

An Analysis of Hominin Cranial Capacity Data Using Simulations

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Abstract

The hominin cranial capacity data was reanalyzed using simulations, which emulated the variability in the estimation of cranial capacity of hominin skulls. First, the data was explored using k-means clustering to establish the presence of two groups in the data. The groups were further confirmed by using Hamming distance on the simulated cluster outcomes. Then, the resulting two datasets arising from two groups were used to estimate the confidence limits for the parameter estimates of Henneberg's double exponential model. Through these parameter estimates and their confidence limits it could be seen that two models for two time spans identified by cluster analysis were better than a single model for the full span of time, which the previous authors considered to be the best option. From an analytical perspective, there are indications for a structural change in cranial capacity growth, which is expressed as a rapid increase after a slow growth period. This structural change scenario does not support the rejection of the concept of punctuated equilibrium on the basis of a gradual change based on the double exponential model.

Keywords: Hominin cranial capacity; K-means clustering; Hamming distance; Simulation; Nonlinear models

Introduction

The hominin cranial capacity has been much discussed in the scientific literature as showing a gradual trend over the later part of Pliocene and the Pleistocene [1-3]. Beals et al. [4] describes gradualism as “the chronological sequence correlates more closely with taxon”. Such gradual growth, supposed to prove Darwinian idea of a gradual continuity, is the standard view of the phyletic gradualism promoted by modern synthesis [5]. According to this view the punctuated equilibrium Eldredge [5,6], which involves periods of stasis, has no relevance in the context of the increase in hominin cranial capacity over time and across various ancestral hominin taxa.

Rightmire [7], based on the available allometric data on *Homo erectus* concluded that little directional change had taken place during the time span of their existence. However, Cronin et al. [8] reject the stasis and punctuation as hominid fossil record provides no well-documented examples for either of them. Several authors assert that the stasis could not be established through their analyses of past cranial capacity data [1,2,9]. In this paper, hominin cranial capacity data available as a compilation in the literature is reanalyzed and the patterns noticed by previous authors De Miguel and Henneberg [1], Henneberg [2] investigated in the light of alternative analytical tools to confirm or question their rejection of punctuated equilibrium on the basis of their formulation of double exponential model.

Materials and Method

Data

The compilation of cranial capacity data over time published by De Miguel and Henneberg [1] had the merit of having multiple estimates on cranial capacity performed on the same specimen. Time values to which the skulls were dated are not regular and thus, the data does not adhere to a standard time series structure. It was decided that any extra specimens found after the original compilation will be ignored as the intended comparison against the previous claims on the original data then becomes unjustifiable and not on the same basis. De Miguel and Henneberg analyzed this extra information on variability in the context of analysis of variance providing within group information to indicate the extent of measurement errors. But these measurements can also be

used to simulate a sample from the universe of all possible values of cranial capacities of the specimen.

In the current study, it was assumed that all the determinations done on the possible time lapsed from the deposition of the specimens to the present are of acceptable quality. Lee and Wolpoff [9] and De Miguel and Henneberg [1] showed reservations about the accuracy of dating of the specimens. Lee and Wolpoff [9] reanalyzed the growth rates of log-transformed cranial capacities from the Pleistocene using an innovative resampling technique to prove the gradual increase in cranial capacity. However, this reassigning of dates to cranial capacities based on the assumed error span in dating is not sufficiently intuitive, as the amount of possible unintended errors introduced by doing so cannot be easily quantified. The author of this article believes that if the widely used standard techniques cannot show up a feature in the data, it is not justifiable to introduce possible errors intertwined with new analytical tools in order to test a hypothesis. The current study takes the stand of Beals et al. [4], De Miguel and Henneberg [1] and Henneberg [10] in determining the relationship between time and cranial capacity, that is, considering dates are as accurate as they can get, i.e., time as the explanatory variable. Model building undertaken in this investigation is only intended to facilitate uncovering any underlying patterns in an exploratory manner rather than serving a predictive or explanatory purpose. Any evident pattern in the form of a fitted model indicates the path probably trodden by the increasing cranial capacity of the hominins.

