

(Reprinted from *Nature*, Vol. 213, No. 5079, pp. 890-893,
March 4, 1967)

Ecology and Taxonomy of the Gorilla

Multivariate analysis shows that the ecological diversity
of the gorilla is reflected in the morphology of the skull
and is of assistance in subspecific taxonomy.

by

COLIN P. GROVES*

Unit of Primatology and Human Evolution,
Royal Free Hospital School of Medicine,
London, W.C.1

The gorilla is the largest living primate, and systematically one of the closest to man. It is probably this closeness as much as anything else that has stimulated a great deal of scientific interest in this animal, from Owen's^{1,2} early osteological studies through the taxonomic era of Matschick's³⁻⁶ to the very recent behaviour study of Schaller⁷. The general range of variability is known largely through the work of Schultze's⁸ and the distribution is well known as a result of the work of Cooldidge⁹ and Schaller.

It is not clear to what extent gorillas are divided into geographical races—races with ecological determinants—partly because of the typological point of view of the earlier workers and the chance that gorillas tended to be collected in the extreme west and east of the total range of the species. The old literature tends either to describe new forms, based on very little information, or merely to contrast the mountain and lowland types as a whole. Actually, as Schaller has shown, many of the eastern gorillas are at low altitudes. Investigations of the influence of ecology on the morphology of man are only just beginning. It can be supposed, however, that gorillas, lacking the mobility of human beings, are more likely to show a comparatively uncomplex pattern of influence.

A further question which has recently been raised by several authors (Simpson, Mayr, Washburn) is the relationship of the gorilla to the chimpanzee. This question is beyond the scope of the present paper, but is indicative of a new trend of taxonomic thought.

* Present address: Department of Anthropology, University of California, Berkeley, California.

The altitudes at which gorillas are found vary from sea-level in West Africa to 13,000 ft. on the Uganda-Rwanda-Congo border. The whole area of distribution is split into two portions—one in West Africa, approximately between the Nigerian border and the lower Congo River, and one in East-Central Africa, between the Upper Congo River and the Uganda border, being mostly (but not entirely) to the west of the Albertine Rift. These two quite separate geographic regions are generally referred to as the areas of "lowland" and "mountain" gorillas respectively. The currently recognized classification, dating from 1929 (ref. 11), allows a single sub-species to each of these two zones, the western or lowland gorilla being the typical form, *Gorilla gorilla gorilla* Savage and Wyman, 1847, and the eastern or mountain gorilla being known as *Gorilla gorilla beringei* Matschie, 1903. Vogel's among others has queried this point of view, basing his judgment on the morphology of the mandible and the frequencies of some non-metrical features.

The first immediately striking feature of this arrangement is that the western gorilla is by no means an exclusive inhabitant of low-lying country: on the plateau of the interior of Cameroun the altitude is around 2,000 ft., while on the Cross River, at the western extreme of the range, altitudes of 5,000 ft. have been recorded for gorillas. Equally, the eastern gorilla is by no means entirely a mountainous form. Schaller⁷ shows that at least two-thirds of the eastern distribution area lies in lowland rain forest at altitudes of 1,600-2,600 ft.

For these reasons, it was felt that a new analysis of gorilla material was required, based on as large a number of specimens as possible, with a view to relating geographic variation to ecological factors. The present investigation therefore includes material from all the major collections of the world*, as well as many minor ones. The five largest collections of the world are located as follows: British Museum (Natural History), London; Powell-Cotton Museum (Natural History), Kent, England; Musée Central africain, Tervuren, Belgium; Institut für spezielle Zoologie und zoologisches Museum, Berlin (East); Natural Science Museum, Cleveland, Ohio, U.S.A. In several other collections there exist a fairly large number of specimens, but these are mostly of unknown locality. In all, including the smaller collections, 469 adult male and 278 adult female skulls were used in this investigation, as well as numerous juveniles which were useful for comparison. The specimens examined included the holotypes of all the many supposed species or sub-species described by Matschie and his contemporaries, with the exception of *Gorilla beringei* Matschie, 1903,

and *Gorilla gorilla schwarzi* Eritze, 1912, both of which were destroyed during the war. The original co-types of Savage and Wyman were also examined.

