# 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

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*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 hominin 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

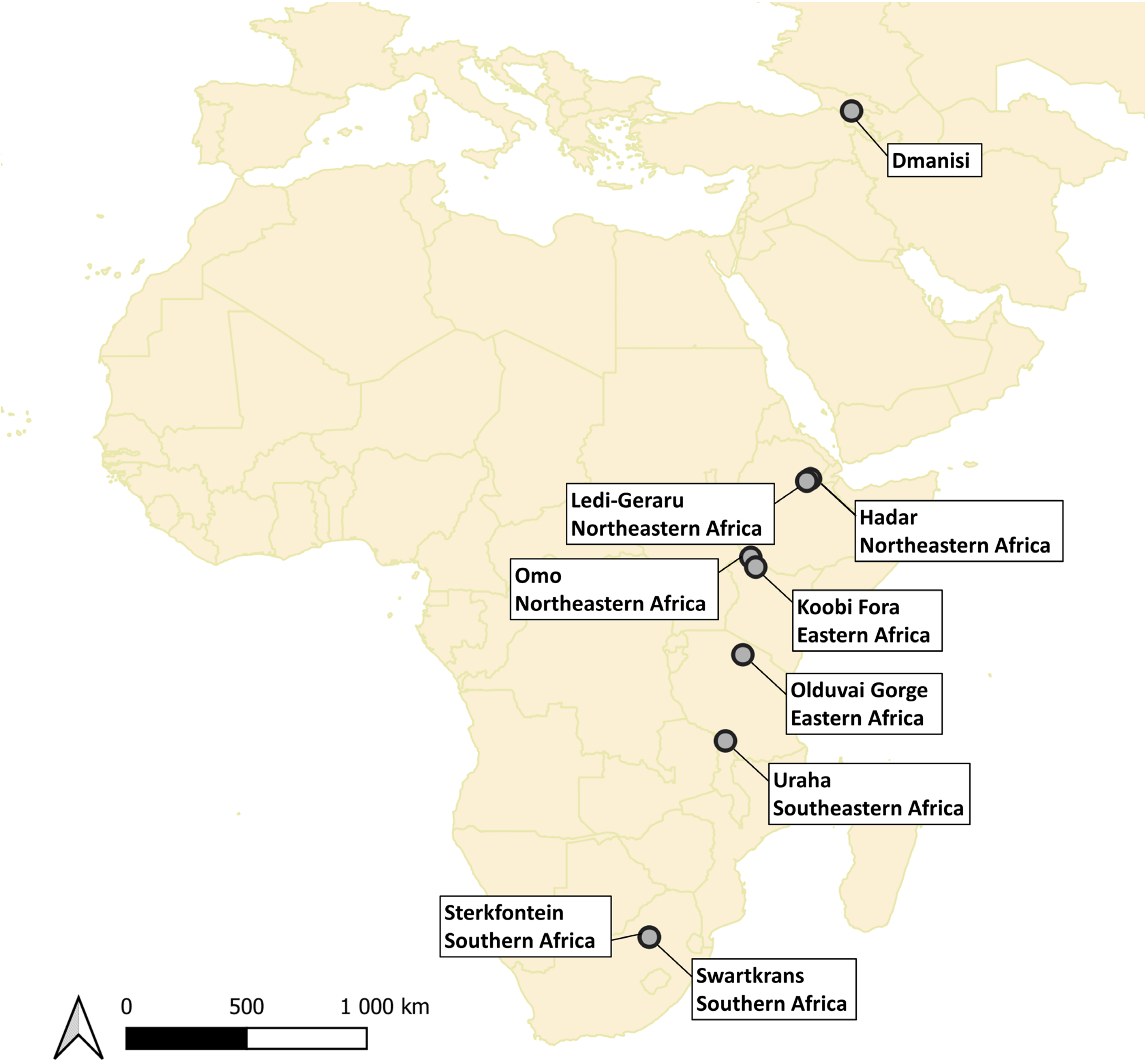

*Figure 1. Map of specimen localities, including the geographic region of the localities utilized in this study (map created with QGIS).*

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 ($Bt \propto P$). 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 resulted 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