The data set used by De Miguel and Henneberg [1] can be found in their published work. They excluded any child or young adult specimens together with any specimen of dubious quality. The specimens used had been listed in bold letters and numbers in the appendix to their paper. Altogether, the number of specimens used, added up to 209 [3].

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A slight difference in the current approach was to split the ranges given in their data to lower and upper limits for the specimen.

Methods

In this study, the first attempt was to see whether there was an underlying structure to the data. If there were such a structure, then it was needed to take this structure into account in any analysis. Such an investigation was highly desirable as different taxa in hominins prevailed in different periods of human evolution. A simple graphical representation of data in two dimensions could not reveal any discernible group structure. It is common practice to use unsupervised machine learning methods to uncover hidden structures. One method popular among the data miners is the use of k-means clustering algorithms, which find a specified number of convex clusters in a dataset. Ignoring the fact that the data was only two-dimensional, the k-means clustering with the default algorithm of Hartigan and Wong [11] available in the software package R Core Team 2013 [12] was used in this study. This analysis was expected to show a structure based on the Euclidean distances between specimens rather than two different axes which contained measurement errors.

To find the number of clusters of cranial capacities along the time axis, it was decided to use specimen means without standardization. Both time and cranial capacity should equally contribute to the distance between any two specimens as each specimen should be treated in the two dimensions without any displacement to the natural space defined by time axis and cranial capacity. The standardization of variables can distort these inter-specimen relationships and thus, was avoided. The number of clusters can be determined by repeatedly using k-means algorithm to change the number of clusters between a single cluster and the number equal to the number of observations in the data set and plotting the within group sum of squares (WSS) for each cluster solution against the number of clusters. The number of possible groups can be identified as the first solution resulting in a substantial drop in WSS value, which only slightly changes for the remaining solutions. The cluster solution thus obtained was further tested for stability using a simulation study the basis of which will be discussed below.

Simulated data for each specimen was assigned to a cluster and the 2.5% and 97.5% points of the empirical distributions for these assignments were compared using Hamming distance, H Hamming [13] defined for this purpose as

$$H = \sum_{i=1}^n h_i \text{ where } h_i = 1 \text{ if } (I_i^{0.025} \neq I_i^{0.975}); h_i = 0 \text{ otherwise}$$

Note that $I_i^{0.025}$ (or) $I_i^{0.975}$ means that the specimen i has been a member of the cluster, I ($=1, \dots, k$) at the 25th (or 975th) quantile resulting, for example, from a set of 1000 trials. The solution with the smallest H is more stable and hence a more probable solution as the Hamming distance measures the sum of differences between the group assignments of a specimen at the 2.5th percentile and 97.5th percentile for all specimens. Once the number of clusters was determined, further analysis was done using the simulated data with the selected number of clusters.

In respect of the cranial capacities, it was assumed that their estimates, Y_i on specimen i follows a lognormal distribution with mean μ_i and standard deviation σ_i .

$$Y_i \sim \text{Lognormal}(\mu_i, \sigma_i)$$

This process introduces the skewness towards higher cranial

capacities as well as a wider spread of simulated values, to make the simulation outcomes more conservative. The values of μ_i and σ_i can be estimated from the estimates done on each specimen y_i . When σ_j cannot be estimated from the data, it was assumed to be:

$$\hat{\sigma}_j = f_j * \mu_j$$

$$f_j \sim \text{Uniform}\left(\min\left(\frac{\sigma_{i \neq j}}{\mu_{i \neq j}}\right), \max\left(\frac{\sigma_{i \neq j}}{\mu_{i \neq j}}\right)\right)$$

where j is values of i without sufficient number of estimates of cranial capacities to calculate a standard deviation. Similarly, \min and \max of $\left(\frac{\sigma_{i \neq j}}{\mu_{i \neq j}}\right)$ are respectively, minimum and maximum values of coefficients of variation for all specimens for which the standard deviation can be computed. Allowing f_j to vary uniformly introduced more freedom in determining the value of standard deviation and thus, accounting for estimation errors in cranial capacities. Following two processes were used to take care of inaccuracies in estimation.

