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Abstract

Increases in brain size over the course of evolutionary time have been observed in multiple mammalian lineages, including hominins. This has inspired a variety of competing proposals to explain the underlying forces driving brain size increase, among them large-scale changes in climate. However multiple aspects of the climate (e.g. trend, variability, and rate of change in temperature and/or aridity) may have simultaneously influenced brain evolution in hominins, and/or other taxa. Here we investigated the relationship between different measures of the global oxygen isotope record (trend, variability, and rate of change) and cranial capacity using a dataset of 222 fossil species representing five different mammalian taxonomic groups, while accounting for the potentially confounding effects of trendedness in these times-series datasets. While cranial capacity was correlated with some aspects of global climate in particular lineages (e.g. Carnivora, Perissodactyla), hominin brain size was shown to be unrelated to climatic forces. By using a statistical approach that can guard against false positive relationships to which time-series data are highly susceptible, we conclude that the results of this study do not support previous assertions that climatic shifts drove hominin brain evolution.

Keywords	Variability selection, brain evolution, paleoclimate, isotopes, temporal autocorrelation
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Cover letter

Dear editors of Journal of Human Evolution,

My co-authors and I are pleased to submit our manuscript titled "*Global climate influenced the evolutionary history of brain size increase in some mammalian lineages, but not in hominins*" for review by Evolution. To our knowledge, this represents the first study that directly tests the proposed relationships between several aspects of global climate (trend, variability, rate of change) and brain size evolution across a multiple taxonomic orders using a statistically rigorous procedure.

 Using cranial capacities of fossil specimens (n = 227), we found that some taxa (e.g. Perissodactyla, Carnivora) did indeed show evidence of relationships between the deep-sea core oxygen isotope records (as a proxy for global temperature/aridity) and evolutionary changes in cranial capacity. However, importantly, hominins (n = 189 individuals) demonstrated no evidence of such brain-climate interactions once data had been properly detrended to guard against the potentially confounding effects of temporal autocorrelation. These results counter previously proposed hypotheses of paleoclimate being a primary driver of brain size increase and behavioral flexibility in hominin evolution. We thus believe that this study provides a much-needed statistically rigorous test of long standing hypotheses of brain-climate interactions in mammalian evolution.

 Thank you very much for your time and consideration. We look forward to the opportunity to publish in Journal of Human Evolution.

Many thanks,

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Title: Global climate influenced the evolutionary history of brain size increase in some mammalian lineages, but not in hominins

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Introduction

25   Since the divergence of hominins from the genus *Pan* ~5–7 million years ago (Ma), our lineage has undergone a massive expansion in brain size, such that modern humans have brains that are over three times larger than those of the other great apes, our closest extant relatives (Dunbar, 1993; Holloway, 2008; Sherwood et al., 2008; Klein, 2009) . However this phenomenon is not unique to hominins, as evolutionary increases

30   in brain size have also been demonstrated in non-human Primates, Carnivora, Artiodactyla and birds (Lefebvre et al., 2004; Shultz and Dunbar, 2010).

While the precise causes of evolutionary brain enlargement remain unclear, many hypotheses revolve around enhanced cognitive flexibility (Lefebvre et al., 2004; Sol et al., 2005; Krubitzer, 2009; Sol, 2009). Organisms may evolve larger brain size as

35   an adaptation to more efficiently solve novel problems and thus flexibly respond to changes in their dietary niche (Broadhurst et al., 1998; Carmody and Wrangham, 2010) or to navigate complex social networks (Dunbar, 1998; Shultz and Dunbar, 2007, 2010). Large-scale changes in climate have also been proposed as a driver of brain evolution. However, which aspects of climatic change are most significant for brain evolution is a

40   matter of ongoing debate, particularly in the field of human origins (Behrensmeyer, 2006; Faith and Behrensmeyer, 2013). Trend-based hypotheses implicate long-term directional changes in aspects of the climate, such as temperature and/or aridity as the primary drivers of evolution (e.g. savannah hypothesis, aridity hypothesis, and aspects of turnover pulse hypothesis) (Vrba, 1994; deMenocal, 2004; Domínguez-Rodrigo, 2014).

45   Alternatively, variability-based hypotheses implicate increasingly severe climatic fluctuations (e.g. variability selection hypothesis, variability pulse hypothesis) (Potts, 1996, 1998a; Bobe et al., 2002; Trauth et al., 2007, 2010, Maslin et al., 2014, 2015). More specifically, variability-based hypotheses posit that increases in the amplitude and periodicity of global environmental fluctuations may induce extinction, migration, and in

50   some instances, influence some species to become more versatile and thus to more effectively adapt to rapidly changing environments. According to this third scenario, hominins responded to an increased demand for versatility by evolving larger brains capable of enhanced behavioral plasticity (Potts, 2012). Lastly, some have suggested the rapidity at which climate change occurs may be a catalyst of evolution, here referred

55   to as rate-based hypotheses (e.g. turnover pulse hypothesis) (Vrba, 1993, 1995, 1996).

While often conceptualized as mutually exclusive, there is in fact considerable overlap among these hypotheses. Changes in trend, variability, and rate are interactive aspects of the global climate that can in turn have complex downstream effects on environment at the level of continents, regions, local habitats, and communities of organisms (Zachos et al., 2001; Maslin and Christensen, 2007). Therefore, it seems more appropriate to test these hypotheses within a single model.

While there have been numerous claims of a relationship between hominin brain size and climate (Vrba, 1994, 1995, 1996, Potts, 1998b, 2012; Shultz and Maslin, 2013; Maslin et al., 2015) only a few studies have attempted to statistically test this relationship. Ash & Gallup (2007) examined the relationship between brain evolution and climate, finding that both global cooling trends and global temperature variability significantly correlated with increasing hominin cranial capacity (CC) (n=109 specimens) over the last 2 Ma. In a subsequent multivariate analysis of the Ash & Gallup (2007) dataset, Bailey & Geary (2009) found that climatic trends towards global cooling and increased variability as well as other predictors of CC (e.g. estimated population density, parasitic load) predicted hominin CC. Despite these efforts, the conclusions that can be drawn from these studies have some notable limitations. First, they did not include measures of the rate or speed of climatic change as factors that might also be associated with brain size evolution. Second, and perhaps more importantly, they did not account for the confounding effects of temporal autocorrelation in time-series data (such as brain size change over time vs. climatic change over time), leaving open the possibility that previous associations between hominin brain size and climate are spurious. Fortunately, there is a wide body of research devoted towards accounting for such statistical complications.

The analysis of time series data is common in many fields, including ecology. Non-stationary data (i.e. data showing a directional trend or cyclicity over time) includes data exhibiting temporal autocorrelation, or the tendency of a dataset to correlate with itself over points in time (Chatfield, 2004). If a correlation is found between two strongly trended time-series, this relationship could be spurious in that the two datasets are in fact not causally related to one another. Just one of numerous examples of this error is the relationship between the westward tectonic movement of North America and the global isotope record (Alroy et al., 2000). Both datasets show directional change over time (i.e., are strongly trended) and thus show strong cross-correlations despite being causally unrelated to one another. This renders any interpretations of causality between

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90   trended time series as highly suspect, as temporal autocorrelation can often cause even random walks to produce significant cross-correlations. Alroy and colleagues (2000) discuss the pitfalls of failing to account for the effects of non-stationarity in the context of relating oxygen isotope time series to biotic data (e.g. Cenozoic mammalian diversity and body mass over time). This clearly demonstrates the potential for spurious

95   correlations (and thus unfounded conclusions) that can come about when correlating time-series data with directional trends. The authors note that while it is tempting to observe two strong trends over time and declare that they are causally related, it is far more informative to observe how the variables change between time intervals, and to ask whether these changes are correlated. Correlations in these "*blow-by-blow, interval-*

100   *by-interval"* differences in time series data are much more informative than correlations in trended time series (Alroy et al., 2000)*.*

        Later work represented a significant methodological advancement over previous attempts to test for brain-climate relationships in hominins in that, importantly, efforts were made to guard against the potential effects of non-stationarity (Shultz et al., 2012;

105   Shultz and Maslin, 2013). Specifically, Shultz, Nelson & Dunbar (2012) regressed hominin CC against time, grouped the resulting CC residuals into bins of 100 Ky, and used a series ANOVAs between adjacent time bins to test for shifts in CC over time. Using this methodology they found little evidence for interactions between global climate and hominin brain size, contrasting previous findings (Ash and Gallup Jr., 2007; Bailey

110   and Geary, 2009). A later study accounted for non-causal correlation by incorporating age as covariate, in addition to hominin CC and several regional climatic measures (derived fro terrigenous dust and deep-sea core oxygen isotope, and lake coverage records), in a stepwise Aikake information criterion model (Shultz and Maslin, 2013). It was found that regional climatic shifts in the East African Rift System were related to

115   evolutionary shifts in hominin brain size evolution during several time periods. However, in all previous investigations, (Ash and Gallup Jr., 2007; Bailey and Geary, 2009; Shultz et al., 2012; Shultz and Maslin, 2013) CCs of non-hominin mammalian taxa were not included in the sample. Employing a broader comparative approach would allow one to determine whether climatic variables are related to brain size variation as a general

120   principle of mammalian evolution outside of hominins. The paleontological record demonstrates that brain size has increased across many different taxa (Jerison, 1973; Montgomery et al., 2010; Boddy et al., 2012) but it remains to be determined whether these increases relate to climatic shifts.

The first goal of the present study was to identify which mammalian taxa (if any) display evidence for evolutionary increases in brain size over time. This was assessed using CC data derived from the fossil record. The fossil record is limited in a number of ways, including the error associated with various dating techniques (Ludwig and Renne, 2000) and the possibility that the earliest representatives of phylogenetic lineages have not yet been discovered. Despite the fragmentary nature the fossil record, we compiled a dataset from the literature with considerable numbers of species from each investigated taxon.

The second goal was to test for potential relationships between changes in CC and changes in global climate, using the deep-sea oxygen isotope record as a proxy. In order to address the possibility of multiple climatic factors simultaneously influencing brain evolution, we used multiple regression models with CC as the response variable and three different measures of climatic change as the predictor variables. Each climatic measure was intended to represent a different climatic hypothesis (Fig. 1):

1) *Trend*: This measure represents directional change-based hypotheses (e.g. deMenocal's (2004) aridity hypothesis), which predict that trends towards colder temperatures and increased aridity correlate with increased CC in hominins. This was quantified as mean oxygen isotope values in a given time interval.

2) *Variability*: This measure represents variability-based hypotheses (e.g. Potts' (1996, 1998a, 2012, 2013) variability selection hypothesis) which predict that increased fluctuations in global temperature and aridity lead to increased CC in hominins. This was quantified as standard deviation of oxygen isotope values in a given time interval.

3) *Rate*: This measure draws from aspects in both trend- and variability-based hypotheses as well as the rapid changes envisioned in turnover-pulse hypothesis (Vrba, 1993, 1996). The rate-based hypothesis proposed here predicts that increases in the rate of change in global temperature and aridity lead to increases in CC. This was quantified as the slope of the linear regression of oxygen isotope values in a given time interval.

The third goal of this study was to assess whether accounting for trendedness has any effects on the relationship between CC and global climate using an alternative statistical method to Shultz, Nelson & Dunbar (2012).

Each taxon has its own evolutionary history, array of ecological niches, and distribution across habitats, which can influence how they respond to a given

environmental pressure. Thus we predicted that each taxon may be differentially affected by various aspects of global climatic shifts over time (i.e. trend, variability, rate),

160   if at all.

Materials and methods

Fossil CC data

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CCs for 227 mammalian fossil species from six different taxa (Artiodactyla (*n* = 20 species), Carnivora (*n* = 129), Cetacea (*n* = 26), Perissodactyla (*n* = 14), and non-hominin Primates (*n* = 19)) were extracted from the Shultz & Dunbar supplementary dataset (2010). For the hominin sample, CC and date (in Ma) for 189 individual

170   specimens were extracted from Shultz, Nelson & Dunbar (2012), Schoenemann (2013), and Berger et al. (2010). These individuals were fit into a scheme of 19 different hominin species including: *Ardipithecus ramidus* (n = 1), *Australopithecus afarensis* (n = 5), *Australopithecus africanus* (n = 8), *Australopithecus garhi* (n = 1), *Australopithecus sediba* (n = 1), *Kenyanthropus platyops* (n = 1), *Homo habilis* (n = 10), *Homo rudolfensis*

175   (n = 3), *Homo ergaster* (n = 6), *Homo georgicus* (*n* = 3), *Homo erectus* (n = 33), *Homo floresiensis* (n = 1), *Homo antecessor* (n = 3), *Homo heidelbergensis* (n = 21), *Homo neanderthalensis* (n = 27), *Homo sapiens* (n = 58), and the robust australopiths *Paranthropus aethiopicus* (n = 1), *Paranthropus boisei* (n = 6), and *Paranthropus robustus* (n = 3). Species averages were calculated when multiple specimens per

180   species were available.

Each specimen was assigned an associated date (Ma) corresponding to the First Appearance Datum (FAD) of that fossil species as an approximation of its emergence. We assume that any error associated with these measures was equally distributed across all taxa (Shultz and Dunbar, 2010).

185   While a complete set of analyses investigating CC, body size, encephalization quotient (EQ) (Martin, 1981, 1984) and their interrelated dynamics would be worthwhile, reliable estimates of body mass in fossil taxa are relatively sparse. In the Shultz & Dunbar (2010) dataset, fossil body mass was often estimated based on cranial orbit measurements. However recent evidence (Elliott et al., 2014) suggests that orbit

190   dimensions are not reliable estimators of hominin body mass, as previously suggested (Aiello and Wood, 1994). This issue is further compounded when comparing specimens

across multiple mammalian taxa with highly variable relationships between orbit dimensions and overall body size. Furthermore, some evidence suggests that total CC is the a better predictor than EQ of measures of intelligence (Deaner et al., 2007) and the

195   ability to adapt to novel environments (Deaner et al., 2007; Sol et al., 2008).

