Severe bottleneck of ancient *Homo* populations: Insights from computational modeling and fossil evidence

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This file includes:

Main Text
Figures 1 to 4
Tables 1 and 2

Abstract

Reconstructing ancient population size history is essential for understanding the evolutionary origin of *Homo sapiens*. Using the fast infinitesimal time coalescent process (FitCoal), which precisely computes the expected site frequency spectrum (SFS), we revisited the debated population bottleneck that occurred approximately 930 thousand years ago. By benchmarking FitCoal against *mushi* and ten billion coalescent simulations, we demonstrate that FitCoal achieves both superior speed and accuracy in expected SFS estimation. Analyses of simulated datasets confirmed that FitCoal reliably recovered the bottleneck, whereas *mushi* failed under identical conditions. Independent fossil and paleoclimate evidence further corroborates the timing and evolutionary impact of this bottleneck, linking it to hominin dispersals, speciation events, and a subsequent increase in brain size. These findings refine the demographic history of *Homo* during the Pleistocene and highlight the importance of high-precision SFS computation for revealing critical evolutionary transitions that shaped modern human ancestry.

Introduction

Over the past four million years, at least 22 hominin taxa have emerged, yet only modern humans (*Homo sapiens*) have persisted to the present day. The Early and Middle Pleistocene epochs represent a pivotal period in *Homo* evolution, during which African *H. erectus* declined (Di Vincenzo and Manzi 2023) and gave rise to a new species ancestral to modern humans, Neanderthals, and Denisovans (Prüfer, et al. 2014). Understanding the evolutionary trajectory leading to modern humans therefore requires reconstructing population size dynamics throughout the Pleistocene.

Site frequency spectrum (SFS)-based methods provide powerful tools for reconstructing population histories (Li and Stephan 2006; DeWitt, et al. 2021; Excoffier, et al. 2021). The SFS comprises (n–1) allele frequency categories, where n is the number of sampled sequences. Previous studies developed methods to estimate the expected branch lengths for each SFS category and calculate the likelihoods of observed SFS data under various demographic scenarios. However, these methods may lack sufficient accuracy for inferring the detailed population history of *Homo* during the Pleistocene. To overcome this limitation, the fast infinitesimal time coalescent process (FitCoal) was recently introduced to precisely infer both recent and ancient population size histories using the SFS (Hu, et al. 2023). FitCoal accurately calculates the expected SFS and associated likelihood. As different theoretical demographic models may yield similar SFS patterns (Myers, et al. 2008), FitCoal prioritizes biologically plausible scenarios and systematically increases model complexity to identify the most appropriate demographic model. Moreover, high-frequency alleles within the SFS are particularly susceptible to confounding factors, such as positive selection (Li 2010; Vy and Kim 2015), introgression (Tagore and Akey 2025), population structure (Kern and Hey 2017), and misclassification of ancestral and derived variants (Baudry and Depaulis 2003). Consequently, excluding such overrepresented alleles reduces biases and enhances the robustness and reliability of inferred demographic histories (Bhaskar, et al. 2015; Liu and Fu 2015; Hu, et al. 2023).

Results and Discussion

It has been widely recognized for nearly four decades that current African and non-African human populations share a common evolutionary history prior to their divergence. Our previous research identified a severe population bottleneck occurring approximately 930 thousand years ago (Ka) in both 12 African and 19 non-African populations (Hu, et al. 2023). However, recent studies have challenged this finding, suggesting that this bottleneck was confined to African populations alone and absent in non-African populations (Cousins and Durvasula 2025; Deng, et al. 2025). To resolve this discrepancy, we re-examined our earlier analyses and confirmed that both the timing

and severity of the bottleneck were virtually identical between African and non-African populations (Fig. 1A, B).

To further validate the efficacy of FitCoal, we compared inferred population histories obtained using both the complete site frequency spectrum (SFS) and a restricted subset of the SFS under an arbitrary bottleneck model. Remarkably, the bottleneck was accurately inferred even when analyzing only 10% of the SFS categories (minor allele frequencies ≤ 0.1) (Fig. 2A). FitCoal effectively captures subtle yet widespread signals present in the SFS due to the bottleneck event, as each coalescent state maintains a non-zero probability when traced back to this event (Hu, et al. 2023). This attribute significantly reduces biases from confounding factors, which predominantly affect high-frequency alleles. Although recent work partially addressed this issue by simulating ancestral and derived variant misclassification, the approach inadvertently increased model complexity (Cousins and Durvasula 2025). In contrast, FitCoal mitigates these confounding influences by specifically excluding high-frequency alleles (Bhaskar, et al. 2015; Liu and Fu 2015). These results highlight the abundant demographic information contained within the SFS and emphasize the robustness of FitCoal in accurately reconstructing complex evolutionary histories.

