

Kamp-Hilt & Bree (1964) reported *P. nathusii* from seven other localities. Hanák (1967) regards this species as rare in Czechoslovakia but Aellen (1961) states that it is common in the Swiss plains.

The question as to whether this English capture is a vagrant or part of an overlooked population is unknown but it seems unlikely that any sizeable population exists in Dorset.

Ectoparasite

One flea was collected from this bat and was identified by A. M. Hutson (Brit. Mus. (Nat. Hist.)) as *Ischnopygillus varibitlis* Wagner, a female. This is the first record for Britain of this flea but *P. nathusii* is the normal host (Aellen, 1960).

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R. E. STEBBINGS

*The Nature Conservancy,
Coastal Ecology Research Station,
Cohey Lane, Norwich,
NOR 70F*

Population systematics of the gorilla

COLIN P. GROVES

Duckworth Laboratory of Physical Anthropology, Cambridge University

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(With 4 figures in the text)

The systematics of the gorilla are reviewed in the light of abundant new material examined with the aid of techniques of multivariate analysis. Defects are pointed out in the usually accepted view that there are two clear-cut subspecies (*G. g. gorilla* and *G. g. beringei*); the existence of morphological intergradation is shown, and an intermediate subspecies, *G. g. graueri*, is recognized in addition.

Contents

Introduction	Page
Material and methods	287
Osteological material	288
Bionometrics	288
Results	290
Discussion	292
Summary	297
References	298
Appendix	299

Introduction

The currently accepted classification of the gorilla recognizes a single species with two subspecies—a view stemming from Coolidge (1929). The subspecies are the Lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman, 1847) and the Mountain gorilla (*G. g. beringei* Matschie, 1903). According to Coolidge the two differ in a series of characters: the Mountain gorilla has a longer palate, narrower skull, thicker pelage, shorter arms and longer legs. To this list Schultz (1934) adds considerably, stating that the amount of difference between the two inclines him to the view that they are distinct species. It may be noted, however, that many of the distinctions listed by Schultz (20 in all) appear to be highly interdependent, reducing to a longer and narrower pelvis, shorter limbs (especially the arms), longer great toe, narrower face and peculiarly curved vertebral border to the scapula. Finally Vogel (1961) reports that in the Mountain gorilla the toothrow is less crowded than in the Lowland form, the mental foramen is more frequently multiple and is further forward on the jaw, while the genioGLOSSAL fossa is more commonly lacking.

The distributions of the two forms are highly distinctive: not only are they separated by the whole Congo basin, where there are no gorillas, but the Mountain gorilla is found at altitudes of above 8000 feet, while terrain occupied by the Lowland form is below 6000

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extending into neighbouring countries; while that of the Mountain gorilla is given as the mountains of the Great Lakes region of the Eastern Congo, Uganda and Rwanda.

The first intimation that this neat picture might be more complicated than had been thought originated from the work of Schaller (1963), who stated clearly that the bulk of so-called "Mountain" gorillas live in lowland forests, lying to the west of the Great Lakes at altitudes of some 2000 feet—the very height at which the Lowland gorilla is most commonly found. Since this brings eastern ("Mountain") gorillas closer both geographically and altitudinally to western ("Lowland") gorillas, it seemed appropriate to examine specimens of these eastern lowland gorillas (i.e. the westerly group of the so-called "Mountain" gorilla) in order to discover whether the differences between the two recognized forms are in fact so clear-cut, especially as Coolidge's biometric techniques have been severely criticized by Haddow & Ross (1951).

The position of *Gorilla graueri* Matschie, 1914, would also appear to merit new enquiry. This is a form living on the Itombwe mountains, between Mwenga and Fizi in the eastern Congo, and which, according to Lorenz von Lieberna (1917), has limb-indices similar to *G. s. gorilla* rather than to *G. s. beringei*—yet according to Coolidge the name *graueri* is a synonym of *beringei*.

It is towards these enquiries that the present study has been directed, an opportunity also having been taken to enquire into the possibility of correlations between variations in the environment and those in the morphology of different groups of gorillas.

Material and methods

Osteological material

Visits to 35 institutions in 13 countries in Europe and North America afforded opportunity to study a total of 747 skulls of adult gorillas (469 male, 278 female) of accurately known locality, as well as 105 complete skeletons. The localities at which specimens were collected are from all parts of the known range of the species, and are listed and depicted in Table A, deposited in the archives of the British Museum (Natural History); many are from the eastern Congo lowland forests, the region intermediate between the ranges of the eastern and western subspecies, and therefore crucial for present purposes.