Climatic data

The deep-sea oxygen isotope record serves as a proxy for mean ocean temperature,

200   which tracks global temperature over long periods of time. A high-resolution oxygen-isotope ($\partial^{18}O$) record calibrated to the standard geomagnetic polarity time scale (GPTS) were extracted from the literature (Zachos et al., 2001). These data were originally culled from deep-sea core isotope records from 40 different sites around the world spanning from present day to 65Ma. Since isotopic values do not vary significantly by site, it is

205   appropriate to use the combined dataset as a proxy for global climate change. This record provides a proxy for global temperature shifts that can in turn affect various regions through a network of complex environmental interactions.

Measures of mean, standard deviation (sd) and slope of the $\partial^{18}O$ record were calculated for a given span of time, referred to as intervals (Fig. 2). All analyses were

210   repeated using different interval lengths: 1My, 400Ky, and 200Ky. For example, if a species appeared at 2Ma, that species' CC would be correlated with each climatic measure (i.e. mean, sd and slope) over the course of 2.0–3.0Ma (1My interval), 2.0–2.4Ma (400Ky interval), and 2.0–2.2Ma (200Ky interval) (Fig. 3). The 400Ky and 200Ky intervals were chosen as they align with Milankovitch cycles (specifically eccentricity, or

215   the periodic shifts in the shape of the earth's orbit around the sun) (Zachos et al., 2001), which have been proposed to influence hominin evolution (Potts, 1998a; Ash and Gallup Jr., 2007). 1Ma intervals were also investigated in an attempt to capture a large number of climatic events per unit, which may be related gradual long-term evolutionary changes in certain taxa (Foley, 1994).

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Analyses of CC vs. time

First, Ordinary Least Squares (OLS) linear regression were performed in R using the lm function in the *stats* package (R Development Core Team, 2017). CC was used as the

225   response variable while time (in terms of Ma) was used as the predictor variable, first

with all taxa grouped together and then divided into five separate taxa to elucidate the relative contribution of each taxon to any potential overall mammalian patterns.

Analyses of CC vs. climate

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Next, multiple regressions analyses were performed also using the lm function in R (R Development Core Team, 2017). Again, CC was the response variable but the previously calculated climatic measures were used as predictor covariates (*CC ~ mean + sd + slope*).

235   There are several well-established methods that can statistically account for non-stationarity (Chatfield, 2004). The goal of these methods is to convert the trended time series into a detrended time series, or a time series that does not show a directional trend over time. The effect of detrending a previous trended dataset is illustrated in Figure 4. A commonly used method is to calculate the first differences of the original

240 time series (Alroy et al., 2000). The corrected (detrended) time series are computed as follows: $y'_t = y_t - y_{t-1}$, where y_t and y_{t-1} are temporally adjacent data points (e.g. oxygen isotope values) from which a differenced data point (y'_t) is calculated. Note that the detrended time series of first differences will be of length $n - 1$ where n is the length of the original pre-detrended time series. Thus, in the new detrended time series each point

245 reflects the difference between adjacent time bins. The resulting detrended time series can be used in subsequent analyses with other detrended time series. By employing this methodology one can be much more confident that any observed cross-correlations are meaningful relationships and not merely misleading coincidences.

      To account for trendedness in our study, we used the aforementioned

250 methodology to detrend both the CC data and the oxygen isotope data by calculating the magnitude of difference between any two adjacent data points in time (Alroy et al., 2000) (Fig. 4). However, in order to do this some of the data had to be averaged as some specimens shared the same points in time. For example, if fossil species A (with a CC of 400mL) and B (with a CC of 500mL) both appeared at 22.1Ma, their CCs would be

255 averaged to get a CC of 450mL for time point 22.1Ma. This reduced the number of observations in the analyses of fossil CC (from 227 to 71 across all taxa) likely due to the fact that many specimens often come from single paleontological sites and/or stratigraphic contexts that are associated with the same geological age. Nevertheless, multiple species averaged into a single time point will still be more likely to provide a

260   more accurate estimate of its respective taxon's typical CC than a single species from
       that taxon.

Evidence Scores

265   In order to summarize the findings of this study, Evidence Scores (how much
       evidence there was overall for CC being influenced by climate) were calculated for each
       taxon matched for time interval (1My, 400Ky, 200Ky) and climatic predictor variable
       (Trend, Variability, Rate terms within the multivariate model, as well as the multivariate
       model as a whole) (Table 1). In the Significance columns, "Y" denotes that the multiple
270   regression analysis revealed a significant relationship between CC and the given
       climatic variable within a given taxon (e.g. All Taxa, Artiodactyla, Carnivora, etc.) within a
       given interval (e.g. 1My, 400Ky, 200Ky) using either raw or detrended datasets, whereas
       "N" denotes a lack of significant relationship ($p > 0.05$). Evidence Scores were calculated
       by taking the number of detrended analyses that yielded a significant relationship
275   between CC and a given climatic variable ("Y") and dividing by the total number of
       detrended analyses ("Y" or "N") within a given taxon (multiplied by 100 to put in terms of
       %). Evidence scores did not include raw results due to the effects of temporal
       autocorrelation discussed above.

280   **Results**

CC vs. time

       Using the fossil CC dataset (natural log scale) (Fig. 5A), when all mammalian taxa were
285   analyzed as one group there was a small but significant trend of increasing CC as time
       approached the present (Adjusted R^2 (aR^2) = 0.193, coefficient estimate (ce) = -0.047, p
       < 0.0001). When separated by taxon, most groups showed evidence of increasing CC
       over time, including Artiodactyla (aR^2 = 0.404, ce = -0.084, p = 0.002), Carnivora (aR^2 =
       0.139, ce = -0.038, p = 0.000), Perissodactyla (aR^2 = 0.337, ce = -0.037, p = 0.018), and
290   Primates (aR^2 = 0.297, ce = -0.057, p = 0.010). Hominins were treated as their own
       separate group to allow for comparisons with other mammalian taxa, and displayed the
       most dramatic increase in CC over time (aR^2 = 0.493, ce = -0.304, p = 0.001). In order to
       explore the effect of increased sample size on the results, these data were reanalyzed

with the hominin CC dataset broken into individual specimens, thus increasing the
sample size from 13 species to 91 individuals, yielding an even stronger trend of
increasing CC over time (aR^2 = 0.834, ce = -0.429, p = 0.000) (see full results in Table
A.1).

CC vs. climate

Multiple regression analyses of raw fossil CC and climatic data were first conducted.
These showed that CC of the pooled sample from all fossil mammalian taxa (*n* = 222)
was significantly predicted by the climatic model (the model with trend, variability and
rate as predictors) at all three time intervals (1My, 400Ky, & 200Ky) (aR^2 = 0.426–0.458,
p < 0.001); Trend was the only significant predictor variable at all three intervals (ce =
2.141–2.292, p < 0.001). Artiodactyla CC was only significantly predicted by the climatic
model at the 400Ky interval (aR^2 = 0.551, p < 0.05) in which Variability was the only
significant predictor variable (ce = -0.454, p < 0.05). Carnivora CC was predicted by the
climatic model at all three intervals (aR^2 = 0.252–0.288, p < 0.01) in which Trend was the
only significant predictor variable in each interval (ce = 1.542–1.645, p < 0.002).
Perissodactyla CC was only predicted by the climatic model at the 400Ky interval (aR^2 =
0.672, p < 0.05) in which Trend was the only significant predictor variable (ce = 1.253, p
< 0.05). Species-averaged hominin CC was predicted by the climatic model at all three
time intervals (aR^2 = 0.365–0.488, p < 0.05) but no single climatic predictor variable
significantly contributed this relationship on its own (p > 0.05). Individualized hominin CC
was even more strongly predicted by the climatic model (aR^2 = 0.759–0.799, p < 0.001)
in which both Trend (ce = 1.312–1.599, p < 0.01) and Variability (ce = 0.499–0.793, p <
0.01) were significant predictors at all time intervals. Neither Cetacea CC nor Primate
CC were predicted by the climatic model at any interval (p > 0.05) (see Table A.2.A).

　　　　Results differed considerably when these analyses were rerun after detrending
the fossil CC and climatic data sets. Consistent with the raw results, neither Cetacea nor
Primate CC were predicted by the climatic models (p > 0.05). Additionally, CC of all taxa
grouped together, as well as Carnivora, Primates, hominins and individualized hominins
were not significantly predicted by the climatic model at any time interval (p > 0.05). This
is particularly noteworthy in individualized hominins, which showed a strong CC-climate
relationship before detrending the data. However, detrending the data did not eliminate

all significant results as Perissodactyla CC was predicted by the climatic model ($aR^2 =$ 0.481–0.711, $p < 0.05$) (see Table A.2.B).

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Evidence Scores

All taxa grouped together yielded an Evidence Score of 8.33, meaning 8.33% of detrended analyses showed a significant relationship between CC and climate. In

335   descending order, Evidence Scores for each taxon were as follows: Perissodactyla (50.00), Carnivora (8.33), Primates (0.00), Artiodactyla (0.00), Cetacea (0.00), hominins (0.00), individualized hominins (0.00).

Discussion

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In the fossil dataset, it was found that across mammals in general, there was a trend towards increased brain size over time. Subdividing the sample by taxon revealed that many, but not all, mammalian lineages contributed to this overall pattern. This is consistent with previous demonstrations of increasing absolute or relative brain size over

345   time in the fossil record of Artiodactyla (Jerison, 1970, 1973), Carnivora (Jerison, 1970, 1973, Finarelli and Flynn, 2007, 2009), Perissodactyla (Edinger, 1948; Jerison, 1970), Primates (Holloway, 1968; Jerison, 1973), and hominins (Shultz et al., 2012; Schoenemann and Begun, 2013) (see also Shultz & Dunbar (2010) for an inter-order comparison). Cetacea were the notable exception to this pattern of increasing brain size,

350   as their average brain size has remained consistently large since their emergence. The contrast of our results with those of previous studies that reported directional increases in Cetacean brain (Marino et al., 2004; Boddy et al., 2012; Montgomery et al., 2013) likely stems from differences in samples and methodology. It should, however, be noted that different taxa of mammals occupy different, partially overlapping time periods over

355   the last 65My. Some taxa have existed much longer than others and thus span a much larger portion of the oxygen isotope record. This means that some taxa would have experienced a wider range of selective pressures, some of which could influence evolutionary shifts, speciation events, and extinctions.

Hominins occupy a particularly short and recent period of time (the last ~5–7Ma).

360   This is, of course, partly due to the fact that they represent a taxonomic tribe rather than an order like most of the other taxa investigated here. Despite having only existed during a relatively brief time, hominins have undergone remarkable evolutionary increases in brain size (Fig. 3 & Fig. 5A) which may have been in response to greater selective pressures for cognitively-mediated adaptability and problem solving in novel

365   environments (Sol et al., 2005, 2008). This rapid increase in brain mass drastically deviates from the allometrically predicted brain mass of a primate of modern human body size and likely relates to many enhanced cognitive capacities including tool manufacture, complex social cognition, and language (Deacon, 2000; Passingham, 2008; Sherwood et al., 2008; Stout and Chaminade, 2012).

370   A number of hypotheses have proposed climatic changes as a driver of brain evolution (Potts, 1996, 1998b, 2012, 2013; Vrba, 1996; deMenocal, 2004). Using a statistically rigorous approach across a taxonomically diverse sample, this study tested these hypotheses and found evidence that in some mammalian taxa (Perissodactyla, and Carnivora) brain size evolution has indeed been influenced by global climate.

375   However it should be noted that the relationship was not always positive. In some cases, an increase in brain size was associated with a decrease in climatic Rate (e.g. detrended fossil Perissodactyla CC at the 1 My interval) or an increase in Variability (e.g. detrended all grouped fossil taxa CC at the 400 Ky interval) (see Table 3SB).

        All three climatic variables (Trend, Rate, and Variability) were shown to

380   contribute in varying degrees and combinations depending on the taxon and time interval investigated. However, once the time-series data had been detrended, this study provided no evidence for a relationship between brain size and climate in several taxa, most notably, hominins (Table 1 & A.2.).

        Based on the fossil record data, it appears that hominins continued the Primate-

385   general trend of increasing brain size, albeit at a greatly accelerated pace in the last 5–7 Ma. Like non-hominin Primates, the rapid brain expansion observed in hominins appears to have been completely decoupled from global climatic events. Thus, hominins most likely inherited this brain-climate decoupling from their non-hominin primate ancestors. We speculate that this decoupling from global climate shifts first arose in non-hominin

390   Primates through the evolutionary elaboration of certain neural structures (e.g. prefrontal cortex) that underlie enhanced capacities for cognitive and behavioral plasticity (Kuboshima-Amemori and Sawaguchi, 2007), driven by selection forces unrelated to climatic change.

The lack of brain-climate relationships in hominins corroborate the overall

395   conclusions of Shultz & Dunbar (2012), albeit that their results indicated some significant hominin brain-climate relationships whereas ours indicate none at all. These slight discrepancies are likely due to differing methodologies (e.g. detrending procedures) and sample (e.g. our inclusion of additional hominin specimens). Our analyses consistently found that, once detrended, hominins displayed no relationship between CC and any of

400   the tested global climatic factors at any intervals. This cannot be explained as a general tendency of detrending time-series data to eliminate significant relationships, as this transformation sometimes revealed new relationships that had not been observed using the raw data (e.g. Perissodactyla, Table 1). Nor does this appear to simply be the result of low statistical power due to a small sample size of hominin species (n=19) since the

405   dataset of individual hominin specimens (n=189) also resulted in no brain-climate relationships.

Conclusions

410   Thus, these results do not support previous claims that hominin brain size was driven by global climatic variables. The fact that previous reports found significant relationships (Ash and Gallup Jr., 2007; Bailey and Geary, 2009) could stem from one or more of the following sources: 1) differing sample sizes, 2) testing single climatic factors at a time, and/or 3) use of non-stationary time-series data without appropriate statistical

415   corrections. In this study we demonstrated that the latter of these three factors consistently and dramatically alters the pattern of results due to the confounding effects of temporal autocorrelation, in this case, spuriously producing a brain-climate relationship in hominins. This clearly illustrates the necessity of accounting for non-stationarity in time-series data before conducting cross-correlation analyses, particularly

420   in the realm of hominin brain evolution. While other investigations have found evidence of a relationship between hominin brain size and climatic factors at the geographic regional level (Shultz and Maslin, 2013), our results indicate that these relationships do not hold at the global level for hominins. This situation contrasts with the significant relationships commonly found between global climate and brain size in other mammalian

425   taxa, though it remains to be tested whether regional climate more strongly influences brain evolution in these taxa. Future work could thus explore the effects of multiple climatic spatial scales and variables on brain evolution across a diversity of taxa.

