Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Human encephalization accelerated late and linked to cultural complexity

Manuel Will

manuel.will@uni-tuebingen.de

University of Tübingen: Eberhard Karls Universitat Tubingen https://orcid.org/0000-0001-8116-2543

Jay T. Stock

Western University

Hannes Rathmann

University of Tübingen

Adam Gordon

University at Albany, State University of New York

Claudio Tennie

University of Tübingen

Research Article

Keywords: Brain size, body size, cognition, Paleolithic archaeology, paleodeme, cultural evolution

Posted Date: September 2nd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10878202/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: The authors declare no competing interests.

Abstract

Paleoanthropology and archaeology employ various proxy measures of hominin cognition, including endocranial volume, the complexity of material culture, or encephalization quotients (EQ). Competing scenarios of hominin encephalization contrast gradual anagenetic change with punctuated models linked to speciation events and major technological innovations. Here, we employ improved estimates of EQ with increased spatiotemporal resolution, including a novel paleodeme approach, and examine their relationship with technological complexity. We found no substantial increase in hominin encephalization associated with the earliest stone tool technologies, the origin of our genus, or the onset of the Acheulean. Instead, segmented regression analysis identified a major breakpoint in encephalization at ~ 1.2–0.7 Mya and another inflection point at ~ 0.1 Mya. Measures of technological complexity correlate highly with EQ, demonstrating a tight, though late, integration of encephalization with cultural evolution. Exponential increases in relative brain size emerge only after the onset of the Middle Paleolithic/Middle Stone Age, coinciding with a marked acceleration in both the diversity and pace of cultural innovation during the Late Pleistocene. Our findings support a model of late, stepwise encephalization co-evolving with cumulative cultural complexity.

Significance statement

Our understanding of human evolution has long assumed that larger brains evolved gradually alongside the earliest stone tools and major technological innovations. We overturn this view by showing that substantial increases in relative brain size occurred much later than previously thought, characterized by a stepwise pattern that coincided with accelerating cultural innovation during the Middle to Late Pleistocene. These findings demonstrate that the evolution of larger brains and increasingly complex culture became tightly coupled only late in human history. This offers a revised biocultural framework for understanding the emergence of modern humans, proving that early technological milestones did not drive initial brain expansion, but that biology and culture later formed an accelerating, co-evolutionary feedback loop.

Introduction

Hominin evolution is characterized by the co-evolution of biology and culture. Key behavioral changes over the Plio-Pleistocene include increased diversity and complexity of artefacts, larger group size, changing subsistence patterns, the occupation of more ecological niches, extended childhoods, and a tendency towards symbolic communication. The main biological macrotrends across this timeframe include the evolution and refinement of bipedal locomotion in connection with changes in body proportions, increases in stature and body mass, and larger absolute and relative brain sizes. Whereas the evolution of body size and shape is relatively well understood (*1–3*), changes in brain size have long been debated (*4,5*) with renewed and recent interest (*6–14*). Although changes in brain size are a particularly relevant area to study the interaction between human biology and cultural evolution on a macro-level, recent work has not explored this relationship in detail.

Various models for hominin cognitive evolution have been proposed in paleoanthropology and archaeology. Based on studying absolute and relative brain sizes, competing models encompass gradual diachronic change (*6,14*) or more step-like and punctuated patterns (*1,11,15*). In punctuated models, proposed key events include the emergence of the genus *Homo* and/or the speciation of *Homo erectus*, followed by a second phase of additional brain size gain and exponential increase in encephalization with the onset of the Middle Pleistocene and including *Homo heidelbergensis* or *Homo sapiens* (*1,11,13,15–17*). Gradual models advocate for major changes that occur mostly within lineages, such as a gradual increase in both brain and body sizes within *Homo erectus*, but also other species (*6,14*), without any substantial breakpoints. In a similar vein, using various measures to assess cognitive complexity based on the archaeological record has resulted in either punctuated changes, such as at the origins of stone tool technology, the Acheulean, Later Stone Age or Upper Paleolithic (*18–21*), but also more gradual, cumulative models (*22*).

Encephalization quotients (EQ), the classic measures of relative brain size in relation to body size, are comparatively underrepresented in recent paleoanthropological debates. Various ways to calculate and analyze EQ have been used, though they suffer limitations (see Text S1). The calculation of EQs requires associated estimates of both brain and body size from the same individuals, but the fragmentary nature of the fossil record poses a fundamental data-scarcity problem, particularly before the Late Pleistocene. A common attempt to circumvent this problem uses 'mean EQ' values for species by combining mean brain sizes and mean body sizes to generate what we shall call here an average 'taxon EQ' (see e.g., *1,14*). This approach has its own limitations as it combines body and brain size estimates taken from different individuals, despite specimens within these groups potentially ranging widely in time, space, and ecology. Intra-species variation, phenotypic plasticity, ecological influences, and within-lineage evolutionary trends add noise to the resulting averages and EQ values. Taxon EQs also lack an expression of variability and are typically based on small sample sizes, and are, as such, prone to the effects of outliers that can skew the means. One way to address the challenges of individual and taxon EQs is to use paleodemes as analytical units (*23,24*), grouping remains of the same taxon, proximate geographic distribution, and similar age. This approach still aggregates various individuals in one category, yet the resulting paleodeme EQs derive from a small sample of closely associated body and brain sizes coming from similar eco-geographical backgrounds and sharing a closer gene pool. Paleodemes thus provide more biologically relevant EQs compared to taxon EQ and allow for intra-species spatial and temporal variation (see Methods for more details).

Regarding the relationship between hominin biological and cultural evolution, there is broad agreement that more complex tool technologies are more demanding, as they require longer sequences and/or a deeper hierarchy of cognitive steps in preparation and execution. To deal with these increasing demands, cognitive powers need to increase via more capable brains or these demands may be met via cumulative cultural solutions, transmitted and shared culturally (or both). However, the latter requires special types of social learning, and therefore brains capable of performing them and storing the cultural information (*25,26*). In both cases, encephalization is therefore expected to track tool complexity and *vice versa*. How best to measure this complexity remains debated, and traditional archaeological typologies may be poor

proxies for real shifts in complexity (see e.g., *27,28*). Exploring the relationship between encephalization and technological complexity while attending to the tempo of change in each may help distinguish the evolution of technological cognition from the evolution of special types of social learning for cumulative culture (*29*) and from the later cultural co-evolution of human cognition and culture (e.g. via symbolic minds). This is because cultural evolution can far outpace biological evolution (*30,31*). Such an analysis is timely as the earliest evidence for the types of social learning necessary for human cumulative culture has recently been shifting away from traditionally considered transition points, and could even postdate the onset of the Acheulean (28,32). With it, the earliest evidence of cumulative culture and the cultural brain may postdate the origin of *Homo* and the origins of stone tools.

Resolving current paleoanthropological and archaeological debates on the patterns and drivers of hominin cognition using EQ requires novel, integrated approaches with datasets from both disciplines. Here, we provide new estimates of EQ on three levels of resolution - individual fossils, paleodemes, and taxa - to better examine spatio-temporal trajectories in hominin evolution. We couple this approach with segmented regression analysis to infer whether temporal patterns were gradual or punctuated, and at which times major changes occurred. Finally, we assess the relationship between brain and cultural evolution by comparing EQ values with archaeology-based measures of technological complexity. Our findings provide substantial insights into hominin cognitive evolution: i) A major breakpoint in encephalization occurred at ~ 1.2–0.7 million years ago (Mya) with another inflection point at ~ 0.1 Mya, well after the emergence of *Homo* and *Homo erectus*, and much later than the origins of stone tools and the Acheulean; ii.) Exponential increases in relative brain size appear only after the beginning of the Middle Paleolithic/MSA. iii.) Combined analyses of bio-cultural datasets demonstrate that technological complexity correlates with EQ and support a model of late, punctuated encephalization linked first to the evolution of special types of social learning which allowed cumulative cultural technology, and, later, culturally evolved cognition.

Encephalization quotients by paleodeme

We calculated three measures of EQs - individual, paleodeme, and taxon - and compared them against each other and published results (Fig. 1; Text S2; Figures S1-3). Individual EQ includes specimens with both brain and postcranial body size estimates, whereas EQ values for taxonomic units or paleodemes are grouped by body and brain sizes of their respective groups (See Methods and Table S2). Since the paleodeme approach (n = 73) provides the highest spatio-temporal resolution and biological relevance, we provide these results in the following. A comparison to the results of the taxon and individual finds can be found in Text S2.

