

DISTRIBUTION AND PLACE OF ORIGIN OF THE GORILLA

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The gorilla (*Gorilla gorilla* (Savage & Wyman 1847)) is the largest living primate, and one of the closest to man. Its distribution within the African rain forest is discontinuous: it occurs in the Cameroon-Gabon area of west Africa, from the upper Cross River in Nigeria to the lower Congo, and is then quite absent from the forests of central Africa until one reaches the district to the east of the Itahaba in eastern Congo-Kinshasa. In the eastern districts most of the gorillas live at relatively low-lying altitudes, but also ascend the mountains of the western, or Albertine, Rift, in the massifs of Tshaberimu, Kahuzi, Iombwe and Virunga, crossing the rift to the montane Kayonza forest in Uganda. Traditionally the eastern gorillas have all been referred to a single subspecies, the Mountain Gorilla (*G.g. beringei* (Marschke 1903)); but the present author has demonstrated (Groves 1970) that only the Virunga and Kahuzi gorillas are true Mountain Gorillas, and that those of the other, less lofty highland areas, together with the east-Congo lowlands, belong to a separate subspecies, the Eastern Lowland Gorilla (*G.g. graueri* Marschke 1914).

Schaller (1963) poses the problem of the gorilla's discontinuous distribution, and postulates that the species was limited in the past, just as it seems to be today, by two factors: 1) the distribution of the rain forest; 2) the animals' inability to swim and cross large rivers. It is the purpose of the present article to assess the evidence of the past distribution of the gorilla, as well as its present range, in the light of these two limiting factors; and to suggest the possibility of other limiting factors. Finally, a hypothesis will be presented concerning the original adaptations of the gorilla, together with an attempt to pinpoint its place of origin.

Distribution of the gorilla

An extensive study of available gorilla material, preserved in the museums of Europe and the United States, has permitted the compilation of a detailed distribution map (fig. 1). In the east of the gorilla's range, a few localities not represented in museum collections have been reported by Schaller (1963) and these too are represented on fig. 1.

Also on fig. 1 are given the outlines of vegetation zones. The dotted line gives the limit of the Tropical Rain Forest; below approximately 1500 m. this is of lowland type; above it the forest is montane. Montane forest differs from lowland in the smaller size of the trees; more open canopy allowing a greater amount of light to reach the ground, so that ground vegetation is much thicker; fewer lianes; and the presence of gymnosperms as well as angiosperms among the trees. Montane forest is not, however, uniform in type; several types are stratified altitudinally, the exact