We further investigated the changes in the SFS induced by the presence or absence of the ancient severe bottleneck event. This bottleneck significantly reduced the proportions of mid- and high-frequency alleles in both African and non-African populations (Fig. 2B). Notably, the reduction was more pronounced in African populations, becoming evident from the 20th SFS category onward, compared to the 50th category in non-African populations. This finding is consistent with the broader range of bottleneck estimates observed in non-African populations (Fig. 1B). To further evaluate the detectability of the bottleneck, we simulated genome-wide polymorphic datasets based on inferred demographic histories from African populations. FitCoal successfully recovered the bottleneck signal (Fig. 2C), whereas *mushi* (DeWitt, et al. 2021) did not detect this signal under the same conditions. The log-likelihood of the demographic history inferred by FitCoal was also significantly higher than that inferred by *mushi* (-1211.63 *vs* -2849.65, *P*-value $< 2.2 \times 10^{-16}$, Fig. 3). These outcomes reinforce FitCoal's effectiveness and reliability in identifying the ancient severe bottleneck from genomic data.

To further explore the differences between FitCoal and *mushi* in inferring population history, we compared their estimations of expected branch lengths, a critical component in calculating the expected SFS. It is known that *mushi* relies on the joint probability density function of coalescent times, making it susceptible to accumulated numerical errors (Polanski, et al. 2003; Polanski and Kimmel 2003; Živković and Wiehe 2008). FitCoal overcomes this limitation by introducing a novel framework, the fast infinitesimal time coalescent process. For a fair comparison, we examined a synthetic demographic model previously associated with misidentification of a severe bottleneck (Deng, et al. 2025). The expected branch lengths estimated by FitCoal and *mushi* differed by up to 6.21%, corresponding to a cumulative discrepancy of 9,981 generations across SFS categories (Fig. 2D). To asses which method more closely reflects true values, we conducted 1×10^{10} *msprime* coalescent simulations (Baumdicker, et al. 2022) as a benchmark. FitCoal's estimates matched simulated values exactly in 194 of 215 SFS categories (90.2%), with only a single-generation deviation in the remaining categories (Table 1). Conversely, *mushi* exhibited deviations two orders of magnitude larger (Fig. 2E), underscoring FitCoal's superior accuracy. A recent study reported no apparent differences between *mushi* and *msprime* simulations (Cousins and Durvasula 2025), likely because their analyses were limited to comparisons analogous to the upper panel of Figure 2D, where differences remain minimal. Furthermore, FitCoal demonstrated remarkable computational efficiency, completing the calculation in only 0.00013 seconds, whereas *mushi* and *msprime* required 1.29 seconds and 4.90 years, respectively. These results highlight FitCoal's advantages in both accuracy and computational speed.

The observed, not the expected, SFSs were used as input for FitCoal (Hu, et al. 2023). A recent study input an expected SFS, leading to the detection of a severe-bottleneck-like event (Deng, et al. 2025). To clarify this issue, we compared expected and observed SFS and found that reliably estimating expected branch lengths requires at least 1×10^{10} simulations (Fig. 2E) and that the genome-wide observed SFS varies significantly among population samples. Considering this inherent variability, FitCoal employs a conservative default threshold of 20% likelihood gain, minimizing false positives in demographic model selection (Hu, et al. 2023). We validated this conservativity by simulating 1,000 genome-wide polymorphic datasets under the previously studied synthetic model (Deng, et al. 2025). FitCoal consistently avoided overfitting the mild population decrease (Fig. 2F), as the conservative threshold effectively minimized false positives. When using the expected SFS as input, a lower threshold (1% likelihood gain) was required to achieve optimized likelihoods without premature termination, yielding accurate demographic histories (Fig. 2F). These findings show the importance of clearly distinguishing between expected and observed SFSs in demographic analyses.

Existence of the ancient severe bottleneck is supported by multiple lines of evidence, including gaps in the African hominin fossil record (Profico, et al. 2016), the timing of ancestral chromosome fusion events (Dreszer, et al. 2007; Poszewiecka, et al. 2022; Poszewiecka, et al. 2023), major cultural and behavioral shifts (Clark and Linares-Matás 2024), climatic transitions during the Early-to-Middle Pleistocene (Jouzel, et al. 2007), and fluctuations in mammalian speciation and extinction rates (Cohen, et al. 2022). Moreover, the timing of the bottleneck coincides with major episodes of hominin dispersals from Africa to Eurasia (Muttoni and Kent 2024), and the evolutionary context inferred from the earliest known human facial fossil in Western Europe (Huguet, et al. 2025) aligns closely with the demographic decline scenario associated with this bottleneck.

Between 1,000 and 100 Ka, at least two significant macroevolutionary events occurred (Fig. 4A), coinciding with the “muddle in the middle”, a period characterized by hominin coexistence and morphological diversity (Bergström, et al. 2021; Ni, et al. 2021; Fu, et al. 2025). Since small population sizes facilitate speciation (Gould and Eldredge 1977), our findings imply that this severe bottleneck significantly impacted phenotypic and behavioral evolution in ancestral humans. Particularly, its role in adaptation and speciation warrant further investigation. The fixation of chromosome 2 fusion and its possible contribution to reproductive isolation remains unresolved. To further explore this, we analyzed endocranial volumes and encephalization quotient data from African fossil specimens. Our analysis revealed a significant increase in brain size following the bottleneck (Fig. 4B, Table 2), suggesting a potential relationship between population contraction and accelerated cognitive and social evolution. Additionally, recent evidence indicates that the last populations of African *H. erectus* experienced extreme aridity at the onset of the bottleneck, potentially driving behavioral adaptations critical for improved survival and resource utilization (Mercader, et al. 2025).