However the current evidence suggests that global climate did not influence brain evolution in at least several taxa, including hominins.

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Acknowledgements

Appendix. Supplementary data

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Supplementary data associated with this article can be found in the on-line version, at…

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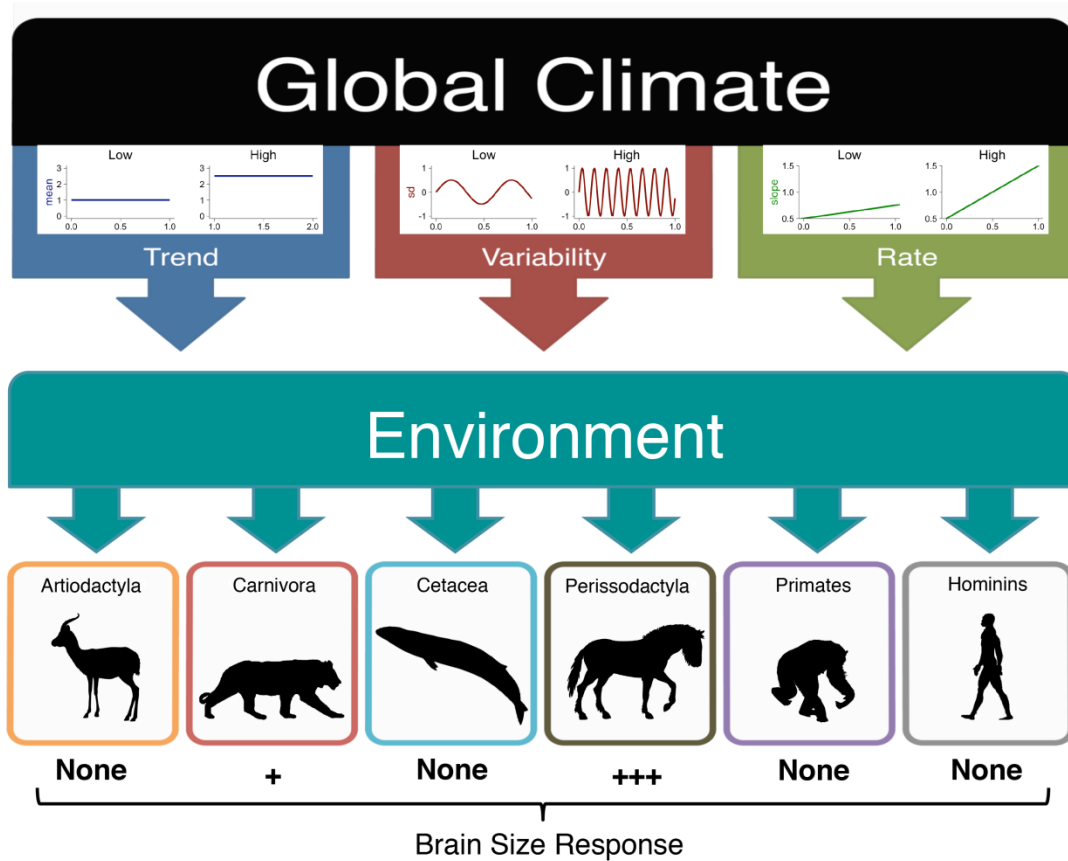
Figure 1. Multiple aspects of global climate change (Trend, Variability, and Rate of change) can simultaneously affect the environment. Cartoon examples of High and Low
605 Trend, Variability, and Rate are shown within their respective climatic variable boxes. These changes in environment can alter the selective pressures acting on the organisms that inhabit it over an evolutionary timescale. Some taxa show a significant relationship between climatic variables (Trend, Variability, and/or Rate) and cranial capacity (CC), suggesting that some taxa have indirectly responded to changing global climate by
610 evolving larger brains. After appropriately detrending the time-series data, it was found that Perissodactyla CC was the most frequently responsive (+++, Evidence Score=50.00) followed by Carnivora CC (+, Evidence Score=8.33),. Artiodactyla, Cetacea, Primates and hominins demonstrated no evidence of a relationship between brain size and global climate for any climatic variable at any tested time interval (1My,
615 400Ky, 200Ky). Silhouettes from phylopic.org.

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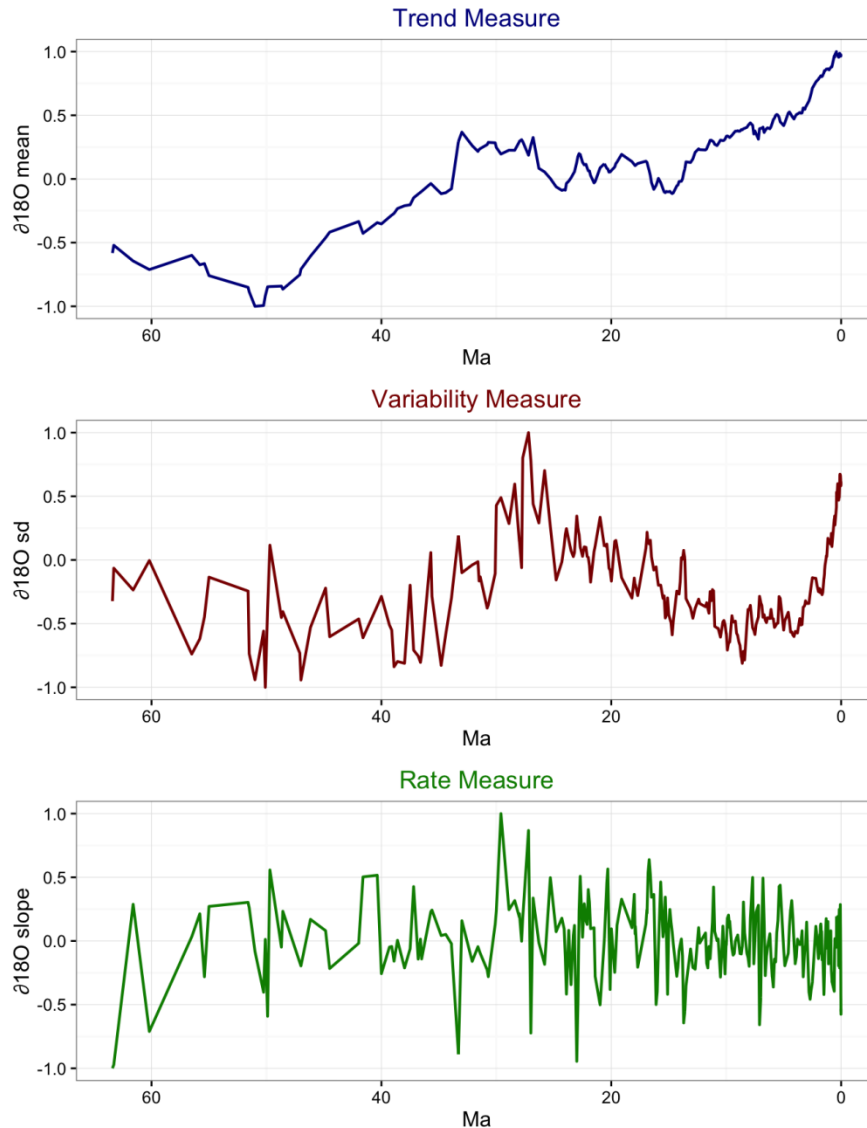
Figure 2. Multiple climatic measures of the oxygen isotope (∂^{18}O) record over the last 65My. Measures were calculated by starting at the age (Ma) of a ∂^{18}O data point, and encompassing all the ∂^{18}O data in the prior 400Ky time interval (e.g. all ∂^{18}O data within 10.2Ma–10.6Ma). This procedure was repeated over all data points in the ∂^{18}O record.
625 Trend was quantified as the ∂^{18}O mean within a time interval, Variability was quantified as the standard deviation (sd) within a time interval, and Rate was quantified as the slope of the ordinary least squares (OLS) regression within a time interval. Some climatic variables display long-term directional changes over time, for example the pattern of increasing Trend (higher mean ∂^{18}O) over the last ~50My, or the pattern of
630 increasing Variability (higher sd) over the last ~10My. If another time-series dataset, CC for example, also shows a strong trend over time, these climatic variables and CC may cross-correlate despite being causally unrelated. Detrending time-series data such as these can help guard against such spurious cross-correlations and reveal true relationships.

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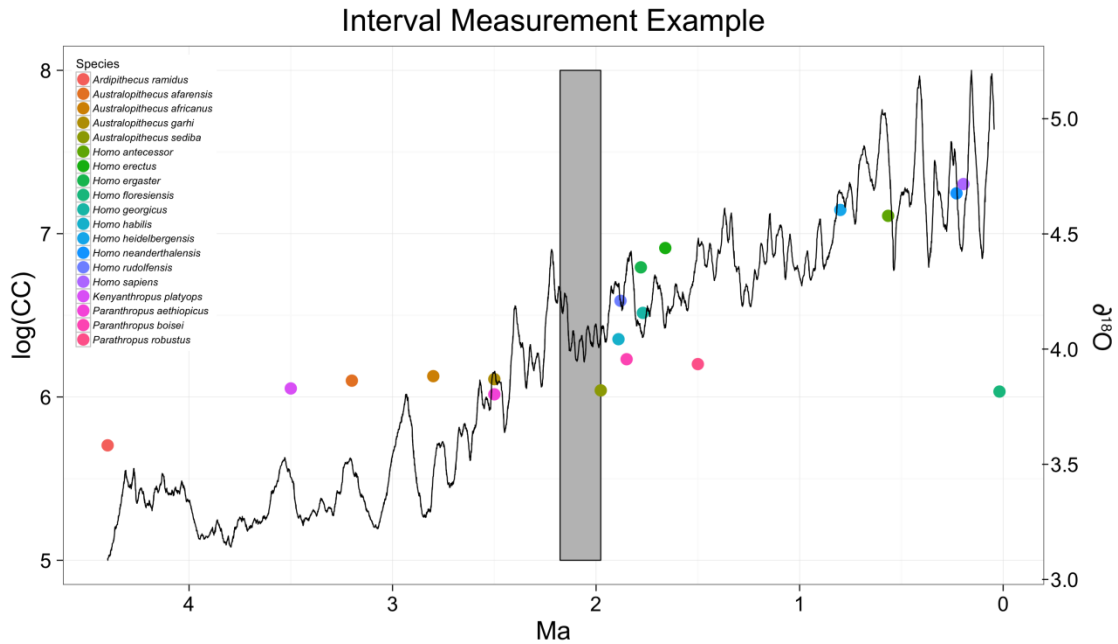
Figure 3. Example of how measures of the oxygen isotope record (black line, $\partial^{18}O$ on right y-axis) were collected from the time intervals preceding the first appearance datum (FAD) associated with a species. Each point is a species averaged fossil cranial capacity (points, log scale CC on left y-axis). In this example, the 200Ky interval preceding the 3.2Ma FAD of *Australopithecus sediba* is enclosed within the grey rectangle, spanning the time period 3.2–3.4Ma.

