

The Evolutionary Origin and Population History of the Grauer Gorilla

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ABSTRACT

Gorillas living in western central Africa (*Gorilla gorilla*) are morphologically and genetically distinguishable from those living in eastern central Africa (*Gorilla beringei*). Genomic analyses show eastern gorillas experienced a significant reduction in population size during the Pleistocene subsequent to geographical isolation from their western counterparts. However, how these results relate more specifically to the recent biogeographical and evolutionary history of eastern gorillas remains poorly understood. Here we show that two rare morphological traits are present in the hands and feet of both eastern gorilla subspecies at strikingly high frequencies (>60% in *G. b. graueri*; ~28% in *G. b. beringei*) in comparison with western gorillas (<1%). The intrageneric distribution of these rare traits suggests that they became common among eastern gorillas after diverging from their western relatives during the early to middle Pleistocene. The extremely high frequencies observed among grauer gorillas—which currently occupy a geographic range more than ten times the size of that of mountain gorillas—imply that grauers originated relatively recently from a small founding population of eastern gorillas. Current paleoenvironmental, geological, and biogeographical evidence supports the hypothesis that a small group of eastern gorillas likely dispersed westward from the Virungas into present-day grauer range in the highlands just north of Lake Kivu, either immediately before or directly after the Younger Dryas interval. We propose that as the lowland forests of central Africa expanded rapidly during the early Holocene, they became connected with the expanding highland forests along the Albertine Rift and enabled the descendants of this small group to widely disperse. The descendant populations significantly expanded their geographic range and population numbers relative to the gorillas of the Virunga Mountains and the Bwindi-Impenetrable Forest, ultimately resulting in the grauer gorilla subspecies recognized today. This founder-effect hypothesis offers some optimism for modern conservation efforts to save critically endangered eastern gorillas from extinction. *Am J Phys Anthropol* 159:S4–S18, 2016. © 2016 Wiley Periodicals, Inc.

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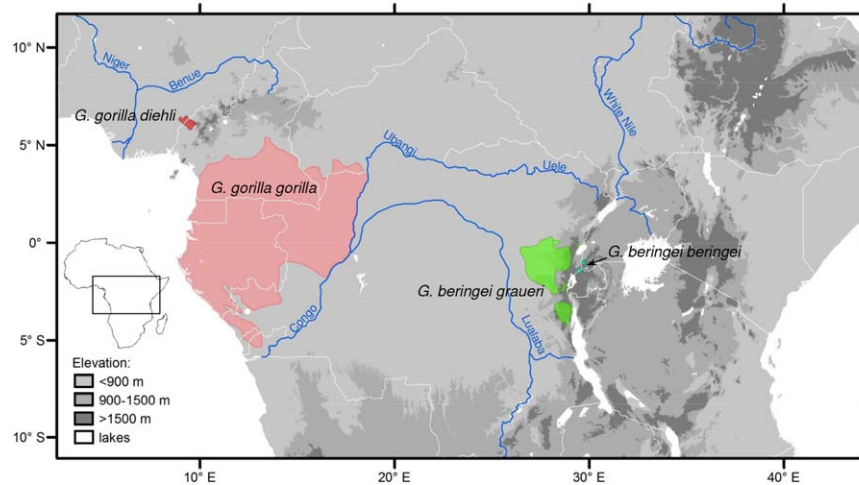


Fig. 1. The current IUCN (2015) ranges of gorilla taxa shown with major river boundaries. Elevations mark approximate boundaries between lowland (<900 m), transitional (900–1,500 m), and highland (>1,500 m) forested habitats. The white lines denote country borders.

Ever since Schaller (1963) first made clear that “mountain” gorillas live in both highland and lowland habitats west of the Virunga Mountains (Fig. 1), grauer gorillas have puzzled researchers with regard to their evolutionary relationships and their morphological, functional, and behavioral affinities. Originally considered true mountain gorillas (Coolidge, 1929; Schultz, 1930, 1934), subsequent work focused on increasing knowledge about grauer gorillas, often highlighting similarities and/or differences to both mountain and western gorillas (Groves, 1967, 1970, 1971; Groves and Stott, 1979; Yamagiwa et al., 1992, 1996; Yamagiwa and Mwanza, 1994; Uchida, 1996; Doran and McNeilage, 1998; Taylor, 2003; Taylor and Groves, 2003; Yamagiwa et al., 2003; Jabbour, 2008; Pilbrow, 2010; Tocheri et al., 2011; Dunn et al., 2014; Knigge et al., 2015). Here we combine an overview of the current state of knowledge about grauer gorillas from genetic, morphological, and paleoenvironmental perspectives, with new evidence of two rare skeletal traits present in the hands and feet of eastern gorillas to articulate a founder-effects hypothesis for the evolutionary origin and population history of the grauer gorilla.

GORILLA PHYLOGENETICS AND POPULATION HISTORIES

Comparative studies of human and great ape morphology and genetics, including recent analyses of whole genomic sequences, leave little doubt that gorillas are the second closest living relative of modern humans (Ruvolo et al., 1994; Ruvolo, 1997a,b; Lockwood et al., 2002, 2004; Salem et al., 2003; Uddin et al., 2004; Scally et al., 2012). Phylogenetic analyses of hominid temporal bone shape based on three-dimensional geometric morphometrics strongly supports a *Pan-Homo* clade with *Gorilla* as the sister taxon (Lockwood et al., 2002, 2004; Pearson et al., 2015). Whole-genome comparisons, in combination with varying assumptions about past mutation rates, suggest that the lineage ultimately leading to living gorillas split from that of modern humans, chimpanzees, and bonobos between 8.8 and 12 million years ago (Scally et al., 2012). Further data on observed generation times in humans and great apes, and observed mutation rates in human families, estimates this split at

8 to 19 million years ago (Langergraber et al., 2012). These results are reasonably consistent with the 10 to 10.5 million-year-old teeth from Ethiopia of *Chororapithecus abyssinicus*, the only fossils to date argued to be basal members of the gorilla clade (Suwa et al., 2007). Unfortunately, here the trail of knowledge about early gorilla evolution goes remarkably cold. New fossil discoveries are a main hope for increasing knowledge of gorilla evolutionary history. However, we can learn much about gorillas and their evolution from those surviving today and the many specimens housed in natural history collections around the world (McFarlin et al., 2009; Gordon et al., 2013).