In conclusion, high-precision calculation of expected SFSs is critical for minimizing artifacts in demographic inference. Recent studies emphasize that these considerations cannot be overlooked (Hilgers, et al. 2025; Ishigohoka and Liedvogel 2025). Collectively, advanced demographic inference and extensive human genomic data promise deeper insights into hominin speciation, genetic impacts of severe population bottleneck, and the evolutionary forces shaping modern humans. Our findings enhance the understanding of critical evolutionary events within the genus *Homo* and highlight the importance of integrating genetic, paleontological, and environmental evidence.

Materials and Methods

The parameters of ancient bottleneck estimated from African and non-African populations were obtained from our previously published results (see the “Severe bottleneck during the Early to

Middle Pleistocene transition" section) (Hu, et al. 2023). The student *t*-test was used to examine whether there is a significant difference between African and non-African estimates in Fig. 1B.

To illustrate the rich demographic information embedded within the SFS, we simulated 200 SFS datasets using *msprime* (Baumdicker, et al. 2022) under a simple bottleneck model in Figure 2C of Hu et al. Mutation and recombination rates were set at 1.2×10^{-8} and 0.96×10^{-8} per base per generation, respectively, across 200 sequences of 100 Mb each. The generation time was 24 years. Demographic inference was performed with FitCoal, specifying three-time intervals for analysis. 10 repeats were performed to maximize the likelihood.

Four models were employed to investigate the effects of ancient severe bottlenecks on present-day human populations. Specifically, bottleneck models I and III from Hu *et al.* (Figure 4a and 4c) were utilized, with bottleneck I representing demographic history analogous to the true population history of African populations and bottleneck III analogous to that of non-African populations. Two additional models, modified versions excluding severe bottlenecks, were also derived from these original models. FitCoal calculated expected SFSs for all four scenarios, assuming n = 200 sequences.

We employed bottleneck model I as the true model, corresponding to the "severe bottleneck model" described by Deng *et al.* Using this model, we simulated 1,000 SFS datasets with *msprime*. Numbers of simulated sequences are 188, and the lengths of simulated sequences are 100 Mb each. These simulated datasets were then analyzed using *mushi* (DeWitt, et al. 2021) with parameters specified by Deng *et al*., yielding 1,000 inferred population histories. FitCoal was also used to infer population histories from the same simulated SFS datasets. Following our previous study, 10 repeats were performed to maximize the likelihood and analyze the simulated SFSs. Because FitCoal and *mushi* calculate the expected SFSs in different ways, to compare their likelihoods, we calculated the expected branch lengths for *mushi*-inferred demography using FitCoal.

The synthetic demographic model was obtained using the scripts from Deng et al. (Deng, et al. 2025). Initially, this model was generated using an expected SFS calculated by *mushi* based on a severe bottleneck scenario for an African population. The expected SFS was derived by multiplying branch lengths by the total mutation rate across the analyzed sequence fragments. To assess this synthetic model, we compared expected branch lengths for each SFS category using three independent methods. We assumed that n = 216 sequences. First, we calculated the expected branch lengths using *mushi*, following the approach described in recent studies (Cousins and Durvasula 2025; Deng, et al. 2025). Second, expected branch lengths were calculated using FitCoal version 1.3, freely available at https://doi.org/10.5281/zenodo.4765446 and released alongside this manuscript. Third, we performed simulations with *msprime*, generating 1×10^{10} coalescent trees for a single locus based on the synthetic model and calculating mean branch length per SFS category. The number of simulations 1×10^{10} was selected after evaluating expected branch length accuracy (Fig. 2E). Due to rounding precision considerations, at least 1×10^{10} coalescent simulations were necessary for accurate inference of expected branch lengths. These simulations were conducted on a CPU server equipped with an Intel Xeon Gold 6248R processor utilizing 60 parallel threads, with total runtime reported in core-hours. We loaded a pre-calculated table merely once to FitCoal, and FitCoal's runtime for calculating expected branch lengths was determined as the average of 5,000 repetitions on the same server, using a single thread.

To examine the robustness of FitCoal in inferring population demography, we simulated 1,000 SFS datasets under the synthetic model using *msprime*. Simulation parameters matched those used by Deng et al. (2025), setting mutation and recombination rates at 1.2×10^{-8} per base per generation across 216 sequences, each 100 Mb in length. Because the simulated data followed a neutral single-population model, exclusion of high-frequency mutations was unnecessary. FitCoal

was run with default parameters, using a logLPRate of 20 (indicating a 20% likelihood gain) to infer 1,000 population size histories. Additionally, population history was inferred using a FitCoal-generated expected SFS with a logLPRate of 1 (indicating a 1% likelihood gain). The logLPRate setting determines the optimal model identification; a smaller logLPRate is appropriate when the expected SFS is used because maximum likelihood corresponds directly to the true model. However, since expected SFSs cannot be derived directly from samples and typically serve to calculate likelihoods for observed SFSs under demographic models, we recommend against using expected SFSs as input of FitCoal.

