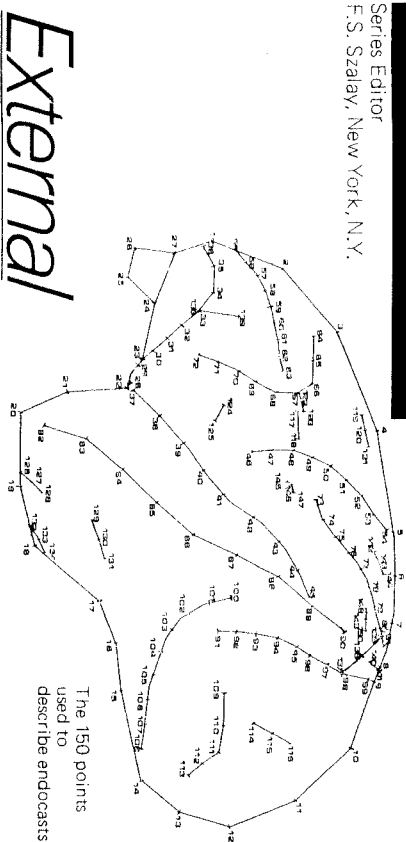


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External Neuroanatomy of Old World Monkeys (Cercopithecoidea)

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This study entails an analysis of cortical brain morphology of all genera of cercopithecooid monkeys. For each genus, computer-drawn plots (which illustrate the mean endocran of infants, juveniles and adults) are provided, along with normal descriptive statistics for lengths of sulci and areas of lobes and limb and face regions. Modern cortical maps of primates (based on cytoarchitectonic analyses and the method of evoked potentials) show that sulci delimit functional areas of cortex such as sensory/motor regions allocated to hindleg, arm and face functions. Sulcal patterns of cercopithecooids are interpreted in

light of these cortical maps, taken from the literature. Differences in brain morphology are determined at the sub-family level, selective pressures which may have been responsible for cortical differences are discussed, and the widely held assumption that Old World monkey cortices are symmetrical is tested and rejected. The results of this study may have implications for understanding the evolution of handedness and language in man.



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Systematic Relationships of Gorillas from Kahuzi, Tshaberimu and Kayonza

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Key Words: *Gorilla* · Virunga · Kahuzi · Tshaberimu · Kayonza · Systematics · Clines · Montane adaptation · Hot-spots

Abstract: Previous classifications of gorillas from Mt. Kahuzi, Mt. Tshaberimu and the Kayonza Forest, placing them in *Gorilla gorilla graueri* or *G.g. beringei*, somewhat oversimplify a complex situation. Both Kahuzi and Tshaberimu gorillas are close to *graueri* and should be placed in that subspecies, but each (in different ways) shows some approach to *beringei*, either through independent adaptation to extreme montane conditions, or because they may be points along a (now disrupted) cline from one race to the other. A hypothesis for the dispersal of *beringei* is presented, making use of geophysical data on the movement of the African plate over the Virunga 'hot-spot'.

Introduction

The question of the subspecific allocation of the gorillas of the Mt. Kahuzi region, Zaire, has recently been renewed [Casimir, 1975; Goodall and Groves, 1977]. Previously, Groves [1970a, b] had proposed to place them in the subspecies *Gorilla gorilla beringei*, along with the topotypical population of the Virunga volcanoes; though with some misgivings. We feel it is now worthwhile, on the basis of certain new information, to review the matter, along with the question of the position of the other border populations between *G.g. beringei* and *G.g. graueri*: those from the Tshaberimu massif and from the Kayonza Forest.

The exact subspecific classification of these populations is, of course, of less importance than the assessment of their genetic relations to one another and to

the two polar forms of the eastern region. Light shed on this problem could in turn suggest solutions to questions of dispersal patterns in the past, and the relative effects of isolation and adaptation in the differentiation of populations.

Results and Discussion

Previous Theories

In the Discriminant Analysis (Mahalanobis D^2), Groves [1970a, p. 296] found that the Kahuzi sample — 1 male, 2 female crania; 2 male, 1 female mandibles — falls close to those from Tshiaberimu and 'Mwenga-Fizi' (= the Itombwe mountains), while the Kayonza sample — 4 male, 3 female crania, 1 male mandible — was close to 'Mwenga-Fizi' and not much further from Virunga. On this basis, it was proposed that the Kayonza forest gorillas belong to *graueri*; but the evidence of postcranial indices suggested that Kahuzi gorillas belong to *beringei*.