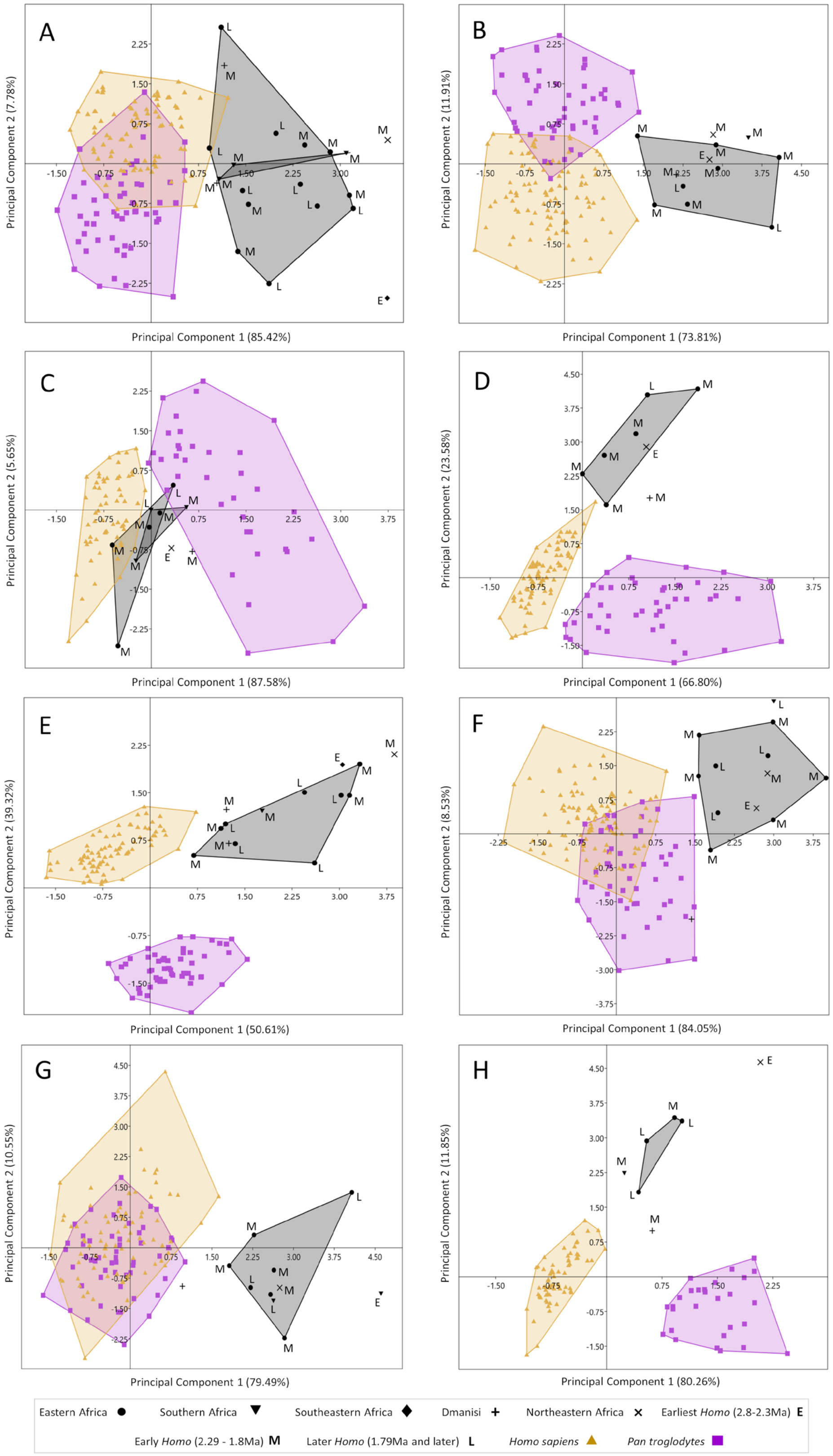

*Figure 2. Principal component plots for each subset. Symbol legend is provided below the figure. Convex hulls are drawn to indicate the species distributions of* Homo sapiens *and* Pan troglodytes *(orange and purple, respectively), as well as various regions in the early* Homo *group (grey, differentiated 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 | | R² | *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.