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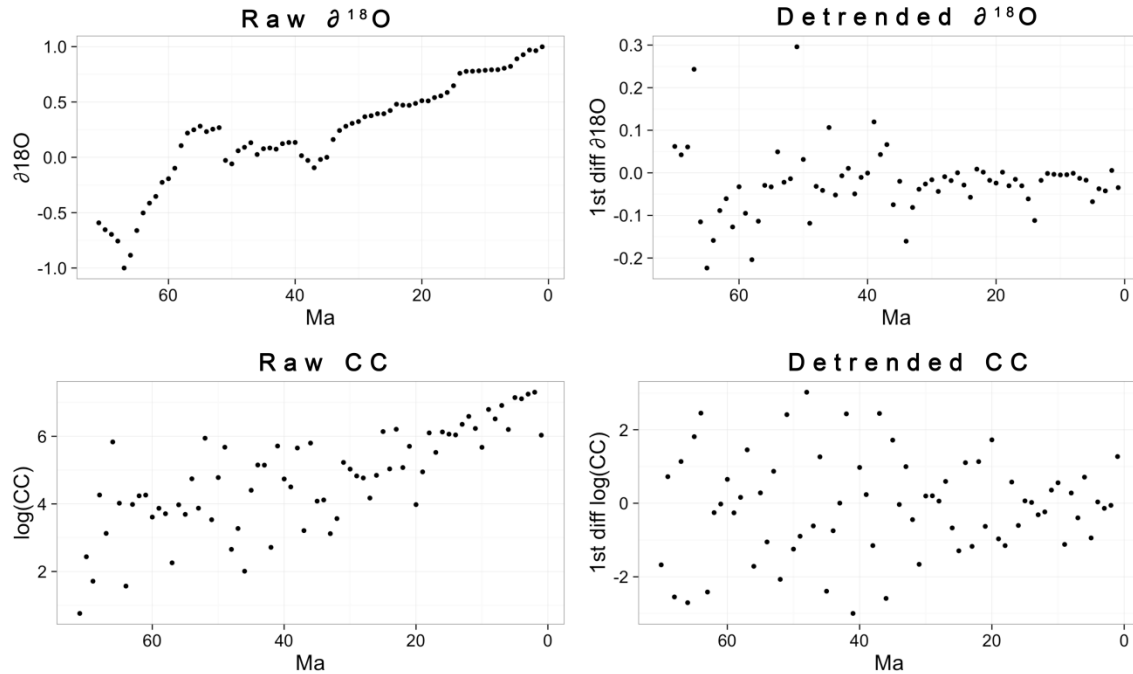
Figure 4. Demonstration of the effect of detrending time-series data (in this case the oxygen isotope record and mammalian CC over the last 65My) by calculating the first difference between temporally adjacent data points. The raw oxygen isotope record ($\partial^{18}O$) indicates a clear trend toward global cooling over time (upper left). After detrending the data, we are left with the degree of $\partial^{18}O$ changes over many time points rather than the raw values. Raw cranial capacity (CC) data similarly showed a trend over time (bottom left) that disappeared once detrended (bottom right).
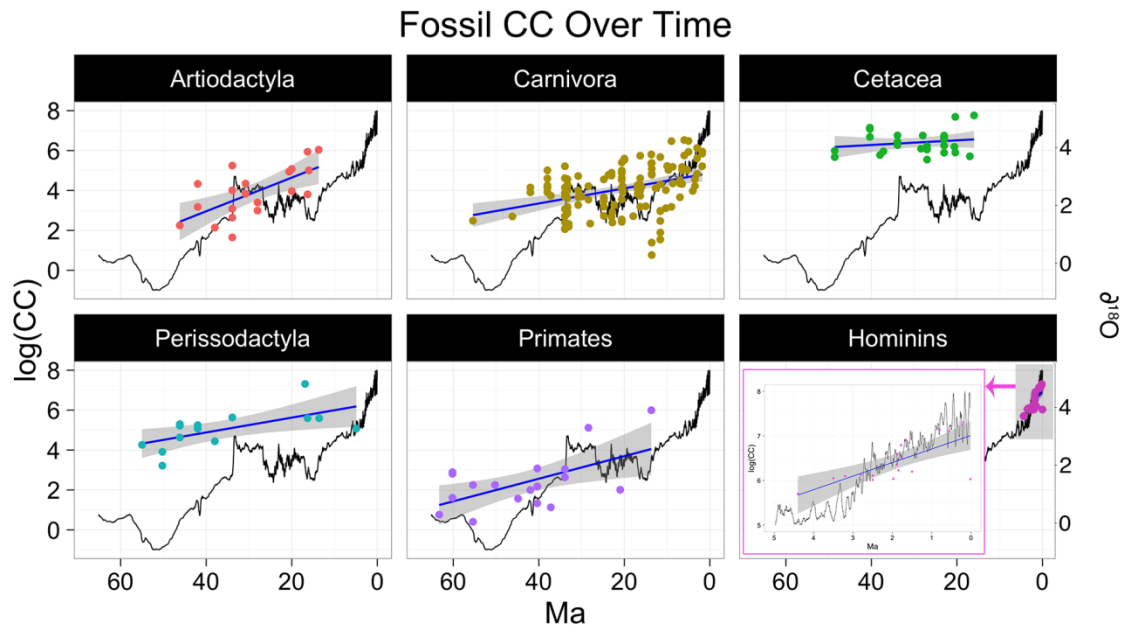
Figure 5. Fossil cranial capacity (CC) (natural log) for six taxa (points, scale on left y-axis) with corresponding best fit lines from ordinary least squares (OLS) regressions (blue line) with confidence intervals (grey shading). The $\partial^{18}O$ record over 65My is illustrated for each taxa (black line, scale on right y-axis). The hominin plot (A) was expanded for visualization purposes due to the relatively short period of time the hominin fossil record occupies. Of the fossil taxa, each taxa showed evidence of increased CC over time (aR^2 = 0.139–0.834, $p < 0.05$), except Cetacea ($p > 0.05$). (see Tables A.1 & A.2 for full results).

Results Summary Table

		Raw Fossil Significance			Detrended Fossil Significance			Results Summary
		1My	400Ky	200Ky	1My	400Ky	200Ky	
All Taxa	Trend	Y	Y	Y	N	N	N	
	Variability	N	N	N	N	Y	N	
	Rate	N	N	N	N	N	N	**Evidence Score**
	MODEL	Y	Y	Y	N	N	N	8.33
Artiodactyla	Trend	N	N	N	N	N	N	
	Variability	N	Y	N	N	N	N	
	Rate	N	N	N	N	N	N	**Evidence Score**
	MODEL	N	Y	N	N	N	N	0.00
Carnivora	Trend	Y	Y	Y	N	N	N	
	Variability	N	N	N	N	N	N	
	Rate	N	N	N	N	Y	N	**Evidence Score**
	MODEL	Y	Y	Y	N	N	N	8.33
Cetacea	Trend	N	N	N	N	N	N	
	Variability	N	N	N	N	N	N	
	Rate	N	N	N	N	N	N	**Evidence Score**
	MODEL	N	N	N	N	N	N	0.00
Perissodactyla	Trend	N	Y	N	Y	N	N	
	Variability	N	N	N	Y	Y	N	
	Rate	N	N	N	Y	N	N	**Evidence Score**
	MODEL	N	Y	N	Y	Y	N	50.00
Primates	Trend	N	N	N	N	N	N	
	Variability	N	N	N	N	N	N	
	Rate	N	N	N	N	N	N	**Evidence Score**
	MODEL	N	N	N	N	N	N	0.00
Hominins	Trend	N	N	N	N	N	N	-
	Variability	N	N	N	N	N	N	-
	Rate	N	N	N	N	N	N	**Evidence Score**
	MODEL	Y	Y	Y	N	N	N	0.00
Individulaized Hominins	Trend	Y	Y	Y	N	N	N	-
	Variability	Y	Y	Y	N	N	N	-
	Rate	Y	N	N	N	N	N	**Evidence Score**
	MODEL	Y	Y	Y	N	N	N	0.00

Table 1. This table provides an overall summary of cranial capacity (CC) vs. climate analysis results. In Significance columns, "Y" denotes that there was a significant relationship found between CC and a given climatic variable, and/or the overall model, whereas "N" denote that no significant CC-climate relationship was found (p<0.05). Evidence Scores were calculated as the percentage of detrended results that showed evidence of CC-climate relationships (to the exclusion of raw results due to confounds associated with temporal autocorrelation). Some taxa demonstrated evidence of CC-climate interactions (i.e. Carnivora, Perissodactyla) while other taxa demonstrated no such evidence (i.e. Artiodactyla, Cetacea, Primates and hominins).

SUPPLEMENTARY MATERIALS

Fossil CC vs. Time

		log(CC) by Taxa							
		All Taxa	Artiodactyla	Carnivora	Cetacea	Perissodactyla	Primates	Hominins	Individualized Hominins
Ma	ce	- 0.047	- 0.084	- 0.038	- 0.012	- 0.037	- 0.057	- 0.304	- 0.429
	se	- 0.006	- 0.023	- 0.008	- 0.013	- 0.013	- 0.019	- 0.071	- 0.014
	t	- 7.424	- 3.727	- 4.655	- 0.923	- 2.76	- 2.934	- 4.302	- 30.788
	p	**0.000***	**0.002**	**0.00001***	0.366	**0.018***	**0.010**	**0.0005***	**0.000***
(Intercept)	ce	5.552	6.332	4.867	6.747	6.368	4.828	7.012	7.262
	se	- 0.175	- 0.688	- 0.193	- 0.389	- 0.525	- 0.873	- 0.153	- 0.017
	t	31.722	9.199	25.271	17.333	12.12	5.528	45.817	433.496
	p	0.000***	0.00000***	0.000***	0.000***	0.00000***	0.00004***	0.000***	0.000***
	Observations	227.0	20.0	129.0	26.0	14.0	19.0	19.0	189.0
	R^2	0.197	0.436	0.146	0.034	0.388	0.336	0.521	0.835
	Adjusted R^2	0.193	0.404	0.139	- 0.006	0.337	0.297	0.493	0.834
	Residual Std. Error	1.386	0.96	1.056	0.584	0.782	1.132	0.35	0.179
	F Statistic	**55.116*****	**13.892****	**21.671*****	0.851	**7.617***	**8.606****	**18.506*****	**947.914*****
	Summary	Increase	Increase	Increase	Stable	Increase	Increase	Increase	Increase

Note: *p<0.05 **p<0.01 ***p<0.001

Table A.1. Results of linear regressions in which fossil cranial capacity (CC) (natural log) was the response variable and time, in terms of millions of years ago (Ma), was the predictor variable. Negative estimate values mean that CC grew larger as we come closer to the present (Increase), positive estimate values mean CC grew smaller as we approach the present, and no significant means that there was no significant trend of CC in either direction (Stable).

A

Fossil CC vs. Climate: Raw

log(CC) by Taxa and Intervals

1 My Intervals

Measure	Stat	All Taxa	Artiodactyla	Carnivora	Cetacea	Perissodactyla	Primates	Hominins	Individualized Hominins
Mean	ce	2.292	0.883	1.645	0.129	1.353	2.26	2.225	1.599
	se	- 0.278	- 1.811	- 0.435	- 0.919	- 0.585	- 1.382	- 1.57	- 0.459
	t	8.247	0.488	3.78	0.141	2.312	1.635	1.417	3.485
	p	**0.000*****	0.641	**0.001*****	0.892	0.061	0.141	0.179	**0.001*****
SD	ce	0.011	1.147	- 0.591	0.111	1.214	1.189	- 0.038	0.499
	se	- 0.317	- 1.059	- 0.304	- 0.484	- 0.827	- 1.244	- 0.698	- 0.156
	t	0.036	1.082	- 1.945	0.229	1.467	0.956	- 0.055	3.191
	p	0.972	0.315	0.059	0.824	0.193	0.368	0.957	**0.002****
Slope	ce	0.794	- 0.331	0.278	0.172	- 1.075	1.402	0.827	0.69
	se	- 0.455	- 1.291	- 0.397	- 1.126	- 0.932	- 2.059	- 1.064	- 0.258
	t	1.744	- 0.257	0.7	0.152	- 1.153	0.681	0.778	2.672
	p	0.086	0.805	0.489	0.883	0.293	0.516	0.45	**0.009****
(Intercept)	ce	4.131	4.388	3.686	6.34	6.309	3.412	4.73	5.347
	se	- 0.172	- 0.53	- 0.166	- 0.312	- 0.585	- 0.637	- 1.284	- 0.38
	t	24.072	8.286	22.223	20.314	10.79	5.359	3.683	14.083
	p	0.000***	0.0001***	0.000***	0.000***	0.00004***	0.001***	0.003**	0.000***
Observations		71	11	43	13	10	12	18	95
R²		0.508	0.348	0.339	0.026	0.604	0.42	0.518	0.799
Adjusted R²		0.486	0.068	0.288	- 0.299	0.406	0.202	0.414	0.792
Residual Std. Error		1.062	1.174	0.842	0.673	0.776	1.398	0.379	0.201
F Statistic		23.097***	1.244	6.676***	0.08	3.049	1.931	5.009*	120.371***

400 Ky Intervals

Measure	Stat	All Taxa	Artiodactyla	Carnivora	Cetacea	Perissodactyla	Primates	Hominins	Individualized Hominins
Mean	ce	2.141	- 0.454	1.58	0.347	1.253	1.362	2.044	1.312
	se	- 0.287	- 1.312	- 0.466	- 0.85	- 0.472	- 1.736	- 1.125	- 0.399
	t	7.473	- 0.346	3.388	0.409	2.654	0.784	1.816	3.29
	p	**0.000*****	0.74	**0.002****	0.693	**0.038***	0.456	0.091	**0.002****
SD	ce	0.044	3.228	- 0.692	- 0.124	1.499	1.624	0.236	0.656
	se	- 0.387	- 1.145	- 0.395	- 0.582	- 0.697	- 1.632	- 0.485	- 0.122
	t	0.114	2.82	- 1.752	- 0.213	2.15	0.995	0.487	5.372
	p	0.91	**0.026***	0.088	0.837	0.076	0.349	0.635	**0.000*****
Slope	ce	0.247	- 1.81	- 0.374	- 0.018	0.75	0.03	0.747	0.035
	se	- 0.402	- 0.913	- 0.419	- 0.46	- 0.684	- 1.13	- 0.419	- 0.099
	t	0.614	- 1.982	- 0.894	- 0.04	1.097	0.027	1.785	0.352
	p	0.542	0.088	0.377	0.97	0.315	0.98	0.096	0.726
(Intercept)	ce	4.272	4.625	3.687	6.37	5.971	3.205	4.986	5.556
	se	- 0.173	- 0.334	- 0.18	- 0.188	- 0.271	- 0.561	- 0.929	- 0.328
	t	24.701	13.831	20.537	33.824	22.049	5.709	5.367	16.944
	p	0.000***	0.00001***	0.000***	0.000***	0.00000***	0.0005***	0.0001***	0.000***
Observations		71	11	43	13	10	12	18	95
R²		0.467	0.685	0.282	0.02	0.78	0.401	0.579	0.792
Adjusted R²		0.443	0.551	0.227	- 0.307	0.671	0.176	0.488	0.785
Residual Std. Error		1.106	0.815	0.878	0.675	0.578	1.421	0.355	0.204
F Statistic		19.563***	5.085*	5.103**	0.061	7.109*	1.786	6.406**	115.741***

200 Ky Intervals

Measure	Stat	All Taxa	Artiodactyla	Carnivora	Cetacea	Perissodactyla	Primates	Hominins	Individualized Hominins
Mean	ce	2.165	0.126	1.542	0.359	0.79	4.129	2.383	1.488
	se	- 0.303	- 1.664	- 0.464	- 0.719	- 0.817	- 1.988	- 1.15	- 0.422
	t	7.155	0.076	3.324	0.499	0.966	2.076	2.072	3.523
	p	**0.000*****	0.942	**0.002****	0.63	0.372	0.077	0.058	**0.001*****
SD	ce	- 0.315	3.745	- 0.992	0.543	2.372	- 2.186	0.051	0.793
	se	- 0.515	- 2.079	- 0.536	- 0.895	- 1.154	- 2.224	- 0.629	- 0.171
	t	- 0.611	1.801	- 1.851	0.606	2.056	- 0.983	0.081	4.633
	p	0.544	0.115	0.072	0.56	0.086	0.359	0.937	**0.000*****
Slope	ce	2.906	- 5.666	- 3.742	5.463	- 7.313	- 8.294	3.137	- 0.287
	se	- 3.709	- 9.082	- 4.425	- 5.423	- 15.17	- 8.227	- 2.71	- 0.685
	t	0.783	- 0.624	- 0.846	1.007	- 0.482	- 1.008	1.158	- 0.42
	p	0.437	0.553	0.403	0.341	0.647	0.347	0.267	0.676
(Intercept)	ce	1.566	10.186	6.987	1.517	12.94	10.486	1.806	5.737
	se	- 3.372	- 8.143	- 4.044	- 4.922	- 13.928	- 7.385	- 2.756	- 0.754
	t	0.465	1.251	1.727	0.308	0.929	1.42	0.655	7.614
	p	0.644	0.252	0.092	0.765	0.389	0.199	0.523	0.000***
Observations		70	11	43	13	10	11	18	95
R²		0.451	0.521	0.305	0.137	0.68	0.459	0.477	0.759
Adjusted R²		0.426	0.316	0.252	- 0.151	0.52	0.227	0.365	0.751
Residual Std. Error		1.092	1.005	0.863	0.633	0.698	1.42	0.395	0.22
F Statistic		18.076***	2.542	5.705**	0.474	4.251	1.98	4.256*	95.649***