The gorillas from Mt. Tshiaberimu, of which a large enough sample was available to make this group part of the main analysis, proved to be very close to 'Mwenga-Fizi', less so to Virunga. The other population of the eastern region, from the Utu lowlands, is not an 'odd-man-out' as might be inferred from all this, as its distance from 'Mwenga-Fizi' was the closest of all in the eastern region.

On the basis of new skull material, Casimir [1975] preferred to allocate the Kahuzi form to *graueri*, without, however, discussing the postcranial data which had been decisive in Groves's [1970a, b] assignment of it to *beringei*. Since then, a number of other correspondents [notably D. Cousins, D. Fossey and A.G. Goodall] have indicated to one or both of us their dissatisfaction with the alliance of the Kahuzi and Virunga populations, while the dangers inherent in any ill-considered judgement have been highlighted by the recent proposal by MacKinnon [1976] to infuse 'new blood' into the declining Virunga population by translocating some gorillas from the increasing Kahuzi population, on the grounds that they were supposed to be the same subspecies: a proposal forcefully confuted by Harcourt [1977].

It is clearly time to reassess the position. The two eastern subspecies, *graueri* and *beringei*, are very easily differentiated and can be distinguished cranially, postcranially and externally: the former is topotypically from the Itombwe mountains, west of the northern end of Lake Tanganyika, and — as instanced by the skull data, above — extends into the Utu region of Schaller [1963], the lowland forests of eastern Zaïre between about 0.30° and 3.00° S; the latter is

the population from the six extinct Virunga Volcanoes (central and eastern clusters), straddling the Zaïre-Rwanda-Uganda border. Three other populations intervene geographically between these two: on Mt. Kahuzi (broadly speaking, the Kahuzi-Biega National Park), Mt. Tshiaberimu (near Lubero at the northern end of the Virunga National Park), and the Kayonza or Impenetrable Forest, in Uganda about 15 mi to the north of the Virunga range. Not only the Kahuzi population, but the other two also, are actually or potentially equivocal in their systematic affiliation.

Eastern Subspecies of Gorilla

The differences between the two well-defined eastern subspecies are as follows:

1. *Gorilla gorilla graueri* Matschie, 1914. Eastern Lowland Gorilla.
 - (a) Skull smaller (from table I, cranial length averages about 187 mm in males, 156–160 mm in females, of both Utu and Itombwe populations); palate shorter in males, but no real difference in females; jaw angles not flaring; ascending ramus low, gonion to condyle [Vogel, 1961].
 - (b) Humerus long (high femur-humerus index, low brachial index and clavicle-humerus index). Great toe short, heel-to-hallux-tip only 84% of heel-to-second-tip.
 - (c) Mental foramen multiple in two-thirds to three-quarters of cases; infra-orbital foramen multiple in 90–100%; mental foramen in forward position (anterior to P.) in under 20%; 'rocking jaws' uncommon.
 - (d) Vertebral border of scapula generally straight.
 - (e) Hair relatively short, especially on scalp and around face.
 - (f) Nose with rounded nostrils, well-padded alae, and tending not to be strongly outlined above; upper lip diffusely padded below nose, the padding extending about two-thirds down the lip [see photos in Schouteden, 1947, fig. 11, 12 (Itombwe), 14 (Utu)]; (fig. 1, from Utu).
2. *Gorilla gorilla beringei* Matschie, 1902. Mountain gorilla.
 - (a) Skull larger (cranial length in male 200 mm, in female 167 mm); palate longer in males, jaw angles enormously flared in both sexes; ascending ramus high, muscularly moulded, more differentiated in females [Vogel, 1961].
 - (b) Humerus short. Great toe long, stout, springing from sole 75% of the distance from heel to tip of second toe [Schulz, 1934].
 - (c) Mental foramen multiple in over 90%; infraorbital foramen less often multiple; mental foramen in forward position in one-third of cases; 'rocking-jaws' common.