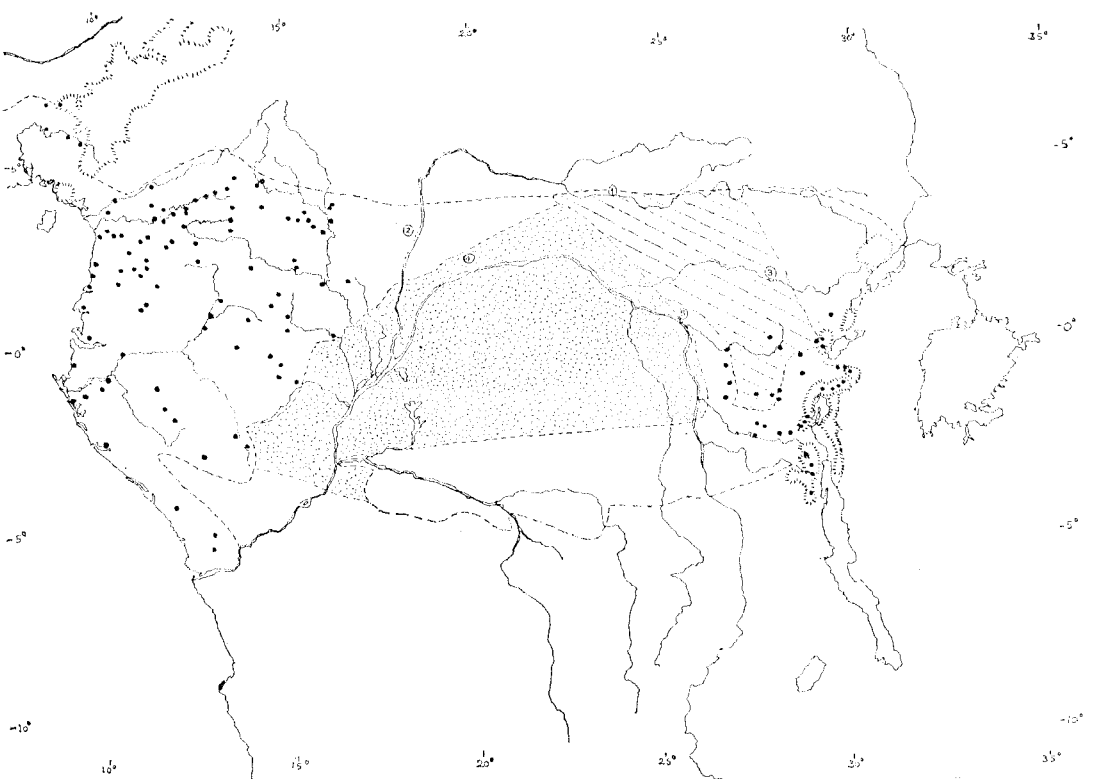


FIGURE 1 (see foot of page)

FIGURE 1. Distribution of the gorilla.

- The dotted line indicates the approximate boundary of the Tropical Rain Forest belt. Fine stipple—'Highly humid forest with freshwater swamp forest' (Phillips 1939) or 'Forêt marécageux' (Dandelot 1965). Dashed lines—single-dominant climax forest of *Gilbertiodendron*. Solid circles: localities of collection of museum specimens, and as recorded by Schaller (1963).
- (1) Diabait (Bondo), Uele valley.
 - (2) West bank of the Ubangui, south of Libenge' (Friedrich 1913).
 - (3) 'Near Avakubi' (Johnson 1908).
 - (4) 'Bwela country, near the River Motima' (Johnson 1908).
 - (5) 'Near Stanleyville' (Christy 1924).

succession varying from place to place. Schaller's study was largely in the Virunga volcanoes, and he gives the altitudinal replacement both in the Kisoro area of the northeastern volcanoes and the Kabara area of the south-western part of the range. It is at Kabara that gorillas are really numerous. The succession is given in table 1.

TABLE 1. Floral succession in Virunga Volcanoes (based on Schaller 1963).

KABARA, Mt. Mikeno		KISORO, Mt. Mahinyira	
Montane mixed forest	up to 2200 m.	Montane mixed forest	up to 2700 m.
Bamboo zone	2200—2800 m.	Bamboo zone	2700—3000 m.
<i>Hagenia</i> forest	2800—3350 m.	<i>Hypertium</i> forest	3000—3350 m.
<i>Hypertium</i> forest	3350—3500 m.	Giant Senecio zone	3350—3550 m.
Giant Senecio zone	3500—4200 m.	Alpine zone	3550—peak
Alpine zone	4200—peak		

Note that no other mountains in the eastern Congo reach heights greater than 3000 m., with consequent lack of typical successional flora other than montane mixed forest and the bamboo zone.

Nor is lowland forest entirely homogeneous. Fig. 1 illustrates two important elements of the heterogeneity: the marshy forest of the Congo basin proper, and the *Gilbertiodendrelia deuerrei* forests which cover much of the north-east of the Congo-Kinshasa. Elsewhere the lowland forest is mixed in type and with few or no swampy areas.

No locality in fig. 1 is in the marshy forest region; both in the Upper and the Lower Congo regions the distribution does not apparently approach the river itself, but stops short where the swampy region begins. The *Gilbertiodendrelia* (= *Macrolobium*) forest is of a single-dominant type characterised by much-branched widely spreading crowns which block out much of the possible light, and reduce ground vegetation to a sparse covering; and gorillas seem not to invade this area to any great extent.

