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Geographic variation in gorilla limb bones

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ABSTRACT

Gorilla systematics has received increased attention over recent decades from primatologists, conservationists, and paleontologists. Studies of geographic variation in DNA, skulls, and teeth have led to new taxonomic proposals, such as recognition of two gorilla species, *Gorilla gorilla* (western gorilla) and *Gorilla beringei* (eastern gorilla). Postcranial differences between mountain gorillas (*G. beringei beringei*) and western lowland gorillas (*G. g. gorilla*) have a long history of study, but differences between the limb bones of the eastern and western species have not yet been examined with an emphasis on geographic variation within each species. In addition, proposals for recognition of the Cross River gorilla as *Gorilla gorilla diehli* and gorillas from Tshiaberimu and Kahuzi as *G. b. rex-pymaeorum* have not been evaluated in the context of geographic variation in the forelimb and hindlimb skeletons.

Forty-three linear measurements were collected from limb bones of 266 adult gorillas representing populations of *G. b. beringei*, *Gorilla beringei graueri*, *G. g. gorilla*, and *G. g. diehli* in order to investigate geographic diversity. Skeletal elements included the humerus, radius, third metacarpal, third proximal hand phalanx, femur, tibia, calcaneus, first metatarsal, third metatarsal, and third proximal foot phalanx. Comparisons of means and principal components analyses clearly differentiate eastern and western gorillas, indicating that eastern gorillas have absolutely and relatively smaller hands and feet, among other differences. Gorilla subspecies and populations cluster consistently by species, although *G. g. diehli* may be similar to the eastern gorillas in having small hands and feet. The subspecies of *G. beringei* are distinguished less strongly and by different variables than the two gorilla species. Populations of *G. b. graueri* are variable, and Kahuzi and Tshiaberimu specimens do not cluster together. Results support the possible influence of higher-altitude Pleistocene refugia on patterns of geographic variation in gorillas.

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1. Introduction

Differences between the gorillas of eastern and western Africa have long been recognized on the basis of external and skeletal features (e.g., Coolidge, 1929; Schultz, 1934). In the past two decades, studies of gorilla DNA have also supported a deep evolutionary split between eastern and western gorillas (Ruvolo et al., 1994; Garner and Ryder, 1996; Gagneux et al., 1999; Scally et al., 2012, 2013; Prado-Martinez et al., 2013). A species-level distinction between eastern gorillas (*Gorilla beringei*) and western gorillas (*Gorilla gorilla*) has been suggested (Groves, 2001) and widely adopted, and studies have increasingly examined variation below the species level. Research on geographic variation in skulls and teeth has shown that differences between the two species are greater than differences among subspecies and populations within each species (Uchida, 1998; Stumpf et al., 2003; Taylor and Groves, 2003; Pilbrow, 2006, 2010), but differences between eastern and western gorillas in the limb bones have not yet been studied with a focus on geographic diversity within each species.

Differences among *Gorilla* subspecies have been identified using their skulls, teeth, and postcrania (e.g., Groves, 1970, 2001; Sarmiento, 1994; Uchida, 1998), but mountain gorillas (*G. beringei beringei*) and western lowland gorillas (*G. g. gorilla*) have received more attention than eastern lowland gorillas (*G. b. graueri*) and Cross River gorillas (*Gorilla. gorilla diehli*). Since the proposal by Sarmiento and Oates (2000) that the Cross River gorillas, long included in *G. g. gorilla*, be recognized as the subspecies *G. g. diehli*, research on Cross River gorilla morphology has increased. A few large multivariate studies of skulls and teeth have indicated that all four subspecies can be distinguished from one another (Stumpf et al., 2003; Pilbrow, 2010), but comparable studies have not been conducted using postcrania. Gorillas from the *G. beringei* populations of Tshiaberimu and Kahuzi have unusual combinations of

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cranial and postcranial morphology when compared to other eastern gorillas (Groves, 1970; Groves and Stott, 1979), and some research suggests there may be morphological support for recognizing them as *G. b. rex-pygmaeorum* (Schwarz, 1927; Pilbrow, 2010).

Separations between gorilla subspecies are apparent in genetic studies as well. Mountain, eastern lowland, and western lowland gorillas are distinct based on mtDNA (Garner and Ryder, 1996; Gagneux et al., 1999). The degree of separation between Cross River and western lowland gorillas is not quite as clear; a mtDNA analysis showed that the Cross River gorillas form a clade with other western gorillas in Cameroon and Gabon (Clifford et al., 2004), but analyses including nuclear DNA found the Cross River gorillas to be distinctive (Thalmann et al., 2011; Prado-Martinez et al., 2013). If *G. b. rex-pygmaeorum* is accepted, mtDNA analyses suggest it should include gorillas from the Kahuzi highlands and lowlands, as well as from the type locality of Tshiaberimu (Saltonstall et al., 1998; Jensen-Seaman and Kidd, 2001).

Study of the forelimb and hindlimb skeleton may be particularly informative with regard to geographic variation, because limb bone morphology has the potential to reflect differences in positional behavior and, therefore, in habitat. In fact, limb bone differences between mountain gorillas (or more broadly eastern gorillas) and western lowland gorillas have been previously identified and generally thought to reflect differences in their degrees of terrestriality or arboreality (Schultz, 1927, 1934; Sarmiento, 1994; Carlson, 2005; Tocheri et al., 2011; Dunn et al., 2014), with exceptions (Taylor, 1997a, b; Inouye, 2003). Western lowland gorillas tend to live in higher-canopied forests containing more fruit trees, and they spend more time climbing trees and foraging for fruit than mountain gorillas, which live in discontinuous montane forests with fewer fruit trees and depend more heavily on terrestrial herbaceous vegetation (Doran, 1996; Doran and McNeilage, 1998; Remis, 1998).