Table 1. Comparisons of Kahuzi gorillas

	Utu		Itombwe		Tshiaberimu		Kahuzi		Virunga		Kahuzi closest to
	X	σ	X	σ	X	σ	X	σ	X	σ	
<i>(a) Skeletal measurements</i>											
Male	(n = 12)		(n = 11)		(n = 12)		(n = 8)		(n = 13)		
Cranial length, mm	186.5	6.3	187.4	7.8	190.0	5.1	188.0	7.4	200.2	11.9	Itombwe
Palate length, mm	126.3	4.9	128.8	3.3	132.7	4.4	135.0	6.1	134.8	4.4	Virunga
Bigonial breadth, mm	128.4	8.1	136.1	5.2	145.2	7.7	129.5	9.3	144.6	8.8	Utu
Female	(n = 11)		(n = 12)		(n = 11)		(n = 4)		(n = 11)		
Cranial length, mm	160.2	5.2	156.2	5.1	162.4	5.1	159.3	3.9	166.8	6.2	Utu
Palate length, mm	100.3	5.4	105.6	3.8	107.8	5.0	109.3	1.0	105.8	2.5	Tshiaberimu
Bigonial breadth, mm	104.0	4.8	106.4	4.1	115.9	7.0	107.0	5.3	121.6	4.8	Itombwe
Combined	(n = 8)		(n = 18)		(n = 10)		(n = 4)		(n = 20)		
Femur-humerus index	118.5	3.0	117.7	2.2	118.0	2.2	115.1	1.5	113.4	3.9	Virunga
Brachial index	79.2	1.1	76.8	1.9	78.1	2.2	80.7	1.4	83.2	2.9	Utu
Clavicle-humerus index	38.1	2.9	37.4	1.7	39.3	2.6	39.9	1.6	42.9	1.7	Tshiaberimu
Hallux ray to foot	—		83.7	1.7	89.3	1.6	87.9	1.4	90.4		Tshiaberimu
			(n = 7)		(n = 2)		(n = 2)		(n = 1)		
<i>(b) External measurements</i>											
Male (only)	(n = 1)		(n = 1)		(n = 1-2)		(n = 1-3)		(n = 8-9)		
Weight, kg	150		—		180		208.6		158.6	29.6	
Height, cm	196 (?)		153		174.5	30.4	176.8	34.5	170.4	13.4	
Girth, cm	155		134		168		149.4	7.7	147.5	10.1	
Foot length, mm	—		—		325		292.0	6.8	295.0	19.1	
Hand length, mm	—		—		250		237.5	5.0	254.0	0.0	(n = 2)
<i>(c) Skeletal frequencies</i>											
	Utu		Itombwe		Tshiaberimu		Kahuzi		Virunga		Kahuzi closest to
	%	n	%	n	%	n	%	n	%	n	
Multiple mental foramina	62.0	36	77.0	31	66.7	30	53.8	13	91.3	46	Utu
Multiple infraorbital foramina	88.1	40	100.0	34	83.8	38	95.0	10	76.8	53	Utu/Itombwe
Mental foramen anterior to P ₁	3.0	36	17.8	31	6.7	30	18.2	11	32.5	46	Itombwe
Bifid mandibular condyle 'Rocking jaws'	42.9	36	8.9	31	39.1	30	80.0	10	47.3	55	—
Vertebral border of scapula sinuous	15.4	36	17.8	31	37.0	30	40.0	5	42.6	47	Tshiaberimu/Virunga
Mean number of mental foramina	18.8	8	0.0	24	11.1	9	100.0	4	84.5	13	Virunga
	2.0	26	2.5	31	2.0	30	1.9	9	2.6	49	Utu/Tshiaberimu



Fig. 1. Typical *Gorilla g. gorilla* adult male, captured in Ulu lowlands by C. Cordier, Antwerp Zoo. Photo C.P. Groves.

(d) Vertebral border of scapula sinuous.

(e) Hair long, shaggy, noticeably on scalp and forming a long beard with cheek whiskers, surrounding and partially obscuring face; supraorbital toms covered with shaggy hair.

(f) Nose with angular nostrils, less padded alae, and well-outlined above and below; upper lip clearly padded only a little below nose, the padding not extending more than halfway down the lip [see, for example, the photos in Schaller, 1963; and Root's photos reproduced in Groves, 1970b].

