

Primate evolution by random genetic drift: Comparing linear and geometric morphometrics of the cranium in testing cercopitheicine divergence

Introduction

Linear measurements and landmark-based geometric morphometrics are both widely used to quantitatively describe primate cranial form and its variation. Each type of data is often subsequently used to study evolutionary aspects of primate cranial form, including the action of microevolutionary processes, such as random genetic drift and natural selection. Previously (Prôa, 2016; Prôa & Matos, 2017), I have applied "Cheverud's conjecture" to a large sample of cranial linear measurements to test what the relative contribution of genetic drift is that have acted on the anthropoid cranium to produce its current diversity of forms. Results have shown that the null hypothesis of diversification by random genetic drift alone is rejected in many (but by no means all) phylogenetic branches; a large contribution of non-random processes like natural selection seems to have occurred, particularly in the Papionini branch. Now I apply the same protocol to 3D landmark-based geometric morphometric data, and compare them to linear measurements taken on a sample of cercopitheicine crania, to assess whether results are concurrent between the two types of data.

Key words: Cercopitheicinae; random genetic drift; linear measurements; cranial form; variance-covariance matrices.

Material & Methods

Ten landmarks were collected on 3D surface models of the cranium of 70 adult individuals, male and female, belonging to 8 cercopitheicine genera (all genera except *Miopithecus*, for which no data could be retrieved): prosthion; nasion; inion; basion; vertex; staphylion; right ectomolare; left ectomolare; right porion; left porion. Six linear measurements (after Ritzman, 2014) were calculated as distances between landmark points: 1. facial height (distance from prosthion to nasion); 2. cranial length (distance from prosthion to inion); 3. cranial height (distance from basion to vertex); 4. palate length (distance from prosthion to staphylion); 5. palate width (distance from right ectomolare to left ectomolare); 6. cranial width (distance from right porion to left porion). The 3D models of primate crania were built from CT scans available at Digital Morphology Museum, KUPRI (<http://dmm.pri.kyoto-u.ac.jp/dmm>).

To study whether or not the observed diversity could be explained by random genetic drift alone, the within- (**W**) and among-group (**B**) variance-covariance matrices were compared. Following the claim (Cheverud, 1988) that, in contemporary populations, the **W** matrix is often proportional to the genetic (**G**) variance-covariance matrix, one can substitute the latter by the former. Comparing **B** and **W** (as a surrogate of the average **G**) was done by using the method of Ackermann and Cheverud (2002). The null hypothesis of random genetic drift is rejected if the slope of the regression (β) deviates significantly from 1. When using a significance level of $\alpha = 0.05$, it is expected that a true null hypothesis has a 5% chance of being rejected (a type I error). This test was proved to be robust in falsifying the underlying assumptions (Prôa et al., 2013). Because primate cranial forms are constrained by their close phylogenetic relationships, a phylogenetic tree (after Fleagle, 2013) is used as a basis for the analyses and for the interpretation of results. In total, 28 analyses were performed all of them run in the R environment: one set of 7 analyses were ran using the raw linear measurement data; a second set using the configuration of raw 3D landmarks; a third set using the Procrustes coordinates after a full GPA; and a fourth set using the Procrustes coordinates after a size-and-shape analysis (registration, but no scaling).

Discussion

Results indicate differences can be substantial when using linear measurements or 3D landmark coordinates, but not in every cercopitheicine group: in the Papionini, divergence by random genetic drift alone was rejected when either type of data was used, in all four sets of analyses. Preliminary results with 3D landmarks on Papionini (Prôa, 2013) were in agreement with results shown here and indicate that genetic drift alone would not have been able to produce the current diversity in form of the cranium in those primates. A considerably large contribution of non-random processes like natural selection seems to have occurred in all groups when landmark configurations are considered. This is not the case when linear measurements are used, where the action of random genetic drift seems likely (only the *Erythrocebus/Chlorocebus* and the *Lophocebus/Papio* groups show a clear rejection of drift). While one interpretation is that the whole of Cercopitheicinae could not have diversified by genetic drift alone when using landmark coordinates (except in shape analyses), the same cannot be said when linear measurements are used. This discrepancy in results, therefore, has important consequences for the interpretation of the action of microevolutionary processes on cranial form in cercopitheicine primates. It is possible, however, that the sample size of only 70 individuals is too small for the multivariate analyses applied here, and that its substantial increase will eventually clarify the actual differences in use of the two types of data. Also, other 3D landmarks to describe cranial form should be tested and considered in further analyses. The extension of the sample to include other extant and fossil primates, as well as humans and fossil hominins would also be a welcomed addition to further the understanding of primate cranial form evolution.