The earliest hominins in our samples between 4.4–3.2 Mya, *Ar. ramidus* (paleodeme EQ = 1.75; n = 1) and *A. afarensis* (paleodeme EQ = 1.94–2.12; n = 2) demonstrate the lowest EQ values. Until about 1.5 Mya, most paleodeme EQs fall slightly higher and range between 2–3 (Fig. 1, Figure S2, Table S2). *Paranthropus* paleodemes (EQ = 2.28–2.85; n = 6) are only slightly lower or equal to various *Homo* taxa, including Early *Homo*, *Homo habilis*, *Homo naledi* and *Homo floresiensis*. The paleodemes of the earliest

Homo in our sample (~ 2.0-1.8 Mya) have a narrow EQ range (EQ = 2.83-3.00) and include both smaller-brained and smaller-bodied individuals from East Turkana assigned to *Homo habilis* at 1.9 Mya (mean = 39 kg; 530 cm^3; e.g., KNM-ER 3735 and KNM-ER 1813) but also larger-bodied representatives from East Turkana > 1.9 Mya with larger brains attributed to Early *Homo* (mean=57kg; 703 cm^3; e.g., KNM-ER 1481 and KNM-ER 1470).

Closer consideration of *Homo erectus* s.l. demonstrates within-lineage changes. The detailed temporal plot (Figure S2) shows marked differences in paleodeme EQ values before 1.3 Mya (mean EQ = 2.86) within the range of early *Homo* taxa, and after (mean EQ = 3.45) within this taxon. The latter group reaches EQs midway between early *Homo* and the mean of Mid-Pleistocene *Homo* paleodemes (EQ = 4.08, n = 5). The low EQ values for early *Homo erectus* s.l. are due to the small-brained and small-bodied Dmanisi individuals (mean = 49.5 kg; 634 cm^3; EQ = 2.86) and the larger-brained but also much larger-bodied individuals from East Turkana (mean = 69 kg; 816 cm^3; EQ = 2.86), dated to between 1.6–1.5 Mya. Higher values of the later paleodemes of *Homo erectus* s.l. derive from the geographically distinct populations of Bouri, Gona, Zhoukoudian, Sangiran, Sambungmacan and Trinil from throughout the late Early and Middle Pleistocene with intermediate body sizes but much larger brains (mean = 62.5 kg; ~980 cm^3; EQ = 3.3–3.88). Overall, paleodeme EQs of *Homo erectus* s.l. have the highest range of values of earlier hominins, indicating spatio-temporal variability that is likely linked to ecological differences, an intra-species diachronic increase, and potential issues with the alpha taxonomy of included fossils. A noticeable and consistent increase in average paleodeme EQs of 4 and beyond can only be seen in paleodemes of the Mid-Pleistocene and later, including Mid-Pleistocene *Homo* (average EQ = 4.07; range = 3.61–4.38; n = 5), Neanderthals (average EQ = 4.74; range = 3.91–5.78; n = 10), and *Homo sapiens* (average EQ = 5.27; range = 4.44–6.77; n = 26). Neanderthals and *Homo sapiens* share comparable paleodeme EQ values, with all other *Homo* paleodemes falling either at the lowest range of this distribution or below.

Segmented regression analysis identifies temporal breakpoints in hominin encephalization

Using segmented regression analyses, we quantified temporal patterns of variation in hominin body size, brain size, and EQ, with EQ estimated at the individual, paleodeme, and taxon level. For each of the five datasets, we tested alternative models containing zero, one, or two breakpoints and selected the model with the highest Akaike weight as the best-supported model in the set (Table 1). Of the best-fitting models, we retained the estimated breakpoint locations and the slopes of each segment between breakpoints, which we interpret as approximate rates of evolutionary change (Table 2 and Fig. 1).

Table 1
Segmented regression model selection based on Akaike weights.

Individual body size					
Nr. breakpoints	Adj. R^2	AIC	AIC_c	Delta AIC_c	Akaike weight
0	0.392	2694.874	2694.943	76.251	0.000
1	0.443	2666.179	2666.353	47.661	0.000
2	**0.516**	**2618.366**	**2618.692**	**0.000**	**1.000**
Individual brain size					
Nr. breakpoints	Adj. R^2	AIC	AIC_c	Delta AIC_c	Akaike weight
0	0.818	3492.935	3493.027	99.213	0.000
1	0.865	3415.465	3415.697	21.882	0.000
2	**0.876**	**3393.379**	**3393.814**	**0.000**	**1.000**
Individual EQ					
Nr. breakpoints	Adj. R^2	AIC	AIC_c	Delta AIC_c	Akaike weight
0	0.669	119.589	119.989	19.669	0.000
1	**0.766**	**99.286**	**100.320**	**0.000**	**0.757**
2	0.768	100.594	102.594	2.273	0.243
Paleodeme EQ					
Nr. breakpoints	Adj. R^2	AIC	AIC_c	Delta AIC_c	Akaike weight
0	0.767	133.668	134.026	35.484	0.000
1	0.860	99.605	100.528	1.986	0.270
2	**0.869**	**96.765**	**98.542**	**0.000**	**0.730**
Taxon EQ					
Nr. breakpoints	Adj. R^2	AIC	AIC_c	Delta AIC_c	Akaike weight
0	0.850	21.241	23.241	10.932	0.004
1	**0.946**	**6.309**	**12.309**	**0.000**	**0.991**
2	0.940	9.108	23.108	10.799	0.004

The model with the highest level of support is highlighted in bold.

Table 2
Estimated breakpoints and slopes for the best-fitting segmented regression models identified in Table 1.

Individual body size	Breakpoint 1 (95% CI)	Breakpoint 2 (95% CI)	Slope 1 (95% CI)	Slope 2 (95% CI)	Slope 3 (95% CI)
	2.470 (2.093–2.848)	**0.040 (0.030–0.051)**	**-7.098 (-14.768–0.572)**	**13.815 (12.121–15.510)**	**-429.000 (-621.360 – -236.640)**
Individual brain size	2.105 (1.760–2.450)	0.113 (0.016–0.210)	60.345 (-58.417–179.11)	423.670 (390.940–456.400)	1858.400 (234.030–3482.800)
Individual EQ	0.947 (0.470–1.424)	NA	0.201 (-0.181–0.583)	2.741 (1.670–3.812)	NA
Paleodeme EQ	1.179 (0.584–1.774)	0.078 (0.013–0.143)	0.390 (0.146–0.634)	1.455 (0.785–2.124)	12.130 (-0.201–24.462)
Taxon EQ	0.714 (0.154–1.274)	NA	0.508 (0.353–0.663)	2.581 (0.584–4.578)	NA

The most-supported model for body size change contained two breakpoints, explained approximately 52% of the variance, and had a probability of 100% of being the best model in the candidate set. According to this model, the first breakpoint occurred at 2.470 Mya (95% CI: 2.093–2.848), where the rate of evolutionary change increased from − 7.098 kg/Mya (95% CI: -14.768–0.572) to 13.815 kg/Mya (95% CI: 12.121–15.510). A second breakpoint occurred at 0.040 Mya (95% CI: 0.030–0.051), at which point the rate of change declined sharply to -429.000 kg/Mya (95% CI: -621.360–-236.640).

When comparing absolute brain size, the most-supported model also contained two breakpoints, explained approximately 88% of the variance, and had a probability of 100% of being the best model in the candidate set. The first breakpoint occurred at 2.105 Mya (95% CI: 1.760–2.450), where the rate of change increased from 60.345 cc/Mya (95% CI: -58.417–179.11) to 423.670 cc/Mya (95% CI: 390.940–456.400). A second breakpoint occurred at 0.113 Mya (95% CI: 0.016–0.210), after which the rate of change increased further to 1858.400 cc/Mya (95% CI: 234.030–3482.800).

Considering EQ estimated at the individual-level, there was only one breakpoint in the most-supported model, which explained approximately 77% of the variance, and had a 76% probability of being the best model in the candidate set. According to this model, the breakpoint was estimated at 0.947 Mya (95% CI: 0.470–1.424), where the rate of evolutionary change increased from 0.201 individual EQ/Mya (95% CI: -0.181–0.583) to 2.741 individual EQ/Mya (95% CI: 1.670–3.812).

The most-supported model for temporal variation in paleodeme EQs contained two breakpoints that explained approximately 87% of the variance, with a 73% probability of being the best model in the set. The first breakpoint occurred at 1.179 Mya (95% CI: 0.584–1.774), where the rate of change increased

from 0.390 paleodeme EQ/Mya (95% CI: 0.146–0.634) to 1.455 paleodeme EQ/Mya (95% CI: 0.785–2.124). A second breakpoint occurred at 0.078 Mya (95% CI: 0.013–0.143), after which the rate of change increased sharply to 12.130 paleodeme EQ/Mya (95% CI: -0.201–24.462).