There are some qualifications needed here. By and large, the Ulu and Lombwe population of *gorilla* are very similar: more alike, perhaps, than would be predicted from their different altitudinal ranges. The Lombwe sample – gorillas living at altitudes which approach those of *beringei* – have more flared jaw angles and slightly higher frequency of multiple mental foramen and of forward-placed mental foramen (table I), suggesting that these features might relate to altitude in some degree; on the other hand, the Ulu sample – gorillas living at much lower altitudes but possibly in former genetic contact, via



Fig. 2. Foot of 'Néagi', adult male gorilla from Kibondo, Alimpongo, Mt. Tshiaberimu, formerly in San Diego Zoo. Photo K.W. Stolt.

Tshiaberimu and/or Kahuzi, with *beringei* – have much higher frequency of the bifid mandibular condyle, and the vertebral border of the scapula is sometimes sinuous, suggesting that these are features unrelated to altitude, but subject to clinal variation of unknown significance.

One of the 'best' features of *beringei*, the short humerus, has turned out to be not so cogent after all. As reported by Goodall and Groves [1977], the humerus in the massacred Tundura troop (Virunga) was unusually long, giving

an intermembral index of 117.0 to 122.6 [the latter figure misprinted in Goodall and Groves, p. 605; as 112.6] which is well above that for all other *beringei*; femur-humerus, brachial and clavicle-humerus index are similarly affected. The new figures for the postcranial indices of *beringei* take this into account: based on a considerable amount of new material including the Tsundura sample, the new figures for *beringei* have a much larger standard deviation than the old, depriving them of much significance although it can still be stated that 'except as an anomaly' this race is characterised by short humeri (table I).

The three equivocal populations can now be fitted in as follows.

Tshaberimu

In previous papers, Groves [1970a, b, 1971; Goodall and Groves, 1977] has always included this population under *graueri*; although it has generally been stated that it does tend towards *beringei* in some respects, its status in this regard has not always been emphasised sufficiently.

Vogel [1961] included a specimen from Alimbongo in his *beringei* sample, on the grounds that this is in the Albert National Park (now called the Virunga National Park); but it is in the Tshaberimu massif, which is also included within the National Park, not in the Virunga Volcanoes. This error was, inferentially, the major reason why Schaller [1963, p. 12] refused to accept Vogel's revision. It should be noted that the specimen in question must be the Brussels Museum one collected by Frechkop [1944], the only one with that locality; and that being a male, its incorrect allocation would not greatly affect the conclusions, since the differences were actually greater among females. All Vogel's other specimens, incidentally, were from localities within the Iombwe and Uru districts.

As seen in table I, Tshaberimu approaches Virunga slightly in its cranial length (greater than *graueri*), and much more so in its palate length and bigonial breadth. In the Generalised Distance, based on these among other measurements, it is closer to Virunga than to Uru, but is so extremely close to 'Mwenga-Fizi' that the three non-Virunga groups form a continuum with a sharp break between them and Virunga. The pattern of relationships sex by sex is interesting: the cranial length of females is in Tshaberimu almost as large as Virunga, but the jaw angles do not flare as much as do those of the males.

The humerus is as long, relatively, as any other *graueri*; but the hallux ray is long relative to the total foot, approaching *beringei*. Comparing the foot of the San Diego gorilla 'Ngagi', imported from Alimbongo (fig. 2), with the figures in Schultz [1934, fig. 2, p. 58], the reality of these figures is illustrated: the hallux



Fig. 3. 'Ngagi', about 1933, shortly after arrival in San Diego Zoo. Photo K.W. Stort.

branches from the sole at about 75% of the way along the foot, as in *beringei*, but the sole itself reaches only to the middle of the medial phalanges like *gorilla*. Although illustrations of true *graueri* [for example, Schouteden, 1947, p. 17, fig. 11, 12] do not place the foot in a comparable position, a *gorilla*-like form is quite clear in such animals. The intermediate nature of the Tshaberimu gorillas is thus emphasised.

On the other hand, the vertebral border of the scapula is completely straight as in true *graueri*, with some slight deviations.

The characters of the mental foramen and mandibular condyle fall within the ranges of the *graueri* groups. There is less tendency to multiply the infra-orbital foramina (like *beringei*) and more 'rocking jaws', again like *beringei*.



Fig. 4. 'Mbongo', male from Kibondo, Alimbongo, Mt. Tshiaberimu, in San Diego Zoo shortly after arrival (about 1953). Photo K.W. Stolt.