Biometrics

A total of 45 measurements was taken on each skull; these are listed and described in Table B, also deposited in the archives of the British Museum (Natural History). These skulls were clustered into 19 geographical groupings for males. Females were also represented in 11 of these. Each of the resulting samples contained at least 11 skulls, some as many as 30. The geographical locations of these samples is indicated in Fig. 1. Three of the groups consisted of skulls from single localities (Ouesso, Ebolowa and Abong Mbang); the others were drawn from several localities within restricted areas of not more than 100 sq. miles in area. The one exception concerned skulls from the eastern Congo lowland forests, an area of about 10,000 sq. miles, all of which were pooled into a single sample.

For each group, means, standard deviations and correlation coefficients were calculated between each pair of dimensions, using the Atlas Computer at the Institute of Computer Science of London University; resultant covariance matrices are deposited in the British Museum (Natural History) archives (Tables C1-67). On the basis of these intercorrelations, measurements of the

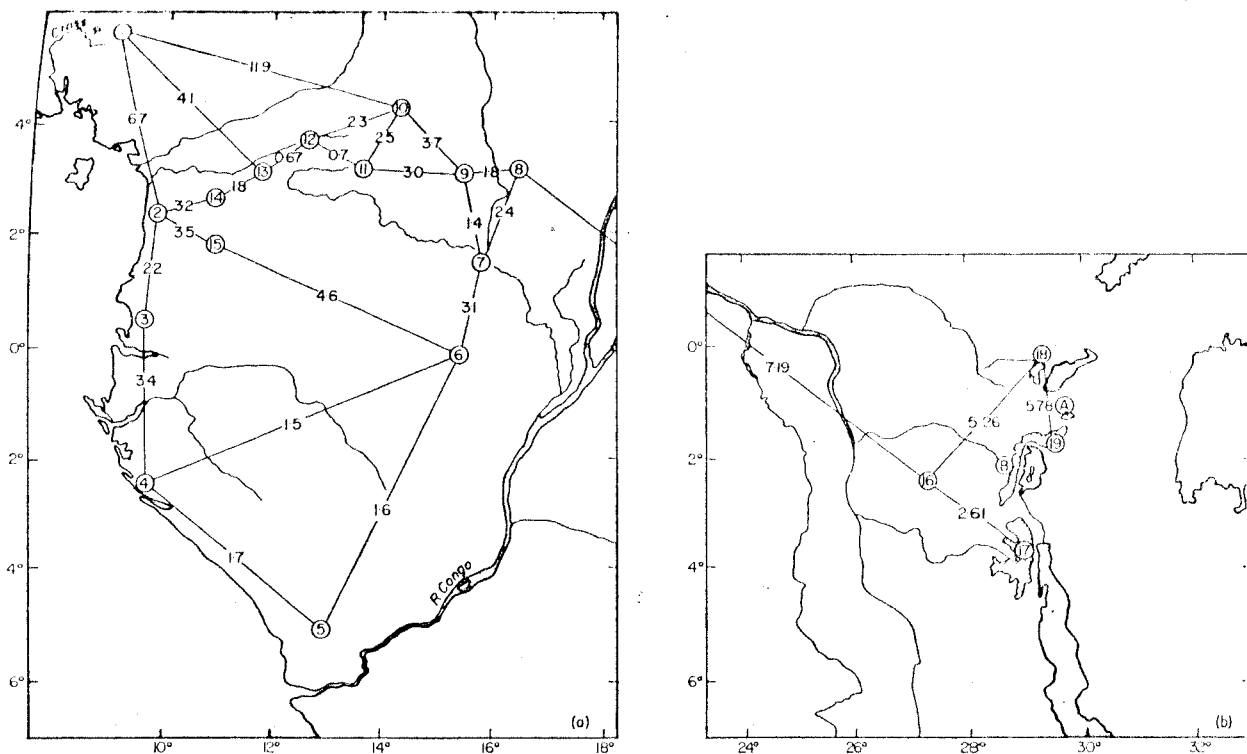


FIG. 1. Geographical locations of the 19 groups of gorillas studied. The name of the chief locality of collection is followed by the maximal number of skulls studied from that area, in parentheses; important subsidiary localities in the same area are also given.