Since the gorilla first became known to science in 1847 (Wyman, 1847; Savage and Wyman, 1847), a plethora of species has been described (see Groves, 2001; Meder and Groves, 2005). The advent and development of molecular analytical methods are clarifying longstanding debates over gorilla taxonomy and systematics based on morphology alone. The emerging consensus is a model of two species with each divided into two subspecies (Fig. 1). This model is based on the fact that gorillas living in west central Africa (*Gorilla gorilla gorilla* and *Gorilla gorilla diehli*) are genetically and morphologically distinguishable from those living roughly 1,000 km farther to the east (*Gorilla beringei beringei* and *Gorilla beringei graueri*) (Schultz, 1930, 1934; Groves, 1967, 1970, 1971; Morell, 1994; Ruvolo et al., 1994; Garner and Ryder, 1996; Ruvolo, 1997a,b; Burrows and Ryder, 1997; Saltonstall et al., 1998; Jensen-Seaman and Kidd, 2001; Groves, 2000, 2001, 2003; Jensen-Seaman et al., 2003, 2004; Stumpf et al., 2003; Lockwood et al., 2002, 2004; Clifford et al., 2004; Guillen et al., 2005; Anthony et al., 2007; Pilbrow, 2010; Tocheri et al., 2011; Scally et al., 2012, 2013; Dunn et al., 2014; Das et al., 2014; Knigge et al., 2015; IUCN, 2015). Most estimated split times of this ancestral population are around 1 million years ago depending on model assumptions (Thalmann et al., 2007; Becquet and Przeworski, 2007; Scally et al., 2012; Prado-Martinez et al., 2013). The recalibrated split time estimates by Langergraber et al. (2012) are probably the most accurate as their methodology minimizes assumptions, incorporates observed human and ape

generation times, and are the most congruent with the human and great ape fossil record as currently understood. They estimate that western and eastern gorillas split sometime between 1.2 and 3.0 million years ago, based on recalibrations of earlier work (Thalmann et al., 2007; Becquet and Przeworski, 2007). Almost all recent studies of gorilla genetics also show evidence of relatively low levels of gene flow between eastern and western gorillas up until around 200,000 to 80,000 years ago (Thalmann et al., 2007) or possibly as recently as about 20,000 years ago (Xue et al., 2015).

Western gorillas show substantially larger past effective population sizes, greater genetic diversity, and greater population genetic substructure than do eastern gorillas (Thalmann et al., 2007, 2011; Scally et al., 2012, 2013; Prado-Martinez et al., 2013; Roy et al., 2014; Xue et al., 2015; Fünfstück and Vigilant, 2015). Based on microsatellite genotypes, Cross River gorillas (*G. g. diehli*) diverged ~17,800 years ago from western lowland gorillas (*G. g. gorilla*) with gene flow occurring until ~420 years ago, followed by a genetic bottleneck in Cross River gorillas ~320 years ago (Thalmann et al., 2011). In contrast, genomic analyses suggest that significant reductions in past population sizes (i.e., one or more bottlenecks) occurred in eastern gorillas subsequent to geographical isolation from their west African counterparts (Thalmann et al., 2007; Scally et al., 2012; Prado-Martinez et al., 2013; Roy et al., 2014; Xue et al., 2015). Moreover, the effective population sizes of both eastern gorilla subspecies (*G. b. beringei* and *G. b. graueri*) continued to decrease after they diverged from one another (Roy et al., 2014; Xue et al., 2015). Estimates based on autosomal genotypes suggest that the population split between mountain and grauer gorillas occurred around 10,000 years ago, with a subsequent split between the Virunga and Bwindi mountain gorilla populations around 5,000 years ago (Roy et al., 2014). The results of these genetic studies shed new and important light on previous interpretations of gorilla morphology and variation generally, and on grauer gorillas (*G. b. graueri*) in particular.

RARE CONGENITAL VARIANTS IN THE HANDS AND FEET OF EASTERN GORILLAS

During data collection for functional morphological studies of western and eastern gorilla hands and feet (Tocheri et al., 2011; Dunn et al., 2014; Knigge et al., 2015), we noted the presence of two rare congenital skeletal variants in the hands and feet of several grauer gorilla specimens from southeastern Democratic Republic of Congo (DRC). One of these two variants is a form of tarsal coalition that occurs between the navicular and intermediate cuneiform (hereafter referred to as naviculo-cuneiform II coalition) in the foot while the second is the absence of a joint between the trapezium and second metacarpal in the hand (Figs. 2–4). These initial observations led to an additional study wherein we systematically scored these two traits in a large sample of gorillas representing diverse populations, including nearly all skeletal hands and feet of eastern gorillas currently available in collections around the world.

Both of these rare traits arise prenatally, are observable in skeletons of young gorillas including infants, and are almost certainly heritable (Figs. 3 and 4). Tarsal coalitions result from malsegmentation anomalies occurring during early embryonic development leaving an abnor-

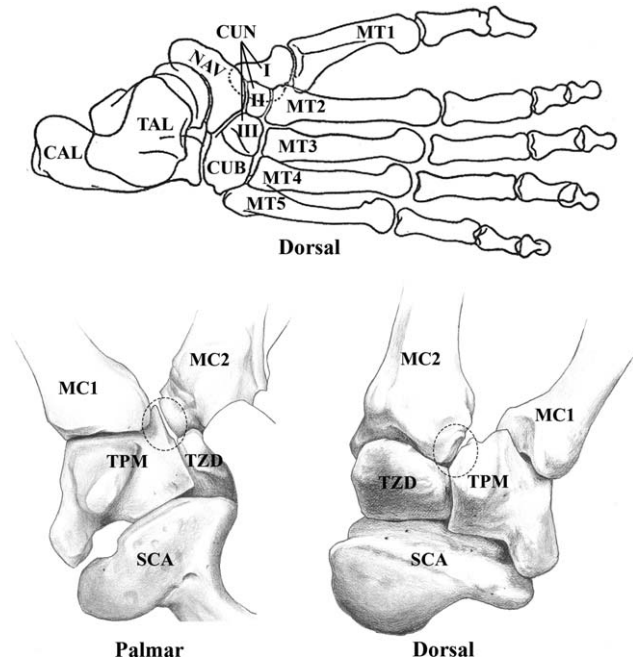


Fig. 2. (Top) Illustration of the skeletal anatomy of a gorilla right foot (CAL, calcaneus; TAL, talus; NAV, navicular; CUB, cuboid; CUN I, medial cuneiform; CUN II, intermediate cuneiform; CUN III, lateral cuneiform; MT1–5, metatarsals 1–5) (modified from Schultz, 1930). The tarsal coalition discussed in the text occurs between the navicular and the intermediate cuneiform. (Bottom) Illustration of the skeletal anatomy of a partial gorilla left hand (SCA, scaphoid; TPM, trapezium; TZD, trapezoid; MC1–2, first and second metacarpal bases) (modified from Tocheri et al., 2005). Articular facets between the trapezium and second metacarpal (highlighted by dotted oval) are often absent in eastern gorillas.

mal bridge of fibrous, cartilaginous, or osseous tissue between two bones. An absence of articular or nonarticular interzone formation in the mesenchyme between two or more presumptive tarsals leads to subsequent failure of joint cavitation, which is observable by the early fetal period (Leboucq, 1890; Trolle, 1948; Cihák, 1972; Kawashima and Uthoff, 1990). The absence of an articular joint between the trapezium and second metacarpal is not an example of carpo-metacarpal coalition. However, it probably has a similar etiology in that the mesenchymal cells ultimately do not form the mutual articular facets between these two bones that are otherwise normally present in the hands of humans, apes, and many other nonhuman primates.