Externally, 'Ngagi' and 'Mbongo', the San Diego gorillas (fig. 3-6), and Frickkop's [1944] gorilla from Alimbongo, resemble *graueri* precisely. The hair is short on the scalp, the supraorbital torus is free of long shaggy hair, and there are no long copious side-whiskers, or beard. The nostrils, better outlined in 'Ngagi' than in 'Mbongo', are none the less not *beringei*-like: they are not angular; and there is more diffuse, spread padding of the upper lip. Both, especially 'Mbongo', show an overhang or 'lip' at the top of the nasal septum,



Fig. 5. 'Ngagi' in 1944, when fully mature (rather obese). Photo K.W. Stolt.

which occurs frequently — not invariably — in *graueri* as in *gorilla*, but never occurs in *beringei*.

Schwarz [1927] described a gorilla from this region under the colourful name of *Gorilla gorilla rex-pygmæorum*; however, he included some gorillas from lower altitudes in this subspecies — a paratype from Walkale, for instance — and later Schouteden [1947] mapped the race all over the Uru lowlands, separating it from *graueri* which he restricted to the Fombwe massif. As we have seen above, if *rex-pygmæorum* were to be retained it would have to be restricted to the Tshiaberimu gorillas; but we do not recommend giving it subspecific status, as it is essentially a point along a cline. Although its transitional nature does seem clear enough on the evidence so far available, it would be advisable to



Fig. 6. 'Mbongo' about 1941 or 1942, fully mature (grossly obese). Photo K.W. Stort.

examine a larger number of specimens, especially with regard to the characters of the foot, before placing it definitively. In the meantime, its external appearance is so clearly different from *beringei*, and some of its skeletal characters (especially humerus length and scapular morphology) are so clearly those of *graueri* that we recommend retaining it, typologically, with this latter subspecies: a placement which accords with its distribution, which in the recent past was certainly continuous with the Utu population, but surely not with that of Virunga.



Fig. 7. Head of a gorilla shot while crop-raiding near Mutungu (Tshibinda), Mt. Kahuzi. Courtesy, the late Dr. J.C. Trevor.

Kahuzi

The Kahuzi gorilla has never been awarded subspecies rank; Goodall and Groves [1977] comment that there is some irony in this, as it seems a fairly distinctive population morphologically — a comment which should not be misread as a hint that it be given a subspecific name!

Casimir [1975] argued strongly that it should be placed in *graueri* rather than in *beringei* where Groves [1970a, b] had placed it. From his new cranial data such a conclusion seemed cogent; but there remained the postcranial characters, apparently *beringei*-like, to explain. As Casimir notes, his new measurements — taken from specimens studied while in Zaïre — in the main do not correspond with those of Groves [1970a, b]; so it is not possible to calculate new Generalised Distances. Some of his measurements, however, are those used by Vogel [1961], notably Ascending Ramus height, which is very low in *graueri* compared to *beringei* such that in females the ranges of variation do not overlap. Placing Casimir's measurements for a male and a female mandible from the

Kahuzi district on Vogel's regression diagrams [1961, fig. 6, 7, pp. 7-8], a curious finding emerges: for the comparison between two ramus heights [to condyle cf. to coronoid, Vogel's fig. 6], Casimir's male jaw falls with *beringei* but between males and females, while the female jaw falls among *graueri*. However, in Vogel's figure 7 [Vogel, 1961] (ramus height to breadth) both Kahuzi jaws fall within the *graueri* range.

In the cranial measurements listed in table 1, the Kahuzi group (which now includes Casimir's new specimens, as well as certain skulls previously [Groves, 1970a, b], perhaps over-cautiously, rejected as being not quite adult or not certainly from Kahuzi) is actually less *beringei*-like than the Tshaberimu group: cranial length is less, the jaw angles are not at all flared. In the non-metrical features, the mental foramen is less often multiple than in any *graueri* sensu stricto, the infraorbital foramen is more often multiple, and the position of the mental foramen is about as in Lombole: note, however, that the small number of specimens makes these conclusions – that Kahuzi diverges from *graueri* in the opposite direction from *beringei* – somewhat suspect. The mandibular condyle is bifid in four out of five jaws (eight out of ten sides), and there are mostly 'locking jaws' as in *beringei*.