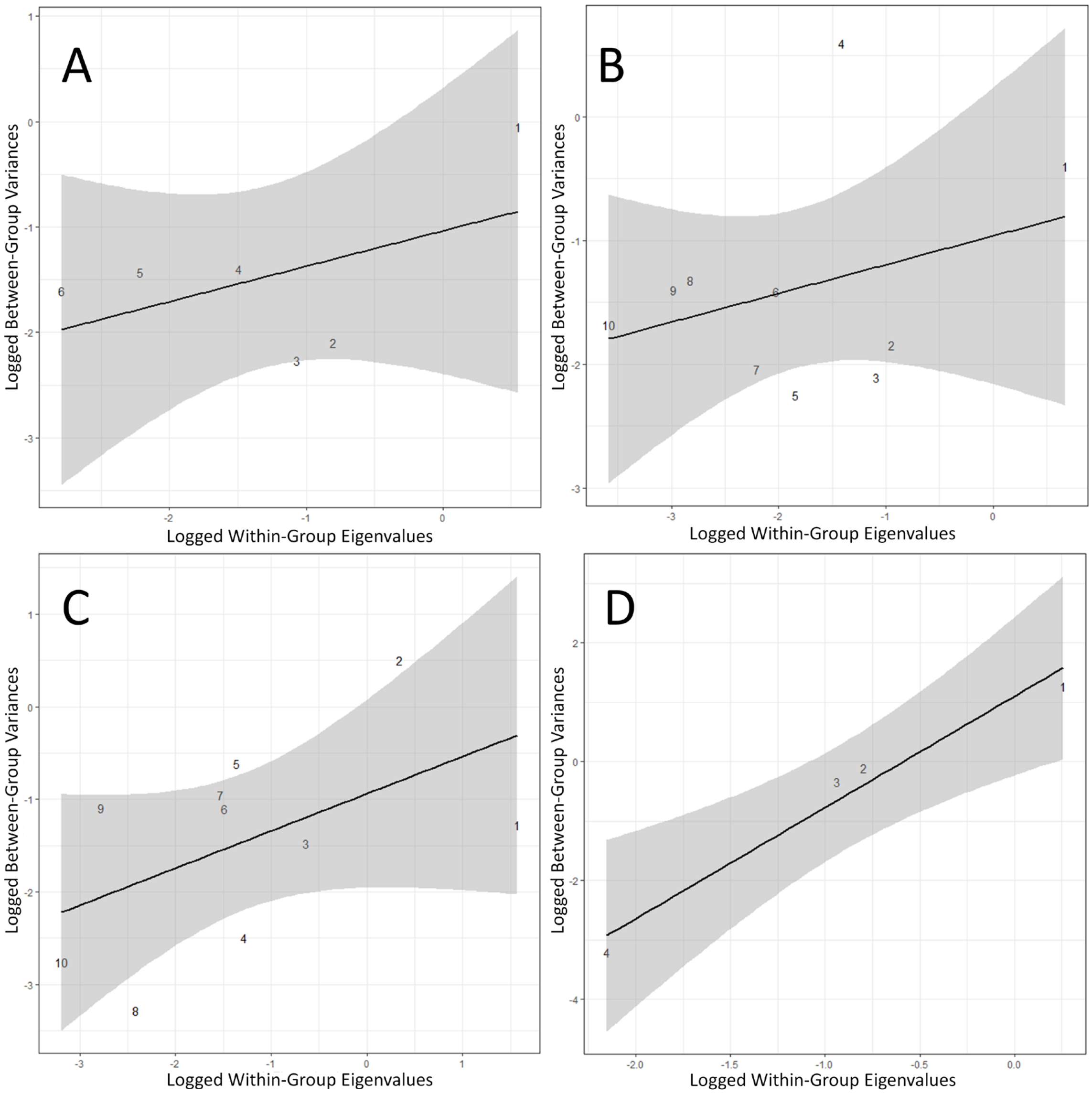

*Figure 3. Regression plots of between versus within-group variance for* ***regional*** *analyses for which the null hypothesis of genetic drift was rejected (indicated in Table 2). Regression points (x, y) are labelled as numbers, which refers to principal component numbers. Within-group variance (logged 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 subset 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 | | R$^2$ | 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-