Familial cases of many different tarsal coalition types have been documented within and between generations of the same family (Rothberg et al., 1935; Webster and Roberts, 1951; Wray and Herndon, 1963; Harris, 1965; Yeates, 1980; Nakajima et al., 1994), including cases occurring in both monozygotic and dizygotic human twins (Harris, 1965; Glessner and Davis, 1966; Yeates, 1980). A positive family history has been noted for affected individuals (Leonard, 1974; Kumar et al., 1992; Rouvreau et al., 1994), with one study identifying tarsal coalition in 39% of first degree relatives of index patients (Leonard, 1974). Tarsal coalition types and frequencies have been shown to vary between geographically distinct human populations (Burnett and Case, 2005; Case and Burnett, 2012; Burnett and Wilczak, 2012), but all

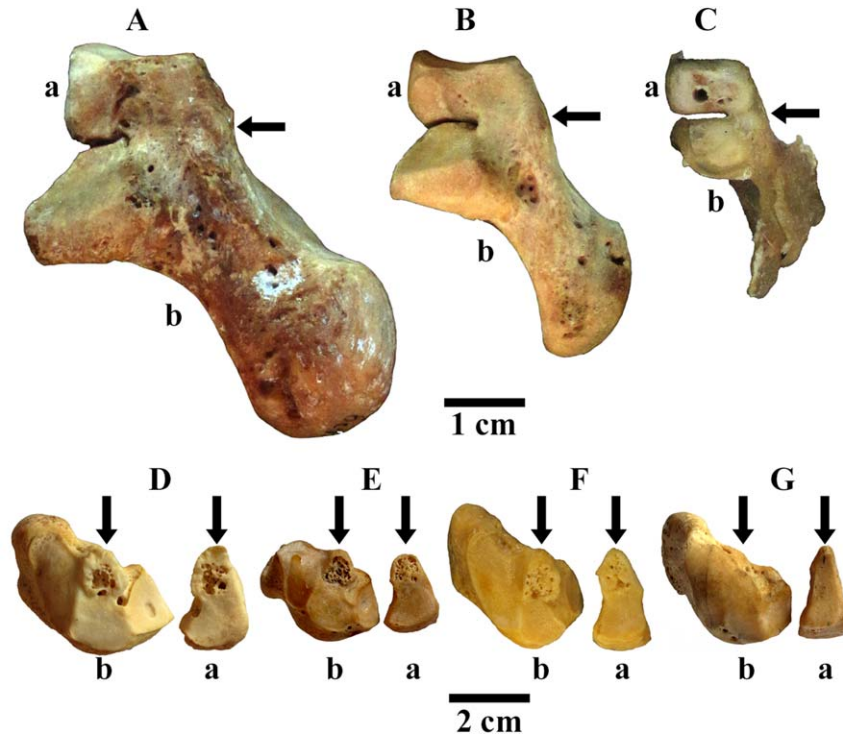


Fig. 3. Intermediate cuneiforms (a) and naviculars (b) that show osseous (A–C) and non-osseous coalitions (D–F) and normal anatomy (G). Black arrows point to the plantar portions of both bones and indicate the typical areas that coalitions occur. A, adult male grauer; B, adult female grauer; C, infant female grauer; D, adult male grauer; E, juvenile female grauer; F, adult male grauer; G, adult female western. Note in C, coalition is clearly visible even though much of the navicular has yet to ossify.

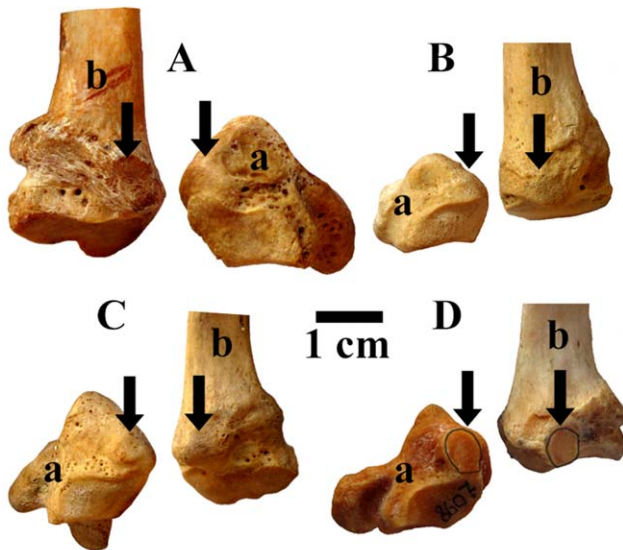


Fig. 4. Trapezia (a) and second metacarpal bases (b) that lack mutual articulating surfaces (A–C), with the expected articulation anatomy outlined and shown in D. Black arrows point to the portions of both bones where articulation is expected (A, adult male grauer; B, juvenile male grauer; C, juvenile female grauer; D, adult female mountain).

human populations seem to be characterized by an absence of isolated naviculo-cuneiform II coalition. Similar coalition patterns in Asian and Native American samples appear to support known genetic links between

native New World and ancestral Asian populations (Burnett and Wilczak, 2012).

In cases of osseous naviculo-cuneiform II coalition, a complete or partial absence of normal joint space occurs due to bony union (Fig. 3A–C). Non-osseous forms involve the two tarsals being united by a bridge of cartilage, fibrous tissue, or some combination of both that results in diagnostic pitting or an irregular bony surface on the opposing articular facets (Fig. 3D–F). In addition, an osseous rim may form on the navicular just plantar (i.e., toward the sole of the foot) to the cuneiform II facet. In cases involving the navicular and one of the cuneiforms in modern humans, the non-osseous bridge usually spans only the plantar portion of the joint with the remainder of the joint space forming normally (Burnett and Case, 2005; Choi et al., 2005). This “typical” pattern was also observed in our gorilla sample (Fig. 3).

We found skeletal evidence of naviculo-cuneiform II coalition in 61% of grauer gorillas ($N = 56$), representing all five major population regions within the DRC (Kahuzi, Itombwe, Tshiaberimu, Utu, and Maiko), and in 28% of mountain gorillas from Virunga ($N = 47$) (Tables 1 and 2; Figs. 3 and 5). These high frequencies contrast with the 0% naviculo-cuneiform II coalition found in western gorillas we examined ($N = 183$) and 0% in modern humans ($N = 1,251$) (Case and Burnett, 2012). A similar pattern is evident in the hand, where 73% of grauer gorillas we observed lacked an articulation between the trapezium and second metacarpal ($N = 48$) (Tables 3 and 4; Figs. 4 and 5). In comparison, only 27% of mountain gorillas from Virunga ($N = 55$) and 0.6% of western gorillas lacked this articulation ($N = 178$).

TABLE 1. *Naviculo-cuneiform II coalition in gorillas*

Taxon	Left side			Right side			Total by side			Total by individual					
	<i>P</i> ^a	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i> ^b	%	<i>P</i>	<i>N</i> ^c	%
Grauer	24	54	44.4	27	59	45.8	51	113	45.1	34	61	55.7	34	56	60.7
Mountain	11	55	20.0	7	56	12.5	18	111	16.2	13	66	19.7	13	47	27.7
Western	0	193	0.0	0	197	0.0	0	390	0.0	0	207	0.0	0	183	0.0

^a *P*, present; *N*, sample size; %, relative frequency.