The endocranial volume data for the Buia specimen were sourced from Bruner et al. (2016), KNM-ER 42700 from Neubauer et al. (2018), and all remaining specimens from Holloway, Broadfield and Yuan (2004). Encephalization quotients for each specimen were calculated following Jerision (1973). Body mass estimates (in kilograms) used in these calculations were obtained from Carretero, et al. (2004), Grabowski, et al. (2015) and Jungers et al. (2016).

Data Availability

FitCoal version 1.3 is freely available at https://doi.org/10.5281/zenodo.4765446.

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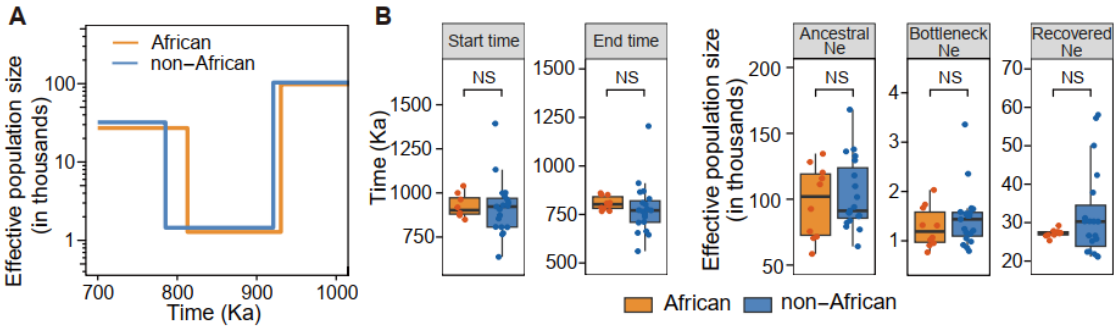

Fig 1. The ancient human severe bottleneck. (**A**) The severe bottleneck inferred in African and non-African populations. Mean values are shown. (**B**) Estimated bottleneck parameters for 10 African and 19 non-African populations. Two South African populations (San and Bantu) were excluded due to small sample sizes. Estimates are based on previously published results (Hu, et al. 2023). Two-tailed Student's *t*-test; NS, not significant.

