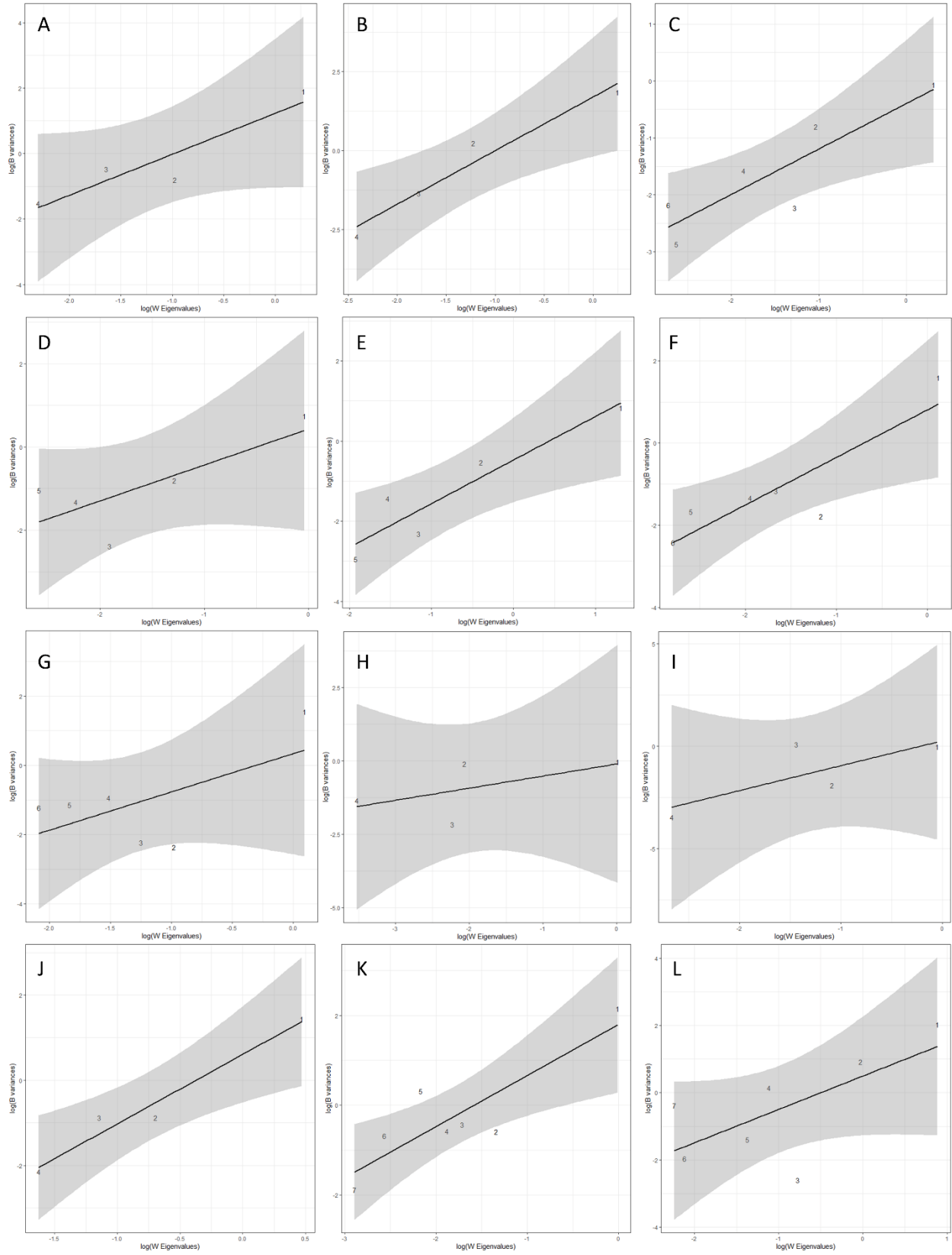| Subset 8						
	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7
I_2 MD	0.33	-0.01	0.64	0.59	-0.02	-0.24	0.28
C_1 MD	0.68	-0.30	-0.61	0.11	-0.04	-0.15	0.19
P_3 MD	0.50	0.11	0.28	-0.30	-0.19	-0.13	-0.72
P_4 MD	0.15	0.58	-0.02	-0.22	-0.63	0.13	0.42
I_2 BL	0.37	-0.01	0.22	-0.21	0.42	0.75	0.19
P_3 BL	0.03	0.53	-0.31	0.62	0.10	0.29	-0.36
P_4 BL	0.11	0.53	-0.05	-0.26	0.61	-0.49	0.17
Eigenvalue	14.11	2.08	0.58	0.29	0.25	0.16	0.11
% variance	80.26	11.85	3.29	1.65	1.41	0.89	0.65