Note: *p<0.05 **p<0.01 ***p<0.001

B

Fossil CC vs. Climate: Detrended

log(CC) by Taxa and Intervals

1 My Intervals

Measure	Stat	All Taxa	Artiodactyla	Carnivora	Cetacea	Perissodactyla	Primates	Hominins	Individualized Hominins
Mean	ce	1.08	- 0.219	- 1.154	- 1.122	4.098	0.222	- 1.937	- 0.28
	se	- 2.139	- 2.559	- 2.111	- 1.751	- 1.219	- 2.931	- 5.446	- 2.241
	t	0.505	- 0.085	- 0.547	- 0.641	3.363	0.076	- 0.356	- 0.125
	p	0.616	0.935	0.588	0.54	**0.021***	0.942	0.728	0.902
SD	ce	0.614	0.017	0.032	0.704	1.977	1.129	1.537	- 0.043
	se	- 0.636	- 0.929	- 0.658	- 0.958	- 0.726	- 1.596	- 1.603	- 0.973
	t	0.965	0.019	0.049	0.735	2.725	0.707	0.959	- 0.044
	p	0.339	0.986	0.962	0.484	**0.042***	0.503	0.356	0.966
Slope	ce	0.263	- 1.229	0.025	- 1.331	- 1.542	2.484	1.994	0.457
	se	- 0.59	- 1.125	- 0.625	- 1.58	- 0.514	- 2.085	- 1.641	- 0.812
	t	0.445	- 1.092	0.04	- 0.843	- 3.002	1.191	1.215	0.563
	p	0.658	0.317	0.969	0.424	**0.031***	0.273	0.246	0.575
(Intercept)	ce	- 0.046	- 0.365	- 0.116	- 0.204	0.428	- 0.472	0.029	- 0.018
	se	- 0.17	- 0.418	- 0.197	- 0.327	- 0.285	- 0.638	- 0.183	- 0.03
	t	- 0.27	- 0.872	- 0.592	- 0.622	1.503	- 0.74	0.16	- 0.616
	p	0.788	0.417	0.558	0.551	0.194	0.484	0.876	0.54
Observations		70	10	42	12	9	11	17	94
R²		0.021	0.174	0.008	0.105	0.766	0.224	0.112	0.008
Adjusted R²		- 0.024	- 0.239	- 0.07	- 0.231	0.625	- 0.109	- 0.093	- 0.025
Residual Std. Error		1.363	1.209	1.184	1.061	0.705	2.05	0.522	0.263
F Statistic		0.471	0.422	0.108	0.313	5.443*	0.672	0.546	0.255

400 Ky Intervals

Measure	Stat	All Taxa	Artiodactyla	Carnivora	Cetacea	Perissodactyla	Primates	Hominins	Individualized Hominins
Mean	ce	- 0.768	- 0.386	- 1.854	- 0.35	1.847	- 3.053	- 2.612	0.239
	se	- 1.724	- 2.457	- 1.605	- 1.912	- 1.141	- 3.123	- 4.179	- 1.953
	t	- 0.445	- 0.157	- 1.155	- 0.183	1.619	- 0.978	- 0.625	0.122
	p	0.658	0.881	0.256	0.86	0.167	0.361	0.543	0.903
SD	ce	1.248	1.897	0.413	- 0.409	2.097	2.365	0.533	- 0.473
	se	- 0.618	- 1.572	- 0.671	- 0.797	- 0.603	- 1.774	- 1.274	- 0.644
	t	2.018	1.207	0.616	- 0.514	3.479	1.333	0.419	- 0.734
	p	**0.048***	0.273	0.542	0.622	**0.018***	0.225	0.683	0.465
Slope	ce	- 0.376	- 1.474	- 0.908	0.258	0.216	0.885	1.064	0.205
	se	- 0.357	- 1.397	- 0.382	- 0.578	- 0.5	- 1.635	- 0.501	- 0.223
	t	- 1.052	- 1.055	- 2.377	0.446	0.432	0.542	2.123	0.919
	p	0.297	0.333	**0.023***	0.668	0.684	0.605	0.054	0.361
(Intercept)	ce	- 0.082	- 0.171	- 0.148	- 0.208	0.065	- 0.578	- 0.102	- 0.023
	se	- 0.161	- 0.424	- 0.178	- 0.343	- 0.268	- 0.623	- 0.162	- 0.029
	t	- 0.508	- 0.403	- 0.829	- 0.607	0.242	- 0.927	- 0.63	- 0.798
	p	0.614	0.702	0.413	0.561	0.819	0.385	0.54	0.428
Observations		70	10	42	12	9	11	17	94
R²		0.089	0.225	0.151	0.067	0.819	0.252	0.258	0.015
Adjusted R²		0.048	- 0.163	0.084	- 0.283	0.711	- 0.068	0.087	- 0.018
Residual Std. Error		1.315	1.171	1.096	1.083	0.619	2.012	0.477	0.262
F Statistic		2.15	0.58	2.258	0.192	7.562*	0.786	1.505	0.447

200 Ky Intervals

Measure	Stat	All Taxa	Artiodactyla	Carnivora	Cetacea	Perissodactyla	Primates	Hominins	Individualized Hominins
Mean	ce	1.691	- 0.344	0.287	- 0.483	0.549	3.793	- 5.03	- 1.297
	se	- 1.448	- 1.966	- 1.422	- 1.824	- 1.856	- 5.257	- 3.975	- 1.318
	t	1.167	- 0.175	0.202	- 0.265	0.296	0.722	- 1.265	- 0.984
	p	0.248	0.867	0.842	0.798	0.78	0.503	0.228	0.328
SD	ce	- 0.016	3.574	0.179	0.56	2.456	- 2.733	0.077	0.034
	se	- 0.737	- 1.95	- 0.956	- 1.457	- 1.082	- 2.707	- 1.1	- 0.583
	t	- 0.021	1.832	0.188	0.385	2.27	- 1.01	0.07	0.059
	p	0.984	0.117	0.853	0.711	0.073	0.359	0.946	0.954
Slope	ce	- 1.935	- 4.671	- 5.036	5.456	- 3.143	- 9.376	2.619	- 0.943
	se	- 3.358	- 5.759	- 3.89	- 6.768	- 10.655	- 15.038	- 2.356	- 1.075
	t	- 0.576	- 0.811	- 1.295	0.806	- 0.295	- 0.623	1.112	- 0.877
	p	0.567	0.449	0.204	0.444	0.78	0.561	0.287	0.383
(Intercept)	ce	0.048	- 0.249	- 0.066	- 0.201	- 0.07	- 0.51	- 0.182	- 0.023
	se	- 0.161	- 0.344	- 0.185	- 0.327	- 0.383	- 0.754	- 0.165	- 0.028
	t	0.298	- 0.725	- 0.359	- 0.614	- 0.182	- 0.677	- 1.101	- 0.8
	p	0.767	0.496	0.722	0.557	0.863	0.529	0.291	0.427
Observations		68	10	42	12	9	9	17	94
R²		0.033	0.445	0.048	0.151	0.676	0.306	0.166	0.023
Adjusted R²		0.012	0.168	- 0.027	- 0.167	0.481	- 0.11	- 0.026	- 0.009
Residual Std. Error		1.309	0.991	1.16	1.033	0.829	2.246	0.506	0.261
F Statistic		0.73	1.605	0.645	0.474	3.473	0.736	0.864	0.709

Note: *p<0.05 **p<0.01 ***p<0.001

Table A.2. Results of multiple regression analyses in which fossil cranial capacity (CC) was the response variable and climatic measures (mean, SD, and slope of the $\partial^{18}O$ curve) were the predictor variables. Analyses were first conducted with all taxa grouped

695   together, and then divided into respective taxa. Hominins were also subdivided into individuals ("Individualized hominins").
        Highlighted p values are significant at <0.05. This time-series data was first analyzed raw (A) and then detrended (B).

Taxon	Species	MYA	CC	Fossil
Hominins	Australopithecus afarensis	3.2	445.8	Yes
Hominins	Australopithecus africanus	2.8	458.25	Yes
Hominins	Australopithecus garhi	2.5	450	Yes
Hominins	Homo erectus	1.66	1004.15597	Yes
Hominins	Homo ergaster	1.78	892.2328333	Yes
Hominins	Homo georgicus	1.77	675	Yes
Hominins	Homo habilis	1.89	574.6819	Yes
Hominins	Homo heidelbergensis	0.8	1268	Yes
Hominins	Homo neanderthalensis	0.229	1403.921593	Yes
Hominins	Homo rudolfensis	1.88	727	Yes
Hominins	Homo sapiens	0.195	1485.833328	Yes
Hominins	Ardipithecus ramidus	4.4	300	Yes
Hominins	Paranthropus aethiopicus	2.5	410	Yes
Hominins	Paranthropus boisei	1.85	508.33	Yes
Hominins	Parathropus robustus	1.5	493.33	Yes
Hominins	Homo floresiensis	0.018	417	Yes
Hominins	Homo antecessor	0.565	1223	Yes
Hominins	Kenyanthropus platyops	3.5	425	Yes
Hominins	Australopithecus sediba	1.977	420	Yes
Artiodactyla	Samotherium	13.7	420	Yes
Artiodactyla	Dicrocerus	16	150	Yes
Artiodactyla	Aletomeryx	16.3	45	Yes
Artiodactyla	Procamelus	16.3	380	Yes
Artiodactyla	Dremotherium	19.9902	53	Yes
Artiodactyla	Promerycochoerus	19.9902	160	Yes
Artiodactyla	Protolabis	20.5975	140	Yes
Artiodactyla	Leptauchaenia	27.99	20	Yes
Artiodactyla	Miniochoerus	27.99	30	Yes
Artiodactyla	Eporeodon_majori	30.797	77	Yes
Artiodactyla	Eporeodon_socialis	30.797	46	Yes
Artiodactyla	Leptomeryx	33.9	22	Yes
Artiodactyla	Archaeotherium	33.9	190	Yes
Artiodactyla	Cainotherium	33.9	5.2	Yes
Artiodactyla	Bathygenys	33.9	14	Yes
Artiodactyla	Merycoidodon	33.9	55	Yes
Artiodactyla	Hypertragulus	37.986	8.5	Yes
Artiodactyla	Agriochoerus	41.9743	76	Yes
Artiodactyla	Protoreodon	41.9743	24	Yes
Artiodactyla	Homacodon	46.1707	9.5	Yes
Carnivora	Smilodon_californicus	1.8	385.61	Yes
Carnivora	Smilodon_fatalis	1.8	345.91	Yes

Carnivora	Smilodon_gracilis	1.8	184.88	Yes
Carnivora	Panthera_atrox	3	459.87	Yes
Carnivora	Panthera_augusta	3	272.66	Yes
Carnivora	Panthera_pardus	3	125.21	Yes
Carnivora	Lynx_issiodorensis	3.5	96.18	Yes
Carnivora	Lynx_shansius	3.5	68.32	Yes
Carnivora	Nyctereutes_donnezani	4	53.45	Yes
Carnivora	Ursus_deningeri	5	378	Yes
Carnivora	Ursus_spelaeus	5	652.59	Yes
Carnivora	Dinofelis_pivateau	5.3	153.68	Yes
Carnivora	Arctodus_simus	6	683.11	Yes
Carnivora	Tremarctos_floridanus	6	314.65	Yes
Carnivora	Canis_armbrusteri	6.4987	153.43	Yes
Carnivora	Canis_dirus	6.4987	177.66	Yes
Carnivora	Canis_edwardii	6.4987	75.38	Yes
Carnivora	Lutra_palaeindica	6.997	38.87	Yes
Carnivora	Hyaenictitherium__hyaenoid	6.997	90.99	Yes
Carnivora	Hyaenictitherium__wongi	6.997	77.43	Yes
Carnivora	Adcrocuta_eximia	8.6876	178.25	Yes
Carnivora	Thalassictis_hipparionum	8.6876	77.63	Yes
Carnivora	Promeles_palaeattica	8.999	24.07	Yes
Carnivora	Indarctos_oregonensis	8.999	646.5	Yes
Carnivora	Lycyaena_chaeretis	9.695	152.82	Yes
Carnivora	Crocuta_sivalensis	9.9894	186.18	Yes
Carnivora	Pliotaxidea_nevadensis	10.2903	22.46	Yes
Carnivora	Eucyon_davisi	10.2903	55.68	Yes
Carnivora	Promephitis_hootoni	11.599	11.87	Yes
Carnivora	Promephitis_majori	11.599	6.64	Yes
Carnivora	Promephitis_parvus	11.599	4.68	Yes
Carnivora	Sinictis_dolichognathus	11.599	19.68	Yes
Carnivora	Machairodus_palanderi	11.599	291.04	Yes
Carnivora	Palinhyaena_reperta	11.599	74.69	Yes
Carnivora	Tungurictis_spocki	11.599	19.37	Yes
Carnivora	Ictitherium__viverrinum	12.7	61.31	Yes
Carnivora	Martinogale_chisoensis	13.6	4.01	Yes
Carnivora	Martinogale_faulli	13.6	2.15	Yes
Carnivora	Borophagus_littoralis	13.6	127.02	Yes
Carnivora	Borophagus_secundus	13.6	119.17	Yes
Carnivora	Barbourofelis_loveorum	13.6	162.88	Yes
Carnivora	Barbourofelis_morrisi	13.6	121.65	Yes
Carnivora	Nimravides_galiani	13.6	217.29	Yes
Carnivora	Homotherium_hadarensis	13.7	211.51	Yes