Apart from the confirmed localities, five other records of gorillas must be considered, numbered consecutively on fig. 1.

1. Djabbir, Uele valley. This is a record based on four specimens in the Koninklijk Museum voor Middenafrika, Tervuren, and described by Schoueteden (1927) as *Gorilla gorilla nellensis*. Coolidge (1929) originally considered that these skulls, which he found to be morphologically indistinguishable from western gorillas, had probably been traded upriver from the Cameroons; later (1936) he changed his opinion and admitted that they were probably indigenous to the area, citing a letter from Schoueteden pointing out that two of the specimens—a female skull and jaw, and a male jaw—were from gorillas shot in that very area by a soldier, while the other two—an adult male and a subadult male cranium—were smoke-blackened, having been kept as trophies in village huts in the area. It is curious that the 'shot' jaw fits the smoke-blackened adult skull. Not only does it fit the cranium, but the tooth-wear patterns are consistent with the view that they might have come from the same animal (U. Welsch, pers. comm.). Whatever the truth, the soldier who shot the female said they were 'assez rare' in the area (Coolidge 1936), and they are probably extinct there now considering the small area of forest north of the Uele River.

2. 'West bank of the Ubangui, south of Libenge'. This locality is said by Friedrich (1913) to be inhabited by gorillas. No grounds for the statement are given, but considering the locality it is entirely possible that gorillas do, or did, live there.

3. 'Near Avakubi . . . in the dense forests of the Aruwimi River as far east as Mawambi'. This locality comes from Johnson (1908), who saw photos of 'an ape of large size like a gorilla' killed in that area. Coolidge doubts this was a gorilla, seeing that on another occasion Johnson had identified as a gorilla a photo which was certainly that of a chimpanzee; none the less it is not far from known gorilla localities and the species' existence on the Aruwimi is not unlikely. Schaller (1963) notes that Stanley had recorded gorillas on the Aruwimi.

4. 'Bwela country, near the river Moima'. This reference, also from Johnson (1908), is more easily disposed of as a chimpanzee. Coolidge (1936) pointed out that not only is it far from all other records of gorillas, but also that the description of the animal as only four feet high, and as being shot from the branches of a tree nearly 150 feet high, make it very unlikely that the animal was a gorilla.

5. Christy (1924) mentions having seen photos of dead gorillas which had been brought into Stanleyville. Though the animals may have been killed within the mapped range of the gorilla, Stanleyville is also placed on the map in view of the possibility that some, at least, were killed in the near vicinity. Interestingly, this author also states: 'the gorilla seems in my recollection to have more resembled the gorilla of the Cameroons than the giant gorilla of the mountain heights to the north of Tanganyika'. He is thus the earliest author to appreciate that the Eastern Lowland gorilla is not identical with the Mountain gorilla.

It can be noted that those records which seem most likely to be factually correct—Schoueteden's and Friedrich's—are within the mixed forest belt where almost all other records lie; the one which is impossible to accept (Johnson's at Moima) is in the swamp forest zone; while the Aruwimi record, distinctly possible, is in the single-dominant *Gilbertiodendrelia* climax forest where there are some records, but not many.

The past environment of the Congo region

The question of Africa's environment and climate during the Pleistocene has been intensively studied by Moreau (1966). This author has tackled the zoogeography of African birds in depth, reviewing geological evidence of the past biotopes of the continent, and reconstructing from this the original distributions of numerous stenotopic bird species. Since all his conclusions are based on dual evidence from two different disciplines, and since the assumptions he employs in integrating this evidence are concerned with *when* certain events happened rather than with *whether* they did, his conclusions will be adopted here. Their relevance to this discussion is that they point to the existence of certain Pleistocene events which bear directly on the problems of gorilla distribution and offer the best explanation yet of the data. According to Moreau's findings:

1. Africa's montane biomes on the whole are of Quaternary date; during the Tertiary almost the whole of Africa was below 1500 m. The whole Congo basin was a lake.