For EQ estimated at the taxon-level, the most-supported model contained a single breakpoint, explained approximately 95% of the variance, and had a 99% probability of being the best model in the candidate set. The breakpoint was estimated at 0.714 Mya (95% CI: 0.154–1.274), where the rate of change increased from 0.508 taxon EQ/Mya (95% CI: 0,.353–0.663) to 2.581 taxon EQ/Mya (95% CI: 0.584–4.578).

Association of EQs with measures of technological complexity

To explore the correspondence between archaeological data and EQs, we first performed ANOVA with EQ or brain size dependent on tool industry across paleodemes or across individuals to determine whether more complex industries were associated with higher EQ and/or larger brain size. All ANOVA showed significant associations, with more complex tool industries consistently associated with higher mean EQ and brain size ($p < 0.001$ in all cases; Table S4; Fig. 2). The paleodeme post-hoc Tukey test results (Table S5; Fig. 2a and b) suggest further associations between EQ values and archaeological industries (see also Figure S4): i) although the origin and initial use of the Acheulean is associated with significantly larger brain size, it does not seem to have coincided with major increases in EQ (significantly larger mean brain size in Acheulean compared to Oldowan, but no significant difference in mean EQ between Oldowan and Acheulean); and ii.) paleodemes associated with the Middle Paleolithic/MSA and Upper Paleolithic do appear to have marked increases in EQ (mean EQ significantly higher in both the Middle and Upper Paleolithic groups than in the Acheulean). There is also no significant difference in mean EQ of the latter two (see also Figure S4).

To correlate EQ with higher resolution measures of technological complexity from the archaeological record, we chose Procedural Units (PU) as a quantitative way to express technological complexity (see *28,33*) using a commonly available dataset (see Methods for more details). For paleodemes, technological complexity as measured by PU was found to be strongly positively correlated with both EQ (median resampled correlation = 0.770, 95% CI = 0.686 to 0.837, Fig. 3a) and brain size (median resampled correlation = 0.745, 95% CI = 0.659 to 0.817, Fig. 3b). EQ accounted for more variance in PU than did brain size alone, although not significantly so (median r^2_{EQ}-$r^2_{Brain\ size}$=0.038, 95% CI for difference=-0.041 to 0.112). The correlation between PU and brain size was similar for paleodemes and the full individual data set (median resampled correlation for individual data set = 0.734, 95% CI = 0.684 to 0.780).

When the individual sample was restricted to those specimens with both brain size and EQ, similar levels of correlation were found between PU and EQ (median resampled correlation = 0.527, 95% CI = 0.399 to 0.644, Fig. 3c) and PU and brain size (median resampled correlation = 0.4607, 95% CI = 0.317 to 0.587, Fig. 3d). Just as in the paleodeme data set, in the individual data set EQ accounted for more variance in

PU than did brain size alone, but not significantly (median r^2_{EQ}-$r^2_{Brain\ size}$=0.067, 95% CI for difference=-0.051 to 0.181).

Discussion and Conclusion

The unique features of human cognition, their evolutionary trajectories, and their relationship to human brain size remain contested, with various measures and scenarios providing conflicting results. We provided three different EQ estimates and combined them with measures of technological complexity, testing the relationship between cultural and brain size evolution. Our analyses consistently support a model of late, stepwise encephalization linked to technological and cultural complexity, well beyond the origins of stone tools and Acheulean technology. These findings can be interpreted as evidence for increasing EQ associated with the emergence of special types of social learning and cumulative culture, discussed further below.

Our approach provides new insights into the temporal patterns of brain evolution across hominins, documenting distinct phases of EQ change across taxa and time. The initial period from ~ 4.5-3.0 Mya starts with consistently low EQs < 2.6 with *Ar. ramidus, Australopithecus anamensis, Australopithecus prometheus*, and *Australopithecus afarensis*, found in all three EQ types. Subsequently, between 3.0-1.5 Mya, we see a mix of stasis with some increase but similar values among various taxa of *Paranthropus*, *Australopithecus*, and *Homo*, with averages mostly between EQ = 3.0-2.6. While *Homo erectus* s.l. shows higher taxon EQ values when considered as one unit (EQ = 3.39), finer-resolved paleodeme EQs found that early *Homo erectus s.l*. between 1.8–1.3 Mya (EQ = 2.86) instead fits within this group. A more marked period of gradual increase in EQs values is visible only between afterwards with later paleodemes of *Homo erectus* s.l. in East Asia showing higher values between EQ = 3.03–3.88. This intra-taxon increase in relative brain size was recently found by another study (*14*) and is most visible in this taxon. In a last phase sometime after 200 ka, specimens and paleodemes of Pleistocene *Homo sapiens* and Neanderthals exhibit consistently higher EQ values for all three EQ approaches we used (with EQs of between 4–6).

The segmented regression analysis provided a more robust way to statistically assess the descriptive temporal trends in encephalization. The analyses of all three EQ values find a breakpoint ranging between 1.2 and 0.7 Mya, much later compared to the results from absolute brain size at about 2.1 Mya (Fig. 1). The paleodeme results also support an additional breakpoint close to 0.1 Mya, and this is equally found in absolute brain size. Accordingly, the evolution of EQs began with a slow and mostly gradual increase between 4.4–1.2 Mya, followed by a phase of heightened linear change and then even more rapid and exponential growth with an inflection point around 0.1 Mya. This, however, was not a uniform process across all hominins. Both *Homo naledi* and *Homo floresiensis* align with earlier members of *Homo* as well as *Paranthropus* and *Australopithecus* instead of broadly contemporaneous taxa such as Neanderthals or *Homo sapiens*. In this late period ~ 0.1 Mya and after, we observe a decoupling of changes in absolute brain and body size, with marked increases in endocranial volume but

reductions in body size (Fig. 1). This change appears to drive the inflection point in encephalization in the Late Pleistocene from an already steady increase to even more exponential growth.

The origins of *Homo* have commonly been associated with an important change in (absolute and relative) brain size and cognitive functions, aligning with the origins of stone tool technology such as the Oldowan and increased reliance on meat-eating and new social strategies and behaviors (*15,20,34–36*). Based on absolute brain sizes, Weber (*13*) recently postulated a first breakpoint at ~ 2.1 Mya - a result reproduced in our analyses of this measure - and a major difference between early *Homo* and australopithecines, associated with the more frequent use of Oldowan stone tools by the former. In addition, *Homo erectus* s.l. has long been interpreted as demonstrating the deep origins of the human biological bauplan and advanced cognitive capacities (e.g., *37,38*), and some analyses found stepwise change in absolute brain size around the emergence of this species ~ 1.8 Mya (*15*). These changes have been connected to the advent of more complex Acheulean technology, requiring higher cognitive abilities compared to Oldowan stone tools around ~ 1.8 Mya (see e.g., *39–41*).

In contrast, we find that EQ values of both the paleodemes of earliest *Homo* and early *Homo erectus* s.l. are more comparable with australopithecines and paranthropines than Middle and Late Pleistocene *Homo*. While there is an increase in absolute brain sizes, these are mostly 'offset' by marked increases in body size, resulting in reduced EQ values. These results suggest that allometric scaling relationships between brain and body size of *Australopithecus* and *Paranthropus* are mostly maintained in early *Homo* and early representatives of *Homo erectus* s.l.. Our results are in line with recent findings of small-bodied and small-brained individuals among the earliest specimens of *Homo erectus* in Africa and Asia (e.g., *42,43*) and re-evaluations of *Homo erectus* as a taxon (e.g., *44,45*). The results presented here also match the lack of a sustained increase in the amount of evidence for hominin carnivory - often argued to fuel encephalization - between 2.6 and 1.2 Mya across *Homo* and even after the appearance of *Homo erectus* (*46*).

Reconsidering the relationship between hominin biology and cognition, the first major shift in relative brain size identified consistently by all EQ analyses occurred around or after 1.2 Mya (between ~ 1.2–0.7 Mya), well beyond the origins of the genus *Homo* and *Homo erectus* – and after the first appearances of both Oldowan and Acheulean. The paleodeme approach also identifies a second major breakpoint in the Late Pleistocene which is also the phase of fastest and most dramatic changes in EQ fitting an accelerated pace of change and increased cultural diversity observed in the later part of the MSA record of Africa (*47,48*). The general macroevolutionary pattern of accelerating brain size relative to body size increase through time – with later taxa such as *H. neanderthalensis* or *H. sapiens* increasing their brain sizes at a faster pace – was recently found by another study (*14*). Different from this study, however, our data suggest that between-species increases in relative brain size do play an important role, though mostly after 1.5 Mya (Figs. 1 & 2; Table 1).