^b Includes individuals wherein only one side was examinable and no evidence of coalition occurred.

^c Excludes individuals wherein only one side was examinable and no evidence of coalition occurred.

TABLE 2. *Naviculo-cuneiform II coalition in grauer gorilla*

Taxon	Left side			Right side			Total by side			Total by individual					
	<i>P</i> ^a	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i> ^b	%	<i>P</i>	<i>N</i> ^c	%
Kahuzi	4	5	80.0	3	4	75.0	7	9	77.8	4	5	80.0	4	5	80.0
Itombwe	14	22	63.6	14	24	58.3	28	46	60.9	18	24	75.0	18	23	78.3
Tshiaberimu	1	8	12.5	3	10	30.0	4	18	22.2	4	10	40.0	4	9	44.4
Uturu	1	8	12.5	2	9	22.2	3	17	17.6	2	9	22.2	2	8	25.0
Maiko	3	9	33.3	3	9	33.3	6	18	33.3	3	10	30.0	3	8	37.5
Unknown	1	2	50.0	2	3	66.7	3	5	60.0	3	3	100	3	3	100.0

^a *P*, present; *N*, sample size; %, relative frequency.

^b Includes individuals wherein only one side was examinable and no evidence of coalition occurred.

^c Excludes individuals wherein only one side was examinable and no evidence of coalition occurred.

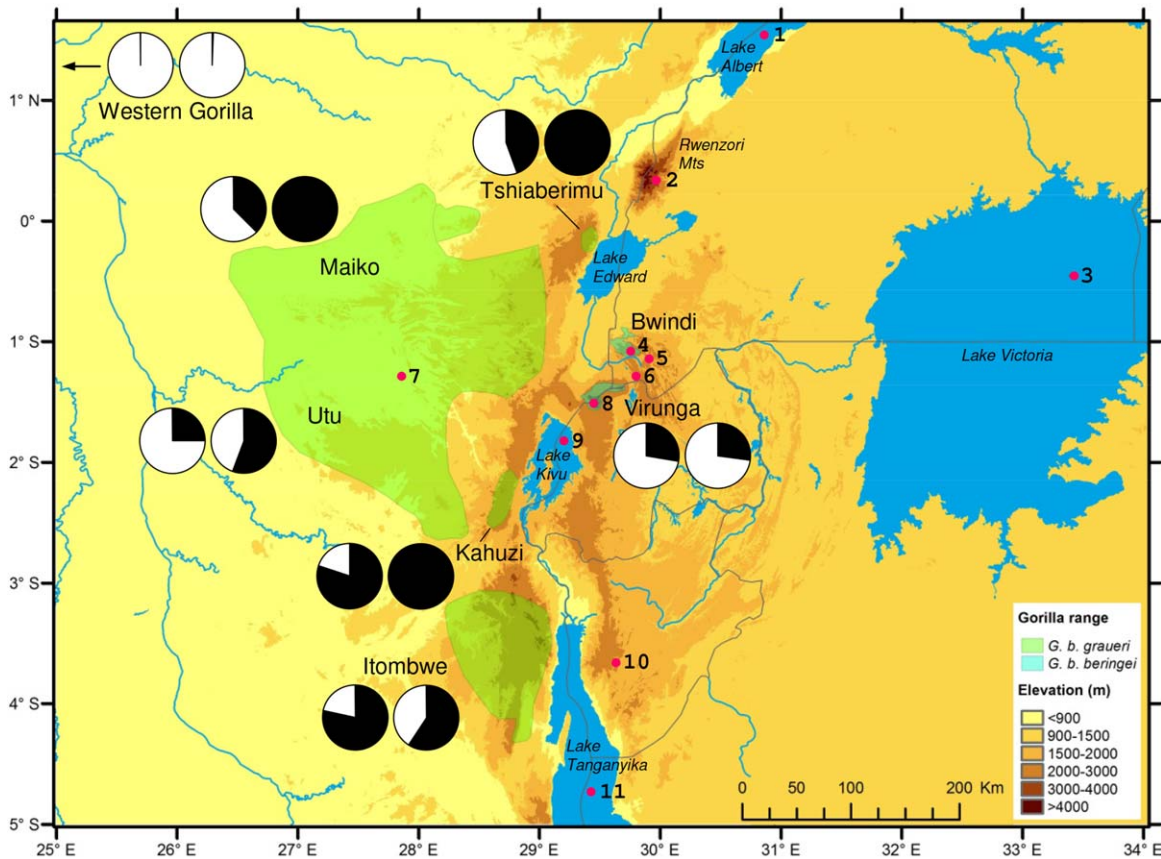


Fig. 5. Map showing the current IUCN (2015) ranges of eastern gorillas against elevation (scale shown at bottom right) and rare trait frequencies (naviculo-cuneiform II coalition shown as left pie diagram, lack of trapezium-second metacarpal articulation as right pie diagram). The numbered dots indicate the sampling locations of the published paleoenvironmental data sets referred to in the text and in Figure 6.

TABLE 3. Lack of trapezium-second metacarpal articulation in gorilla

Taxon	Left side			Right side			Total by side			Total by individual					
	<i>P</i> ^a	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i> ^b	%	<i>P</i>	<i>N</i> ^c	%
Grauer	27	41	65.9	32	54	59.3	59	95	62.1	35	55	63.6	35	48	72.9
Mountain	13	60	21.7	9	57	15.8	22	117	18.8	15	66	22.7	15	55	27.3
Western	1	184	0.5	1	189	0.5	2	373	0.5	1	195	0.5	1	178	0.6

^a *P*, present; *N*, sample size; %, relative frequency.

^b Includes individuals wherein only one side was examinable and articulation was present.

^c Excludes individuals wherein only one side was examinable and articulation was present.

TABLE 4. Lack of trapezium-second metacarpal articulation in grauer gorillas

Taxon	Left side			Right side			Total by side			Total by individual					
	<i>P</i> ^a	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i>	%	<i>P</i>	<i>N</i> ^b	%	<i>P</i>	<i>N</i> ^c	%
Kahuzi	5	5	100	5	5	100	10	10	100	5	5	100	5	5	100.0
Itombwe	12	22	54.5	11	22	50.0	23	44	52.3	13	23	56.5	13	22	59.1
Tshiaberimu	5	5	100	7	8	87.5	12	13	92.3	7	8	87.5	7	7	100.0
Utu	4	8	50.0	4	9	44.4	8	17	47.1	5	9	55.6	5	9	55.6
Maiko	0	0	0.0	3	7	42.9	3	7	42.9	3	7	42.9	3	3	100.0
Unknown	1	1	100	2	3	66.7	3	4	75.0	2	3	66.7	2	2	100.0

^a *P*, present; *N*, sample size; %, relative frequency.

^b Includes individuals wherein only one side was examinable and articulation was present.

^c Excludes individuals wherein only one side was examinable and articulation was present.

