

## 2. Patterns of molar variation in great apes and their implications for hominin taxonomy

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### Abstract

In studying the nature of variation and determining the taxonomic composition of a hominin fossil assemblage the phylogenetically closest and thus the most relevant modern comparators are *Homo* and *Pan* and following these, *Gorilla* and *Pongo*. Except for *Pan*, however, modern hominids lack taxonomic diversity, since by most accounts each one is represented by a single living species. *Pan* is the sister taxon to modern humans and it is represented by two living species. As such the species of *Pan* have greater relevance for studying interspecific variation in fossil hominin taxonomy. Despite their relatively impoverished species representations *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus* are, nevertheless, represented by subspecies. This makes them relevant for studying the nature of intraspecific variation, in particular for addressing the question of subspecies in hominin taxonomy. The aim of this study is to examine the degree and pattern of molar variation in species and subspecies of *P. pygmaeus*, *G. gorilla*, *P. troglodytes* and *P. paniscus*. I test the hypothesis that measurements taken on the occlusal surface of molars are capable of discriminating between species and subspecies in commingled samples of great apes. The results of this study are used to draw inferences about our ability to differentiate between species and subspecies of fossil hominins. The study samples include *P. t. troglodytes* (n = 152), *P. t. verus* (n = 64), *P. t. schweinfurthii* (n = 79), *G. g. gorilla* (n = 208), *G. g. graueri* (n = 61), *G. g. beringei* (n = 30), *P. p. pygmaeus* (n = 140), and *P. p. abelii* (n = 25). Measurements taken from digital images were used to calculate squared Mahalanobis distances between subspecies pairs. Results indicate that molar metrics are successful in differentiating between the genera, species and subspecies of great apes. There was a hierarchical level of differentiation, with the greatest separation between genera, followed by that between species within the genus *Pan* and finally between subspecies within species. The patterns of molar differentiation showed excellent concordance with the patterns of molecular differentiation, which suggests that molar metrics have a reasonably strong phylogenetic signal. *Pan troglodytes troglodytes* and *P. troglodytes schweinfurthii* were separated by the least dental distance. *P. troglodytes verus* was separated by a greater distance from these two, but on the whole the distances among subspecies of *P. troglodytes* were less than among subspecies of *G. gorilla* and *P. pygmaeus*. The dental distance between *G. g. gorilla* and *G. g. graueri* was greater than that observed between *P. troglodytes* and *P. paniscus*. With size adjustment intergroup distances between gorilla subspecies were reduced, resulting in distances comparable to subspecies of *P. troglodytes*. A contrast between size-preserved and

size-adjusted analyses reveal that size, sexual dimorphism and shape are significant factors in the patterning of molar variation in great apes. The results of this study have several implications for hominin taxonomy, including identifying subspecies among hominins. These implications are discussed.

## Introduction

Molars make up a disproportionately large part of early hominin fossil collections and figure prominently in taxonomic assessments. When determining whether the differences observed among sets of fossil hominin molars can be attributed to that of a species, or are part of the variation to be expected within a species, paleoanthropologists generally look to modern analogs. Because the fossil record does not present us with the requisite numbers of specimens, or the anatomical, behavioral and ecological details needed to gauge the nature of variation in fossil hominins, extant hominids<sup>1</sup>, namely humans and great apes, provide the next best alternative for modeling variation. The justification behind using closely related extant taxa for models is fairly sound: through recency of common ancestry in closely related taxa are likely to have shared similar patterns and ranges of variation. Therefore, they likely provide reasonably accurate estimates of the type of variation to be expected in the fossils (see papers in Kimbel and Martin, 1993). Just as important, we have a fairly good understanding of patterns of variation in extant hominids in external morphology, breeding patterns, habitat preferences and genetic structure and we can see how these match up with variation in fossilizable attributes such as cranial and dental features. The extant hominids thus provide a comprehensive comparative model for understanding variation in the molars of fossil hominins. If we are to ultimately reconstruct the biology and lifeways of fossil forms in a manner that is consistent with living forms this modeling of variation is essential.

A consensus opinion emerging from molecular systematists (Goodman, 1962;

Goodman et al., 1982; 1998; Caccone and Powell, 1989; Ruvolo, 1994; 1997), corroborated by morphological data (Begun, 1992; Gibbs et al., 2000; Guy et al., 2003; Lockwood et al., 2004), is that chimpanzees are the closest extant relatives of modern humans. Chimpanzees are therefore especially relevant for studying the nature of variation in fossil hominins. Additionally, chimpanzee patterns of variation are well documented. Two species of chimpanzees, *Pan paniscus* and *Pan troglodytes*, are recognized by a plethora of morphological, behavioral, ecological and genetic studies (Coolidge, 1933; Johanson, 1974; Shea, 1981, 1983a, b, c, 1984; Sibley and Ahlquist, 1984; Caccone and Powell, 1989; Kinzey, 1984; Shea et al., 1993; Wrangham et al., 1994; Uchida, 1996; Guy et al., 2003; Taylor and Groves, 2003; Lockwood et al., 2004; Pilbrow, 2006a, b; but see Horn, 1979). Diversity within *P. troglodytes* is also substantial. The traditional taxonomy recognizes three subspecies (Hill, 1967; 1969), but mtDNA studies have suggested that an additional one should be recognized (Gonder et al., 1997). They also suggest that the West African subspecies *P. t. verus* should be recognized as a distinct species, *P. verus* (Morin et al., 1994). Certain morphological data sets have registered the distinctiveness of *P. t. verus* compared to the other two subspecies (Braga, 1995; Uchida, 1996; Pilbrow, 2003, 2006a, b; Taylor and Groves, 2003). The substantial diversity exhibited by *Pan* at the inter- and intra-specific level, together with a close phylogenetic relationship to humans makes them particularly germane to discussions about hominin taxonomy.

Gorillas and orangutans are more distantly related to humans. According to the consensus view (above) gorillas are a sister taxon to