Carnivora	Homotherium_serus	13.7	332.29	Yes
Carnivora	Herpestes_lemanensis	15	24.79	Yes
Carnivora	Plesiogulo_crassa	16	65.89	Yes
Carnivora	Ischyrocyon_gidleyi	16.3	311.41	Yes
Carnivora	Parataxidea_crassa	16.3	41.79	Yes
Carnivora	Pekania_palaeosinensis	16.3	24.23	Yes
Carnivora	Carpocyon_compressus	16.3	71.62	Yes
Carnivora	Carpocyon_webbi	16.3	100.8	Yes
Carnivora	Paratomarctus_euthos	16.3	62.83	Yes
Carnivora	Paratomarctus__temerarius	16.3	53.99	Yes
Carnivora	Potamotherium_valletoni	16.8876	45.68	Yes
Carnivora	Catopuma_temninckii	16.8876	68.03	Yes
Carnivora	Profelis_aurata	16.8876	57.97	Yes
Carnivora	Pseudaelurus_validus	16.8876	71.79	Yes
Carnivora	Kinometaxia_guangpui	17.9235	15.1	Yes
Carnivora	Amphicyon_galushai	19.9902	253.42	Yes
Carnivora	Amphicyon_ingens	19.9902	257.94	Yes
Carnivora	Amphicyon_longiramus	19.9902	270.3	Yes
Carnivora	Protomarctus_optatus	20.3853	54.78	Yes
Carnivora	Tomarctus_brevirostris	20.3853	51.3	Yes
Carnivora	Tomarctus_hippophaga	20.3853	68.05	Yes
Carnivora	Pliocyon_medius	20.5975	222.22	Yes
Carnivora	Leptarctus_primus	20.5975	12.79	Yes
Carnivora	Plionictis_parviloba	20.5975	11.37	Yes
Carnivora	Aelurodon__asthenostylus	20.5975	92.31	Yes
Carnivora	Aelurodon_ferox	20.5975	134.03	Yes
Carnivora	Aelurodon_mcgrewi	20.5975	62.59	Yes
Carnivora	Aelurodon_taxoides	20.5975	148.65	Yes
Carnivora	Epicyon_haydeni	20.5975	131.27	Yes
Carnivora	Epicyon_saevus	20.5975	104.11	Yes
Carnivora	Microtomarctus__conferta	20.5975	34.93	Yes
Carnivora	Paracynarctus_sinclairi	20.5975	59.59	Yes
Carnivora	Herpestides_antiquus	22.3518	26.37	Yes
Carnivora	Bathygale_lemanensis	22.7983	10.98	Yes
Carnivora	Paragale_huerzeleri	22.7983	18.45	Yes
Carnivora	Cynelos__rugosidens	22.9971	115	Yes
Carnivora	Daphoenodon_superbus	22.9971	133	Yes
Carnivora	Promartes_darbyi	22.9971	14.54	Yes
Carnivora	Enhydritherium__terraenovae	23.6983	119.07	Yes
Carnivora	Adilophontes_brachykolos	24.7972	95.33	Yes
Carnivora	Zodiolestes__daimonelixensi	24.7972	31.99	Yes
Carnivora	Desmocyon_matthewi	24.7972	38.62	Yes

Carnivora	Desmocyon_thompsoni	24.7972	36.76	Yes
Carnivora	Leptocyon_gregorii	24.7972	15.27	Yes
Carnivora	Leptocyon_vafer	24.7972	24.21	Yes
Carnivora	Pseudobassaris_riggsi	27.99	10.4	Yes
Carnivora	Pseudocyonopsis__ambiguus	28.3995	68	Yes
Carnivora	Otocolobus_manul	28.3995	34.47	Yes
Carnivora	Paraenhydrodon_josephi	29.9994	40.04	Yes
Carnivora	Pachycynodon_tedfordi	30.797	39	Yes
Carnivora	Cormocyon_copei	30.797	26.4	Yes
Carnivora	Sunkahetanka__geringensis	30.797	54.69	Yes
Carnivora	Pogonodon_platycopis	30.797	112.53	Yes
Carnivora	Stenogale_julieni	32.9983	10.23	Yes
Carnivora	Paleoprionodon__lamandini	32.9983	8.92	Yes
Carnivora	Cynodesmus_thooides	33.297	37.42	Yes
Carnivora	Enhydrocyon_basilatus	33.297	73.68	Yes
Carnivora	Enhydrocyon__pahinsintewakṇ	33.297	54.12	Yes
Carnivora	Enhydrocyon__stenocephalus	33.297	69.11	Yes
Carnivora	Phlaocyon_leucosteus	33.297	18.97	Yes
Carnivora	Phlaocyon_multicuspus	33.297	23.86	Yes
Carnivora	Rhizocyon_oregonensis	33.297	17.27	Yes
Carnivora	Nimravus_brachyops	33.297	96.1	Yes
Carnivora	Paradaphoenus_cuspigerus	33.9	21.52	Yes
Carnivora	Plesictis_palustris	33.9	8.04	Yes
Carnivora	Amphicticeps__shackelfordi	33.9	15.11	Yes
Carnivora	Cephalogale_ursinus	33.9	184.11	Yes
Carnivora	Mesocyon_brachyops	33.9	39.35	Yes
Carnivora	Mesocyon__coryphaeus	33.9	48.17	Yes
Carnivora	Osbornodon_fricki	33.9	101.22	Yes
Carnivora	Osbornodon_iamonensis	33.9	63.36	Yes
Carnivora	Otarocyon_cooki	33.9	11.04	Yes
Carnivora	Otarocyon_macdonaldi	33.9	7.87	Yes
Carnivora	Eusmilus_bidentatus	37.1961	42	Yes
Carnivora	Dinictis_cyclops	37.986	63.49	Yes
Carnivora	Dinictis_felina	37.986	70.44	Yes
Carnivora	Hoplophoneus__occidentalis	37.986	150.3	Yes
Carnivora	Hoplophoneus_primaevus	37.986	62.71	Yes
Carnivora	Hoplophoneus_primaevus_I	37.986	65	Yes
Carnivora	Hoplophoneus_primaevus_II	37.986	50	Yes
Carnivora	Hoplophoneus_sicarius	37.986	99.83	Yes
Carnivora	Daphoenus_hartshornianus	41.9743	49.64	Yes
Carnivora	Daphoenus_vetus	41.9743	63.38	Yes
Carnivora	Hesperocyon__gregarious	46.1707	14.88	Yes

Carnivora	Miacis_cognitus	55.3969	11.98	Yes
Cetacea	new_species	16	2348.4	Yes
Cetacea	incertae_sedis_1	16.99	302.4	Yes
Cetacea	Orycterocetus__crocodilinus	20.3853	2188.9	Yes
Cetacea	Pomatodelphis_sp	20.3853	365.3	Yes
Cetacea	indet	20.5975	486.5	Yes
Cetacea	Eurhinodelphis_bossi	22.9971	770.82	Yes
Cetacea	Eurhinodelphis_cristatus	22.9971	792.66	Yes
Cetacea	Eurhinodelphis_indet	22.9971	518.79	Yes
Cetacea	Kentriodon_pernix	22.9971	362.35	Yes
Cetacea	Allodelphis_pratti	22.9971	854.8	Yes
Cetacea	Squaloziphius_emlongi	22.9971	706.9	Yes
Cetacea	new_species	26.996	425.5	Yes
Cetacea	incertae_sedis_2	26.996	507.5	Yes
Cetacea	incertae_sedis_3	26.996	256.7	Yes
Cetacea	new_species	27.99	857.1	Yes
Cetacea	Schizodelphis__longirostris	28.3995	442.81	Yes
Cetacea	Simocetus_rayi	33.9	530.6	Yes
Cetacea	Squalodon_calvertensis	33.9	623.91	Yes
Cetacea	Xenorophus_sp.	33.9	861.4	Yes
Cetacea	Saghacetus_osiris	37.1961	388	Yes
Cetacea	new_species	37.986	323	Yes
Cetacea	Basilosaurus_cetoides	40.36	1271.4	Yes
Cetacea	Dorudon_atrox	40.36	1185.4	Yes
Cetacea	Zygorhiza_kochii	40.36	800.8	Yes
Cetacea	Rodhocetus_kasrani	48.576	291	Yes
Cetacea	Dalanistes_ahmedi	48.576	400	Yes
Perissodactyl	Neohipparion	4.9	160	Yes
Perissodactyl	Pliohippus	13.6	270	Yes
Perissodactyl	Merychippus	16.3	270	Yes
Perissodactyl	Teleoceras	16.8876	1500	Yes
Perissodactyl	Subhyracodon	33.9	280	Yes
Perissodactyl	Mesohippus	37.986	85	Yes
Perissodactyl	Amynodon	41.9743	190	Yes
Perissodactyl	Hyracodon	41.9743	160	Yes
Perissodactyl	Hyrachus	46.1707	103	Yes
Perissodactyl	Mesatirhinus	46.1707	185	Yes
Perissodactyl	Palaeosyops	46.1707	200	Yes
Perissodactyl	Heptodon	50.2487	50	Yes
Perissodactyl	Hyracotherium	50.2487	25	Yes
Perissodactyl	Colonoceras	55	71	Yes
Primates	Oreopithecus	13.7	402	Yes

Primates	Chilecebus	20.9721	7.46	Yes
Primates	Proconsul	28.3995	167	Yes
Primates	Aegyptopithecus	33.9	21	Yes
Primates	Parapithecus_grangeri	33.9	14	Yes
Primates	Catopithecus	37.1961	3.1	Yes
Primates	Adapis_parisiensis	40.36	8.8	Yes
Primates	Adapis_parisiensis_2	40.36	8.8	Yes
Primates	Leptadapis_magnus	40.36	21.7	Yes
Primates	Necolemur_antiquus	40.36	3.8	Yes
Primates	Rooneyia_viejaensis	41.9743	7.4	Yes
Primates	Pronycticebus_gaudryi	44.8559	4.8	Yes
Primates	Smilodectes_gracilis	50.2487	9.5	Yes
Primates	Notharctus_tenebrosus	55.3969	9.5	Yes
Primates	Tetonius_homunculus	55.3969	1.5	Yes
Primates	Plesiadapis	60.19	18	Yes
Primates	Plesiadapis_cookei	60.19	5	Yes
Primates	Plesiadapis_tricuspidens	60.19	16.6	Yes
Primates	Ignacius_graybullianus	63.2832	2.14	Yes
Artiodactyla	Hylochoerus_meinertzhageni	NA	140	No
Artiodactyla	Potamochoerus_porcus	NA	138	No
Artiodactyla	Sus_scrofa	NA	180.4	No
Artiodactyla	Cervus_elaphus	NA	311.1	No
Artiodactyla	Cervus_nippon	NA	201	No
Artiodactyla	Camelus_bactrianus	NA	576	No
Artiodactyla	Phacochoerus_africanus	NA	131.7	No
Artiodactyla	Mazama_americana	NA	56	No
Artiodactyla	Odocoileus_virginianus	NA	143.8	No
Artiodactyla	Dama_dama	NA	215	No
Artiodactyla	Babyrousa_babyrussa	NA	127	No
Artiodactyla	Alces_alces	NA	435	No
Artiodactyla	Capreolus_capreolus	NA	100.2	No
Artiodactyla	Rangifer_tarandus	NA	270.4	No
Artiodactyla	Lama_glama	NA	232	No
Artiodactyla	Lama_pacos	NA	178	No
Artiodactyla	Antilope_cervicapra	NA	165	No
Artiodactyla	Muntiacus_muntjak	NA	122	No
Artiodactyla	Giraffa_camelopardalis	NA	703.9	No
Artiodactyla	Okapia_johnstoni	NA	501	No
Artiodactyla	Hydropotes_inermis	NA	53	No
Artiodactyla	Tragulus_javanicus	NA	14.55	No
Artiodactyla	Tragulus_napu	NA	17.6	No
Artiodactyla	Tayassu_pecari	NA	105.1	No

Artiodactyla	Hyemoschus_aquaticus	NA	24.95	No
Carnivora	Leopardus_pardalis	NA	63.43	No
Carnivora	Oncifelis_geoffroyi	NA	34	No
Carnivora	Proteles_cristatus	NA	35.16	No
Carnivora	Alopex_lagopus	NA	35.52	No
Carnivora	Felis_chaus	NA	39.25	No
Carnivora	Felis_nigripes	NA	20.09	No
Carnivora	Felis_silvestris	NA	37.34	No
Carnivora	Atelocynus_microtis	NA	62.18	No
Carnivora	Chrysocyon_brachyurus	NA	120.3	No
Carnivora	Lycaon_pictus	NA	129	No
Carnivora	Pseudalopex_culpaeus	NA	51.5	No
Carnivora	Pseudalopex_gymnocercus	NA	40	No
Carnivora	Speothos_venaticus	NA	40.45	No
Carnivora	Panthera_leo	NA	223.63	No
Carnivora	Panthera_onca	NA	151.41	No
Carnivora	Panthera_tigris	NA	278.66	No
Carnivora	Puma_concolor	NA	125.21	No
Carnivora	Lynx_lynx	NA	70.11	No
Carnivora	Lynx_rufus	NA	57.97	No
Carnivora	Neofelis_nebulosa	NA	68.71	No
Carnivora	Nyctereutes_procyonoides	NA	28.5	No
Carnivora	Acinonyx_jubatus	NA	111.05	No
Carnivora	Caracal_caracal	NA	55.15	No
Carnivora	Leptailurus_serval	NA	56.8	No
Carnivora	Conepatus_chinga	NA	14.78	No
Carnivora	Conepatus_humboldtii	NA	12.57	No
Carnivora	Conepatus_leuconotus	NA	14.44	No
Carnivora	Conepatus_mesoleucus	NA	15.5	No
Carnivora	Conepatus_semistriatus	NA	18.92	No
Carnivora	Mephitis_macroura	NA	10.07	No
Carnivora	Mephitis_mephitis	NA	10.28	No
Carnivora	Spilogale_putorius	NA	5	No
Carnivora	Cerdocyon_thous	NA	41.8	No
Carnivora	Herpailurus_yaguarondi	NA	40.04	No
Carnivora	Uncia_uncia	NA	101.49	No
Carnivora	Helarctos_malayanus	NA	345.25	No
Carnivora	Melursus_ursinus	NA	304.9	No
Carnivora	Ursus_americanus	NA	259.82	No
Carnivora	Ursus_arctos	NA	338.3	No
Carnivora	Ursus_maritimus	NA	459.44	No
Carnivora	Ursus_thibetanus	NA	314.19	No