Traditionally, increases in absolute brain measures have often been linked either to the earliest stone tools or to the onset of the Acheulean (*15,17,34–36,39–41*). Our study, however, documents major EQ

increases neither with the earliest stone tools nor with the earliest Acheulean. Early *Homo*, *Australopithecus*, and *Paranthropus* remained broadly similar in EQ for a long period. These findings are consistent with emerging evidence that Lomekwian and early Oldowan industries were produced not only by multiple Homo species, but also by australopithecines (*49–52*), and with the long co-occurrence of Oldowan and early Acheulean technologies in Africa and Asia beyond 1.0 Mya, including assemblages associated with *Homo erectus* (e.g., *53*). Claims linking the beginning of the Acheulean to enlarged cognitive capacities (*31,40*) and derived brain structure (*8*) are likewise not corroborated by our paleodeme EQ analysis. They also do not match recent experimental evidence (e.g., *54*). Instead, our data support a later and stepwise pattern, with shifts around ~ 1.2–0.7 Ma and another inflection point around ~ 0.1 Mya.

The first shift, from roughly ~ 1.2–0.7 Mya onward, broadly coincides with changes within the later Acheulean record after ca. 1.0 Mya, including more symmetrical and intensely shaped handaxes, more elaborate technical sequences, additional knapping techniques, and increasing levels of organization within action hierarchies (*32,55–57*). The period < 1.0 Mya may contain the first robust archaeological evidence for specialized mechanisms of cultural transmission, namely those relevant to the transmission of the structural gist of production techniques (*32,54,58*). More cautiously, it may mark a phase in which technological traditions became increasingly dependent on more stable or more demanding types of cultural transmission. In addition, or separately, major ecological changes around this time may have created the technological context in which more stable or more demanding types of cultural transmission became advantageous or even necessary (e.g., *59*).

The first shift in the EQ trajectories may reflect the beginning of a new phase in which enhanced transmission capacities and technological differentiation became more tightly coupled. On this reading, cumulative cultural evolution still emerged only later. At first, however, the number and diversity of culturally differentiated outputs grew slowly. Comparative archaeological work has been interpreted as suggesting that the first recognizable instances of cumulative culture proper emerged around 0.6 Mya. This inference combines an ape technological and minimal cultural baseline established by Tennie and colleagues (see *60*) with procedural unit counts that Paige and Perreault argue mark the archaeological threshold (*28*). Whether or not that threshold proves definitive, it fits the broader possibility that the first EQ shift opened a new cultural regime whose consequences accumulated gradually before accelerating much later.

The second inflection point in EQ trajectories, from roughly ~ 0.1 Mya onward, is more pronounced than the first, driven by an accelerated increase in endocranial volume plus reductions in body size. While a late, abrupt, and coordinated ‘revolution’ in human cognition was proposed in earlier work (e.g., *18,19*), the last decades of research have shown that there is no revolution or dramatic shift based on the emergence of a single innovation or ability visible in the archaeological, fossil or genetic record at this or a later time (e.g., genetic mutation, neurological switch, language). What we do see, however, is a generally accelerated tempo of cultural evolution with regard to the complexity and diversity of material culture in the Late Pleistocene, including increasing (non-linear) evidence for abstract patterns and

symbols. The different parts of the constellation that constitute the unique cultural capacities and behavioral repertoire of *Homo sapiens* seem to appear in a piecemeal and mosaic manner, yet come fully in place sometime during this period (e.g., *31,48*). Highly diversified and, with it, highly evolvable culture at the time also likely provided the means for rapid expansion and niche invasion (e.g., *61,62*). The period from roughly 0.3 Mya onward (the MSA/Middle Paleolithic) marks the beginning of more highly demanding, diverse technologies, including a marked increase in non-lithic material culture, fire use and heat-treatment of raw materials, and stronger spatio-temporal patterning of stone tools (*48*). These trends become more pronounced into the Later Stone Age and Upper Paleolithic (*19,63*). Regarding lithic technology, hierarchical flaking associated with prepared core methods emerging with the MSA/Middle Paleolithic has been argued to be cognitively demanding, perhaps even more so than later prismatic blade technologies (*27*). Matching this second EQ shift, modern human brain *shapes* likewise arrived only between 100 – 35 ka in the late *Homo sapiens* lineage (*64*).

We note that Weber (*13*), using the same approach of a segmented regression analysis, identified a breakpoint in absolute brain size at a similar age (~ 110 ka; see also Shultz et al.'s (*15*) postulation of a step change at ~ 100 ka) and associated it with increasing evidence for the emergence of symbolic culture and potentially language (see also *65*). On the cultural side, this period indeed marks the advent of new social technologies. Symbolic culture itself is demanding to transmit, especially once it culturally diversified. However, once diversified symbols exist, they can ease other cognitive demands, such as memory load via information compression (*66*) or demands of technological transmission, via language-based transmission (*67*). Longer childhoods, larger EQs and symbolic minds could then co-evolve, producing, transmitting and sustaining (also via increased cooperative abilities) higher and more diversified cumulative culture in both the social and the technical domain (compare *66*). Recent accounts include even special cognitive abilities themselves under such cumulative cultural products (as "cognitive gadgets"; sensu *68*). This suggests that cognition and culture were closely linked in *Homo sapiens* in a feedback cycle that led to the increase in encephalization found for the Late Pleistocene. By combining and comparing biology and biocultural proxies of cognition from paleoanthropology and archaeology, our results support a late linkage and increasingly tight co-evolution between life history, encephalization, cultural minds, and social and material cultural complexity.

Materials and methods summary

EQ dataset

We present a large, curated Plio-Pleistocene database of body and brain size estimates for individual fossil hominins to test the validity of previous studies and more reliably assess variation and spatio-temporal trends in EQ evolution. We do so by using our enlarged dataset to generate three successive measures of EQ - in descending resolution: 1) taxon EQ; 2) paleodeme EQ; 3) individual EQ. The database required for our new approach only recently became available, stemming from our own recent compilations of body and brain size estimates (*3,9,69*) combined with other recent publications on body size (*2,70–72*) and containing data on endocranial volumes (e.g., *8,10,11,13,14,73*; see Supplementary

Data 1 for full reference list) and updated chronometric information on key specimens (e.g., *74–76*). For body mass, recent research showed that the values provided in Grabowski et al. (*2*) for earlier hominins were too low based on various methodological issues, and so we endeavored to use other, more recent estimates for these fossils (see e.g., *70,72*).

We calculate EQ as follows to be comparable to previous large-scale studies (*1,77*): EQ=(brain mass / 11.22) * body mass^0.76. Brain mass is derived from endocranial volume as: Brain mass= (1.147*BrainSize)^0.976 (after *77*). We calculate taxon EQ as the mean body mass and brain mass of all individuals assigned to the respective taxon. As a new alternative to using taxon EQs, we introduce the paleodeme EQ. Following Howell (*24*) p. 204), this approach "groups in association remains of proximate geographic distribution and closely similar age, at a level between that of the individual specimen(s) and a higher taxonomic category" (see also *23*). While he did not provide absolute numbers, we pool body and brain size estimates of specimens of the same taxon from the same site or geographically proximate find regions (e.g., East Turkana) within roughly 100 km² and similar chronometric ages (+/-10% <1.0 Mya, 100 ka brackets > 1.0 Mya) into 'paleodemes' (see *78,79*) for a broader usage and recent application of the concept). These units can also be represented by single individuals with associated body and brain size. An important consequence of calculating 'paleodeme EQ' is that individual taxa can be represented by several paleodemes, allowing for both intra-species spatial and temporal variation. This approach still aggregates various individuals in one category, yet the resulting (paleodeme) EQs derive from a small sample of closely associated body and brain sizes coming from similar eco-geographical backgrounds by a local population sharing a closer gene pool. This therefore provides better approximations of biologically relevant EQs compared to taxon EQs (see Data S1 & S2). In total, we calculated EQ values for n = 73 paleodemes. As a final analysis - and the one with the *highest possible* resolution of the parameter itself - we calculate 'individual EQs' for n = 66 individual hominin specimens by applying the EQ formula to their associated body and brain size estimates.

In an effort to alleviate the additional error introduced in EQ calibrations (e.g., *6,15*), we only used body mass estimates derived from the postcranium as these are considered to be more reliable compared to cranial predictions based on basic biomechanical grounds (*70,71*), which differs from some recent EQ studies that also included body mass estimates from much less reliable cranial measurements (*7,14*). Our raw dataset and all EQ calculations can be found in Supplementary Data 1, encompassing n = 361 body size, n = 270 brain size estimates for fossil specimens as a basis for EQ calculations, ranging from 4.4 – 0.01 Mya and including the genera *Homo*, *Australopithecus*, *Paranthropus*, and *Ardipithecus*. The finer taxonomic subdivisions were taken from the literature, with the principle of majority rule applied (see Supplementary Data 1 for references). Using these attributions, we also sought maximum comparability to previous studies that estimated body mass, brain size, and EQ with explicit taxonomic assessment (see *2,3,9,11,14,15,69,71*).