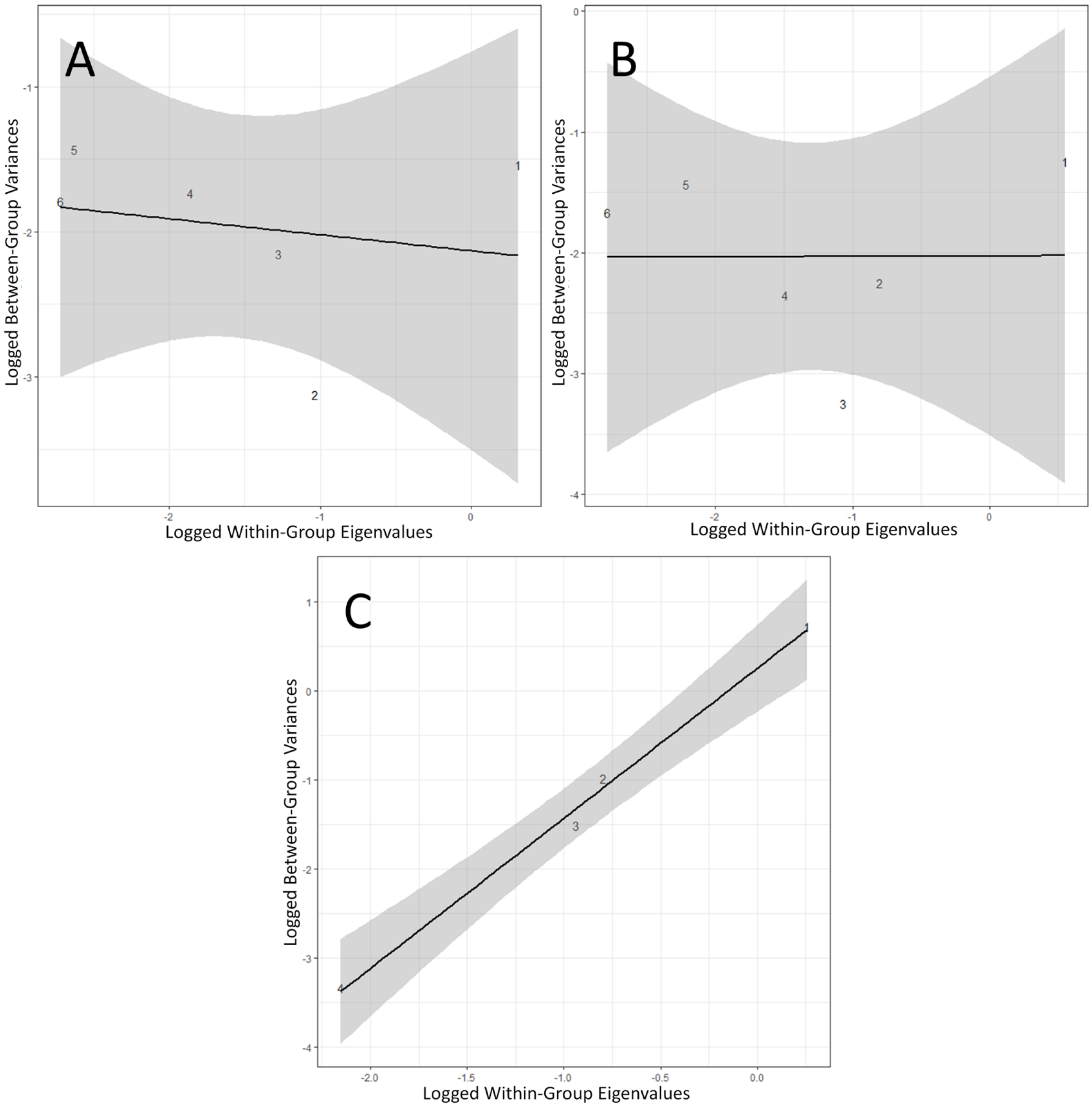

*Figure 4. Regression plots of between versus within-group variance for* ***temporal*** *analyses for which the null hypothesis of genetic drift was rejected (indicated in Table 3). Regression points (x, y) are labelled as numbers, which refers to principal component numbers. Within-group variance (logged 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 | | $R^2$ | 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 | | $R^2$ | 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 | | $R^2$ | 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 dentition 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.