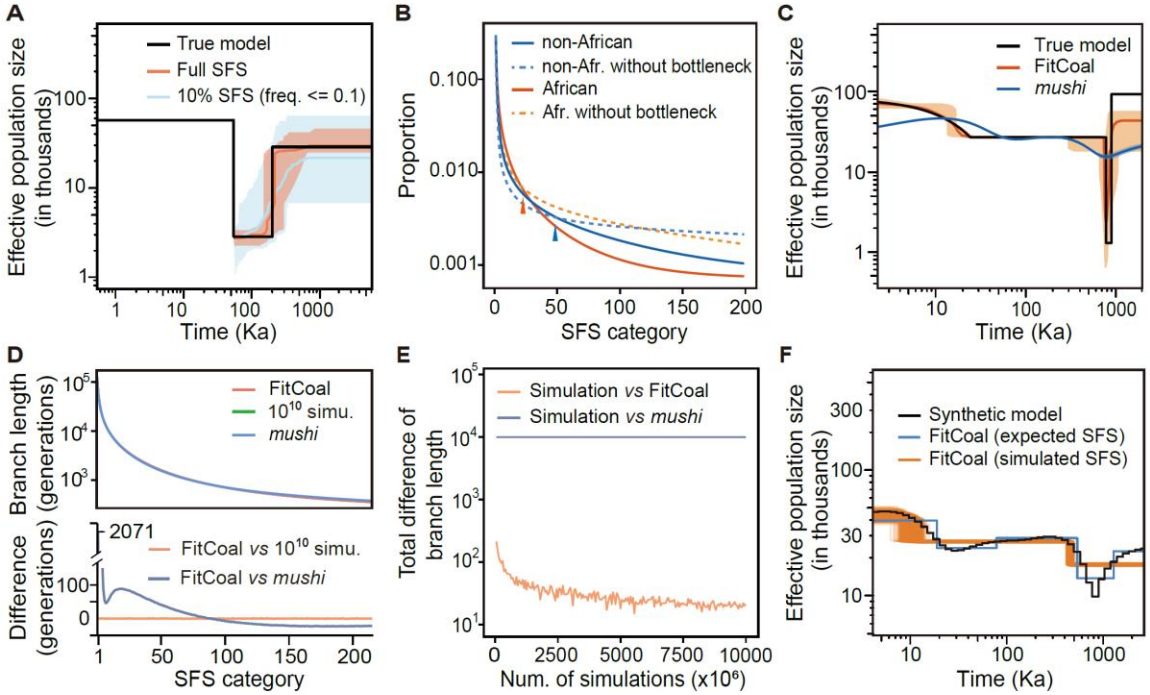

Fig. 2. Implications of FitCoal's high-precision computation. (**A**) FitCoal-inferred population size histories using complete-SFS and minor alleles ($freq \leq 0.1$). Colored bands represent estimated ranges spanning the 2.5th to the 97.5th percentiles. (**B)** Impact of the ancient severe bottleneck on the SFS. Solid orange and blue lines show the normalized expected SFS under African and non-African the demographic histories, respectively, while dashed lines represent cases without the ancient severe bottleneck. Arrows indicate the onset of allele deficiency. (**C**) Population size histories inferred by FitCoal and *mushi*. Shaded areas denote estimated ranges between the 2.5th and 97.5th percentiles. The black line represents the true model, mimicking the demographic history of African agriculturalist populations. (**D**) Upper panel: expected branch lengths for each SFS category calculated by FitCoal, *mushi*, and 1×10^{10} *msprime* simulations under the synthetic model. Lower panel: deviations from FitCoal estimates. (**E**) Effect of simulation number on the accuracy of averaged branch lengths, compared with FitCoal and *mushi* estimates under the synthetic model. (**F**) FitCoal-inferred population size histories from simulated and the expected SFSs under the synthetic model. Red lines indicate histories inferred from 1,000 simulated datasets (*n*=200, *L*=100 Mb), and the blue line represents the history inferred from the expected SFS.

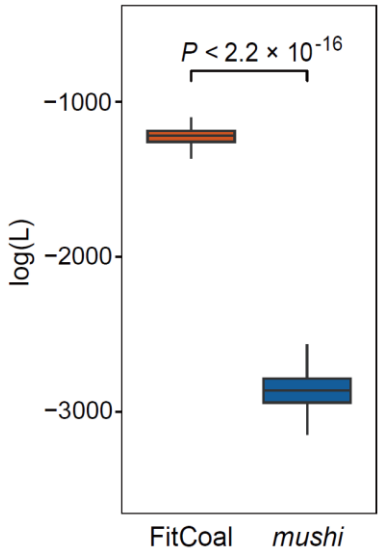

Fig. 3. Log-likelihood values of FitCoal- and *mushi*-inferred histories. The true model is shown in Fig. 2C. Demographic histories were inferred from 1,000 simulated genome-wide datasets using FitCoal and *mushi*. Statistical significance was determined by two-tailed Student's *t*-test.

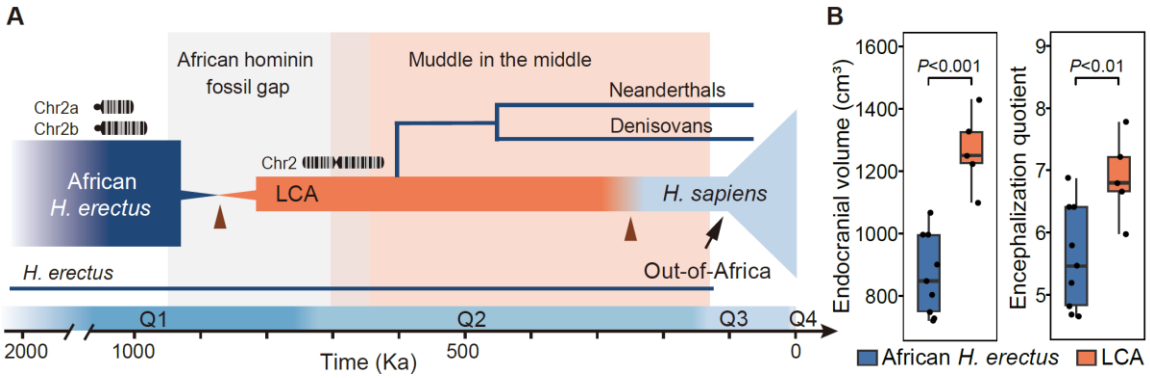

Fig. 4 Integration of genetic evidence and fossil record. (**A**) Evolutionary history of hominins over the past one million years. LCA refers to the last common ancestor shared by Denisovans, Neanderthals, and modern humans. Triangles indicate speciation events. Q1 – Q4 denote the Early Pleistocene, Middle Pleistocene, Late Pleistocene, and Holocene, respectively. (**B**) Endocranial volumes and the encephalization quotients of African fossil specimens before and after the severe bottleneck. Central lines of boxplots represent the medians and box limits denote the 25th and 75th quantiles. Statistical significance was determined by two-tailed Student's *t*-test.

Table 1. Expected branch lengths for each SFS category.