Figure S1. Regression plots of between versus within-group variance for regional analyses. A) Subset 1 – *Homo sapiens* V/CV model; B) Subset 1 – *Pan troglodytes* V/CV model; C) Subset 2 – *Homo sapiens* V/CV model; D) Subset 3 – *Homo sapiens* V/CV model; E) Subset 3 – *Pan troglodytes* V/CV model; F) Subset 5 – *Homo sapiens* V/CV model; G) Subset 5 – *Pan troglodytes* V/CV model; H) Subset 6 – *Homo sapiens* V/CV model; I) Subset 6 – *Pan troglodytes* V/CV model; J) Subset 7 – *Homo sapiens* V/CV model; K) Subset 8 – *Homo sapiens* V/CV model; L) Subset 8 – *Pan troglodytes* V/CV model
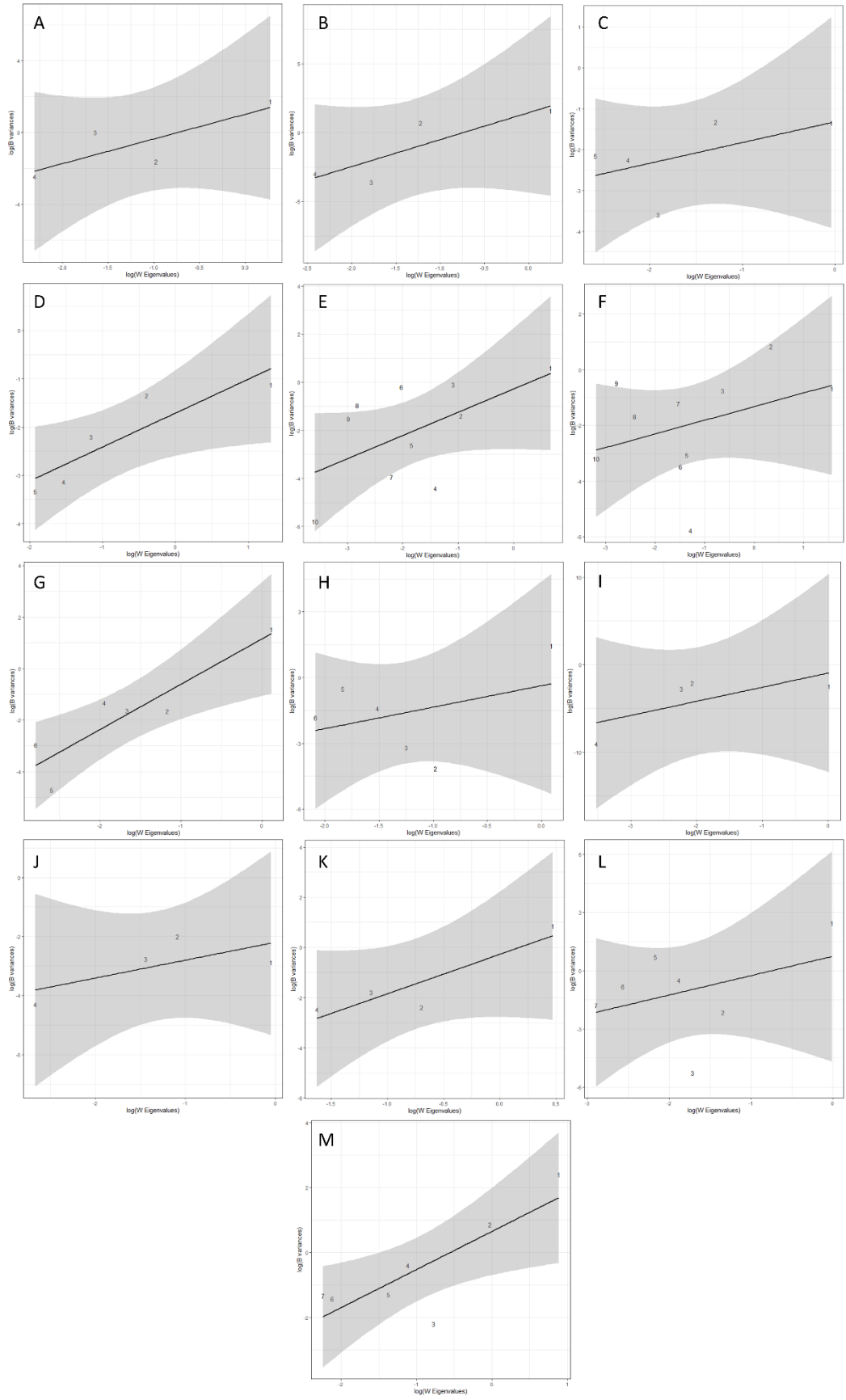
Figure S2. Regression plots of between versus within-group variance for temporal analyses. A) Subset 1 – *Homo sapiens* V/CV model; B) Subset 1 – *Pan troglodytes* V/CV model; C) Subset 3 – *Homo sapiens* V/CV model; D) Subset 3 – *Pan troglodytes* V/CV model; E) Subset 4 – *Homo sapiens* V/CV model; F) Subset 4 – *Pan troglodytes* V/CV model; G) Subset 5 – *Homo sapiens* V/CV model; H) Subset 5 – *Pan troglodytes* V/CV model; I) Subset 6 – *Homo sapiens* V/CV model; J) Subset 6 – *Pan troglodytes* V/CV model; K) Subset 7 – *Homo sapiens* V/CV model; L) Subset 8 – *Homo sapiens* V/CV model; M) Subset 8 – *Pan troglodytes* V/CV model