Carnivora	Urocyon_cinereoargenteus	NA	40.85	No
Carnivora	Urocyon_littoralis	NA	27.66	No
Carnivora	Hyaena_hyaena	NA	97.51	No
Carnivora	Parahyaena_brunnea	NA	106.7	No
Carnivora	Mellivora_capensis	NA	72.97	No
Carnivora	Tremarctos_ornatus	NA	195.27	No
Carnivora	Otocyon_megalotis	NA	26.84	No
Carnivora	Canis_adustus	NA	51.94	No
Carnivora	Canis_aureus	NA	72.24	No
Carnivora	Canis_latrans	NA	88.23	No
Carnivora	Canis_lupus	NA	131.6	No
Carnivora	Canis_mesomelas	NA	51.42	No
Carnivora	Canis_simensis	NA	80.67	No
Carnivora	Cuon_alpinus	NA	95	No
Carnivora	Amblonyx_cinereus	NA	38.08	No
Carnivora	Aonyx_capensis	NA	94.63	No
Carnivora	Enhydra_lutris	NA	125.21	No
Carnivora	Lontra_canadensis	NA	52.98	No
Carnivora	Lontra_felina	NA	38.86	No
Carnivora	Lutra_lutra	NA	42.1	No
Carnivora	Lutra_maculicollis	NA	40.04	No
Carnivora	Lutrogale_perspicillata	NA	64.72	No
Carnivora	Pteronura_brasiliensis	NA	85.63	No
Carnivora	Arctonyx_collaris	NA	49.4	No
Carnivora	Galictis_cuja	NA	15.03	No
Carnivora	Galictis_vittata	NA	24.3	No
Carnivora	Ictonyx_libyca	NA	4.48	No
Carnivora	Ictonyx_striatus	NA	9.78	No
Carnivora	Meles_meles	NA	50.4	No
Carnivora	Melogale_moschata	NA	15.07	No
Carnivora	Melogale_personata	NA	13.83	No
Carnivora	Poecilogale_albinucha	NA	4.76	No
Carnivora	Vormela_peregusna	NA	4.76	No
Carnivora	Crocuta_crocuta	NA	144.03	No
Carnivora	Nasua_narica	NA	29.96	No
Carnivora	Procyon_cancrivorus	NA	59.45	No
Carnivora	Procyon_lotor	NA	40.04	No
Carnivora	Vulpes_bengalensis	NA	25.8	No
Carnivora	Vulpes_chama	NA	33.5	No
Carnivora	Vulpes_pallida	NA	25.03	No
Carnivora	Vulpes_rueppellii	NA	24.29	No
Carnivora	Vulpes_velox	NA	32.14	No

Carnivora	Vulpes_vulpes	NA	43.38	No
Carnivora	Vulpes_zerda	NA	17.29	No
Carnivora	Arctictis_binturong	NA	40.85	No
Carnivora	Arctogalidia_trivirgata	NA	21.98	No
Carnivora	Cynogale_bennettii	NA	29.96	No
Carnivora	Hemigalus_derbyanus	NA	18.92	No
Carnivora	Paguma_larvata	NA	30.88	No
Carnivora	Paradoxurus_hermaphroditus	NA	18.5	No
Carnivora	Paradoxurus_zeylonensis	NA	17.81	No
Carnivora	Ailuropoda_melanoleuca	NA	235.1	No
Carnivora	Eupleres_goudotii	NA	16.95	No
Carnivora	Galidia_elegans	NA	10.7	No
Carnivora	Salanoia_concolor	NA	11.02	No
Carnivora	Herpestes_edwardsii	NA	10.49	No
Carnivora	Herpestes_ichneumon	NA	23.34	No
Carnivora	Herpestes_javanicus	NA	7.24	No
Carnivora	Herpestes_smithii	NA	13.74	No
Carnivora	Herpestes_urva	NA	20.91	No
Carnivora	Herpestes_vitticollis	NA	25.79	No
Carnivora	Genetta_angolensis	NA	15.49	No
Carnivora	Genetta_genetta	NA	14.01	No
Carnivora	Genetta_servalina	NA	15.03	No
Carnivora	Genetta_tigrina	NA	15.18	No
Carnivora	Eira_barbara	NA	35.87	No
Carnivora	Gulo_gulo	NA	78.26	No
Carnivora	Martes_americana	NA	15.8	No
Carnivora	Martes_flavigula	NA	34.12	No
Carnivora	Martes_foina	NA	20.91	No
Carnivora	Martes_martes	NA	20	No
Carnivora	Martes_pennanti	NA	31.82	No
Carnivora	Martes_zibellina	NA	18.5	No
Carnivora	Mustela_altaica	NA	4.5	No
Carnivora	Mustela_erminea	NA	4	No
Carnivora	Mustela_frenata	NA	4.01	No
Carnivora	Mustela_kathiah	NA	4.41	No
Carnivora	Mustela_lutreola	NA	8.5	No
Carnivora	Mustela_nigripes	NA	1.99	No
Carnivora	Mustela_nivalis	NA	1.82	No
Carnivora	Mustela_putorius	NA	8.3	No
Carnivora	Mustela_sibirica	NA	6.75	No
Carnivora	Mustela_vison	NA	8.82	No
Carnivora	Bassaricyon_alleni	NA	18.48	No

Carnivora	Bassariscus_astutus	NA	16.44	No
Carnivora	Bassariscus_sumichrasti	NA	19.3	No
Carnivora	Potos_flavus	NA	25.53	No
Carnivora	Ailurus_fulgens	NA	40.85	No
Carnivora	Prionailurus_bengalensis	NA	29.37	No
Carnivora	Prionailurus_rubiginosus	NA	18.92	No
Carnivora	Prionailurus_viverrinus	NA	46.53	No
Carnivora	Bdeogale_crassicauda	NA	16.95	No
Carnivora	Crossarchus_obscurus	NA	9.78	No
Carnivora	Helogale_parvula	NA	4.76	No
Carnivora	Cynictis_penicillata	NA	10.49	No
Carnivora	Galerella_pulverulenta	NA	11.02	No
Carnivora	Galerella_sanguinea	NA	8.76	No
Carnivora	Ichneumia_albicauda	NA	24.29	No
Carnivora	Paracynictis_selousi	NA	15.8	No
Carnivora	Rhynchogale_melleri	NA	16.95	No
Carnivora	Atilax_paludinosus	NA	28.5	No
Carnivora	Herpestes_naso	NA	25.53	No
Carnivora	Mungos_mungo	NA	10.49	No
Carnivora	Suricata_suricatta	NA	10.28	No
Carnivora	Cryptoprocta_ferox	NA	32.14	No
Carnivora	Fossa_fossana	NA	19.69	No
Carnivora	Mydaus_javanensis	NA	19.49	No
Carnivora	Taxidea_taxus	NA	48.91	No
Carnivora	Civettictis_civetta	NA	36.97	No
Carnivora	Viverra_megaspila	NA	36.6	No
Carnivora	Viverra_tangalunga	NA	24.05	No
Carnivora	Viverra_zibetha	NA	36.97	No
Carnivora	Viverricula_indica	NA	16.78	No
Carnivora	Nandinia_binotata	NA	17.29	No
Carnivora	Prionodon_linsang	NA	8.5	No
Carnivora	Prionodon_pardicolor	NA	9.03	No
Cetacea	Inia_geoffrensis	NA	627.8	No
Cetacea	Lipotes_vexillifer	NA	510	No
Cetacea	Globicephala_macrorhynchus	NA	4165.9	No
Cetacea	Globicephala_melas	NA	2861.7	No
Cetacea	Delphinus_delphis	NA	814.3	No
Cetacea	Tursiops_truncatus	NA	1759.2	No
Cetacea	Lagenorhynchus_obliquidens	NA	1045	No
Cetacea	Lagenorhynchus_obscurus	NA	886.1	No
Cetacea	Sotalia_fluviatilis	NA	688	No
Cetacea	Cephalorhynchus_heavisidii	NA	763	No

Cetacea	Pseudorca_crassidens	NA	3512	No
Cetacea	Stenella_clymene	NA	666	No
Cetacea	Stenella_coeruleoalba	NA	938.5	No
Cetacea	Stenella_longirostris	NA	660	No
Cetacea	Grampus_griseus	NA	2384.4	No
Cetacea	Pontoporia_blainvillei	NA	219.6	No
Cetacea	Delphinapterus_leucas	NA	2083	No
Cetacea	Monodon_monoceros	NA	2993.7	No
Cetacea	Steno_bredanensis	NA	1541.9	No
Cetacea	Phocoena_phocoena	NA	522.7	No
Cetacea	Phocoena_spinipinnis	NA	597	No
Cetacea	Phocoenoides_dalli	NA	861.4	No
Cetacea	Lagenorhynchus_acutus	NA	1100.5	No
Cetacea	Orcinus_orca	NA	5028	No
Cetacea	Kogia_breviceps	NA	1011.5	No
Cetacea	Kogia_simus	NA	621.5	No
Cetacea	Ziphius_cavirostris	NA	2004	No
Cetacea	Platanista_gangetica	NA	298.9	No
Cetacea	Physeter_catodon	NA	7999.4	No
Cetacea	Mesoplodon_densirostris	NA	1457	No
Cetacea	Mesoplodon_europaeus	NA	2146.7	No
Cetacea	Mesoplodon_mirus	NA	2354.7	No
Perissodactyl	Equus_asinus	NA	391.02	No
Perissodactyl	Equus_caballus	NA	588.06	No
Perissodactyl	Equus_burchellii	NA	561.05	No
Perissodactyl	Equus_zebra	NA	607.3	No
Perissodactyl	Ceratotherium_simum	NA	641.21	No
Perissodactyl	Diceros_bicornis	NA	612.35	No
Perissodactyl	Rhinoceros_unicornis	NA	786	No
Perissodactyl	Tapirus_indicus	NA	265	No
Perissodactyl	Tapirus_terrestris	NA	180.51	No
Primates	Homo_sapiens	NA	1250.43	No
Primates	Ateles_paniscus	NA	108.96	No
Primates	Cebus_albifrons	NA	62.95	No
Primates	Macaca_nigra	NA	97.5	No
Primates	Macaca_nemestrina	NA	110	No
Primates	Cebus_capucinus	NA	70.14	No
Primates	Macaca_assamensis	NA	90.5	No
Primates	Cebus_apella	NA	71.3	No
Primates	Cebus_olivaceus	NA	72.5	No
Primates	Lagothrix_lagotricha	NA	89.35	No
Primates	Macaca_sinica	NA	58.15	No

Primates	Theropithecus_gelada	NA	130	No
Primates	Cercocebus_agilis	NA	95.3	No
Primates	Mandrillus_sphinx	NA	159.2	No
Primates	Ateles_geoffroyi	NA	104.96	No
Primates	Lophocebus_albigena	NA	96.8	No
Primates	Pan_paniscus	NA	329.7	No
Primates	Cercopithecus_cephus	NA	76	No
Primates	Macaca_mulatta	NA	87.99	No
Primates	Semnopithecus_entellus	NA	111.5	No
Primates	Cercopithecus_mona	NA	67	No
Primates	Macaca_fascicularis	NA	66.93	No
Primates	Hylobates_lar	NA	93.99	No
Primates	Hylobates_muelleri	NA	95.31	No
Primates	Saimiri_sciureus	NA	23.35	No
Primates	Papio_hamadryas	NA	142	No
Primates	Hylobates_agilis	NA	88.1	No
Primates	Pongo_pygmaeus	NA	341.99	No
Primates	Chlorocebus_aethiops	NA	64.13	No
Primates	Saimiri_oerstedii	NA	22.45	No
Primates	Ateles_fusciceps	NA	113.6	No
Primates	Aotus_lemurinus	NA	113.5	No
Primates	Pan_troglodytes	NA	354.81	No
Primates	Erythrocebus_patas	NA	100.2	No
Primates	Hylobates_syndactylus	NA	134.8	No
Primates	Macaca_maura	NA	94.48	No
Primates	Macaca_arctoides	NA	100.7	No
Primates	Saimiri_boliviensis	NA	24.06	No
Primates	Pithecia_monachus	NA	35	No
Primates	Gorilla_gorilla	NA	454.55	No
Primates	Trachypithecus_francoisi	NA	94.4	No
Primates	Cercopithecus_mitis	NA	75	No
Primates	Eulemur_rubriventer	NA	24.9	No
Primates	Alouatta_seniculus	NA	45.5	No
Primates	Daubentonia_madagascariens	NA	45.15	No
Primates	Procolobus_badius	NA	78	No
Primates	Pygathrix_nemaeus	NA	77	No
Primates	Colobus_guereza	NA	83.9	No
Primates	Macaca_sylvanus	NA	87.7	No
Primates	Callicebus_moloch	NA	19	No
Primates	Aotus_trivirgatus	NA	16.04	No
Primates	Leontopithecus_rosalia	NA	13.05	No
Primates	Alouatta_caraya	NA	50.7	No

Primates	Colobus_angolensis	NA	74.4 No
Primates	Saguinus_oedipus	NA	9.64 No
Primates	Saguinus_geoffroyi	NA	14.27 No
Primates	Eulemur_mongoz	NA	24.03 No
Primates	Varecia_variegata	NA	31.2 No
Primates	Alouatta_palliata	NA	50.04 No
Primates	Nycticebus_coucang	NA	12.74 No
Primates	Callithrix_pygmaea	NA	4.64 No
Primates	Galagoides_demidoff	NA	3.38 No
Primates	Callithrix_jacchus	NA	7.73 No
Primates	Eulemur_macaco	NA	22.6 No
Primates	Lemur_catta	NA	21.63 No
Primates	Indri_indri	NA	38.3 No
Primates	Propithecus_verreauxi	NA	26.7 No
Primates	Perodicticus_potto	NA	12.07 No
Primates	Tarsius_bancanus	NA	2.7 No
Primates	Galago_senegalensis	NA	5.9 No
Primates	Nycticebus_pygmaeus	NA	7.8 No
Primates	Loris_tardigradus	NA	6 No
Primates	Cheirogaleus_major	NA	6.8 No
Primates	Microcebus_murinus	NA	1.84 No
Primates	Cheirogaleus_medius	NA	3.34 No
Primates	Avahi_laniger	NA	10.49 No