Impute only the unknown standard deviations with $\hat{\sigma}_j$

Estimate new standard deviations for all specimens in the form of $\hat{\sigma}_j$

The ordinary linear, polynomial, exponential, power law models and the double exponential model of the form

$$\hat{Y}_i = ab^{cT_i}; a \geq 1, b \neq 0, 0 < c < 1$$

De Miguel and Henneberg [1], Henneberg [2,10] methods were fitted to the full set as well as the identified subsets of data. The letters a , b and c in the above equation represent estimated parameters. The analysis of the output from these models mainly confirmed the conclusion arrived at by De Miguel and Henneberg [1] on the goodness of fit of their double exponential model. This would be again looked into in the discussion section of this article.

The above can be also approximated as

$$\hat{Y}_i = d^{cT_i}$$

Henneberg [10] considers a as intercept and, b and c as slope parameter estimates. The second formulation let us see d , hence a and b , to be intercept estimate and c to be rate of change estimate. As Henneberg [2] also assures, this model is well suited to the cranial capacity data; the parameter c , which drives rate of cranial capacity growth over time, changes to fit the end values of T well. In the current study, the originally proposed and the second form of the model in its linearized form, given below, were fitted:

$$\widehat{\log(\log Y_i)} = d + cT_i$$

Thus, using the above-described two imputation types for the standard deviations, ten thousand simulations of cranial capacities for each of 209 specimens were generated. Then, to the groups identified via k-means clustering the above non-linear form of the model was fitted using the optimization routine $nlinb()$ available with the software package R (R Core Team 2013) to minimize the sum of squared error of prediction. Based on the ten thousand simulations for each model, the 95% confidence limits for each parameter of the double exponential model and its linearized form were constructed and compared. For the non-linear models, the calculations were done after allowing for non-convergence. The direct computations as well as simulated values of the confidence intervals for the linearized model were studied to investigate whether the simulated intervals in general were sensible. For model comparison purposes, the normalized root mean squared

deviation (NRMSD), pseudo R^2 and, in case of the linearized forms, the coefficient of determination, R^2 were used. The pseudo R^2 in this study was defined as follows:

$$pseudo R^2 = \frac{\sum (\hat{Y}_i - \bar{Y})^2}{\sum (Y_i - \bar{Y})^2}$$

where \bar{Y} is the mean value of the cranial capacity. This should always be cautiously used as the algebraic relationship between residual sum of squares, regression sum of squares and total sum of squares is not fully defined in a form to make the pseudo R^2 meaningful in isolation. Note that NRMSD was always defined with respect to the minimum and maximum of the mean cranial capacities of each dataset and, when dealing with transformed data, their equivalents for the purpose of making the RMSDs across various simulations comparable. The minimum and maximum values used are given in table.

Results

The following graph shows the WSS chart for different cluster solutions on mean cranial capacities of 209 specimens. It clearly shows that two-cluster solution is the one, which reduces WSS by the largest magnitude (Figure 1).

To test whether the three and four cluster solutions can be excluded, Hamming distance as described above was used. Table 1 below shows the Hamming distance and the time to the start of each cluster from the modern times in thousand years. The cluster separation points were determined by the mode of the cluster each specimen was assigned to in 10,000 simulations, which were carried out using the first approach described in the methodology section. It is clear from the table that the two-cluster solution had by far the smallest Hamming distance and the clusters separated at 1,150,000 years. Even if Hamming Distance is adjusted for the number of clusters two-cluster solution could not be excelled. Thus, following De Miguel and Henneberg [1], it is safer to place the separation of clusters at one million years.