Were it just for the cranial morphology, therefore, the Kahuzi gorilla would be frankly *graueri*. But, as continually emphasised above, the data of the postcranial skeleton have until now seemed to be just as frankly *beringei*: indeed, gorillas from both Virunga and Kahuzi were included by Schultz [1934] in his sample of '*beringei*' without any difference between them being apparent. But the evidence of the Tsundura troop shows that *beringei* can have a long humerus, if only as an anomaly; and new postcranial data (from the previously unstudied Terruven specimens) show that the means for the postcranial indices are not quite as close to *beringei* as had previously appeared. The femur-humerus and hallux-foot indices are now intermediate, not precisely like Virunga, although in the case of the latter, still much closer to Virunga; while the brachial and claw-humerus indices now even appear slightly closer to *graueri*. The vertebral border of the scapula, however, is invariably sinuous – in fact more markedly so even than Virunga!

Externally, we now have plenty of photographic material available for the Kahuzi gorilla, which must rank as the only gorilla population anywhere which seems to be flourishing, and whose future seems – as of now – secure. Full photographic documentation exists of a gorilla shot near Mulungu (= Tshibinda), on Mt. Kahuzi, whose remains were retrieved for the Cambridge University Physical Anthropology Department by the late Dr. J. C. Trevor; hand and foot

photos have already been published by Groves [1970b, p. 16]. The head (fig. 7) cannot be distinguished from those of *graueri* in Schouteden's work, or from those of 'Ngagi' and 'Mbongo': hair is everywhere short, exposing the supra-orbital torus, and the nose is exceptionally low, poorly outlined, even the alae being flush with the cheek; padding on the upper lip is very poorly developed, the nostrils, though elongated, are not angular in contour. The gorillas in Gregory and Raven [1937], Grzimek [1974] and other sources differ little from this. The foot (of the Trevor specimen), however, is very *beringei*-like: the hallux branches nearly 80% of the distance along the foot (there is, however, some foreshortening due to the angle of the shoe) and is very long, and the sole extends to the base of the medial phalanges of the lateral toes, and actually to the middle of the medial phalanges on toes 2-3.

A comparison of the Kahuzi and Tshaberimu gorillas is very interesting, and not entirely coherent. Both are intermediate between *graueri* and *beringei*, though nearer the former; but the Tshaberimu population is more *beringei*-like in its skull, the Kahuzi one in its postcranial skeleton; and in both the structure of the foot resembles *beringei*, perhaps slightly more so in one than in the other. Presumably, at some distant time in the past, both were in contact with the Virunga population; when the contact was broken, gene-flow from one direction only (Ulu) gradually influenced them, but in somewhat different ways, though why this should be is mysterious.

Kayonza

Evidence on the Kayonza Forest gorillas is still not impressive. Table II shows that the skulls of 3-4 males and 1 female have a long braincase and flaring jaw angles like Virunga, but the palate is shorter in males; yet in the single female skull the palate is one of the longest in the whole series of female gorillas from any locality. Frequencies of metric features probably mean very little on such a small sample, but would not be inconsistent with an interpretation as *beringei*. The Generalised Distance statistic [Groves, 1970a] makes Kayonza near to Virunga but also to 'Mwenga-Fizi', a result probably due as much to sampling error as anything else. One of us (K.W.S.) has seen living specimens from the Kayonza Forest in the flesh, and notes their general similarity to those from the Virunga Volcanoes.

The Kayonza Forest was formerly joined by forest to the Virunga Volcanoes: the stumps of enormous trees can still be seen in the cultivated fields that now lie between the two regions. On the other hand, there is no trace of forest at any time across the Rutshuru plains, between the Kayonza region and

Table 11. Gorillas from Kayonza forest

	Male		n	Female	
	X	s		X	s
Cranial length, mm	204.7	11.02	3	165 (n = 1)	
Palate length, mm	126.0	2.83	4	112 (n = 1)	
Bigonial breadth, mm	142.8	4.99	4	—	
Multiple mental foramen, %				80.0 (n = 5)	
Multiple infraorbital foramen, %				92.9 (n = 10)	
Blifid mandibular condyle, %				40.0 (n = 5)	
Mean number of mental foramina				1.9 (n = 5)	
Mental foramen anterior to P ₁ , %				20.0 (n = 5)	
Rocking jaws, %				22.2 (n = 9)	

the nearest *grazeri* area (Tshaberimu). This implies that the Kayonza forest could only have been populated via the Virunga Volcanoes.