Table S3. Results of regression analyses by region, excluding non-*Homo* specimens identified in Zanolli et al. 2022, testing the null hypothesis of genetic drift*

Subset	Extant Model	Rejection of Drift?	Slope	95% Slope Confidence Interval		R^2	t-stat	*p*-value
Subset 1 (Mandibular)	*Homo sapiens*	No	1.22	-0.32	2.77	0.85	0.62	0.60
	Pan troglodytes	No	1.70	0.51	2.89	0.95	2.54	0.13
Subset 2 (Maxillary)	*Homo sapiens*	No	0.80	0.20	1.40	0.77	0.92	0.41
	Pan troglodytes	Possibly	0.34	-0.47	1.14	0.25	2.29	**0.08**
Subset 3 (Maxillary)	*Homo sapiens*	No	0.86	-0.47	2.19	0.59	0.33	0.77
	Pan troglodytes	No	1.09	0.32	1.86	0.87	0.37	0.74
Subset 4 (Maxillary)	*Homo sapiens*	Yes	0.23	-0.32	0.79	0.10	3.19	**0.01**
	Pan troglodytes	Yes	0.40	-0.14	0.95	0.27	2.53	**0.04**
Subset 5 (Mandibular)	*Homo sapiens*	No	1.16	0.29	2.03	0.77	0.50	0.64
	Pan troglodytes	No	1.11	-0.90	3.12	0.37	0.15	0.89
Subset 6 (Maxillary)	*Homo sapiens*	No	0.80	-0.87	2.47	0.68	0.52	0.66
	Pan troglodytes	No	1.43	-1.09	3.95	0.75	0.74	0.54
Subset 7 (Maxillary)	*Homo sapiens*	No	1.62	-0.03	3.28	0.90	1.62	0.25
	Pan troglodytes	Possibly	2.00	0.94	3.06	0.97	4.06	**0.06**
Subset 8 (Mandibular)	*Homo sapiens*	No	1.14	0.38	1.89	0.75	0.46	0.66
	Pan troglodytes	No	0.99	-0.26	2.24	0.45	0.01	0.99

* Significant *p*-values at an alpha level of 0.1 are shown in bold.

References

Blumenschine, R.J., 2003. Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. Science 299, 1217–1221.

Bromage, T.G., Schrenk, F., Zonneveld, F.W., 1995. Paleoanthropology of the Malawi Rift: an early hominid mandible from the Chiwondo Beds, northern Malawi. J. Hum. Evol. 28, 71–108.

Brown, B., Walker, A., 1993. The Dentition. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectu*s Skeleton. Harvard University Press, Cambridge, MA, pp. 161–192.

Brown, F.H., 1994. Development of Pliocene and Pleistocene chronology of the Turkana Basin, East Africa, and its relation to other sites. In: Corruccini, R.S., Ciochon, R.L. (Eds.) Integrative Paths to the Past. Prentice Hall, Englewood Cliffs, pp. 285–312.

Calvo-Rathert, M., Goguitchaichvili, A., Sologashvili, D., Villalaín, J.J., Bógalo M.F., Carrancho, A., Maissuradze, G., 2008. New paleomagnetic data from the hominin bearing Dmanisi paleo-anthropologic site (southern Georgia, Caucasus). Quatern. Res. 69(1), 91–96.

Clarke, R.J., Howell, F.C., Brain, C.K., 1970. More evidence of an advanced hominid at Swartkrans. Nature 225, 1219–1222.

Curnoe, D., Tobiás, P.V., 2006. Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. J. Hum. Evol. 50, 36–77.

DiMaggio, E.N., Campisano, C.J., Rowan, J., Dupont-Nivet, G., Deino, A.L., Bibi, F., Lewis, M.E., Souron, A., Werdelin, L., Reed, K.E., Arrowsmith, J.R., 2015. Late Pliocene fossiliferous sedimentary record and the environmental context of early *Homo* from Afar, Ethiopia. Science 347 (6228), 1355–1359.