The primary method used was the multivariate technique of generalized distance, which is well described by Trevor¹³ and Talbot and Mulhally¹⁴; the analysis was done by the canonical variates method (see refs. 15 and 16). Although the results of the canonical analysis were of great interest, space precludes their detailed description in the present paper. A total of forty-five measurements was taken on each skull. This large number was reduced by means of correlation coefficients to sixteen, of which ten pertained to the cranium (cranial length and breadth, bi-orbital breadth, palate length and breadth, bi-canine breadth, facial height, post-orbital breadth, tooth row length and nasal surface height), and six to the mandible (bicondylar and bi-gonial breadths, ramus height and breadth, tooth row length and jaw body breadth). The cranium and mandible were treated separately in the analysis because of a comparative lack of specimens possessing both; thus, there were four analyses to perform because males and females were also taken separately. Taking the smallest geographical units possible (one area or district if there were sufficient specimens, otherwise a fairly circumscribed area) it was possible to use nineteen different groups for the male crania and mandibles, but only eleven for female crania and ten for female mandibles. In each case four of the groups were from the eastern area; the remainder, from the western.

Ecologically the western group can be divided into four sections: (A) Coast, which includes the high rainfall area down the coastal strip in West Africa from the lower Njong River, Cameroun, the mouth of the Congo, and extending inland to the low-lying Mambili River region. (B) Plateau; the lower rainfall area of the Cameroun hinterland, above 2,000 ft.; most of the groups large enough to be used in the analysis were from districts within this area, for example, Batouri, Lomié, Abong Albang, Ebolowa. (C) Sangha, a zone ecologically intermediate between (A) and (B); on both sides of the Sangha River, from three localities: Youkadouma (includes, for example, Zindi), Nola and Onesso. (D) Nigeria, the Cross River district, from 1,000 ft. to nearly 6,000 ft. in hilly country, and rather isolated from the other three. These areas are shown on the map in Fig. 1.

The four eastern groups used in the analysis were, to use Schaller's terminology: Yirunga, from 8,000-13,000 ft., in the Yirunga Volcanoes; Tshaberimu, from about 5,000-8,000 ft.; the mountains west of Lake Edward; Mwenza-Tizi, of similar altitude but less precipitous topographically; it is west of the north end of Lake Tanganyika; Uru, lowland rain forest west of the mountainous region, averaging 2,000 ft. high.

* For a catalogue of the gorilla material in the British Isles, see Groves and Napier⁸.

Table 1. MEAN GENERALIZED DISTANCES FOR GORILLA SKULLS: COMBINED DATA FOR MALES AND FEMALES, CRANIA AND MANDIBLES

	Deme A	Deme B	Deme C	Deme D	Utu	Mwenga-Fizi	Tshiaberimu	Virunga
<i>G.g.gorilla</i> : Deme A								
Deme B	3.42							
Deme C	2.36	1.87						
Deme D	3.75	3.64	2.78					
<i>G.g.manyema</i> : Utu	10.58	7.19	8.98	12.00				
Mwenga-Fizi	13.97	9.63	12.01	13.39	2.61			
Tshiaberimu	18.32	12.80	17.69	19.91	5.26	2.85		
<i>G.g.beringei</i> : Virunga	19.35	14.27	15.63	19.55	8.10	5.78	4.06	