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Taxon	Species	MYA	CC	Fossil
Indiv_Hominins	Australopithecus afarensis	3	550	Yes
Indiv_Hominins	Australopithecus afarensis	3.15	400	Yes
Indiv_Hominins	Australopithecus afarensis	3.2	387	Yes
Indiv_Hominins	Australopithecus afarensis	3.2	400	Yes
Indiv_Hominins	Australopithecus afarensis	3.2	492	Yes
Indiv_Hominins	Australopithecus africanus	2.5	435	Yes
Indiv_Hominins	Australopithecus africanus	2.5	400	Yes
Indiv_Hominins	Australopithecus africanus	2.5	457	Yes
Indiv_Hominins	Australopithecus africanus	2.6	515	Yes
Indiv_Hominins	Australopithecus africanus	2.8	510	Yes
Indiv_Hominins	Australopithecus africanus	2.8	436	Yes
Indiv_Hominins	Australopithecus africanus	2.8	485	Yes
Indiv_Hominins	Australopithecus africanus	2.8	428	Yes
Indiv_Hominins	Australopithecus garhi	2.5	450	Yes
Indiv_Hominins	Homo erectus	0.236	1249.333	Yes
Indiv_Hominins	Homo erectus	0.4	911	Yes
Indiv_Hominins	Homo erectus	0.412	1012.5	Yes
Indiv_Hominins	Homo erectus	0.412	1121.429	Yes
Indiv_Hominins	Homo erectus	0.412	1109	Yes
Indiv_Hominins	Homo erectus	0.412	1266.167	Yes
Indiv_Hominins	Homo erectus	0.412	1115.714	Yes
Indiv_Hominins	Homo erectus	0.412	1135	Yes
Indiv_Hominins	Homo erectus	0.412	1090	Yes
Indiv_Hominins	Homo erectus	0.412	1000	Yes
Indiv_Hominins	Homo erectus	0.412	1056.333	Yes
Indiv_Hominins	Homo erectus	0.412	1006	Yes
Indiv_Hominins	Homo erectus	0.54	1000	Yes
Indiv_Hominins	Homo erectus	0.55	900	Yes
Indiv_Hominins	Homo erectus	0.581	1100	Yes
Indiv_Hominins	Homo erectus	0.59	1030	Yes
Indiv_Hominins	Homo erectus	0.59	937.5	Yes
Indiv_Hominins	Homo erectus	0.59	1220	Yes
Indiv_Hominins	Homo erectus	0.59	850	Yes
Indiv_Hominins	Homo erectus	0.59	1225	Yes
Indiv_Hominins	Homo erectus	0.59	1015	Yes
Indiv_Hominins	Homo erectus	0.59	1030	Yes
Indiv_Hominins	Homo erectus	0.85	940	Yes
Indiv_Hominins	Homo erectus	1.15	779	Yes
Indiv_Hominins	Homo erectus	1.25	1020	Yes
Indiv_Hominins	Homo erectus	1.29	868.6	Yes
Indiv_Hominins	Homo erectus	1.3	800	Yes

Indiv_Hominins	Homo erectus	1.49	792.571	Yes
Indiv_Hominins	Homo erectus	1.49	900	Yes
Indiv_Hominins	Homo erectus	1.6	856	Yes
Indiv_Hominins	Homo erectus	1.6	850	Yes
Indiv_Hominins	Homo erectus	1.66	951	Yes
Indiv_Hominins	Homo erectus	1.66	1000	Yes
Indiv_Hominins	Homo ergaster	1.04	995	Yes
Indiv_Hominins	Homo ergaster	1.1	732.33	Yes
Indiv_Hominins	Homo ergaster	1.44	904.5	Yes
Indiv_Hominins	Homo ergaster	1.45	1070.5	Yes
Indiv_Hominins	Homo ergaster	1.575	825.667	Yes
Indiv_Hominins	Homo ergaster	1.78	825.4	Yes
Indiv_Hominins	Homo georgicus	1.77	775	Yes
Indiv_Hominins	Homo georgicus	1.77	650	Yes
Indiv_Hominins	Homo georgicus	1.77	600	Yes
Indiv_Hominins	Homo habilis	1.7	662.286	Yes
Indiv_Hominins	Homo habilis	1.74	639.2	Yes
Indiv_Hominins	Homo habilis	1.75	475	Yes
Indiv_Hominins	Homo habilis	1.75	507	Yes
Indiv_Hominins	Homo habilis	1.75	570	Yes
Indiv_Hominins	Homo habilis	1.78	674	Yes
Indiv_Hominins	Homo habilis	1.84	500	Yes
Indiv_Hominins	Homo habilis	1.85	616	Yes
Indiv_Hominins	Homo habilis	1.855	597	Yes
Indiv_Hominins	Homo habilis	1.89	506.333	Yes
Indiv_Hominins	Homo heidelbergensis	0.11	1250	Yes
Indiv_Hominins	Homo heidelbergensis	0.2	1400	Yes
Indiv_Hominins	Homo heidelbergensis	0.2	1316.667	Yes
Indiv_Hominins	Homo heidelbergensis	0.205	1160	Yes
Indiv_Hominins	Homo heidelbergensis	0.215	1334.571	Yes
Indiv_Hominins	Homo heidelbergensis	0.225	1111.192	Yes
Indiv_Hominins	Homo heidelbergensis	0.2255	1400	Yes
Indiv_Hominins	Homo heidelbergensis	0.25	1375	Yes
Indiv_Hominins	Homo heidelbergensis	0.255	1266.556	Yes
Indiv_Hominins	Homo heidelbergensis	0.259	1280	Yes
Indiv_Hominins	Homo heidelbergensis	0.3	1310	Yes
Indiv_Hominins	Homo heidelbergensis	0.35	1100	Yes
Indiv_Hominins	Homo heidelbergensis	0.399	1432	Yes
Indiv_Hominins	Homo heidelbergensis	0.4	1138.667	Yes
Indiv_Hominins	Homo heidelbergensis	0.4	1185	Yes
Indiv_Hominins	Homo heidelbergensis	0.4	1305	Yes
Indiv_Hominins	Homo heidelbergensis	0.6	1250	Yes

Indiv_Hominins	Homo heidelbergensis	0.8	1216.667	Yes
Indiv_Hominins	Homo antecessor	0.565	1390	Yes
Indiv_Hominins	Homo antecessor	0.565	1125	Yes
Indiv_Hominins	Homo antecessor	0.565	1153.333	Yes
Indiv_Hominins	Homo neanderthalensis	0.036	1457.5	Yes
Indiv_Hominins	Homo neanderthalensis	0.036	1487.4	Yes
Indiv_Hominins	Homo neanderthalensis	0.04	1486.2	Yes
Indiv_Hominins	Homo neanderthalensis	0.04	1337.75	Yes
Indiv_Hominins	Homo neanderthalensis	0.045	1650	Yes
Indiv_Hominins	Homo neanderthalensis	0.045	1550	Yes
Indiv_Hominins	Homo neanderthalensis	0.0455	1310	Yes
Indiv_Hominins	Homo neanderthalensis	0.0455	1345.25	Yes
Indiv_Hominins	Homo neanderthalensis	0.047	1400	Yes
Indiv_Hominins	Homo neanderthalensis	0.051	1626	Yes
Indiv_Hominins	Homo neanderthalensis	0.054	1226.75	Yes
Indiv_Hominins	Homo neanderthalensis	0.054	1551	Yes
Indiv_Hominins	Homo neanderthalensis	0.06	1362	Yes
Indiv_Hominins	Homo neanderthalensis	0.06	1581	Yes
Indiv_Hominins	Homo neanderthalensis	0.0625	1745	Yes
Indiv_Hominins	Homo neanderthalensis	0.071	1650.2	Yes
Indiv_Hominins	Homo neanderthalensis	0.107	1320	Yes
Indiv_Hominins	Homo neanderthalensis	0.122	1270.5	Yes
Indiv_Hominins	Homo neanderthalensis	0.125	1234.333	Yes
Indiv_Hominins	Homo neanderthalensis	0.125	1295	Yes
Indiv_Hominins	Homo neanderthalensis	0.13	1205	Yes
Indiv_Hominins	Homo neanderthalensis	0.13	1450	Yes
Indiv_Hominins	Homo neanderthalensis	0.13	1200	Yes
Indiv_Hominins	Homo neanderthalensis	0.13	1450	Yes
Indiv_Hominins	Homo neanderthalensis	0.143	1065	Yes
Indiv_Hominins	Homo neanderthalensis	0.219	1200	Yes
Indiv_Hominins	Homo neanderthalensis	0.23	1450	Yes
Indiv_Hominins	Homo rudolfensis	1.85	782.5	Yes
Indiv_Hominins	Homo rudolfensis	1.88	776	Yes
Indiv_Hominins	Homo rudolfensis	1.88	622.5	Yes
Indiv_Hominins	Homo sapiens	0.0102	1430	Yes
Indiv_Hominins	Homo sapiens	0.012	1555	Yes
Indiv_Hominins	Homo sapiens	0.012	1434	Yes
Indiv_Hominins	Homo sapiens	0.012	1700	Yes
Indiv_Hominins	Homo sapiens	0.012	1500	Yes
Indiv_Hominins	Homo sapiens	0.012	1370	Yes
Indiv_Hominins	Homo sapiens	0.012	1565	Yes
Indiv_Hominins	Homo sapiens	0.012	1569	Yes

Indiv_Hominins	Homo sapiens	0.012	1560	Yes
Indiv_Hominins	Homo sapiens	0.012	1484	Yes
Indiv_Hominins	Homo sapiens	0.015	1354	Yes
Indiv_Hominins	Homo sapiens	0.022	1500	Yes
Indiv_Hominins	Homo sapiens	0.022	1380	Yes
Indiv_Hominins	Homo sapiens	0.022	1290	Yes
Indiv_Hominins	Homo sapiens	0.024	1775	Yes
Indiv_Hominins	Homo sapiens	0.024	1375	Yes
Indiv_Hominins	Homo sapiens	0.024	1580	Yes
Indiv_Hominins	Homo sapiens	0.024	1464	Yes
Indiv_Hominins	Homo sapiens	0.0248	1880	Yes
Indiv_Hominins	Homo sapiens	0.026	1600	Yes
Indiv_Hominins	Homo sapiens	0.026	1500	Yes
Indiv_Hominins	Homo sapiens	0.026	1304	Yes
Indiv_Hominins	Homo sapiens	0.027	1600	Yes
Indiv_Hominins	Homo sapiens	0.027	1590	Yes
Indiv_Hominins	Homo sapiens	0.027	1538	Yes
Indiv_Hominins	Homo sapiens	0.027	1481	Yes
Indiv_Hominins	Homo sapiens	0.027	1378	Yes
Indiv_Hominins	Homo sapiens	0.027	1547	Yes
Indiv_Hominins	Homo sapiens	0.027	1322	Yes
Indiv_Hominins	Homo sapiens	0.0275	1522	Yes
Indiv_Hominins	Homo sapiens	0.0275	1452	Yes
Indiv_Hominins	Homo sapiens	0.0275	1608	Yes
Indiv_Hominins	Homo sapiens	0.0275	1518	Yes
Indiv_Hominins	Homo sapiens	0.0275	1555	Yes
Indiv_Hominins	Homo sapiens	0.0285	1620	Yes
Indiv_Hominins	Homo sapiens	0.0285	1500	Yes
Indiv_Hominins	Homo sapiens	0.037	1420	Yes
Indiv_Hominins	Homo sapiens	0.0385	1605	Yes
Indiv_Hominins	Homo sapiens	0.0455	1420	Yes
Indiv_Hominins	Homo sapiens	0.051	1570	Yes
Indiv_Hominins	Homo sapiens	0.087	1535	Yes
Indiv_Hominins	Homo sapiens	0.09	1280	Yes
Indiv_Hominins	Homo sapiens	0.09	1531	Yes
Indiv_Hominins	Homo sapiens	0.1	1235	Yes
Indiv_Hominins	Homo sapiens	0.11	1380	Yes
Indiv_Hominins	Homo sapiens	0.115	1480	Yes
Indiv_Hominins	Homo sapiens	0.115	1450	Yes
Indiv_Hominins	Homo sapiens	0.115	1300	Yes
Indiv_Hominins	Homo sapiens	0.115	1554.5	Yes
Indiv_Hominins	Homo sapiens	0.115	1499.5	Yes

Indiv_Hominins	Homo sapiens	0.115	1587.3	Yes
Indiv_Hominins	Homo sapiens	0.117	1550	Yes
Indiv_Hominins	Homo sapiens	0.16	1450	Yes
Indiv_Hominins	Homo sapiens	0.16	1305	Yes
Indiv_Hominins	Homo sapiens	0.16	1400	Yes
Indiv_Hominins	Homo sapiens	0.16	1283.5	Yes
Indiv_Hominins	Homo sapiens	0.1635	1510	Yes
Indiv_Hominins	Homo sapiens	0.195	1432.5	Yes
Indiv_Hominins	Ardipithecus ramidus	4.4	300	Yes
Indiv_Hominins	Paranthropus aethiopicus	2.5	410	Yes
Indiv_Hominins	Paranthropus boisei	1.5	500	Yes
Indiv_Hominins	Paranthropus boisei	1.85	510	Yes
Indiv_Hominins	Paranthropus boisei	1.7	500	Yes
Indiv_Hominins	Paranthropus boisei	1.7	475	Yes
Indiv_Hominins	Paranthropus boisei	1.4	545	Yes
Indiv_Hominins	Paranthropus boisei	1.8	520	Yes
Indiv_Hominins	Paranthropus robustus	1.5	500	Yes
Indiv_Hominins	Paranthropus robustus	1.5	450	Yes
Indiv_Hominins	Paranthropus robustus	1.5	530	Yes
Indiv_Hominins	Homo floresiensis	0.018	417	Yes
Indiv_Hominins	Kenyanthropus platyops	3.5	425	Yes
Indiv_Hominins	Australopithecus sediba	1.977	420	Yes

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