Then, the double exponential models were fitted to the full set of specimens and two subsets separated by the time point at one million years before the present. The modern humans mainly represented the recent part of the last million years. Table 2 shows the parameters

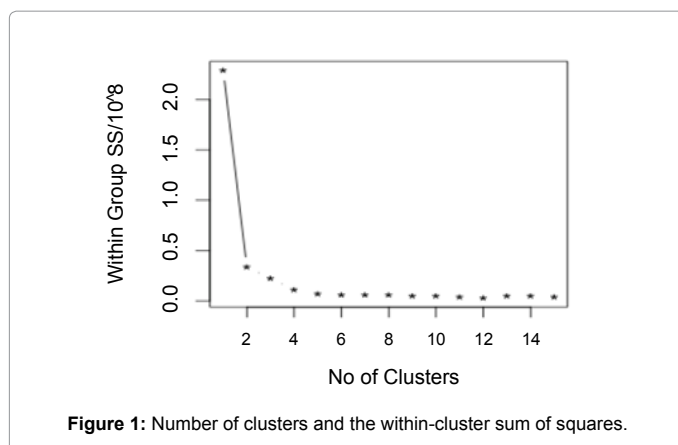


Figure 1: Number of clusters and the within-cluster sum of squares.

Number of Clusters	Hamming Distance	Separation Points in Time BP (in kyr)
2	4	1150
3	141	840,2250
4	162	300,1150,2250

Table 1: Hamming distances for different cluster solutions.

Dataset	No of Specimens	Mean CC in ml (Min-Max)	a	b	c
Full set	209	1130.30 (286-1814)	272.81 (306.63)	5.46 (4.83)	0.9996 (0.9995)
>=1 mio yrs	61	167.62 (286-1082.3)	244.74 (185.68)	8.85 (7.12)	0.9995 (0.9994)
<1 mio yrs	148	962.69 (736.8-1814)	788.66 (433.8)	1.92 (3.25)	0.9984 (0.9997)

Table 2: Parameter estimates of the double exponential models [1], model parameters a, b and c is given within brackets.

fitted and the descriptive statistics for the data sets. It also shows the corresponding parameters from De Miguel and Henneberg [1] in italicized form within brackets. Most noticeable difference was for the parameter estimates of the model with the <1 million years data.

To see whether the conclusions about the double exponential model on the cranial capacity data reached by the previous authors are justifiable, a model as good or better needs to be found. The model fitted in the current study was tested against the previous model by comparing the residual sum of squared deviations around the fitted curves. For the De Miguel and Henneberg [1] model, the residual sum of squared deviations around the models fitted to the subsets exceeded the residual sum of squares for the combined model covering the full span of time. This made the models on the subsets weaker than the combined model [14]. On the contrary, the models fitted in the current study showed that even though not at 5% level of significance, the separate models were better than the combined model. The following relationship shows the probability of the F statistic of 2.55, computed from the improvement of two models over the combined model, exceeding the tabulated F value for the 3 and 203 degrees of freedom.

$$\Pr(2.55 > F_{203}^3) = 0.057$$

The assumption about the homogeneity of the residual sum of squared deviations around two curves fitted to the subsets was only met at 0.061 probability. The result was highly influenced by three outliers detected using a box-plot on the combined residuals of the models fitted to two subsets of data; these were Minatogawa IV, Sambungmacan 3 and Sangiran 31. The only inclusion, obviously dubious was Minatogawa IV. According to Suzuki [15] "...the Minatogawa IV is considered to be a young adult female individual, probably less than 25 years of age".

As all the young were excluded from this analysis it is reasonable to exclude Minatogawan IV as well and see its impact on the model. This change obviously made the separate models significantly better at 5% level than the combined model.

$$\Pr(3.76 > F_{202}^3) = 0.012$$

This also made the residual variation around the separate curves homogeneous by changing probability level from 0.061 to 0.090. On the balance, it can thus be considered that the separate models better represented the data.

In the remainder of the study, this data point would not be excluded to be in agreement with the previous authors. The models fitted with the simulated data did not have an impact big enough to change any conclusions, which were arrived at with the data inclusive of Minatogawa IV specimen. However, any noticeable differences will be discussed as necessary.

