

Morphological integration in the hominin dentition: Evolutionary, functional and developmental factors

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As the most common and best-preserved remains in the fossil record, teeth are central to our understanding of evolution (Tucker and Sharpe, 2004), including that of hominin species. However, many evolutionary analyses based on dental traits seem to overlook the constraints that limit dental evolution. These constraints are diverse, ranging from developmental interactions between the individual elements of a homologous series (the whole dentition) to functional constraints related to occlusion.

Morphological integration, analysed in this study as covariation in shape between teeth, is the result of these interactions. The relationship between morphological integration and evolution is discussed using an extensive sample of hominin fossils, representing the majority of the spatiotemporal distribution of Plio- and Pleistocene hominin species.

The European fossil record, which is continuous along the whole Pleistocene and includes up to four different species, accounts for a high proportion of the whole morphological hominin variation. Hence, the analysis of a broad sample of original European fossils is fundamental in this study because it aims to explain the variability observed in the complete hominin phylogeny.

Geometric morphometric techniques (rev. in Adams et al., 2004) provide a natural framework to study integration and the covariation among structures. Complementarily, phylogenetic comparative methods (Felsenstein, 1985) allow for the study of integration while accounting for non-independence among samples owing to their common evolutionary history.

This study combines geometric morphometrics with comparative methods (Arnqvist and Rowe, 2002; Drake and Klingenberg, 2010) in order to evaluate both the patterns of integration and the mode of evolution of the complete hominin postcanine dentition.

Classic morphogenetic field theory (Butler, 1939) holds that dental classes are determined by partially independent developmental programs. Nevertheless, the results of this study demonstrate that the claim for independence is not met, as teeth belonging to different classes display significant levels of covariation. These results also show how integration impacts the evolution of the different hominin teeth by generating stasis in elements with strong functional and/or developmental interactions (Polly, 2004; Wood et al., 2007; Piras et al., 2009). Alternatively, directional evolution occurs in the elements with marginal roles in occlusion and mastication (Lockwood et al., 2000), probably in response to other selective pressures.

This study highlights the need to reevaluate hypotheses about hominin evolution based on dental characters, given the complex evolutionary and developmental scenarios in which they have evolved.

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References: Adams, D.C., Rohlf, F.J., Slice, D. 2004. Geometric morphometrics: Ten years of progress following the 'revolution'. *It. J. Zool.* 71, 5-16. Arnqvist, G., Rowe, L. 2002. Correlated evolution of male and female morphologies in water striders. *Evolution* 56, 936-947. Butler, P.M. 1939. Studies of the mammalian dentition.—differentiation of the post-canine dentition. *Proc. Zool. Soc. London* B109, 1-36. Drake, A.G., Klingenberg, C.P. 2010. Large-scale diversification of skull shape in domestic dogs: Disparity and modularity. *Am. Nat.* 175, 289-301. Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125, 1-15. Lockwood, C.A., Kimbel, W.H., Johanson, D.C. 2000. Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. *J. Hum. Evol.* 39, 23-55. Piras, P., Marcolini, F., Raia, P., Curcio, M.T., Kotsakis, T. 2009. Testing evolutionary stasis and trends in first lower molar shape of extinct Italian populations of *Terricola savii* (Arvicolidae, Rodentia) by means of geometric morphometrics. *J. Evol. Biol.* 22, 179-191. Polly, P.D. 2004. On the simulation of the evolution of morphological shape: Multivariate shape under selection and drift. *Palaeontologia Electronica* 7, 1-28. Tucker, A., Sharpe, P. 2004. The cutting-edge of mammalian development; how the embryo makes teeth. *Nat. Rev. Genet.* 5, 499-508. Wood, A.R., Zelditch, M.L., Rountrey, A.N., Eiting, T.P., Sheets, H.D., Gingerich, P.D. 2007. Multivariate stasis in the dental morphology of the Paleocene-Eocene condylarth *Ectocion*. *Paleobiology* 33, 248-260.