It seems most likely, in any case, the Virunga Volcanoes and Kayonza Forest are a last refuge for gorillas to the east of the Albertine Rift, rather than outposts. One of us (C.P.G.) was shown by D. Fossey several denuded hillsides in Rwanda, at some distance from the Virunga range but within sight of it, where according to her informants gorillas still lived as late as the 1950s. Where else they might have lived in historical times is a matter for speculation, with perhaps some attention to folk traditions preserved by tribal historians; but it may be relevant that an incisor from the early Pleistocene Kaiso beds, near Kazinga and so somewhat north of present-day gorilla distribution, has been tentatively identified as a gorilla [van Barthold et al., 1970]. But the absence of gorilla from apparently suitable habitat in the Ruwenzoris must be borne in mind when reconstructing the past distribution of the species.

Dispersal of Eastern Gorillas

It is possible to go a little further, and make a hypothesis on the dispersal of gorillas eastward across the Rift Valley. Faulting in the Albertine Rift began in the Miocene and was renewed in the early Pleistocene or possibly the Pliocene [Bishop, 1968], at which time the Virunga Volcanoes may have been formed. The Virunga range is a record of the passing of the earth's crust over a 'hot-spot': an active volcanic centre in the lower mantle, independent of the upper mantle

convection pattern [Stacey, 1977] so that the motion of a crustal plate relative to it produces a chain of volcanoes as the hot-spot successively punctures the plate. The volcanoes become extinct as the plate carries them beyond the hot-spot that produced them.

Minster et al. [1974] calculate the motion of the African plate to be some 2 cm per annum in a north-easterly direction. At this rate — the distance from Nyirangongo (the more easterly of the two active volcanoes in the range) to Muhavura (the furthest east of the range) being about 50 km — the formation of the hot-spot, and so of Mt. Muhavura itself, can be extrapolated to some 2½ million BP (½ × 100,000 × 50).

The three eastern volcanoes form a cluster and are separated by a 12-km saddle from the three central volcanoes; the saddle presumably represents a period of quiescence, after which the hot-spot sprang into life again, forming the central cluster. The distance from Nyirangongo to Visoke, easternmost of the central cluster, is 24 km, giving a date of 1.2 million BP for the initiation of the second phase of activity: this may be taken as the safest date for the time when the three eastern volcanoes would have become habitable, although it could have been earlier than this.

The distance from Nyirangongo to Mikeno, the furthest west of the central cluster, is 16 km, giving a date of 800,000 BP for the ending of the activity of the central cluster. At about this time or somewhat later, therefore, the whole of the eastern group would have become habitable by gorillas and other animals of narrow ecological tolerance.

It must be noted that the African plate moves predominantly eastwards, so that the active volcanoes are always between the Mitumba range and the extinct volcanoes: that is, the gorilla cannot have dispersed across the Virunga range itself, but must have crossed the Albertine Rift either by some other route, or else earlier. The Rutshuru Plains, 1,000–1,500 m a.s.l., could have been such a route; we have no evidence whether they were at any time forested, but inferentially they might have been during an interglacial, since Livingstone [1975] shows that desiccation in Africa was contemporaneous with temperate glaciation, contra Groves [1971]. (Note that this route would bring the gorillas first of all of the Kayonza forest.) Alternatively, the gorilla could have crossed the rift before the renewal of tectonic activity, but as the pre-Pleistocene rift deposits suggest a lacustrine environment, this route might have been closed: besides which, such an extremely early date would seem implausible.

We hypothesise then, that (1) the Virunga Volcanoes must have been invaded by gorillas from east to west; (2) the central cluster (Visoke, Karisimbi

and Mikeno) with its unique *Higania* forest is a youthful habitat; (3) the last connexion of populations across the Albertine Rift is not likely to have been later than the last interglacial while the initial dispersal across the Rift was probably much earlier. The gorillas of the northern end of the Mitumba range (especially Tshiberimu) would therefore have been subjected for nearly 100,000 years to gene-flow from the Ulu lowlands alone, determining the morphology of the population despite selection for high altitude adaptations such as could proceed unchecked in the isolated population which was to become *beringei*.

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