Table 3 shows the models built by De Miguel and Henneberg [1] and the present author on the comparable sets of data. As evident from NRMSD and pseudo- R^2 current models fit as well or better than the previous models. Thus, the extension of these current models to

Dataset	De Miguel and Henneberg Fit		Current Fit		Log of log Fit*	
	NRMSD	Pseudo -R ²	NRMSD	Pseudo -R ²	NRMSD	Pseudo -R ²
Full set	0.0909	90%	0.0906	86%	0.0932	83%
>=1 mio yrs	0.1544	79%	0.1476	85%	0.1495	86%
<1 mio yrs	0.1482	63%	0.1325	91%	0.1356	86%

*These values are based on the back-transformed log of log values to be on par with the other two fits.

Table 3: Comparison current double exponential fits and the log of log form fitted to specimens [1].

Dataset	(Pseudo R ²) (NRMSD)	a		b		c	
		0.025	0.975	0.025	0.975	0.025	0.975
Full-missing SDs replaced	(61-75%) (0.15-0.21)	50.52	432.82	3.58	29.51	0.9992	0.9998
>=1 mio yrs-missing SDs replaced	(20-51%) (0.16-0.29)	15.39	425.24	5.90	179.14	0.9987	0.9999
<1 mio yrs-missing SDs replaced	(39-53%) (0.12-0.15)	576.23	909.98	1.68	2.61	0.9975	0.9991
Full-all SDs replaced	(69-81%) (0.12-0.17)	114.58	408.32	3.77	12.98	0.9993	0.9998
>=1 mio yrs-all SDs replaced	(29-52%) (0.15-0.23)	30.78	351.27	7.03	48.83	0.9992	0.9999
<1 mio yrs-all SDs replaced	(42-54%) (0.12-0.14)	600.25	901.64	1.69	2.51	0.9976	0.9991

Table 4: 95% Confidence limits for simulated values of pseudo R², NRMSD, and the estimated parameters of the double exponential models.

simulated data sets as described in the methodology section was useful in a comparative analysis with De Miguel and Henneberg [1]. The residual sum of squares around the fitted curves, NRMSD and pseudo- R² clearly showed that the current models are as good as or better than the models fitted by the previous authors. Fitting a model to the >=1 million years data after the exclusion of Minatogawa IV specimen maintained the pseudo R² of 91% for the current fit (Table 3). It also reduced the NRMSD for the model fitted to the <1 million year data to 0.129 from 0.133. Again, for conservatism, the Minatogawa IV specimen would not be excluded from this model comparison phase.

The 95% confidence limits of parameters, fitted to the full set and two subsets were simulated using two ways of estimating standard deviations as described in the methodology and are listed with the respective 95% confidence limits for NRMSDs and the pseudo -R² in Table 4. Models fitted to subsets showed clear separation between intercept parameters while their rates of change were significantly different only for the simulations with all standard deviations replaced.

To see whether the linear form also confirmed the presence of two lines in the data, the linearized models were fitted to mean cranial capacity in the log of log form and the models for the two subsets of data and the full set were compared. The comparison was supposed to indicate whether the separate models were better than a single model or otherwise. Simultaneously, the models were tried on the two types of simulated subsets of data and the result can be found in Table 5.

Given the heterogeneity of residuals around the separate lines ($\text{Pr}(3.83 > F_{146}^{59}) \ll 0.001$), the very significant superiority of separate models ($\text{Pr}(3.04 > F_{205}^2) < 0.01$) cannot be readily accepted. However, the simulated confidence limits for the parameter \bar{c} clearly showed the significant non-parallel nature of the OLS regression lines.

Discussion

De Miguel and Henneberg [1] pointed out that from many statistical models they investigated to model the growth of cranial capacity over time, the double exponential model turned out to be the best model for the past 3.2 million years as well as two stretches of time on either side of one million years before the present. The k-means clustering justified the choice of two subsets by De Miguel and Henneberg [1]. The current study also could assert the superiority of their model over several models such as exponential, power law, simple linear regression and polynomial. However, the power law model showed a better fit for the period between 3.2 to 1 million years before present. It showed a R² of 52% and a NRMSD of 0.329 against a R² of 51% and a NRMSD of 0.333 displayed by the log of log model. These differences further supported the change in cranial capacity growth between the two periods considered in this study.