Segmented regression analysis

To quantify temporal changes in hominin brain size, body size, and EQ, the latter estimated at the individual-, paleodeme-, and taxon-level, we applied segmented regression analyses (also referred to as

piecewise or broken-stick regression). In a segmented regression, the relationship between a response variable and an explanatory variable is partitioned into two or more intervals, with a separate linear relationship segment fitted within each interval. The points at which adjacent line segments join are termed breakpoints (also known as change points or inflection points). This approach enables the identification of shifts in temporal trends while retaining the interpretability of a linear regression framework (*80*). All analyses were conducted in R version 4.5.1 (*81*) using the segmented package version 2.1-4 (*82*). To determine the number of breakpoints that best characterized each dataset, we fitted and compared three competing models containing zero, one, or two breakpoints, specified via the *npsi* argument in the segmented() function. This approach does not specify the locations of the breakpoints, only their number, with the locations estimated directly from the data. Because some datasets were relatively small (e.g., the taxon EQ dataset comprised only 18 data points), models with more than two breakpoints were excluded to reduce the risk of overfitting. Model selection was based on Akaike weights derived from Akaike Information Criterion (AIC) scores, which quantify the conditional probability that a given model is the best-supported model within the candidate set. For the best-supported model, we report the estimated breakpoint locations and the slopes of each segment, together with their corresponding 95% confidence intervals (CIs). The best-fitting segmented regression models were visualized using the ggplot2 package version 4.0.0 (*83*). Following previous work (e.g., *13*), we excluded the small-brained Middle and Late Pleistocene fossils of *Homo floresiensis* and *Homo naledi* from the analyses.

Phylogenetic segmented regression analyses were also undertaken but provided inconclusive results (see Text S3). Limitations of the phylogenetic analyses of this dataset may come from many points: limited sample sizes for most included groups, high variance across repeated measures within taxa, debated or unclear ancestor/descendant relationships, application of different species concepts and valuation of intra- vs. inter-species, reticulation, and interbreeding among proposed taxa taking place at least from the Mid-Pleistocene (e.g., *84,85*).

Relationship with technological complexity

Finally, we assessed the potential relationship between encephalization or brain size on the one hand and technological evolution on the other for the paleodeme and individual datasets. We did this in two ways: using one-way ANOVA to explore the association between EQ or brain size and categorical tool industry, and performing a resampling analysis correlating EQ values or brain size with a quantitative measure of technological complexity.

For the categorical analysis, we assigned each paleodeme/individual to one of four tool industries where confident associations were possible: Oldowan, Acheulean, MSA/Middle Paleolithic, or Upper Paleolithic. This resulted in 54 paleodemes having an assigned tool industry, all of which also had paleodeme values for brain size and EQ, and 134 individuals with tool industry and brain size data, of which 56 individuals also had EQ data (see Supplementary Data 1). We then performed four ANOVA: EQ or brain size dependent on tool industry for the paleodeme or individual data set (see Text S4). Tukey's Honest

Significant Differences tests were used to test for significant differences for all pairwise comparisons of tool industries.

For the correlation analysis, we chose Procedural Units (PU) as a quantitative way to express technological complexity (see *28,33*) using a commonly available dataset that stretches from ~ 2.5 Mya until the Upper Paleolithic (*28*, SI Appendix). The assemblages in this data set were further assigned into the four tool industries.

We then performed iterative resampling procedures for paleodeme- and individual-level datasets as follows. In each iteration, every paleodeme (for paleodeme-level analyses) or individual specimen (for individual-level analyses) was paired with the PU value for a randomly-selected assemblage in the PU dataset corresponding to the same broad archaeological period (e.g., a paleodeme assigned to "MSA/Middle Paleolithic" would be paired with the PU value for one randomly selected assemblage from the 20 MSA/Middle Paleolithic assemblages in Table S6, see also Text S5 and Figures S8-11). The correlations between EQ and PU, as well as brain size and PU, were calculated for each iteration (note: for individual-level analysis, correlations between brain size and PU values were calculated for both the full data set and a reduced data set that only included those individuals that also had EQ data). 10,000 iterations were used for both sets of analyses, after which 95% confidence intervals for correlation coefficients were calculated by excluding the largest 2.5% and smallest 2.5% of resampled correlation coefficients in each analysis.

Declarations

Acknowledgments

We acknowledge support from the many people from different institutions who gave access to the important human and fossil collections under their care, and kindly assisted. J. Beier gave access to her literature database of (Upper) Paleolithic human remains that helped greatly in assigning chronometric ages for all fossils included in this study.

Funding: HR's contribution to this work was financially supported by a grant from the Federal Ministry of Education and Research (BMBF) and the Baden-Württemberg Ministry of Science as part of the Excellence Strategy of the German Federal and State Governments. CT was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC 3101 – Project 533763844.

Author contributions: Conceptualization: M.W., C.T., J.T.S.; Methodology: M.W., H.R., A.G.; Formal analysis: M.W., H.R., A.G.; Investigation: M.W., C.T., J.T.S., H.R., A.G; Resources: M.W., J.T.S., C.T.; Writing – original draft: M.W., C.T.; Writing – review & editing: M.W., C.T., J.T.S., H.R., A.G; Visualization: H.R., A.G.

Competing interests: The authors declare that they have no competing interests.

Data, code, and materials availability: All data are available in the manuscript or the supplementary materials.

References

1. Ruff, C. B., Trinkaus, E. & Holliday, T. W. 1997 Body mass and encephalization in Pleistocene Homo. Nature 387, 173–176.
2. Grabowski, M., Hatala, K. G., Jungers, W. L. & Richmond, B. G. 2015 Body mass estimates of hominin fossils and the evolution of human body size. J. Hum. Evol. 85.
3. Will, M., Pablos, A., Stock, J.T. 2017 Long-term patterns of body mass and stature evolution within the hominin lineage. Royal Society Open Science 4(11), 171339.
4. Holloway, R. L. 1967 The evolution of the human brain: Some notes toward a synthesis between neural structure and the evolution of complex behavior. General Systems 12, 3-19.
5. Tobias, P. V. 1971 Human skeletal remains from the Cave of Hearths, Makapansgat, Northern Transvaal. Am. J. Phys. Anthropol. 34, 335–367.
6. Du, A., Zipkin, A. M., Hatala, K. G., Renner, E., Baker, J. L., Bianchi, S., Bernal, K. H., Wood, B. A. 2018 Pattern and process in hominin brain size evolution are scale-dependent. Proc. R. Soc. B 285.
7. Püschel, H. P., Bertrand, O. C., O'reilly, J. E., Bobe, R., & Püschel, T. A. 2021 Divergence-time estimates for hominins provide insight into encephalization and body mass trends in human evolution. Nature ecology & evolution 5(6), 808-819.
8. Ponce de León, M. S., Bienvenu, T., Marom, A., Engel, S., Tafforeau, P., Alatorre Warren, J. L., ... & Zollikofer, C. P. 2021 The primitive brain of early Homo. Science, 372(6538), 165-171.
9. Will, M., Krapp, M., Stock, J.T., Manica, A. 2021 Different environmental variables predict body and brain size evolution in Homo. Nature Communications 12, 4116.
10. DeSilva, J. M., Traniello, J. F., Claxton, A. G., & Fannin, L. D. 2021 When and why did human brains decrease in size? A new change-point analysis and insights from brain evolution in ants. Frontiers in Ecology and Evolution, 712.
11. Gingerich, P. D. 2022 Pattern and rate in the Plio-Pleistocene evolution of modern human brain size. Scientific Reports 12, 11216.
12. Pestana, C., de Sousa, A. A., Todorov, O. S., Beaudet, A., & Benoit, J. 2023. Evolutionary history of hominin brain size and phylogenetic comparative methods. Progress in brain research, 275, 217-232.
13. Weber, G.W. 2023 Quantum leaps in human biocultural evolution and the relationship to cranial capacity. Life, 13(4), 1030.
14. Püschel, T. A., Nicholson, S. L., Baker, J., Barton, R. A., & Venditti, C. (2024). Hominin brain size increase has emerged from within-species encephalization. Proceedings of the National Academy of Sciences, 121(49), e2409542121.