While differences between gorilla taxa have been identified in a number of limb bones, differences in the hands and feet have long attracted attention. In particular, shorter hands and feet in mountain gorillas have frequently been documented (e.g., Schultz, 1934; Inouye, 1992; Sarmiento, 1994) and interpreted as adaptations for greater terrestriality (Schultz, 1927; Sarmiento, 1994). Further, mountain gorillas from the Virungas, which live at the highest altitudes of any gorillas, have been reported to have shorter hands and feet than gorillas from eastern populations at lower altitudes, where there are more fruit trees (Groves and Stott, 1979; Sarmiento et al., 1996).

The functional explanation for why gorillas might have longer hands and feet in habitats where they spend more time climbing trees has been left implicit by most researchers. However, it is presumably the same as the usual explanation for why chimpanzees and orangutans have longer hands and feet than gorillas: longer metapodials and phalanges increase potential grasp diameters (Preuschoft, 1973; Susman, 1979; Langdon, 1986; Gebo, 1992), hence more arboreal taxa experience selection for an increase in their length. Gorillas in habitats where they climb trees less frequently may have shorter hands and feet because of an absence or lesser degree of selection for greater hand and foot length. Alternatively, shorter hands and feet may be advantageous in terrestrial contexts because they minimize bending moments (Sarmiento, 1994) and are less likely to catch on vegetation (Tuttle, 1970). Finally, in the Virungas, shorter appendages, including hands and feet, may be an adaptation for heat retention at colder temperatures (Sarmiento et al., 1996). Further work on identifying gorilla morphology that varies with ecology may provide tools for reconstructing the ecological contexts for the evolutionary divergences of gorilla taxa and for reconstructing the habitats and behaviors of fossil hominoids. In addition, as living apes, gorillas provide a model for patterns and extents of limb bone variation among geographic groups that can be applied to taxonomic interpretations of differences between limb bones in the hominoid fossil record.

The history of climate change during recent gorilla evolution may provide a useful context for the observed patterns and extents of limb bone variation within each species. After the split between eastern and western gorillas, the formation of forest refugia during Pleistocene glacial maxima, which were associated with cool and dry periods in Africa, may have played a role in the diversification of gorillas (Jensen-Seaman and Kidd, 2001; Clifford et al., 2004; Anthony et al., 2007). These dry periods would have led to forest fragmentation and isolation of forest-dependent animal taxa in the remaining patches of tree cover, with the resulting cessation of gene flow potentially leading to the evolutionary divergence of populations in different forest refugia. During wetter periods, forests would have expanded and gene flow between animal populations may have resumed.

Phylogeographic patterns of gorilla diversity based on mitochondrial and nuclear DNA reveal four major haplogroups, each of which is geographically associated with one or more postulated Pleistocene forest refugia. Three of these haplogroups are each represented by one currently-recognized gorilla subspecies (mountain, eastern lowland, and western lowland gorilla), while one includes both the Cross River gorilla and individuals from some western lowland gorilla populations (Anthony et al., 2007). The eastern gorillas, including a *G. b. beringei* haplogroup and a *G. b. graueri* haplogroup, most likely found refuge in the montane forests that formed in the mountains of the Albertine Rift during periods of cooling and drying, making their homes in the highlands on either side of the rift lakes and adopting a more herbivorous diet to take advantage of abundant herbaceous vegetation (Pilbrow, 2010). Eastern lowland gorillas show molecular evidence of population fragmentation and subsequent expansion during the Pleistocene, consistent with hypothesized isolation of populations in various mountainous regions (including Tshiaberimu and Mt. Kahuzi) followed by expansion back down to the lowlands, whereas the evidence for demographic expansion in mountain gorillas, which only live in highlands today, is inconsistent (Jensen-Seaman and Kidd, 2001; Anthony et al., 2007). The ancestors of the Cross River gorilla are likely to have inhabited a highland refugium in the region of the border between Cameroon and Nigeria today (Sarmiento and Oates, 2000; Clifford et al., 2004). While some of the forest refugia to which western lowland gorillas retreated during periods of forest fragmentation may have been at relatively higher elevations (Anthony et al., 2007), the range of this subspecies is characterized by low-relief topography that may have made it easy for populations to resume reproductive contact during periods of forest expansion, resulting in the complex genetic substructuring seen in this subspecies today (Clifford et al., 2004; Pilbrow, 2010). The apparent relationship between gorilla phylogeography and ecological variation in the past suggests the possibility that phylogeographic patterns may be reflected in gorilla limb bones, whether due to adaptation, drift, or both.

In order to study geographic variation in terms of either taxonomy or ecology, a geographically diverse sample is necessary. Most studies of gorilla skeletal morphology compare samples at the levels of species or subspecies, but more fine-grained studies that compare smaller geographic groups (roughly comparable to populations) make an important contribution toward understanding how variation is structured and testing whether patterns of variation at the population level support the current taxonomy (see Albrecht et al., 2003, on "population thinking"). Further, because evolution occurs at the level of the population, it makes sense to study patterns of variation at the population level.

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