1, Nigeria (14): includes all Cross River localities; 2, Bipindi (12): includes Campo, Lolodorf, Kribi; 3, Gabon (11): includes Sangatanga, Cap Lopez, Libville; 4, Sette Camma (13): includes Fernan Vaz; 5, Mayombe (13); 6, Mambili (13): includes Opa, Bade, Zalangoye; 7, Ouesso (20); 8, Nola (11); 9, Youkadour (11): includes Ziendi, Kadei, M'Bimou; 10, Batouri (12); 11, Lomie (24); includes Djaposten, Obala, Meyoss; 12, Abong Mbang (30); 13, Metet (11): includes Lobomouth, Akonolinga; 14, Ebolowa (24); 15, Acam (11): includes all localities in Northeast Rio Muni; 16, Utu (12): includes all localities in eastern Congo lowlands; 17, Mwenga-Fizi (11): includes Wabembe, Baraka, Itombwe; 18, Tshiaberimu (12): includes Lubero, Luofu, Alimbongo, Butembo; 19, Virung (13): includes all localities in Virunga Volcanoes. *Additional*: A, Kayonza forest (including Kumbi); B, Mt. Kahuzi (including Tshibinda, Mt. Nakalongi).

The area comprising the great bend of the Congo, where there are no gorillas, has been omitted.

The numbers on the lines between adjoining groups are the mean squared generalized distances between them.

...statement was selected from each series as being the most prominent anatomically. The 10 resulting cranial measurements were: Cranial length, Biorbital breadth, Palate breadth (outside teeth), Bleamie breadth, Facial height, Postorbital breadth, Bipriontic breadth, Tooth-row length, Palate length and Nuchal surface length. Those on the mandible were Bicondylar breadth, Ramus height, Ramus breadth, Bigonial breadth, Toothrow length and Breadth across jaw body. These were then returned to the computer in their four sections (male crania, female crania, male mandibles, female mandibles) and subjected to canonical analysis (Rao, 1953). Finally the canonical co-ordinates (also deposited in the British Museum, Tables D1-4) were used to calculate a squared generalized distance (D^2) between all pairs of geographical subgroups (Mahalanobis, 1936). This provides a measure of overall separation between the groups. These techniques are used, and their implications discussed, by (for example) Ashton, Healy & Lipton, 1957; Talbot & Mulhall, 1962; Healy, 1964.

Results

The full results of the D^2 analysis are deposited in the British Museum (Tables E1-4), and only an abbreviated version is reproduced here (summarized in Fig. 1). The figures in this diagram are derived from a mean of the four matrices, and records the average squared generalized distances between geographically adjoining subgroups.

TABLE 1

Mean squared generalized distances for gorilla skulls: combined data for males and females, crania and mandibles

	Coast	Plateau	Sangha	Nigeria	Uru	Mwenga-Fizi	Tshaberimu	Virunga
(1) Western								
Coast	xxxx							
Plateau	3.42	xxxx						
Sangha	2.36	1.87	xxxx					
Nigeria	3.75	3.64	2.76	xxxx				
(2) Intermediate eastern								
Uru	10.58	7.19	8.98	12.00	xxxx			
Mwenga-Fizi	13.97	9.63	12.01	13.39	2.61	xxxx		
Tshaberimu	18.32	12.80	17.69	19.91	5.26	2.85	xxxx	
(3) Extreme eastern								
Virunga	19.35	14.27	15.63	19.55	8.10	5.78	4.06	xxxx

The pattern of distances thus displayed shows that the subgroups from the western part of the gorilla's range fall into four clusters. These are: (a) a "Nigerian" group (no. 1 in Fig. 1); (b) a Coastal group (nos 2-5), with which was also closely associated a group from the Mambili river region (no. 6); (c) a group from the valley of the Sangha river (nos 7-9); (d) a group from the Cameroon plateau (nos 10-15).

The remaining samples, from the eastern segment of the range, fall into four groups, of which the three lying in the more westerly portion (nos 16-18 in Fig. 1) were quite similar

while the fourth group, the extreme eastern end of the range in the Virunga volcanoes (no. 19), was distinct. Mean square generalized distances between these eight resultant clusters are presented in Table 1. This indicates clearly that the intermediate eastern cluster (Uru, Mwenga-Fizi and Tshaberimu) differs from each of the four western groups (Coast, Plateau, Sangha and Nigeria) by amounts comparable in scale with that separating it from the fourth eastern group (Virunga). Examination, first of the absolute differences shown by the means of individual dimensions, and secondly of the sizes of the associated loading factors of the canonical variates, showed that most discrimination was being effected by contrasts in jaw size, especially length of toothrow and palate; increasingly large jaws being shown in the sequence Western-Intermediate Eastern-Virunga. Additionally, the Intermediate Eastern group was differentiated by a longer, narrower face than the other two.