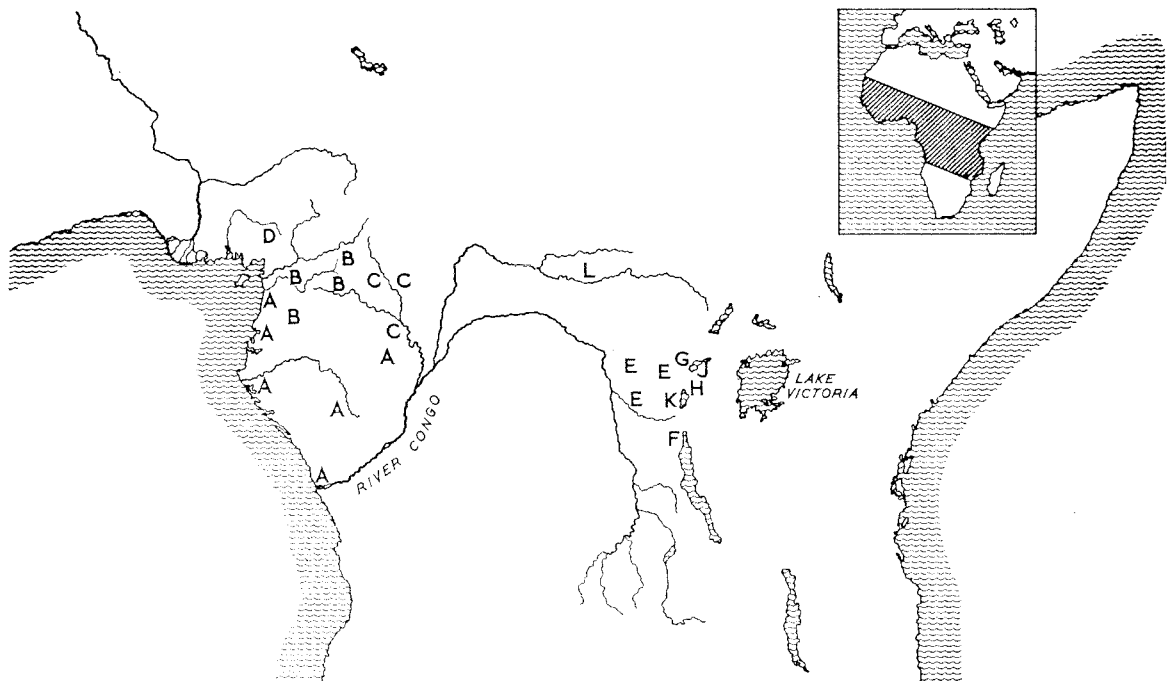


Fig. 1. Map to show distribution of gorilla demes and sub-species. (A) *G.g.gorilla*, coast; (B) *G.g.gorilla*, plateau; (C) *G.g.gorilla*, Sangha; (D) *G.g.gorilla*, Nigeria; (E) *G.g.manyema*, Utu; (F) *G.g.manyema*, Mwenga-Fizi; (G) *G.g.manyema*, Tshiaberimu; (H) *G.g.beringei*, Virunga; (J) Kayonza forest; (K) Mt. Kahuzi; (L) Bondo, Uele valley.

The generalized distance analysis shows that this ecological diversity is reflected in morphological diversity (Table 1). At first all nineteen groups (or eleven, or ten, according to which section of the analysis was being examined) were compared, and the western ones were seen to fall into larger groups which were therefore pooled; the larger groups corresponded exactly to the four-fold division described here, even to the extent of the coast group (A) which includes the inland Mambili skulls. Division was fairly sharp between neighbouring groups in different areas, for example, between Bipindi (on the Cameroonian coast) and Ebolowa (a few miles inland, on the plateau); here it seems that gene exchange has not been sufficient to counteract the ecological difference. Likewise the uniformity of the Sangha gorillas (C) was maintained, even though the very considerable isolating barriers of the rivers Sangha and Dja separate the three groups concerned; morphology seems here to be affected more by environment than by isolation. Thus reduced in number, the remaining eight broad divisions show an interesting pattern of diversity. The Nigerian gorillas are fairly distinct from all others in the western area; the coast group is distinct from the plateau group, but the Sangha group is intermediate. For none of the canonical variates (from which the generalized distance table was calculated) do the means of these groups lie more than one standard deviation apart; no sub-specific distinction is involved.

Among eastern gorillas, the Virunga skulls stand out from the other populations more than any of the western groups differ from one another. The other three eastern groups do not differ very much from each other, but show varying degrees of resemblance to the western or the Virunga gorillas. The Uru group of skulls, it will be seen, is almost equidistant from the Virunga group and from the western groups generally; among the latter it bears rather more resemblance to the Plateau group than to the others. By reference to the original canonical variates it is possible to show that there is a significant difference at the 90 per cent level from both Virunga and the western populations, and that the Uru gorilla merits separation at the sub-specific level from both of the others. This is a not unexpected consequence of the discovery, largely pinpointed by Schaller, that this is an eastern gorilla that is decidedly not a "mountain" gorilla. The Mveinga-Fizi and Tshiaberimu gorillas are intermediate between Uru and Virunga, but nearer to the former, that is, the cline is "stepped"; they would therefore be most justifiably placed with the Uru population in the same sub-species. Renewed examination of the canonical variates showed that it was characters of the jaws and teeth that most weighted the results.

The newly recognized race, being largely a lowland

forest form, may be referred to as the eastern lowland gorilla. The two mountain-living populations have been known as *Gorilla graueri* Matschie, 1914, and *Gorilla gorilla rex-pygmaeorum* Schwarz, 1927, names given to the Mveinga-Fizi and Tshiaberimu populations respectively. It would be unfortunate were the race to be known under a name given to an atypical population. Fortunately it is possible to determine that there is a valid, earlier name attached to the Uru population. In 1908, Rothschild¹⁷ referred to a skull in his possession as that of "*Gorilla gorilla mangena* Alix and Bonnier, from the south Congo region". The intention is to indicate a form described by Alix and Bonnier as *G. mangena*; the misspelling would seem to indicate that there was confusion here with Manyema, a province of the Belgian Congo on the upper Congo (Lualaba) region—an area where the eastern lowland gorilla is found. (The actual type locality of Alix and Bonnier's form was Conde, near Landana, on the lower Congo.) If this reading of the evidence is correct, then clearly Rothschild was referring to the eastern lowland gorilla, and *mangena* will be the valid name for the sub-species. Additionally, it must be stated that there is in the British Museum (Natural History) a skull, number 1939.945, from the Rothschild bequest, which bears no information on the label; but on the brain-case can be discerned, in faded ink, the inscription "*Gorilla gorilla mangema*, Upper Congo". Rothschild never indicated in any of his papers that he possessed more than one skull of this form, and so B.M. No. 1939.945 is doubtless the holotype of the race. Indeed, metrically, it would be difficult to find a more typical skull of the eastern lowland gorilla.