2. In the Pleistocene, extensive rifting occurred; the Congo Lake was captured

and drained by a river; the Virunga volcanoes were formed. These renewed tectonics were presumably Middle Pleistocene in date, at a time when the Balabai Depression and other faults occurred in east Africa (Leakey 1965); rift tectonics had begun however in Lower Miocene times (Gautier 1967).

3. Temperature changes in the Pleistocene were in step with those elsewhere; during the last glaciation in the high latitudes, the temperature must have been depressed at least 5°C in sub-Saharan Africa, so that the boundary between lowland and montane forest fell to 500 m. or less. There would thus have been a bloc of montane forest around the north end of the Congo basin, from Cameroon to the eastern Congo.

4. The decreased evaporation consequent upon lowered temperatures favoured the extension of forest conditions.

5. During *interglacials*, arid conditions replaced much of the present Congo forest: forest refugia were restricted to montane forest, gallery forest, and perhaps a belt of lowland forest to the north of the Congo, apart from the west African coastal forest which appears to have expanded and contracted, but never to have been entirely eliminated.

6. Interglacial conditions last took effect around 75-52,000 B.P. according to one estimate; the greatest montane expansion was in the last phase of the last (Würm) glaciation, 25-18,000 B.P., soon after which the Congo-Cameroon montane connexion was severed.

From this reconstruction, it is difficult to escape the conclusion that the true forest fauna of the Congo basin consists of two elements: a) invaders from west Africa, true lowland forest types, which would have begun to filter in during the last glaciation as the central African forest bloc was gradually reforested; b) montane forest forms, which spread their ranges from refugia in the Albertine Rift as the montane forest spread at the height of the last glaciation. Then montane forest withdrew as Würm III receded in higher latitudes, element (b) would have suffered a discontinuous distribution; in the east, the montane forest was confined to the Mitumba-Virunga area, and in the west to Mt Cameroon and the Obudu Plateau of Nigeria. The eastern population would either undergo a severely reduced range, with consequent reduction in numbers, or would be forced to adapt to lowland conditions.

By and large, it would seem likely that the west African element (a) is today the more widespread; not only still existing in west Africa, but also adapting easily to the swamp forest conditions of the central Congo basin. Element (b) would very likely have been unable to extend its range into the strict lowland—often severely swampy, even mangrove—forests of west Africa, and not into the central Congo basin either; on the other hand, east African forest islands, having a recent montane origin if not actually montane today, would be populated by it.

Except for its lack of extension into the east African rift forests, the gorilla is strongly of type (b), of montane origin. Two factors probably militated against its eastward extension: the River Nile and Lake Victoria, and possibly other smaller rivers which would have been a bar to its dispersal in the first place; and the small size of the east African forest islands that remained after the cold conditions had gone, preventing its survival there.

Montane adaptations of the gorilla

The gorilla lives at altitudes well over 10,000 feet in the Virunga volcanoes, and at great altitudes in the Mitumba range. On the other hand, chimpanzees were not encountered by Schaller in the volcanoes; only in the Kayonza forest do they extend up to 8,000 feet. In the Ruwenzorics chimpanzees live at 9,000 feet—but there are no gorillas there, an unexplained absence. It would seem that at high altitudes the gorilla replaces the chimpanzee in most cases.

TABLE 2. Population densities of gorillas
(from Schaller 1965; Sabater Pi 1964; March 1957).