Type[1]	FitCoal (Generations)	1×10^{10} simulations (Generations)	*Mushi* (Generations)	Absolute diff. FitCoal *vs* simulations	Absolute diff. FitCoal *vs* *mushi*
1	129059	129059	126988	0 (0.00%)	2071 (1.60%)
2	57514	57514	56423	0 (0.00%)	1091 (1.90%)
3	35743	35743	35270	0 (0.00%)	473 (1.32%)
4	25931	25931	25730	0 (0.00%)	201 (0.78%)
5	20441	20441	20349	0 (0.00%)	92 (0.45%)
6	16922	16922	16867	0 (0.00%)	55 (0.33%)
7	14455	14455	14409	0 (0.00%)	46 (0.32%)
8	12617	12617	12568	0 (0.00%)	49 (0.39%)
9	11187	11187	11132	0 (0.00%)	55 (0.49%)
10	10039	10039	9977	0 (0.00%)	62 (0.62%)
11	9096	9096	9026	0 (0.00%)	70 (0.77%)
12	8306	8306	8231	0 (0.00%)	75 (0.90%)
13	7634	7634	7554	0 (0.00%)	80 (1.05%)
14	7056	7056	6972	0 (0.00%)	84 (1.19%)
15	6552	6552	6466	0 (0.00%)	86 (1.31%)
16	6110	6110	6023	0 (0.00%)	87 (1.42%)
17	5719	5719	5631	0 (0.00%)	88 (1.54%)
18	5371	5371	5282	0 (0.00%)	89 (1.66%)
19	5059	5059	4970	0 (0.00%)	89 (1.76%)
20	4778	4778	4689	0 (0.00%)	89 (1.86%)
21	4523	4523	4435	0 (0.00%)	88 (1.95%)
22	4291	4291	4204	0 (0.00%)	87 (2.03%)
23	4080	4080	3994	0 (0.00%)	86 (2.11%)
24	3886	3886	3801	0 (0.00%)	85 (2.19%)
25	3708	3708	3624	0 (0.00%)	84 (2.27%)
26	3544	3543	3461	1 (0.03%)	83 (2.34%)
27	3392	3392	3311	0 (0.00%)	81 (2.39%)
28	3251	3251	3172	0 (0.00%)	79 (2.43%)
29	3120	3120	3042	0 (0.00%)	78 (2.50%)
30	2998	2998	2922	0 (0.00%)	76 (2.54%)
31	2884	2884	2810	0 (0.00%)	74 (2.57%)
32	2777	2777	2705	0 (0.00%)	72 (2.59%)
33	2678	2677	2607	1 (0.04%)	71 (2.65%)
34	2584	2584	2515	0 (0.00%)	69 (2.67%)
35	2496	2496	2429	0 (0.00%)	67 (2.68%)
36	2413	2413	2348	0 (0.00%)	65 (2.69%)
37	2334	2334	2271	0 (0.00%)	63 (2.70%)
38	2260	2260	2199	0 (0.00%)	61 (2.70%)
39	2190	2190	2131	0 (0.00%)	59 (2.69%)
40	2124	2124	2066	0 (0.00%)	58 (2.73%)
41	2062	2061	2005	1 (0.05%)	57 (2.76%)
42	2002	2002	1947	0 (0.00%)	55 (2.75%)
43	1945	1945	1892	0 (0.00%)	53 (2.72%)
44	1892	1891	1840	1 (0.05%)	52 (2.75%)
45	1840	1840	1791	0 (0.00%)	49 (2.66%)
46	1791	1792	1743	1 (0.06%)	48 (2.68%)
47	1745	1745	1698	0 (0.00%)	47 (2.69%)

48	1700	1701	1656	1 (0.06%)	44 (2.59%)
49	1658	1658	1615	0 (0.00%)	43 (2.59%)
50	1617	1617	1576	0 (0.00%)	41 (2.54%)
51	1579	1578	1538	1 (0.06%)	41 (2.60%)
52	1541	1541	1503	0 (0.00%)	38 (2.47%)
53	1506	1506	1468	0 (0.00%)	38 (2.52%)
54	1472	1471	1436	1 (0.07%)	36 (2.45%)
55	1439	1439	1404	0 (0.00%)	35 (2.43%)
56	1407	1407	1374	0 (0.00%)	33 (2.35%)
57	1377	1377	1345	0 (0.00%)	32 (2.32%)
58	1348	1348	1318	0 (0.00%)	30 (2.23%)
59	1320	1320	1291	0 (0.00%)	29 (2.20%)
60	1293	1293	1265	0 (0.00%)	28 (2.17%)
61	1267	1267	1241	0 (0.00%)	26 (2.05%)
62	1242	1242	1217	0 (0.00%)	25 (2.01%)
63	1218	1218	1194	0 (0.00%)	24 (1.97%)
64	1195	1195	1172	0 (0.00%)	23 (1.92%)
65	1173	1173	1151	0 (0.00%)	22 (1.88%)
66	1151	1151	1131	0 (0.00%)	20 (1.74%)
67	1131	1131	1111	0 (0.00%)	20 (1.77%)
68	1110	1111	1092	1 (0.09%)	18 (1.62%)
69	1091	1091	1074	0 (0.00%)	17 (1.56%)
70	1072	1072	1056	0 (0.00%)	16 (1.49%)
71	1054	1054	1039	0 (0.00%)	15 (1.42%)
72	1036	1037	1022	1 (0.10%)	14 (1.35%)
73	1019	1020	1006	1 (0.10%)	13 (1.28%)
74	1003	1003	991	0 (0.00%)	12 (1.20%)
75	987	987	976	0 (0.00%)	11 (1.11%)
76	972	972	961	0 (0.00%)	11 (1.13%)
77	957	957	947	0 (0.00%)	10 (1.04%)
78	942	942	934	0 (0.00%)	8 (0.85%)
79	928	928	921	0 (0.00%)	7 (0.75%)
80	914	914	908	0 (0.00%)	6 (0.66%)
81	901	901	895	0 (0.00%)	6 (0.67%)
82	888	888	883	0 (0.00%)	5 (0.56%)
83	876	876	872	0 (0.00%)	4 (0.46%)
84	864	864	860	0 (0.00%)	4 (0.46%)
85	852	852	849	0 (0.00%)	3 (0.35%)
86	840	840	839	0 (0.00%)	1 (0.12%)
87	829	829	828	0 (0.00%)	1 (0.12%)
88	819	819	818	0 (0.00%)	1 (0.12%)
89	808	808	808	0 (0.00%)	0 (0.00%)
90	798	798	799	0 (0.00%)	1 (0.13%)
91	788	788	789	0 (0.00%)	1 (0.13%)
92	778	778	780	0 (0.00%)	2 (0.26%)
93	769	769	771	0 (0.00%)	2 (0.26%)
94	759	759	763	0 (0.00%)	4 (0.53%)
95	751	750	755	1 (0.13%)	4 (0.53%)
96	742	742	746	0 (0.00%)	4 (0.54%)
97	733	733	738	0 (0.00%)	5 (0.68%)
98	725	725	731	0 (0.00%)	6 (0.83%)