Several skulls were available of populations whose status is in doubt, and of which large enough samples were impossible to obtain for the primary analysis. From application of the results of the analysis to these skulls, it would seem that the gorillas from the Kayonza forest, Uganda, may be *G. mangema*, while those from Mount Kabuzi, west of Lake Kivu, are very possibly *G. gaberigae*. The skulls from Bondo, in the Cole valley (a locality intervening between the eastern and western zones¹⁹), are decidedly *G. g. gorilla*.

In conclusion, the gorilla forms but a single species, whose characters overlap in the different races. There are three valid sub-species, at least two of which have ecologically differing demes (for an earlier use of demes as quasi-taxonomic units, see ref. 18). They are as follows: *Gorilla gorilla gorilla* Savage and Wyman, 1847; western gorilla. *Gorilla gorilla mangema* Rothschild, 1908; eastern lowland gorilla. *Gorilla gorilla beringei* Matschie, 1903; eastern mountain gorilla. It may be noted that Vogel¹² similarly concluded that two full sub-species exist in the eastern region, but on quite different grounds. An

examination of post-cranial features also supports this conclusion.

I thank all who made gorilla material available for this investigation, especially Dr. G. B. Corbet, Miss J. H. King, Mr. J. E. Hill, Mr. R. W. Hayman and Miss J. Ingles; Mr. L. Barton and Mrs. H. B. Powell-Cotton; Dr. F. Poll and Monsieur D. F. E. Thijs; Professor K. Zimmermann and Dr. G. H. W. Stern; and Mr. W. Schole and Mr. R. Hansen. Mr. Michael Clarke of the Mandstey Biometrics Unit and the staff of the University of London Institute of Computer Science gave computational help and Professor M. R. Healy gave statistical advice. I also thank Dr. J. R. Napier, of the Royal Free Hospital, and his assistant, Miss R. I. Dickson.

Received November 8, 1966.

- 1 Owen, E., *Trans. Zool. Soc.*, **3**, 281 (1845).
- 2 Owen, R., *Trans. Zool. Soc.*, **4**, 75, 89 (1862).
- 3 Martschke, P., *S.B. Ges. Naturf. Fr. Berlin*, **258** (1903).
- 4 Martschke, P., *S.B. Ges. Naturf. Fr. Berlin*, **45** (1904).
- 5 Martschke, P., *S.B. Ges. Naturf. Fr. Berlin*, **277** (1905).
- 6 Martschke, P., *S.B. Ges. Naturf. Fr. Berlin*, **323** (1914).
- 7 Schaller, G. B., *The Mountain Gorilla* (Chicago, 1963).
- 8 Schultz, A. H., *Exp. Lab. Mus. Zool. Soc. Philadelphia*, **58**, 34 (1930).
- 9 Schultz, A. H., *J. Mamm. Baltimore*, **15**, 51 (1934).
- 10 Goodridge, H. J., *Proc. Acad. Nat. Sci., Philadelphia*, **88**, 479 (1936).
- 11 Goodridge, H. J., *Mem. Mus. Comp. Zool., Harvard*, **50**, 293 (1929).
- 12 Vogel, G., *Z. Säugetierk., Berlin*, **26**, 2, 1 (1961).
- 13 Trevor, J. C., *J. H. Harbord, Inst.*, **77**, 61 (1950).
- 14 Taylor, P. A., and Mithall, H., *The Physical Anthropology of S. Nigeria* (Kambridge, 1962).
- 15 Ashton, F. H., Healy, M. J. R., and Linton, S., *Proc. Roy. Soc. Edinburgh*, **B**, **146**, 552 (1957).
- 16 Deacon, V. M. J., and Healy, M. J. R., *Proc. Roy. Soc., B*, **161**, 200 (1964).
- 17 Rothschild, W., *Nord. Zool.*, **15**, 301 (1908).
- 18 Fairfield, A. W. F., *Nat. Mus. Canada Bull.*, **177**, 161, ser. 66, Ottawa (1961).
- 19 Groves, C. P., and Napier, J. R., *J. Zool.*, **148**, 133 (1966).