Locality	No. gorillas per sq. km.
Kabara	2.6
Sabinio & Muhavura	0.7
Kayonza forest	0.6
Mt Tshaberimu	0.55
Eastern region as a whole	0.4
Rio Muni	1.3
Cross River	0.7

The comparative densities of gorilla populations are very suggestive (table 2). The highest density of any gorilla population is at Kabara, in the open *Hagenia* forest with its abundant vegetation; the next highest is in Río Muni, where there is a great deal of secondary forest and agricultural land, which provides gorillas also with abundant food (Sabater Pi 1964). Densities are higher in montane forests (such as Kayonza and Cross River) than in the Uru Lowlands. Schaller (1963) notes also that bamboo shoots are a favoured food of gorillas, and the density in any one area rises during the season when the shoots are coming up. On the assumption that gorillas are most numerous in the type of environment to which they are most adapted (areas of open montane forest, with *Hagenia* climax and/or seasonal bamboo) and supposing (as seems reasonable) that human interference in the forest has been of fairly recent date, it may be postulated that their environment *par excellence* is a montane forest one.

The gorilla differs from the chimpanzee in various ways in which montane forms often differ from their lowland relatives—and in many respects the differences between *G.g. beringei* and the lowland races are simply a reflection of the differences between the gorillas as a whole and the chimpanzee. The deep, barrel chest with broad sternum; small ears; expanded nostrils; large size ('Bergmann's rule'); shortened extremities such as arms, legs and penis ('Allen's rule'); and large teeth and jaw musculature, suitable for tackling the heavy vegetable matter eaten in highland areas but which seem altogether superfluous to a largely fruit-eating animal such as a lowland gorilla, at least in primary forest (Schaller 1963).

The demes of *G.g. gorilla*, for all that they inhabit rather different environments, are close together morphologically and cannot be separated at a taxonomic level (Groves 1970). The Ule gorillas fit well into the range of variation of the western race (Coolidge 1929). On the other hand there are two distinct subspecies in the eastern area, and one of these (*G.g. graueri*) has several morphologically differentiated demes which are rather more distinctive than those of *G.g. gorilla*. This implies that the eastern populations have been isolated from one another for a longer time than the western, and that dispersal has been from east to west.

Conclusions

Gorillas seem thus to have evolved in response to a montane forest environment: one with abundant fodder at ground level, selecting for a large body size (of which sexual dimorphism may be a consequence) and heavy masticatory apparatus. The species probably evolved during an interglacial in the eastern Congo; when montane forest spread north of the Congo-Ubangui system and into Cameroon, the range of environment open to the gorilla expanded, and the distribution was extended. When, following the end of the last glaciation, the montane forest zone shrank, the gorilla was left with an uneven distribution: the Mitumba-Virunga area, the Cameroon-Gabon lowland forest to which it managed to adapt, and a small refugium north of the Uele river. During the glaciation the gorillas remaining in the east Congo mountains became adapted to even more extreme montane conditions, while the less extreme environment elsewhere led to the evolution of *G. g. gorilla*, which is in many respects less specialised. In the eastern Congo, the recession of montane forests left gorillas in three refugia: Virunga-Kahuzi (which has been continuous or discontinuous in the past, according to whether the volcanoes between them (Nyiragongo and Nyamulagira) have been active or not); the Tshiaberimu massif; and the Irombe mountains. Both these latter are continuous with lowland forest, whereas Mt Kahuzi is separated from lowland forest by open prairie (U. Rahm, pers. comm.). Hence a single subspecies of gorilla has evolved in what ultimately became the Irombe-Utu (i.e. lowland)-Tshiaberimu continuum, while a separate one is restricted to Virunga and Kahuzi. The Kayonza forest gorillas are unknown, both as to history and subspecies; but the forest was probably populated from the Tshiaberimu region.

Gorilla-like forms existed in Africa in the early Miocene, and probably in response to the same type of environment, which Bishop (1964) specifically compares to the present-day Virunga Volcanoes. When one considers the adaptive nature of a gorilla-like morphology, it becomes unnecessary to postulate, as Pilbeam (1970) has done, that the Miocene *Dryopithecus major* is actually ancestral to the gorilla, and that the gorilla and chimpanzee separated so long ago.

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