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## 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.

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# 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.

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**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 (Villmoare 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 |

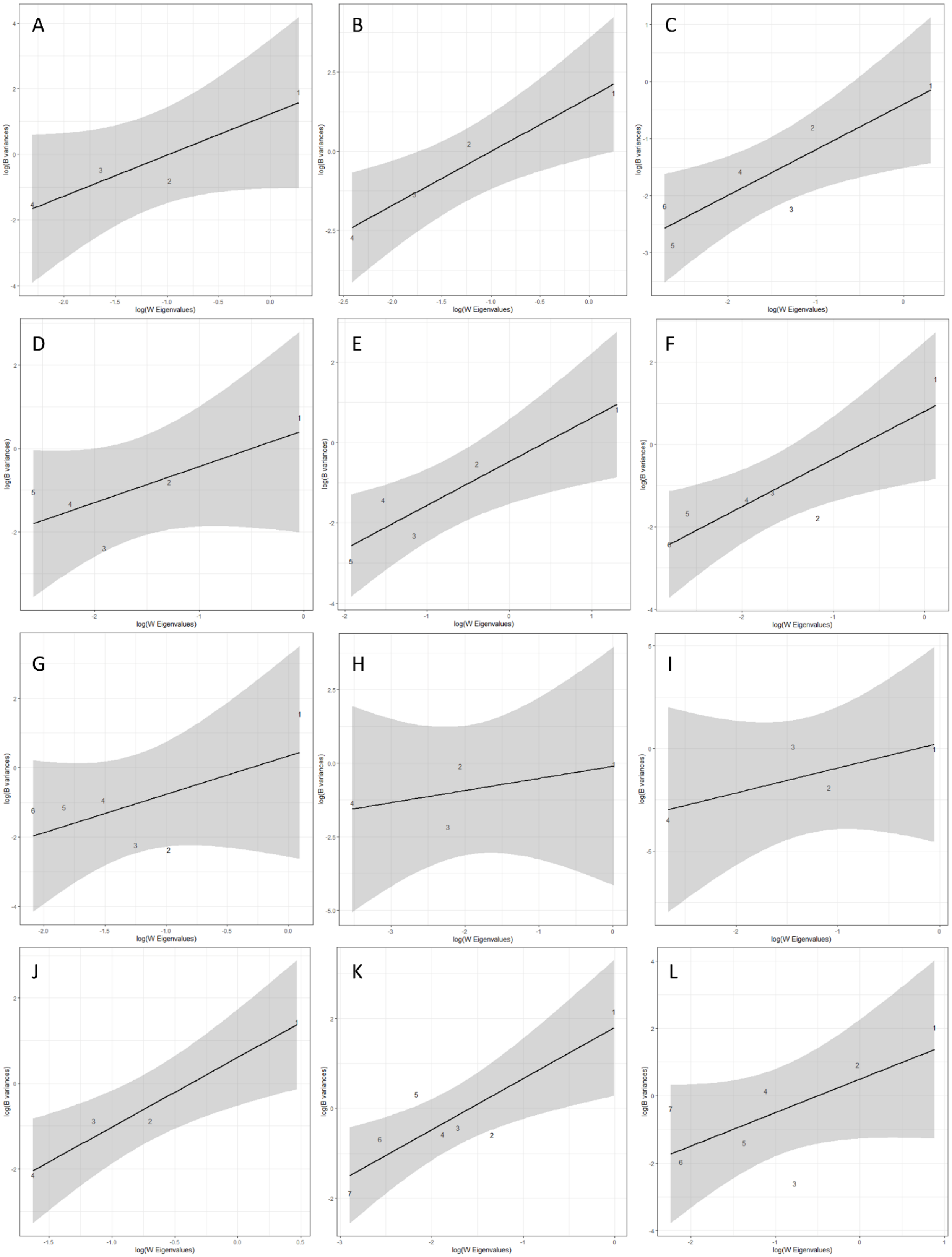
A
B
C
D
E
F
G
H
I
J
K
L
log(B variances)
log(W Eigenvalues)