IMPLICATIONS OF THE MORPHOLOGICAL EVIDENCE FOR UNDERSTANDING THE ORIGINS AND POPULATION HISTORIES OF THE GRAUER GORILLA

The surprising and remarkably high frequencies of two otherwise rare hominid skeletal variants in eastern gorilla hands and feet (Figs. 3–5; Tables 1–4) provide new evidence to the emerging, complex genetic story of gorilla evolution during the Quaternary (Thalmann et al., 2007, 2011; Becquet and Przeworski, 2007; Scally et al., 2012; Prado-Martinez et al., 2013; Roy et al., 2014; Xue et al., 2015). There are three possible but not necessarily mutually exclusive explanations for why these skeletal variants are common among eastern gorillas: natural selection, hybridization, and genetic drift/founder effect.

It is difficult to imagine a correlated selective advantage that would drive such rare congenital variations to such high frequencies among eastern gorillas given the altitudinal range of the different forests they inhabit. Mountain gorillas and some populations of grauer gorillas (e.g., Tshiaberimu, Kahuzi, and Itombwe) live in high-altitude habitats (typically >1,300 m asl) that consist of afro-montane forests (Mehlman, 2008). Other populations of grauer gorillas (e.g., those from the lowland sector of Kahuzi-Biega National Park as well as those from Maiko National Park) survive at much lower altitudes (~600–1,300 m asl) where their habitats consist of transitional and lowland equatorial forests (Mehlman, 2008). Lowland grauers consume more fruit and climb more often than highland grauer and mountain gorillas, and their ranging patterns are also more extensive and seasonally variable, all of which is more similar to western lowland gorillas (Casimir, 1975; Goodall and Groves, 1977; Yamagiwa et al., 1992; Yamagiwa and Mwanza, 1994; Uchida, 1996; Yamagiwa et al., 1996; Doran and McNeilage, 1998, 2001; Robbins and McNeilage, 2003). It is possible that these rare skeletal traits are selectively neutral in highland environments where climbing behaviors and concomitant morphology (e.g., more mobile hands

and feet) are less frequently required (Dunn et al., 2014; Knigge et al., 2015). In contrast, these traits are probably selected against in lowland habitats where gorillas climb significantly more often (e.g., Doran and McNeilage, 1998) and this may explain the lower frequencies of naviculo-cuneiform II coalition we observed in the lowland grauer populations (Table 2) as well as the otherwise extreme rarity of these two traits in western gorillas (Tables 1 and 3). Overall, however, natural selection offers only a weak causal explanation for the high frequencies of these two traits among eastern gorillas.

Ackermann and Bishop (2010) hypothesized that there has been recent hybridization (i.e., secondary admixture) among diverging gorilla lineages based on evidence of rare craniodental traits in some populations (e.g., relatively high frequencies of anomalous fourth molars in grauer and Cross River gorillas). More specifically, they suggested that grauer gorillas may represent evidence of a hybrid zone between western and mountain gorillas or the result of a hybrid zone that occurred sometime earlier (Ackermann and Bishop, 2010). This hypothesis has received little support from the growing body of gorilla genetic evidence (Thalmann et al., 2011; Scally et al., 2012; Prado-Martinez et al., 2013). Instead, low levels of gene flow appear to have occurred over long periods of time subsequent to gorilla population splits (Thalmann et al., 2011; Scally et al., 2012; Prado-Martinez et al., 2013) but likely ceased between western and eastern populations by around 200,000 to 80,000 years ago (Thalmann et al., 2007) or perhaps by about 20,000 years ago (Xue et al., 2015). An important parallel case involves Bornean orangutans for which fourth molars have been documented in unusually high relative frequencies (~20%) (Selenka, 1896, 1898; Hrdlička, 1906). Analysis of mtDNA haplotypes suggests that a small refugium population of Bornean orangutans survived through a substantial rainforest contraction that was accompanied by an extended cold period between 190,000 and 130,000 years ago (Arora et al., 2010).

Prado-Martinez et al. (2013) found that Bornean orangutans (and grauer gorillas) show substantially reduced relative levels of X chromosome and autosomal diversity compared with other ape species and neutral expectations. Thus, comparatively lower past effective population sizes exacerbated by severe bottlenecks and associated founder effects offer a much better explanation for high frequencies of rare skeletal and dental traits in eastern gorillas compared with those invoking significant hybridization/secondary admixture.

The fact that these rare traits are more than twice as common in grauer than mountain gorillas raises important evolutionary and biogeographical questions because grauers occupy a present (or at least recently historic) range more than ten times the size of that of mountain gorillas (Mehlman, 2008). The most parsimonious explanation, and one that is consistent with current genetic evidence (e.g., Scally et al., 2012; Prado-Martinez et al., 2013; Roy et al., 2014; Xue et al., 2015), is that one or more severe bottleneck events after the divergence with western gorillas enabled these rare traits to establish a foothold within the ancestral eastern gorilla gene pool. Moreover, the higher frequencies of these rare traits in grauer gorillas underscore the likelihood that the grauer lineage is the result of a relatively recent founder effect from a late Pleistocene/early Holocene refugium of eastern gorillas (Leigh et al., 2003; Mehlman, 2008; Dunn et al., 2014), which were probably highland-adapted in ways similar to living mountain gorillas (Schultz, 1934; Groves, 2001; Tocheri et al., 2011; Ruff et al., 2013; Dunn et al., 2014; Knigge et al., 2015).

Many other studies of gorilla morphology (Uchida, 1998; Albrecht et al., 2003; Inouye, 2003; Leigh et al., 2003; Taylor and Groves, 2003; Pilbrow, 2010; Barks et al., 2014) are also consistent with low levels of genetic diversity observed among grauer gorillas (Ruvolo et al., 1994; Garner and Ryder, 1996; Ruvolo, 1997a; Saltonstall et al., 1998; Yu et al., 2004; Prado-Martinez et al., 2013). Using a combination of metric and discrete cranial data, Leigh et al. (2003) suggested that grauer populations may have been considerably smaller during the late Pleistocene than in the present day and that, conversely, mountain gorilla populations may have been larger but subsequently diminished more recently. Furthermore, male grauers exhibit the lowest craniofacial metric diversity among all gorillas (Albrecht et al., 2003) and strikingly high frequencies of a rare neuroanatomical feature—fusion of the temporal cortex and posterior insula—occur in mountain (62%) and grauer gorillas (100%) (Barks et al., 2014).