99	717	717	723	0 (0.00%)	6 (0.84%)
100	709	709	716	0 (0.00%)	7 (0.99%)
101	701	701	709	0 (0.00%)	8 (1.14%)
102	694	694	702	0 (0.00%)	8 (1.15%)
103	686	686	695	0 (0.00%)	9 (1.31%)
104	679	680	688	1 (0.15%)	9 (1.33%)
105	672	672	682	0 (0.00%)	10 (1.49%)
106	666	665	675	1 (0.15%)	9 (1.35%)
107	659	659	669	0 (0.00%)	10 (1.52%)
108	652	653	663	1 (0.15%)	11 (1.69%)
109	646	646	657	0 (0.00%)	11 (1.70%)
110	640	640	651	0 (0.00%)	11 (1.72%)
111	634	634	646	0 (0.00%)	12 (1.89%)
112	628	628	640	0 (0.00%)	12 (1.91%)
113	622	622	635	0 (0.00%)	13 (2.09%)
114	616	616	629	0 (0.00%)	13 (2.11%)
115	611	611	624	0 (0.00%)	13 (2.13%)
116	605	605	619	0 (0.00%)	14 (2.31%)
117	600	600	614	0 (0.00%)	14 (2.33%)
118	595	595	609	0 (0.00%)	14 (2.35%)
119	590	590	605	0 (0.00%)	15 (2.54%)
120	585	585	600	0 (0.00%)	15 (2.56%)
121	580	580	595	0 (0.00%)	15 (2.59%)
122	575	575	591	0 (0.00%)	16 (2.78%)
123	571	570	587	1 (0.18%)	16 (2.80%)
124	566	566	582	0 (0.00%)	16 (2.83%)
125	561	561	578	0 (0.00%)	17 (3.03%)
126	557	557	574	0 (0.00%)	17 (3.05%)
127	553	553	570	0 (0.00%)	17 (3.07%)
128	549	549	566	0 (0.00%)	17 (3.10%)
129	544	544	562	0 (0.00%)	18 (3.31%)
130	540	540	558	0 (0.00%)	18 (3.33%)
131	536	536	554	0 (0.00%)	18 (3.36%)
132	532	532	551	0 (0.00%)	19 (3.57%)
133	529	529	547	0 (0.00%)	18 (3.40%)
134	525	525	544	0 (0.00%)	19 (3.62%)
135	521	521	540	0 (0.00%)	19 (3.65%)
136	517	517	537	0 (0.00%)	20 (3.87%)
137	514	514	533	0 (0.00%)	19 (3.70%)
138	510	510	530	0 (0.00%)	20 (3.92%)
139	507	507	527	0 (0.00%)	20 (3.94%)
140	504	504	523	0 (0.00%)	19 (3.77%)
141	500	500	520	0 (0.00%)	20 (4.00%)
142	497	497	517	0 (0.00%)	20 (4.02%)
143	494	494	514	0 (0.00%)	20 (4.05%)
144	491	491	511	0 (0.00%)	20 (4.07%)
145	488	488	508	0 (0.00%)	20 (4.10%)
146	485	485	505	0 (0.00%)	20 (4.12%)
147	482	482	503	0 (0.00%)	21 (4.36%)
148	479	479	500	0 (0.00%)	21 (4.38%)
149	476	476	497	0 (0.00%)	21 (4.41%)