**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

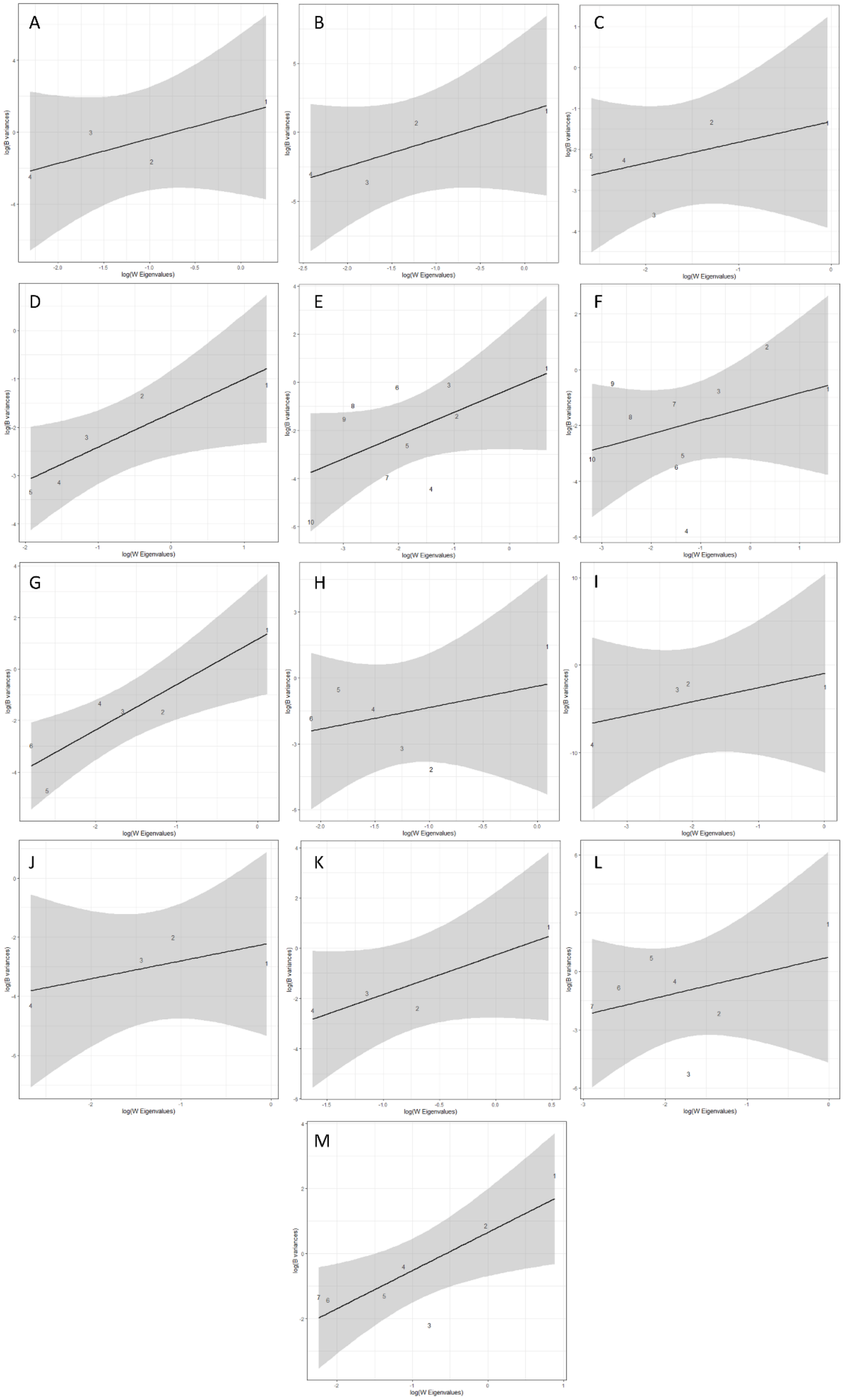
A
B
C
D
E
F
G
H
I
J
K
L
M
log(B variances)
log(W Eigenvalues)

**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.

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