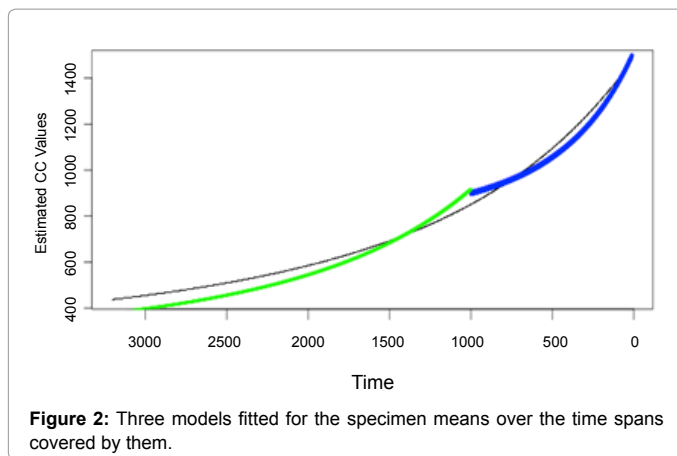
The previous authors De Miguel and Henneberg [1] failed to compare the models on the subsets of cranial capacity data using direct statistical tests, i.e., the comparison of two curves for the subsets vs. single curve across the data or the separation of confidence intervals between corresponding parameters. Mainly using the visual proximity of the predicted curves they assumed that two subsets behaved similarly and thus, the growth in hominin cranial capacity over the last 3.2 million years represented a steady and gradual increase. However, as shown in the results section, there can be at least one set of alternative model parameters, which are equally good as or better than the models used by De Miguel and Henneberg [1]. Through an analysis of residual sum of squares, it could be shown that the separate models were an obvious better option than a single model for the cranial capacity data when the outlier Minatogawa IV was removed. Fitting models to simulated data for the two time periods before and after one million years before present showed significantly different intercept parameters a and b . Parameter c was significantly different for the set of simulations where all standard deviations were replaced even though the simulations with only the missing SDs replaced didn't show separation between two models at 95% confidence level. In both cases, in the more recent times the cranial capacity showed steeper growth, i.e., smaller rates of change for growth. Thus, the simulation results have showed that two models on subsets were better than the combined model. The significant differences in the slope parameters of the linearized models clearly showed that the parallel lines were not an option. Thus, the change in cranial capacity was significantly different for the two periods considered.

Many evolutionary theorists opposing the punctuated equilibrium find the linearity in the gradual growth of cranial capacity over hominin lineage [5]. Exponential model fitted by Henneberg [2] for

Dataset	(R ²) (NRMSD) [^]	d		c	
		0.025	0.975	0.025	0.975
>=1 mio yrs-missing SDs replaced	(29-51%) (0.35-0.49)	1.941 (1.929)	1.976 (1.991)	-0.000064 (-0.000071)	-0.000049 (-0.000042)
<1 mio yrs-missing SDs replaced	(44-56%) (0.30-0.36)	1.985 (1.975)	1.988 (1.999)	-0.000095 (-0.000099)	-0.000079 (-0.000075)
>=1 mio yrs-all SDs replaced	(20-48%) (0.39-0.57)	1.923	1.990	-0.000071	-0.000042
<1 mio yrs-all SDs replaced	(42-55%) (0.31-0.37)	1.985	1.989	-0.000095	-0.000079

[^]Fitted using simulated data with the OLS regressions: parameters d and c with their theoretical 95% CIs for the model fitted with mean values are given in brackets (R²) and (NRMSD) are also based on the simulated data.