Most gorilla social groups are led by one adult male (i.e., a silverback), with multiple adult females and their offspring, but approximately half of mountain gorilla social groups have multiple resident adult males (Schaller, 1963; Fossey, 1974; Harcourt, 1979; Robbins, 1995; Watts, 1996; Bradley et al., 2005; Vigilant et al., 2015). The dominant silverback has been shown to sire the majority of offspring (~72%) in these stable multimale groups (Bradley et al., 2005; Vigilant et al., 2015). Given the mating strategies and social behaviors of gorillas, and that grauer males show the lowest craniofacial diversity among all gorillas (Albrecht et al., 2003), these rare traits were probably initially present in at least one or more founding silverback males. Any alternative hypothesis requires many additional steps to explain why such a large percentage of grauer gorillas living during the past century and across such a relatively large geographical/

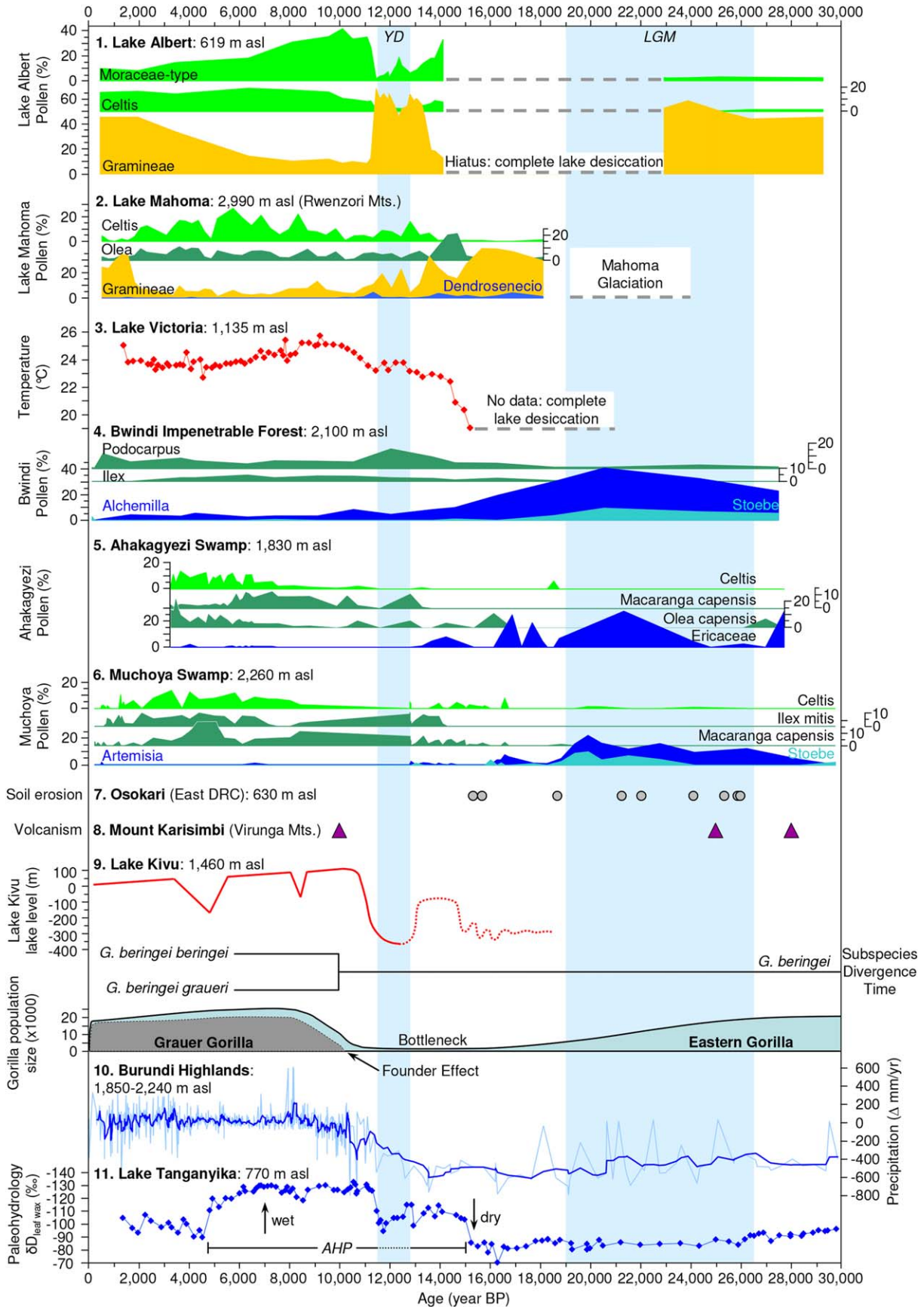
altitudinal range display these two congenital variants that otherwise occur in less than 1% of western gorillas.

Living mountain gorillas from the Virungas offer a potential modern analog for the founder-effect hypothesis for grauer gorilla origins. Group 5, a well-documented group of mountain gorillas from the Virunga Volcanoes, was first studied by Dian Fossey in 1967 (Fossey, 1983). Daily monitoring of descendants of Group 5 continues to the present day by Karisoke Research Center staff (Robbins et al., 2011). Group 5 is arguably the most successful of those first observed by Fossey that survived the severe population crash in the 1960s and 1970s and descendants of this group have contributed significantly to the increasing numbers of mountain gorillas over the past three decades (Robbins et al., 2011). Of the 13 mountain gorillas observed by us with naviculo-cuneiform II coalition, five (38%) are either first or second-generation descendants of Group 5 (Fossey, 1983; Williamson and Gerald-Steklis, 2001; Bradley et al., 2005; Stoinski et al., 2009; Robbins et al., 2011; Vigilant et al., 2015), demonstrating, as expected, how rare trait frequencies can increase substantially in small populations of gorillas over the course of a few generations. Although more research on mountain gorilla skeletal material from the Virungas is needed to calculate precise heritability estimates for these rare morphological traits, it is logical that the original founders of the grauer lineage were probably similar demographically to Group 5.

THE PALEOENVIRONMENTAL CONTEXT OF GRAUER GORILLA ORIGINS

The Pleistocene undoubtedly presented extreme survival challenges for all gorillas unable to find suitable refugia, as African paleoclimate and paleoenvironmental records show significant reductions in suitable forest habitats compared with today (Livingstone, 1967; Hamilton, 1982; Bonnefille et al., 1990; Taylor, 1990, 1993, 1996; Johnson et al., 1996; Beuning et al., 1997; Jolly et al., 1997; Marchant et al., 1997; Street-Perrott et al., 1997; Bonnefille and Chalié, 2000; Gasse, 2000; Runge, 2000, 2001a, 2001b; Schefuß et al., 2005; Anthony et al., 2007; Tierney et al., 2008; Kelly et al., 2014). These data provide key context for interpreting the recent evolutionary history of eastern gorillas, including where populations ancestral to all living mountain and grauer gorillas survived during the late Pleistocene (Fig. 6). During the Last Glacial Maximum (LGM), which occurred 26,500 to 19,000 years before present (BP) (Clark et al., 2009), temperatures in equatorial Africa were reduced by around 4°C as compared with today (Bonnefille et al., 1990; Tierney et al., 2008). Lower temperatures in conjunction with weakened monsoon circulation and reduced moisture transport from the Atlantic Ocean led to a significant reduction in rainfall (Gasse, 2000; Schefuß et al., 2005; Tierney et al., 2008). In central equatorial Africa, where the mean annual precipitation is between 1,360 and 1,750 mm today, annual rainfall was ~400 mm lower during the LGM (Figs. 5 and 6) (Bonnefille and Chalié, 2000).