15. Shultz, S., Nelson, E., & Dunbar, R. I. 2012 Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. Philosophical Transactions of the Royal Society B: Biological Sciences 367(1599), 2130-2140.
16. Rightmire, G. P. 2004 Brain size and encephalization in early to Mid-Pleistocene Homo. Journal of Physical Anthropology 124, 109–123.
17. Holloway, R. L. 2015 The evolution of the hominid brain. In: Henke, W., Tattersall, I. (eds) Handbook of Paleoanthropology. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_81
18. Mellars, P., Stringer, C. (Eds.), 1989. The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Hominids. Edinburgh University Press, Edinburgh
19. Klein, R.G., 2000. Archeology and the evolution of human behavior. Evol. Anthropol. 9, 17e36.
20. Stout, D., Toth, N., Schick, K., & Chaminade, T. (2008). Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1499), 1939.
21. De la Torre, I. (2016). The origins of the Acheulean: past and present perspectives on a major transition in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1698), 20150245.
22. McBrearty, S., & Brooks, A. S. (2000). The revolution that wasn't: a new interpretation of the origin of modern human behavior. *Journal of human evolution*, *39*(5), 453-563.
23. Howell, F .C., 1996 Thoughts on the Study and Interpretation of the Human Fossil Record. In Meikle, W.E., Howell, F.C., Jablonski, G.J. (eds.) Contemporary Issues in Human Evolution. California Academy of Sciences Memoir 21, pp. 1-45, San Francisco.
24. Howell, F. C. 1999 Paleo-demes, species clades, and extinctions in the Pleistocene hominin record. Journal of Anthropological Research 55(2), 191-243.
25. Muthukrishna, M., Doebeli, M., Chudek, M., & Henrich, J. (2018). The cultural brain hypothesis: How culture drives brain expansion, sociality, and life history. PLoS computational biology, 14(11), e1006504.
26. Tennie, C., Snyder, W. D., & Planer, R. J. (2025). Costs of Early Stone Toolmaking cannot Establish the Presence of Know-how Copying. *Human Nature*, *36*(2), 180-218.
27. Muller, A., Clarkson, C. & Shipton, C. 2017 Measuring behavioural and cognitive complexity in lithic technology throughout human evolution. J. Anthropol. Archaeol. 48, 166–180.
28. Paige, J., & Perreault, C. 2024. 3.3 million years of stone tool complexity suggests that cumulative culture began during the Middle Pleistocene. Proceedings of the National Academy of Sciences, 121(26), e2319175121.
29. Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of human evolution*, *63*(1), 180-190.
30. Laland, K. N., Odling-Smee, J., & Feldman, M. W. (2000). Niche construction, biological evolution, and cultural change. *Behavioral and brain sciences*, *23*(1), 131-146.

31. Perreault C (2012) The Pace of Cultural Evolution. PLoS ONE 7(9): e45150.
32. Tennie, C. (2025). 33 The Earliest Tools and Cultures of Hominins. *Oxford Handbook of Cultural Evolution*, 431.
33. Perreault, C., Brantingham, P. J., Kuhn, S. L., Wurz, S., & Gao, X. (2013). Measuring the complexity of lithic technology. *Current anthropology*, *54*(S8), S397-S406.
34. Aiello, L. C. & Wheeler, P. 1995 The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. Curr. Anthropol. 36, 199–221.
35. Antón, S. C., Potts, R. & Aiello, L. C. 2014 Evolution of early Homo: an integrated biological perspective. Science 345, 1236828.
36. Schrenk, F., Kullmer, O., Bromage, T. 2015 The Earliest Putative Homo Fossils. In: Henke, W., Tattersall, I. (eds) Handbook of Paleoanthropology. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_52
37. Walker, A. & Leakey, R. 1993 The Nariokotome Homo erectus Skeleton. Cambridge MA: Harvard University Press.
38. Antón, S.C. 2003 Natural history of Homo erectus. Yrbk. Phys. Anthropol. 46, 126–170.
39. Shipton, C. 2010 Imitation and shared intentionality in the Acheulean. Cambridge Archaeological Journal 20(2), 197-210.
40. Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J. P., ... & Feibel, C. S. 2011. An earlier origin for the Acheulian. Nature 477(7362), 82-85.
41. Stout, D., Hecht, E., Khreisheh, N., Bradley, B., & Chaminade, T. 2015 Cognitive demands of Lower Paleolithic toolmaking. PLoS One 10(4), e0121804.
42. Spoor, F., Leakey, M. G., Gathogo, P. N., Brown, F. H., Antón, S. C., McDougall, I., Kiarie, C., Manthi, F. K. & Leakey, L. N. 2007 Implications of new early Homo fossils from Ileret, east of Lake Turkana, Kenya. Nature 448, 688–691.
43. Lordkipanidze, D., Ponce de León, M. S., Margvelashvili, A., Rak, Y., Rightmire, G. P., Vekua, A. & Zollikofer, C. P. E. 2013 A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo. Science 342, 326–331.
44. Antón, S. C, Spoor, F., Fellmann, C.D. & Swisher III, K.C. 2007 Defining Homo erectus: size considered. Handbook of Paleoanthropology Vol. 3, Chapter 11.
45. Baab, K.L. 2015 Defining Homo erectus. In: Henke, W., Tattersall, I. (eds) Handbook of Paleoanthropology. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_73
46. Barr, W. A., Pobiner, B., Rowan, J., Du, A., & Faith, J. T. (2022). No sustained increase in zooarchaeological evidence for carnivory after the appearance of Homo erectus. Proceedings of the National Academy of Sciences, 119(5), e2115540119.
47. Wadley, L. (2015). Those marvellous millennia: the Middle Stone Age of southern Africa. *Azania: Archaeological Research in Africa*, *50*(2), 155-226.

48. Scerri, E. M., & Will, M. (2023). The revolution that still isn't: The origins of behavioral complexity in Homo sapiens. *Journal of Human Evolution*, *179*, 103358.
49. Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., Boës, X., Quinn, R. L., Brenet, M. & Arroyo, A. et al. 2015 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 310–315.
50. Plummer, T. W., Oliver, J. S., Finestone, E. M., Ditchfield, P. W., Bishop, L. C., Blumenthal, S. A., ... & Potts, R. 2023 Expanded geographic distribution and dietary strategies of the earliest Oldowan hominins and Paranthropus. Science 379(6632), 561-566.
51. Prat, S. (2023). Beyond the genus stereotype. Who were the first toolmarkers in Africa? Crossed views between archaeology and anatomy. *L'anthropologie*, *127*(4), 103187.
52. Williams, E. M., Key, A., de la Torre, I., & Wood, B. (2025). Who made the Oldowan? Reviewing African hominin fossils and archaeological sites from 3.5 million years ago. *Journal of Anthropological Archaeology*, *79*, 101704.
53. Semaw, S., Rogers, M. J., Simpson, S. W., Levin, N. E., Quade, J., Dunbar, N., ... & Everett, M. 2020 Co-occurrence of Acheulian and Oldowan artifacts with Homo erectus cranial fossils from Gona, Afar, Ethiopia. Science Advances 6(10), eaaw4694.
54. Ferar, N., Moos, E. T., Karakostis, F. A., Snyder, W. D., Bolzmann, M., Haas, M., ... & Tennie, C. (2026). Stone tool shaping without direct cultural transmission. *Journal of Archaeological Science*, *187*, 106485.
55. Stout, D., Apel, J., Commander, J., & Roberts, M. (2014). Late Acheulean technology and cognition at Boxgrove, UK. *Journal of Archaeological Science*, *41*, 576-590.
56. Schick, K., & Toth, N. (2017). Acheulean industries of the early and middle Pleistocene, middle Awash, Ethiopia. *L'anthropologie*, *121*(5), 451-491.
57. Moncel, M. H., Cucart-Mora, C., Arzarello, M., Ashton, N., Baena, J., Barsky, D., ... & Bae, C. J. (2026). What Is the Acheulean?. *Evolutionary Anthropology: Issues, News, and Reviews*, *35*(2), e70029.
58. Planer, R. J., Bandini, E., & Tennie, C. (2025). Hominin tool evolution and its (surprising) relation to language origins.
59. Timmermann, A., Yun, K. S., Raia, P., Ruan, J., Mondanaro, A., Zeller, E., ... & Ganopolski, A. (2022). Climate effects on archaic human habitats and species successions. *Nature*, *604*(7906), 495-501.
60. Tennie, C., Bandini, E., Van Schaik, C. P., & Hopper, L. M. (2020). The zone of latent solutions and its relevance to understanding ape cultures: C. Tennie et al. *Biology & Philosophy*, *35*(5), 55.
61. Hallett, E. Y., Leonardi, M., Cerasoni, J. N., Will, M., Beyer, R., Krapp, M., ... & Scerri, E. M. (2025). Major expansion in the human niche preceded out of Africa dispersal. *Nature*, *644*(8075), 115-121.
62. Perreault, C. (2026). Cultural evolution accelerated human range expansion by more than two orders of magnitude. *Proceedings of the National Academy of Sciences*, *123*(11), e2523038123.
63. Conard, N.J., 2015. Cultural evolution during the Middle and Late Pleistocene in Africa and Eurasia. In: Henke, W., Tattersall, I. (Eds.), Handbook of Paleoanthropology. Springer Berlin Heidelberg, Berlin,

Heidelberg, pp. 2465e2508.