Gabunia, L., Vekua, A., 1995. A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. Nature 373(6514), 509–512.

Gathogo, P.N., Brown, F.H., 2006. Revised stratigraphy of Area 123, Koobi Fora, Kenya, and new age estimates of its fossil mammals, including hominins. J. Hum. Evol. 51(5), 471–479.

Grine, F.E., 1993. Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans formation. In: Brain, C.K. (Ed.), Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 75–116.

Grine, F.E., 2005. Early *Homo* at Swartkrans, South Africa: A review of the evidence and an evaluation of recently proposed morphs. S. Afri. J. Sci. 101, 43–52.

Grine, F.E., Leakey, M.G., Gathago, P.N., Brown, F.H., Mongle, C.S., Yang, D., Jungers, W.L., Leakey, L.N., 2019. Complete permanent mandibular dentition of early Homo from the upper Burgi Member of the Koobi Fora Formation, Ileret, Kenya. J. Hum. Evol. 131, 152–175.

Herries, A.I., Martin, J.M., Leece, A.B., Adams, J.W., Boschian, G., Joannes-Boyau, R., Edwards, T.R., Mallett, T., Massey, J., Murszewski, A., Neubauer, S., 2020. Contemporaneity of *Australopithecus*, *Paranthropus*, and early *Homo* erectus in South Africa. Science 368(6486), eaaw7293.

Herries, A.I.R., Shaw, J., 2011. Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: implications for the age of the hominin fossils and stone tool industries. J. Hum. Evol. 60, 523–539.

Joordens, J.C., Dupont-Nivet, G., Feibel, C.S., Spoor, F., Sier, M.J., van der Lubbe, J.H., Nielsen, T.K., Knul, M.V., Davies, G.R., Vonhof, H.B., 2013. Improved age control on early *Homo* fossils from the upper Burgi Member at Koobi Fora, Kenya. J. Hum. Evol. 65(6), 731–745.

Keyser, A.W., 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. S. Afr. J. Sci. 96(4), 189–193.

Kimbel, W.H., Johanson, D.C., Rak, Y., 1997. Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. Am. J. Phys. Anthropol. 103, 235–262.

Kuman, K., Clarke, R.J., 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. J. Hum. Evol. 38(6), 827–847.

Leakey, M.G., Spoor, F., Dean, M.C., Feibel, C.S., Antón, S.C., Kiarie, C., Leakey, L.N., 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. Nature 488(7410), 201–204.

Leakey, R.E, Leakey, M.G., Behrensmeyer, A.K., 1978. The hominid catalogue. In: Leakey, M.G., Leakey, R.E. (Eds.), Koobi Fora Research Project Vol. 1. Clarendon Press, Oxford, pp. 86–182.

McDougall, I., Brown, F.H., 2006. Precise 40Ar/39Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. J. Geol. Soc. 163(1), 205–220.

McHenry, L.J., 2012. A revised stratigraphic framework for Olduvai Gorge Bed I based on tuff geochemistry. J. Hum. Evol. 63(2), 284–299.

Moggi-Cecchi, J., Grine, F.E., Tobiás, P.V., 2006. Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966-1996 excavations): catalogue, individual associations, morphological descriptions and initial metrical analysis. J. Hum. Evol. 50, 239–328.

Moggi-Cecchi, J., Menter, C., Boccone, S., Keyser, A., 2010. Early hominin dental remains from the Plio-Pleistocene site of Drimolen, South Africa. J. Hum. Evol. 58(5), 374–405.

Pickering, R., Herries, A.I., 2020. A new multidisciplinary age of 2.61–2.07 Ma for the Sterkfontein Member 4 australopiths. In: Hominin Postcranial Remains from Sterkfontein, South Africa, 1936–1995, pp. 21–30.

Pickering, R., Kramers, J.D., Hancox, P.J., de Ruiter, D.J., Woodhead, J.D., 2011. Contemporary flowstone development links early hominin bearing cave deposits in South Africa. Earth Planet. Sci. Lett. 306(1), 23–32.

Prat, S., 2005. First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3-2.4 Myr. J. Hum. Evol. 49, 230–240.

Suwa, G., White, T.D., Howell, F.C., 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. Am. J. Phys. Anthropol. 101, 247–282.

Tobias, P.V., 1991. Olduvai Gorge, Volume 4: The Skulls, Endocasts and Teeth of *Homo habilis*. Cambridge University Press, Cambridge.

Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan, J., Braun, D.R., Arrowsmith, J.R., Reed, K.E., 2015. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science 347(6228),1352–1355.

Wood, B.A., 1991. Koobi Fora Research Project. In: Leakey, R.E. (Ed.), Hominid Cranial Remains. Clarendon Press, Oxford.