The cold and arid conditions during the LGM resulted in an eastern central African environment with limited habitat suitable for gorillas in the current and surrounding eastern gorilla ranges. To the north, pollen data from Lake Albert (619 m asl) indicate that the regional vegetation was dominated by savanna and grasslands between 29,000 and 23,000 years ago (Beuning et al.,



1997) (Figs. 5 and 6). If any eastern gorilla populations had survived in this region earlier during the Pleistocene, they would have been forced to disperse west or face extinction as forested habitats disappeared completely by 29,000 years ago. It is possible that the signals of gene flow between eastern and western gorillas found by genetic analyses are the result of eastern gorillas dispersing westwards north of the Ubangi River during middle to late Pleistocene glacial periods, probably following patchy forest corridors surviving along the banks of the river.

In the highlands along the Albertine Rift, glacial climatic conditions depressed montane forest belts by more than 1,500 m in elevation (e.g., Hamilton, 1982) and resulted in substantial glacier advance in the Rwenzori Mountains (Kelly et al., 2014). Glaciers extended down the Rwenzori Mountains to elevations of 3,000 m and in some valleys even to ~2,000 m asl, over 2,700 m lower than today (Livingstone, 1967; Kelly et al., 2014). The prevailing aridity together with lowered atmospheric CO₂ concentrations throughout the LGM favored the spread of grasslands on East African mountains (Street-Perrott et al., 1997), including the Rwenzori's where alpine grasslands dominated the vegetation at least until 15,000 years BP (Livingstone, 1967) (Figs. 5 and 6). If eastern gorillas ever inhabited the Rwenzori's, these late Pleistocene conditions would have ensured their extinction. Eastern chimpanzees (*Pan troglodytes schweinfurthii*) clearly populated this area following the return of lowland forests well after the LGM whereas gorillas have not, despite the fact that montane forests have returned as well.

Most East African equatorial lakes, including Lakes Victoria, Kivu, Tanganyika, Albert, and Edward, either dried up completely or maintained comparatively low lake levels between about 30,000 and 15,000 years BP (Haberyan and Hecky, 1987; Johnson et al., 1996; Beuning et al., 1997; Snoeks et al., 1997; Laerdal et al., 2002; Verheyen et al., 2003; Elmer et al., 2009) (Fig. 6). The arid conditions resulted in savanna and grasslands spreading extensively across the regions surrounding these lakes (e.g., Tshiaberimu, Itombwe) that were formerly forested (e.g. Beuning et al., 1997) (Figs. 5 and 6), leaving few if any potential refugia for eastern gorillas in these locations.

A Pleistocene rainforest refugium in the eastern DRC has been suggested by some authors (e.g., Hamilton, 1982; Endler, 1982), and largely corresponds to the pres-

ent lowland ranges of grauer gorillas in Utu and Maiko (Fig. 5). However, in the center of this range at Osokari (630 m asl), geomorphological evidence of strong erosional and depositional activity during the LGM indicates open savanna vegetation that could not stabilize the soil surface as the dense tropical rainforest does there today (Runge, 2000, 2001a,b) (Figs. 5 and 6). This finding suggests that the proposed forest refugium was likely much smaller and discontinuous, as previously indicated by Colyn et al. (1991). Instead of harboring rainforest vegetation, the land below ~1,000 m in the present grauer gorilla range was covered by open savanna woodland, and closed forests were restricted to a few highland areas above ~1,000 to 2,000 m (e.g., Kahuzi) or along river valleys (Colyn et al., 1991; Runge, 2000). However, pollen-analytical studies from the eastern Congo lowlands are needed to clarify the true extent of rainforest during the LGM and afterwards. While it is possible that eastern gorillas may have survived in this area during the LGM, the likelihood appears low. Instead, the late Pleistocene and LGM refugium for eastern gorillas was probably located within the range of mountain gorillas living today.

Although the Bwindi Impenetrable Forest is often considered to have been a LGM refugium for eastern gorillas (e.g., Roy et al., 2014), detailed inspection of the available paleoenvironmental reconstructions suggests otherwise. Pollen records from the southwestern highlands of Uganda (including Bwindi, Muchoya, and Ahakagyezi), between 1,800 and 2,300 m asl, indicate that montane Ericaceous scrublands dominated by Ericaceae, *Artemisia* spp., *Alchemilla* spp., and *Stoebe* spp. largely replaced moist montane forests from about 30,000 years BP until around 16,000 to 15,000 years BP (Figs. 5 and 6) (Taylor, 1990, 1993, 1996; Jolly et al., 1997; Marchant et al., 1997). At present, this Ericaceous scrub community is found above 2,700 to 3,000 m in the East African highlands (Hedberg, 1951). Moreover, montane forest belts would not have shifted to higher elevations because of lower atmospheric CO₂ concentrations and glacial aridity across the greater region (Hamilton, 1982). During the LGM and presumably during earlier glacial periods as well, montane forests were strongly reduced in area and separated into isolated pockets by open savanna and grasslands that dominated the intervening lowlands. Thus, we hypothesize that the Virunga Mountains acted as the primary refugium for eastern gorillas

Fig. 6. Summary of the African paleoclimate and paleoenvironmental records from along the Albertine Rift used to reconstruct eastern gorilla evolution during the past 30,000 years (AHP, African Humid Period; YD, Younger Dryas; LGM, Last Glacial Maximum). All radiocarbon dates of pollen data sets (except from Lake Albert) and of the Osokari erosion record were recalibrated with the SHCal13 calibration curve. The numbered records are arranged from north (top) to south (bottom) and correspond to the numbered locations shown in Figure 5. For pollen data, only selected pollen types are shown and the pollen percentages are based on an upland pollen sum (lowland tree taxa of moist forests, light green; montane forest tree taxa [elevation range ~2,000–3,000 m], dark green; grasses, yellow; high-altitude shrub and herb taxa of the ericaceous and alpine vegetation belts currently largely restricted to elevations above 3,000 m [e.g., Hedberg, 1951], dark and light blue, respectively). From top to bottom: (1) Lake Albert pollen record (Beuning et al., 1997); (2) Lake Mahoma pollen record (Livingstone, 1967) and Mahoma glaciation of the Rwenzori Mountains based on dated moraines (Kelly et al., 2014); (3) lake surface temperature record of Lake Victoria (Berke et al., 2012) based on the TEX86 paleotemperature proxy; (4) Bwindi pollen record (MB3 core) (Marchant et al., 1997); (5) Muchoya pollen record (MC2 core) (Taylor, 1990); (6) Ahakagyezi pollen record (AH2 core) (Taylor, 1990, 1993); (7) Osokari soil erosion record represents radiocarbon dates of wood/tree trunks that were buried by hillwash in presumably open savanna woodland (Runge, 2000, 2001a,b); (8) volcanic eruptions of Mount Karisimbi based on K-Ar dates of lavas (De Mulder and Pasteels, 1986); (9) lake level record of Lake Kivu (Hecky and Degens, 1973 (dotted line); Zhang et al., 2014 (continuous line)), eastern gorilla subspecies divergence estimates (Roy et al., 2014), and scenario of eastern gorilla effective population sizes (i.e. reproducing individuals) based on Roy et al. (2014) for the past 10,000 years and possible earlier changes based on paleoenvironmental data; (10) Burundi highlands precipitation reconstruction based on pollen transfer functions from nine pollen sequences (Bonnefille and Chalié, 2000); (11) Lake Tanganyika deltaD leaf wax record (Tierney et al. 2008) with more negative isotope values indicating wetter climatic conditions.

during the late Pleistocene. It is the only area within this region that likely maintained enough suitable montane forested habitat for gorillas due to its multiple peaks, wide elevation range, and the absence of glaciation (e.g., Osmaston, 2004).