150	473	473	494	0 (0.00%)	21 (4.44%)
151	470	470	492	0 (0.00%)	22 (4.68%)
152	467	467	489	0 (0.00%)	22 (4.71%)
153	465	465	486	0 (0.00%)	21 (4.52%)
154	462	462	484	0 (0.00%)	22 (4.76%)
155	460	459	481	1 (0.22%)	21 (4.57%)
156	457	457	479	0 (0.00%)	22 (4.81%)
157	454	454	476	0 (0.00%)	22 (4.85%)
158	452	452	474	0 (0.00%)	22 (4.87%)
159	449	449	472	0 (0.00%)	23 (5.12%)
160	447	447	469	0 (0.00%)	22 (4.92%)
161	445	445	467	0 (0.00%)	22 (4.94%)
162	442	442	465	0 (0.00%)	23 (5.20%)
163	440	440	462	0 (0.00%)	22 (5.00%)
164	438	438	460	0 (0.00%)	22 (5.02%)
165	436	435	458	1 (0.23%)	22 (5.05%)
166	433	433	456	0 (0.00%)	23 (5.31%)
167	431	431	454	0 (0.00%)	23 (5.34%)
168	429	429	452	0 (0.00%)	23 (5.36%)
169	427	427	450	0 (0.00%)	23 (5.39%)
170	425	425	447	0 (0.00%)	22 (5.18%)
171	423	423	445	0 (0.00%)	22 (5.20%)
172	421	421	443	0 (0.00%)	22 (5.23%)
173	419	419	441	0 (0.00%)	22 (5.25%)
174	417	417	440	0 (0.00%)	23 (5.52%)
175	415	415	438	0 (0.00%)	23 (5.54%)
176	413	413	436	0 (0.00%)	23 (5.57%)
177	411	411	434	0 (0.00%)	23 (5.60%)
178	409	409	432	0 (0.00%)	23 (5.62%)
179	407	407	430	0 (0.00%)	23 (5.65%)
180	406	406	428	0 (0.00%)	22 (5.42%)
181	404	404	427	0 (0.00%)	23 (5.69%)
182	402	402	425	0 (0.00%)	23 (5.72%)
183	400	400	423	0 (0.00%)	23 (5.75%)
184	399	398	421	1 (0.25%)	22 (5.51%)
185	397	397	420	0 (0.00%)	23 (5.79%)
186	395	395	418	0 (0.00%)	23 (5.82%)
187	393	393	416	0 (0.00%)	23 (5.85%)
188	392	392	415	0 (0.00%)	23 (5.87%)
189	390	390	413	0 (0.00%)	23 (5.90%)
190	389	389	411	0 (0.00%)	22 (5.66%)
191	387	387	410	0 (0.00%)	23 (5.94%)
192	386	386	408	0 (0.00%)	22 (5.70%)
193	384	384	407	0 (0.00%)	23 (5.99%)
194	382	382	405	0 (0.00%)	23 (6.02%)
195	381	381	404	0 (0.00%)	23 (6.04%)
196	379	379	402	0 (0.00%)	23 (6.07%)
197	378	378	401	0 (0.00%)	23 (6.08%)
198	377	377	399	0 (0.00%)	22 (5.84%)
199	375	375	398	0 (0.00%)	23 (6.13%)
200	374	374	396	0 (0.00%)	22 (5.88%)

201	372	372	395	0 (0.00%)	23 (6.18%)
202	371	371	393	0 (0.00%)	22 (5.93%)
203	370	369	392	1 (0.27%)	22 (5.95%)
204	368	368	390	0 (0.00%)	22 (5.98%)
205	367	367	389	0 (0.00%)	22 (5.99%)
206	365	365	388	0 (0.00%)	23 (6.30%)
207	364	364	386	0 (0.00%)	22 (6.04%)
208	363	363	385	0 (0.00%)	22 (6.06%)
209	362	361	384	1 (0.28%)	22 (6.08%)
210	360	360	382	0 (0.00%)	22 (6.11%)
211	359	359	381	0 (0.00%)	22 (6.13%)
212	358	358	380	0 (0.00%)	22 (6.15%)
213	357	357	378	0 (0.00%)	21 (5.88%)
214	355	355	377	0 (0.00%)	22 (6.20%)
215	354	354	376	0 (0.00%)	22 (6.21%)
Total diff.	–	–	–	21	9,981

[1]The number of sampled sequences is 216, following Deng *et al* (2025).

Table 2. Endocranial volume and the encephalization quotient of African *Homo erectus* and the LCA.

Taxon	Specimen	Endocranial volume (cm^3)	Encephalization quotient
H. erectus (Africa)	KNM-ER 3732	750	4.83
	KNM-ER 3733	848	5.46
	KNM-ER 3883	804	5.18
	Daka	995	6.41
	Buia	995	6.41
	KNM-ER 42700	721	4.64
	KNM-WT 15000	900	5.79
	OH 9	1,067	6.87
	OH 12	727	4.68
LCA	Bodo	1,250	6.80
	Broken Hill 1	1,325	7.21
	Saldanha	1,225	6.66
	Omo-Kibish 2	1,430	7.77
	Ndutu	1,100	5.98