Table 5: Comparison of the log of log form of cranial capacity.



hominin cranial capacity across the last 3.2 million years, despite being non-linear, is considered as proof of such gradualism and continuity [16]. Rightmire [7] pointed out the stasis of *Homo erectus* through million-year period as evidence for punctuated equilibrium hypothesis while McHenry [17] noted the little change occurring within most hominid species through time. Wolpoff [18], using the early, middle and late *H. erectus* specimens and the arguable process of multiple significance testing showed significant differences among these time spans and hence, incompatibility with stasis. Eldredge [6] considers that the adaptive change is relatively rare, and thus typically rather rapid. Thus, there seems to be an agreement between Wolpoff's claim about the growth of cranial capacity of *H. erectus* and the presence of stasis. If *H. erectus* remained a single species even with the significant variability across time, the typical characteristics of the species had been recognizably static and the directional change due to positive selection pressures didn't lead to speciation. Thus, data showed the stasis in a background of slow directional change. When speciation finally occurred, the emerging species, the modern humans, was clearly noticeable, i.e. there was a morphological break clear enough for the scientists to work with. In the models this time span of change appeared as a relatively steep curvature.

The said curvature can be seen from the Figure 2, which shows the three nonlinear curves (Table 2) estimating the cranial capacities, in cubic centimeters, of 209 specimens over a series of 0.05 million year intervals through the fitted models. The fitted curves are not expected to be best fits for any specific segment of the time line represented by each curve. However, they are the best fits for total time span covered by each curve. The longer curve describes the general pattern that the cranial capacity followed over the past 3.2 million years. The other two are better fits for the two shorter time spans considered. Short curves turning up to cross the longer curve can be deemed to show the times with a sharp trend.

The slow growth of the period between 3.2 and 1.5 million years before the present might have masked periods with rapid change, which were occupied by several hominid species across several biogeographies. Thus, what can be seen in the cranial capacity studies is a slow change over time. However, between 1.5 to 1 million years ago, against a backdrop of slow growth displayed by the combined data model, there was a relatively rapid increase in cranial capacity, which coincided with the emergence and establishment of *H. erectus*. In the light of the good fit of the power law model over the log of log model to the data for this time span, it is reasonable to view punctuated equilibrium in the light of power law based ideas popularized by

some authors [19]. Gribbin [19] maintains a compromise between gradualism through the Red Queen effect and "punctuation" which manifests in short intervals of dramatic change. Henneberg [2] in reference to hominin cranial capacity attributed this steeper change to "self-amplifying nature of hominid evolution" which is a reference to an autocatalytic process [20]. However, Godfrey and Jacobs [21] while leaning towards punctuations and stasis rejected a power law based process as misleading and inappropriate. Irrespective of the contradictory claims, the rapid change was discussed in the context of the punctuation. In the current study, there was a noticeable increase in cranial capacity associated with the time during which *H. erectus* prevailed.

Again, after a lull until about 0.4 million years before present, a very noticeable increase in cranial capacity leading to modern humans was observable in the fitted curves. The view expressed by Futuyma [22] that without the claim of association between speciation and evolutionary change, the concept of punctuated equilibrium is merely about the variability of the rate of evolution, is very notable. He also proposes that the speciation locks in the otherwise ephemeral change in a species. Thus, the change within a species is not something totally external to the theory of punctuated equilibrium. Eldredge [6] himself made the point that the gradual change even susceptible to explanation in adaptive terms doesn't lead to the advent of the truly new. The present author believes that the analysis discussed in the current paper points towards an association between speciation and a rather rapid change in morphological characteristics

Conclusion

It is sufficiently clear from the above analysis that apart from the short spell of rapid change in relation to *H. erectus* before one million years before the present, there had been a substantial structural change in hominin cranial capacities during the last five hundred thousand years. During this time the modern man arrived on the hominin landscape. Irrespective of the different theoretical viewpoints, this change resulted in a steeper increase in the cranial capacity during the later part of the last half million years. The rate of change, which is usually less than unity and modified as a power of time in the models fitted, traces this steeper increase in cranial capacity as time reaches modern times. As can be seen from the above discussion, the change in cranial capacity through time makes the punctuated equilibrium hypothesis harder to reject, if the slow gradual growth had been disturbed by a span of time with a rapid growth. What could be seen from the above analysis was that the path of cranial capacity growth over last few million years was reasonably well traced by two separate growth curves indicating time spans of slow change followed by rapid rate of cranial capacity increase and thus, supporting a process comparable to a punctuated equilibrium.

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