During the LGM and the early deglacial period that followed, more than 12,000 years of adverse environmental conditions likely resulted in the extinction of all isolated eastern gorilla groups, except those surviving in the Virungas. However, even the Virunga population probably experienced a dramatic decline due to these adverse environmental conditions. A bottleneck before the divergence of the eastern gorilla into the mountain and grauer gorilla lineages is supported by whole-genome sequencing (Xue et al., 2015). The lower temperatures and reduced precipitation that characterize the LGM also persisted during the early deglacial period until around 15,000 years BP. Temperatures and precipitation then increased abruptly at the onset of the so-called African Humid Period (~15,000–5,000 years BP) (deMenocal et al., 2000). This humid period was interrupted by the Younger Dryas cold period (12,800–11,700 years BP), which caused a return to quasi-glacial conditions as exemplified by a 380 m lower lake level at Lake Kivu (Zhang et al., 2014) and the spread of grasslands in both the highlands and lowlands (Fig. 6). Following the Younger Dryas, temperatures and precipitation rose to their absolute maxima for the past 30,000 years at the onset of the Holocene. For instance, 10,000 years ago, the level of Lake Kivu was 100 m higher than at present (Zhang et al., 2014). These humid conditions prevailed until around 5,000 years BP across equatorial East Africa (e.g., Tierney et al., 2008) (Fig. 6).

With the onset of humid conditions, either immediately before or directly after the Younger Dryas interval, a group of eastern gorillas likely dispersed westward from the Virungas with the expanding forests into present-day grauer range in the highlands northwest of Lake Kivu. This group probably became separated from the main Virunga population by volcanic activity and extensive lava flows of Mt. Karisimbi at ~10,000 years ago (De Mulder, 1985; De Mulder and Pasteels, 1986) (Fig. 6) as well as by the formation of the presently active Nyiragongo and Nyamuragira volcanoes around this same time (Pouclet, 1977). Eruptions from the caldera of Mt. Karisimbi and a southwest chain of more than 100 parasitic cones have formed a broad lava plain that extends all the way to the modern shores of Lake Kivu (Pouclet, 1977; De Mulder, 1985; MacKay et al., 1998), and neither Nyiragongo nor Nyamuragira are inhabited by gorillas today. The individuals within this group almost certainly had a disproportionately high frequency of the two congenital variants discussed above compared with the entire eastern gorilla population at that time and represent the founders of the grauer lineage.

The humid and warm climate of the early Holocene, in concert with rising CO₂ concentrations, resulted in rapid expansion of forests across the lowlands as well as upward migration of montane forests in the highlands (Figs. 4 and 6). The presently disjunct ranges of living grauer gorillas were one contiguous forest sector during this time and the founding group likely underwent rapid expansion in numbers as descendants dispersed widely into the available forests. The Virunga population, now cut off by volcanic barriers to the west, dispersed northward into the larger Bwindi region and upwards on the

Virungas, while also rapidly increasing in numbers as suggested by genetic analysis (Roy et al., 2014) (Figs. 5 and 6).

The end of the African Humid Period at around 5,000 years BP marks the onset of rainforest decline, the spread of grassland and savanna in the lowlands (Beuning et al., 1997), and the separation of the Bwindi and Virunga mountain gorilla populations (Roy et al., 2014) (Figs. 5 and 6). Human induced deforestation in western Uganda began around 2,000 years ago as shown by the decline of montane tree taxa and the increase of grass pollen in available palynological records (Livingstone, 1967; Taylor, 1990). In the Virungas, forest clearance began around 1,000 years ago (McGlynn et al., 2013). Together, climatic and anthropogenic deforestation clearly led to the fragmentation of formerly connected forest areas and the consequent separation of Virunga and Bwindi gorilla populations into their present ranges followed by reductions in population sizes. Genetic evidence suggests that the separation of the Bwindi and Virunga mountain gorilla populations started around 5,000 years ago (Roy et al., 2014).

CONCLUSION

Teasing apart the respective contributions of genetic drift and natural selection to the patterns of genetic, morphological, and behavioral diversity observed in living and fossil organisms is a central goal underlying all fields of evolutionary biology. A founder effect explains the genetic and phenotypic consequences of colonization of a new area by a small number of individuals that become reproductively isolated from the larger population from which they derive (Mayr, 1954). The power of the founder effect in explaining the origins of new taxa has been continuously debated on both theoretical and experimental grounds (Lewontin, 1965; Carson, 1968; Lande, 1980; Barton and Charlesworth, 1984; Carson and Templeton, 1984; Meffert and Bryant, 1991; Rice and Hostert, 1993; Galiana et al., 1995; Gavrilets and Hastings, 1996; Slatkin, 1996; Templeton, 1996; Grant et al., 2001; Clegg et al., 2002; Grant, 2002). A major confounding issue with regard to detecting unambiguous founder effects in natural populations is that the effects are easily obscured or erased entirely by processes such as repeated immigration of new individuals or subsequent bottlenecks (Grant, 2002). Thus, most examples of founder effects are historical (i.e., within hundreds of years) and the evolutionary implications over longer periods of time are less certain. In this respect, eastern gorillas—and grauers especially—may offer a useful comparative model for further studies of longer-term founder effects in general, and the role of extreme bottlenecks and possible founder events during human and great ape evolution in particular.

Finally, low genetic diversity negatively affects adult survivorship (Wright, 1977; Caughley, 1994; Nei, 1997; Amos and Balmford, 2001; Reed and Frankham, 2003; Frankham, 2005; Bergl et al., 2008) and puts eastern gorillas at severe risk of extinction. Further complicating matters, the continuing deforestation of gorilla habitat, high levels of human predation and bushmeat trafficking, infectious disease, including the reduction of western gorilla populations by the ebola virus, greatly increases the risk of gorilla extinction (Harcourt, 1996; Walsh et al., 2003; Yamagiwa, 2003; Leroy et al., 2004; Bermejo et al., 2006; McNeilage et al., 2006; Rizkalla

et al., 2007; Robbins et al., 2011). Given the current threats to eastern gorillas and their low levels of genetic diversity (Xue et al., 2015; Fünfstück and Vigilant, 2015), both eastern subspecies are at grave risk of extinction as their currently depleted numbers would suggest. Conservation efforts to protect both eastern gorillas must therefore be treated with continued and increasing urgency (e.g., Robbins et al., 2011). However, if grauer gorillas have truly rebounded from such an extreme bottleneck roughly 10,000 years ago, then there is a glimmer of hope that they could do it again, albeit this time with concerted and continued help from one of their closest living relatives, *Homo sapiens*.

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