64. Neubauer, S., Hublin, J. J., & Gunz, P. (2018). The evolution of modern human brain shape. *Science advances*, *4*(1), eaao5961.
65. Miyagawa, S., DeSalle, R., Nóbrega, V. A., Nitschke, R., Okumura, M., & Tattersall, I. (2025). Linguistic capacity was present in the Homo sapiens population 135 thousand years ago. *Frontiers in Psychology*, *16*, 1503900.
66. Enquist, M., Lind, J., & Ghirlanda, S. (2023). The human evolutionary transition: from animal intelligence to culture.
67. Smith, J. M., & Szathmary, E. (1997). The major transitions in evolution. Oxford University Press.
68. Heyes, C. (2018). Cognitive gadgets: The cultural evolution of thinking. Harvard University Press.
69. Will, M., Stock, J.T. 2015 Spatial and temporal variation of body size among early Homo. Journal of Human Evolution 82, 15-33.
70. Ruff, C. B., Burgess, M. L., Squyres, N., Junno, J. A., & Trinkaus, E. 2018 Lower limb articular scaling and body mass estimation in Pliocene and Pleistocene hominins. Journal of Human Evolution 115, 85-111
71. Ruff C. B., Sylvester A. D., Rahmawati N. T., Suriyanto R. A., Storm P., Aubert M., Joannes-Boyau R., Berghuis H., Pop E., Batenburg K. J., Coban S. B., Kostenko A., Noerwidi S., Renema W., Adhityatama S., & Joordens J. C. 2022 Two Late Pleistocene human femora from Trinil, Indonesia: Implications for body size and behavior in Southeast Asia. Journal of Human Evolution,172, 103252.
72. Ruff, C. B., & Wood, B. A. 2023 The estimation and evolution of hominin body mass. Evolutionary Anthropology: Issues, News, and Reviews, 32(4), 223-237
73. Wu, X. J., Bae, C. J., Friess, M., Xing, S., Athreya, S., & Liu, W. (2022). Evolution of cranial capacity revisited: A view from the late Middle Pleistocene cranium from Xujiayao, China. Journal of Human Evolution, 163, 103119.
74. Rizal, Y., Westaway, K. E., Zaim, Y., van den Bergh, G. D., Bettis III, E. A., Morwood, M. J., ... & Ciochon, R. L. 2020 Last appearance of Homo erectus at Ngandong, Java, 117,000–108,000 years ago. Nature, 577(7790), 381-385.
75. Grün, R., & Stringer, C. 2023 Direct dating of human fossils and the ever-changing story of human evolution. Quaternary Science Reviews, 322, 108379.
76. Pop E., Hilgen S., Adhityatama S., Berghuis H., Veldkamp T., Vonhof H., Sutisna I., Alink G., Noerwidi S., Roebroeks W., & Joordens J. 2023 Reconstructing the provenance of the hominin fossils from Trinil (Java, Indonesia) through an integrated analysis of the historical and recent excavations. Journal of Human Evolution, 176, 103312.
77. Rosenberg, K. R., Zuné, L., & Ruff, C. B. 2006 Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China. Proceedings of the National Academy of Sciences 103(10), 3552-3556.

78. Antón, S. C., Taboada, H. G., Middleton, E. R., Rainwater, C. W., Taylor, A. B., Turner, T. R., ... & Williams, S. A. (2016). Morphological variation in Homo erectus and the origins of developmental plasticity. Philosophical Transactions of the Royal Society B: Biological Sciences, 371(1698).
79. Kaifu, Y., & Athreya, S. 2025 What's in a name? Late Middle and Early Late Pleistocene hominin systematics diversity and evolution of archaic eastern Asian hominins: A synthetic model of the fossil and genetic records. Paleoanthropology 2025:2.
80. Muggeo, V. M. R. 2003. Estimating regression models with unknown break-points. Stat. Med. 22: 3055–3071
81. R Core Team. 2025. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
82. Muggeo, V. M. R. 2008. Segmented: An R package to fit regression models with broken-line relationships. R News 8: 20–25.
83. Wickham, H. 2016. Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
84. van Holstein, L. A., & Foley, R. A. 2022. A process-based approach to hominin taxonomy provides new perspectives on hominin speciation. Evolutionary Anthropology, 31(4), 166-174
85. Wood, B., & Smith, R. J. 2022 Towards a more realistic interpretation of the human fossil record. Quaternary Science Reviews, 295, 107722.

Figures

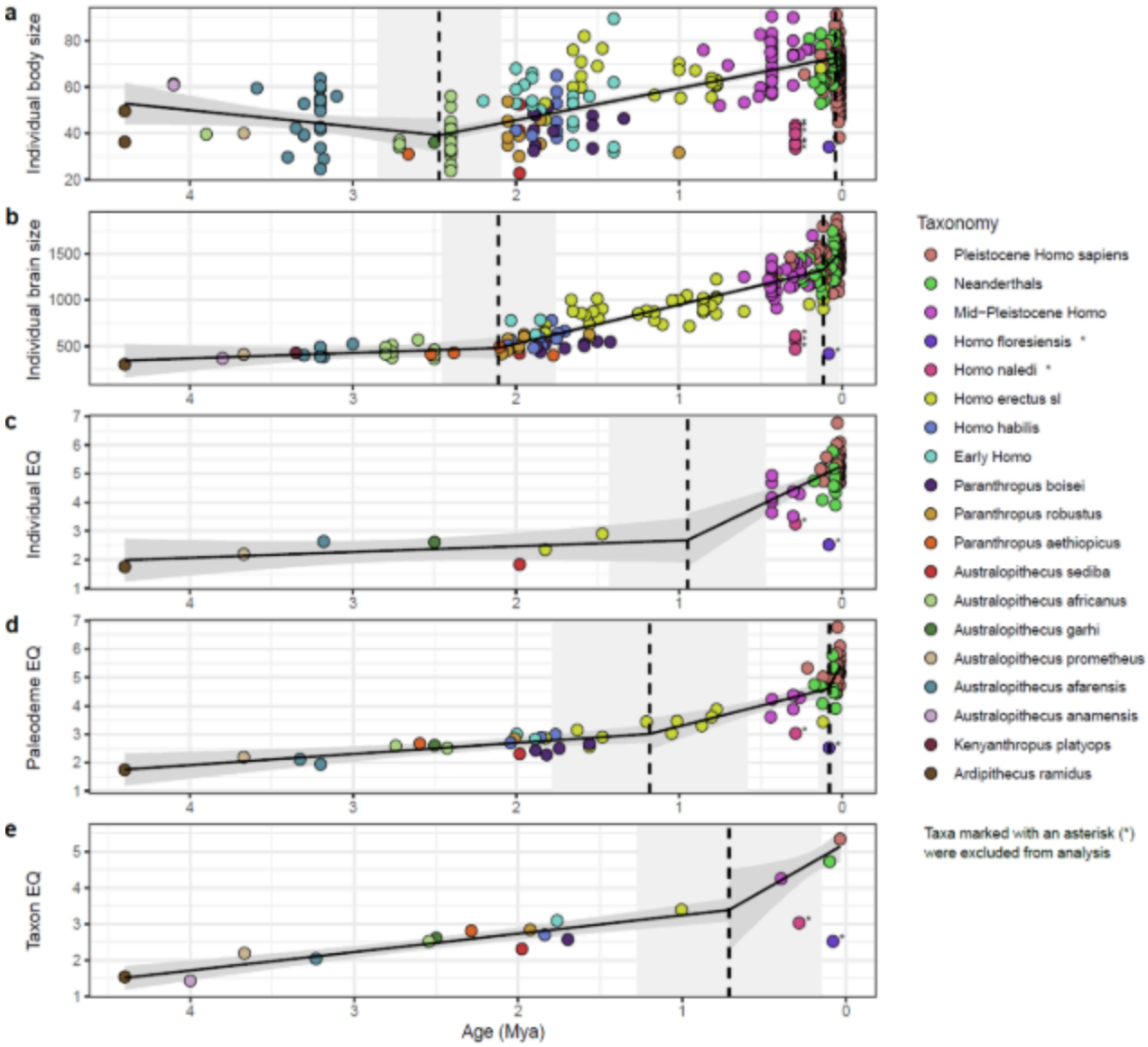


Figure 1

Segmented regression models of hominin (a) individual body size, (b) individual absolute brain size, (c) EQ estimated at the individual-level, (d) EQ estimated at the paleodeme-level, and (e) EQ estimated at the taxon-level through time. Panels show the best-fitting models identified in Table 1. Dots display raw data with color coding indicating taxon affiliation; solid lines represent segment slopes; dashed lines denote breakpoints; and shaded areas indicate 95% confidence intervals.