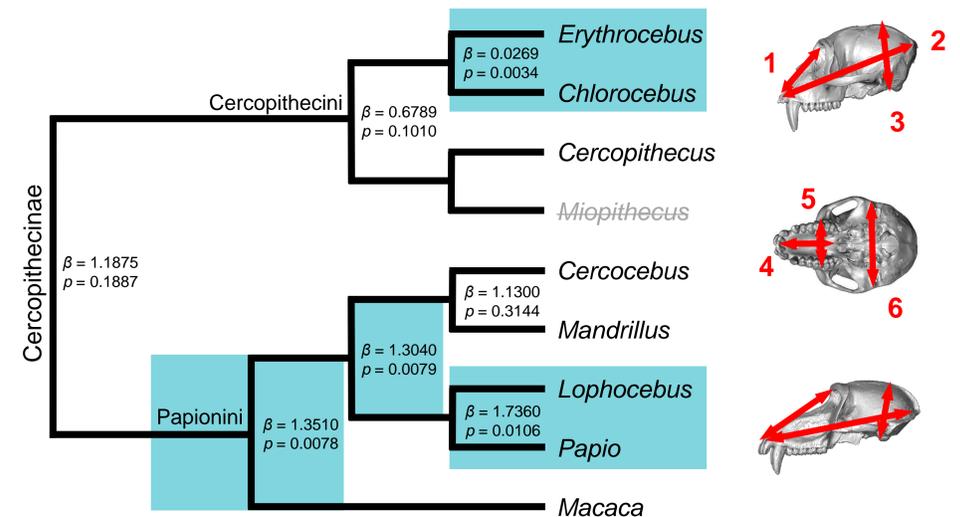
References

Ackermann & Cheverud (2002) *American Journal of Physical Anthropology* 117, 260–271. Cheverud (1988) *Evolution* 42, 958–968. Fleagle (2013) *Primate Adaptation and Evolution* 3rd ed, Academic Press. Prôa (2013) PhD thesis, Hull York Medical School, University of York. Prôa, O'Higgins & Monteiro (2013) *Evolution*, 67, 185–195. Prôa (2016) *Proceedings of ESHE* 5:194. Prôa & Matos (2017) *Proceedings of ESHE* 6:151. Ritzman (2014) PhD thesis, Arizona State University.

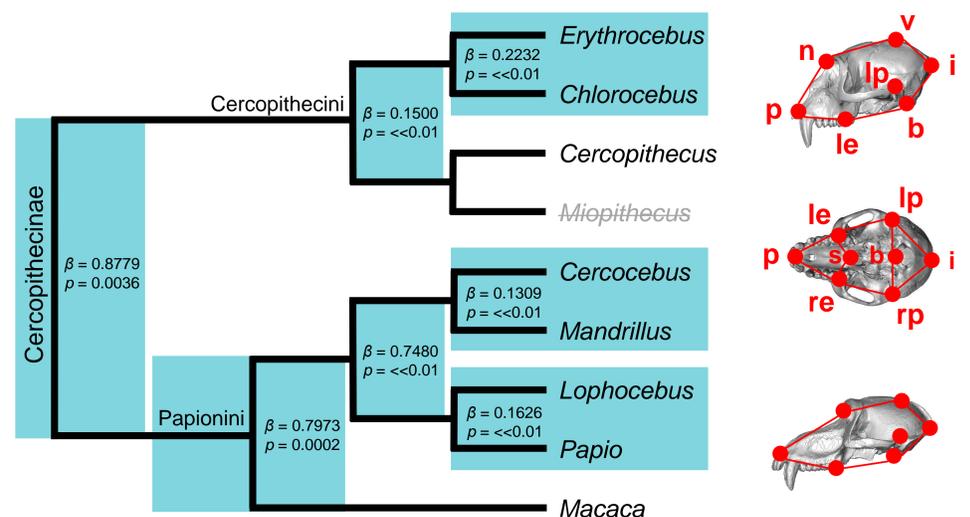
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Results

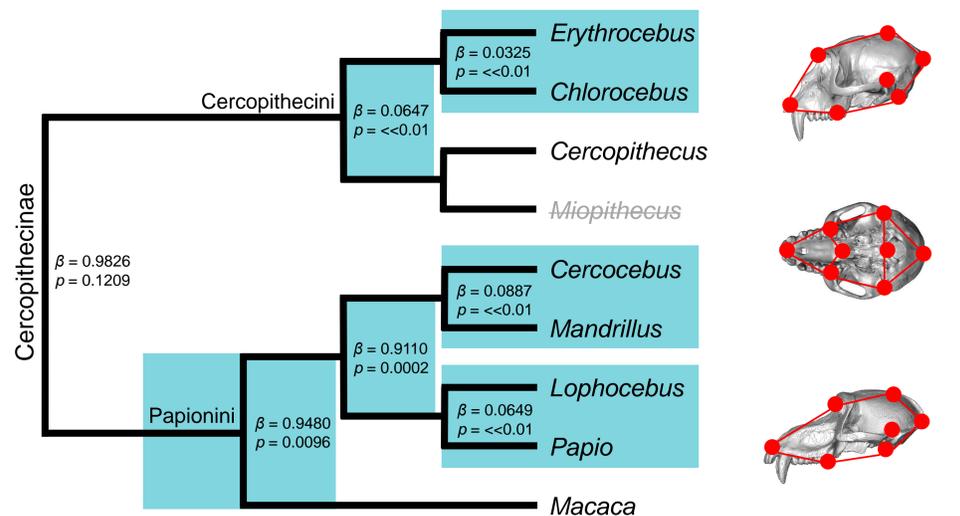
Linear morphometrics (Raw data analyses)



Landmark configurations (Raw data analyses)



Geometric morphometrics (Shape analyses)



Geometric morphometrics (Size-and-shape analyses)