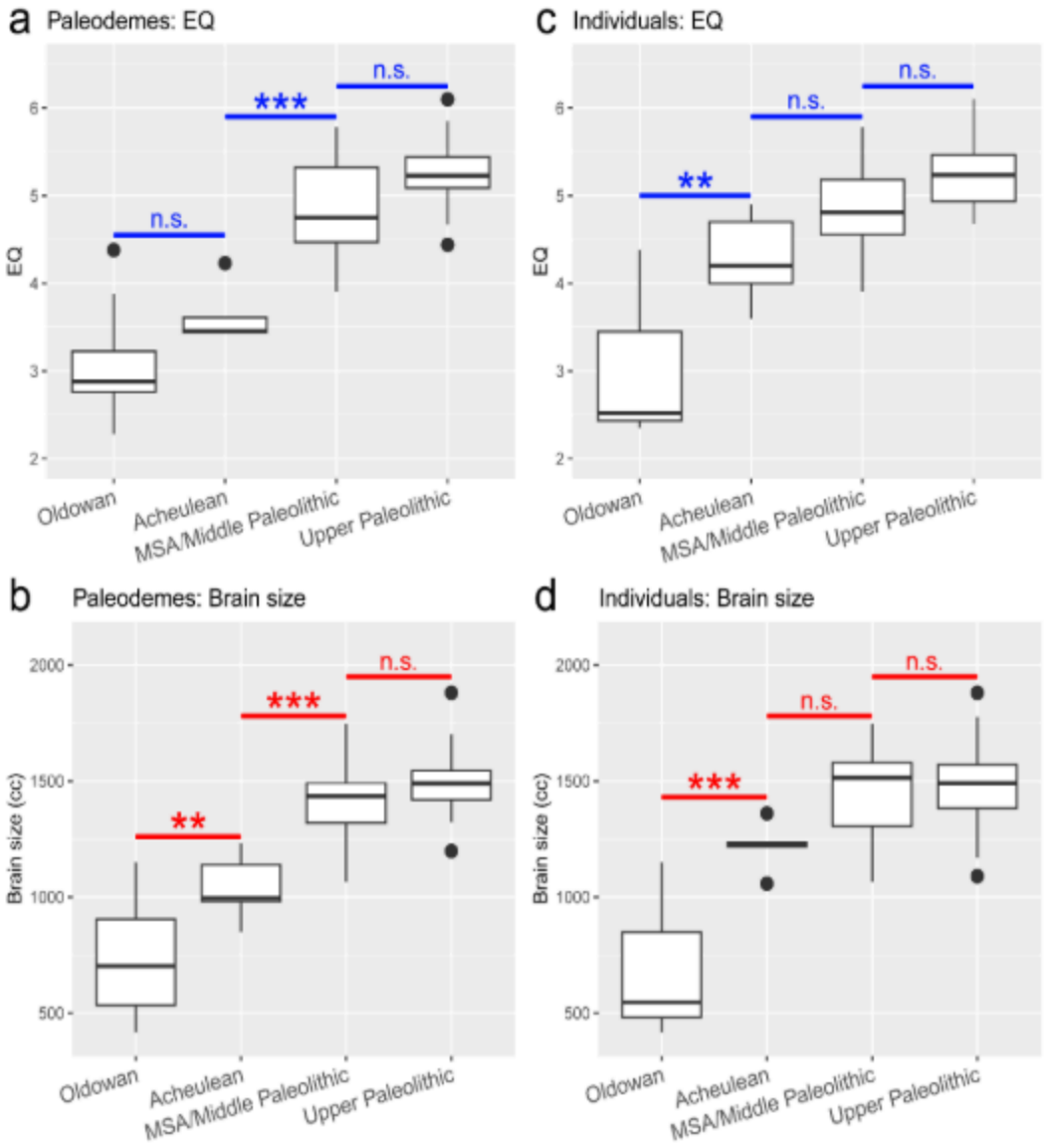


Figure 2

Boxplots by tool industry of (a) paleodeme EQ, (b) paleodeme brain size, (c) individual EQ, and (d) individual brain size. Symbols above horizontal bars indicate multiple-comparison adjusted p-values for pairwise comparison of means between adjacent categories using Tukey's Honest Significant Differences test (comparisons in blue for EQ and red for brain size): n.s., not significant at α =0.05; *, p ≤ 0.05; **, p ≤ 0.01; ***, p ≤ 0.001.

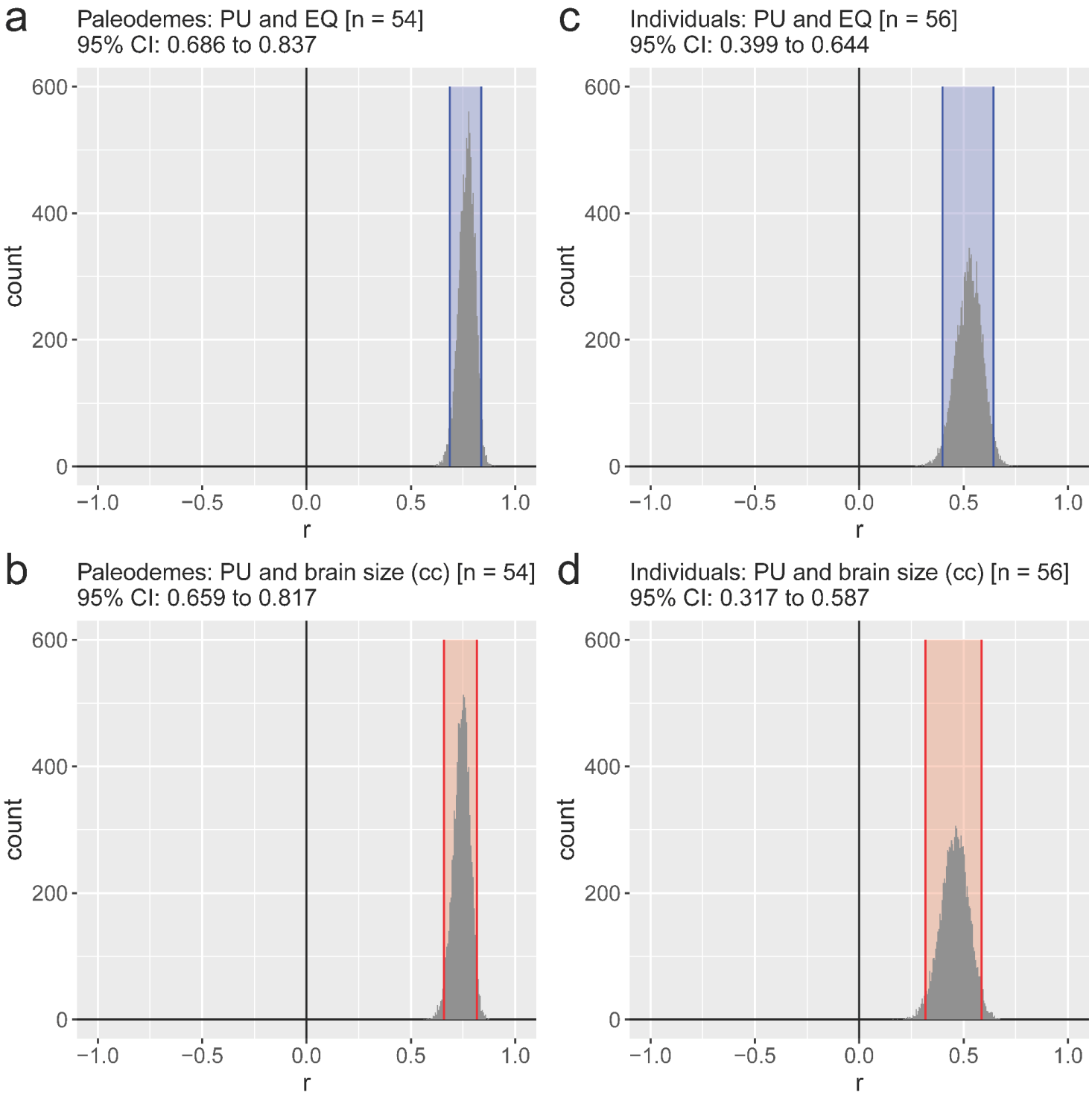


Figure 3

Histograms of resampled correlations between number of procedural units (PU) and (a) paleodeme EQ, (b) paleodeme brain size, (c) individual EQ, and (d) individual brain size. Vertical lines show the extent of 95% confidence intervals for correlation coefficients of PU with EQ (blue) and brain size (red).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryInformation.docx