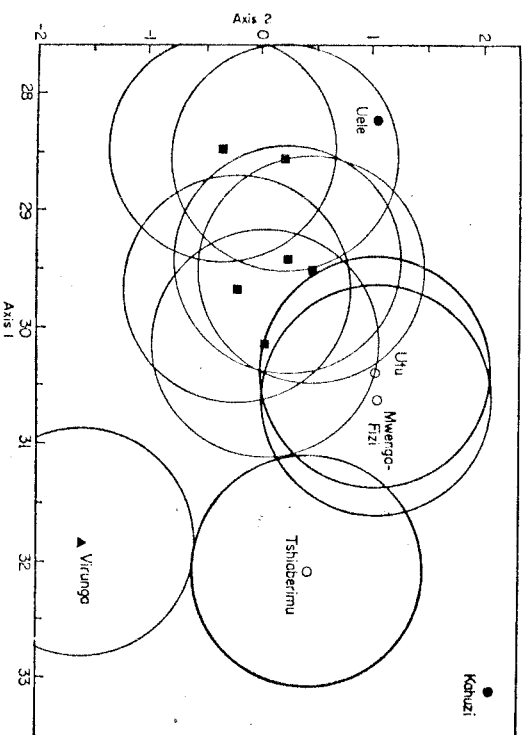


FIG. 2. The relative contrast between geographical subgroups as shown by the first two canonical axes: data from female mandibles. ■, Western group; ○, intermediate eastern group; ▲, extreme eastern group; ●, isolated specimens from other areas.

A similar pattern emerges if the positions of the various groups on the first two canonical co-ordinates (these contributing maximally to the value of the squared generalized distance) are plotted. An example of these results, based on the female mandibles, is presented in Fig. 2, where the easternmost group (Virunga) is completely distinct; the remaining eastern subgroups forming a bridge between it and the western cluster. The total overlap between the three major groups (Western, Intermediate Eastern, and Virunga) is not greater than

The results of this analysis extend the accepted concept of the taxonomy of *Gorilla gorilla* (as comprising two subspecies), in showing that the eastern group comprises two distinct divisions. At the extreme eastern end of the range is the group from the Virunga Volcanoes (topotypes of *Gorilla gorilla beringei*), while somewhat to the west of this, although almost continuous geographically, is a further group centring on the three districts of Mt. Tshiaberimu (west of Lake Edward), the Itombwe mountains (between Mwenga and Fizi, west of Lake Tanganyika) and Utu (in the eastern Congo lowlands).

A further extension to the accepted taxonomy is the finding that within the western (Lowland) subspecies of the gorilla, samples from different parts of the range do, in fact, show a number of significant contrasts. The question therefore arises as to whether or not any or all of these additional subgroups should be given distinct subspecific status, as was done by several authors whose work was reviewed in Coolidge's (1929) revision.

TABLE II
Frequencies of certain meristic features in gorilla population samples

	Per cent with Mental foramen multiple	Per cent with Infraorb. foramen multiple	Per cent with Mandib. condyle bifid	Per cent with Palate incomplete behind
(1) Western Coast	15.5 (120)	56.7 (126)	0.0 (120)	23.1 (126)
Plateau	21.8 (113)	57.9 (159)	11.7 (113)	21.2 (159)
Sangha	25.2 (56)	62.5 (80)	14.7 (56)	15.0 (80)
Nigeria	5.6 (18)	25.3 (63)	0.0 (18)	22.4 (63)
	17.0	50.6	6.6	20.4
(2) Intermediate eastern Utu	62.0 (36)	88.1 (40)	42.9 (36)	2.5 (40)
Mwenga-Fizi	77.0 (31)	100.0 (34)	8.9 (31)	0.0 (34)
Tshiaberimu	66.7 (30)	83.8 (38)	39.1 (30)	0.0 (38)
	68.6	90.6	30.3	0.8
(3) Extreme eastern Virunga	91.9 (37)	74.7 (42)	56.5 (37)	0.0 (42)
(4) Others Kahuzi	66.7 (9)	95.0 (10)	80.0 (10)	0.0 (10)
Kayanza	80.0 (5)	92.9 (10)	40.0 (5)	0.0 (7)

The following differences were found to be significant at the 5% level of χ^2 :

- (1) Multiple mental foramen: all western from all eastern; all intermediate eastern from extreme eastern.
- (2) Multiple infraorbital foramen: Nigeria from other western; all western from all eastern; Mwenga-Fizi from extreme eastern.
- (3) Bifid condyle: Coast and Nigeria from Plateau and Sangha; all western, plus Mwenga-Fizi, from all other eastern.
- (4) Incomplete palate: all western from all others.

The geographical distribution of the genus is becoming increasingly clear. The extreme of the Lowland gorilla and the westernmost extent of the "Mountain" form. Despite this discontinuity, the findings of the present craniometric analysis indicate that a cline in overall cranial pattern can be made out, extending from the Nigerian group in the extreme west through the Plateau and Sangha groups, thence to the "Mountain"

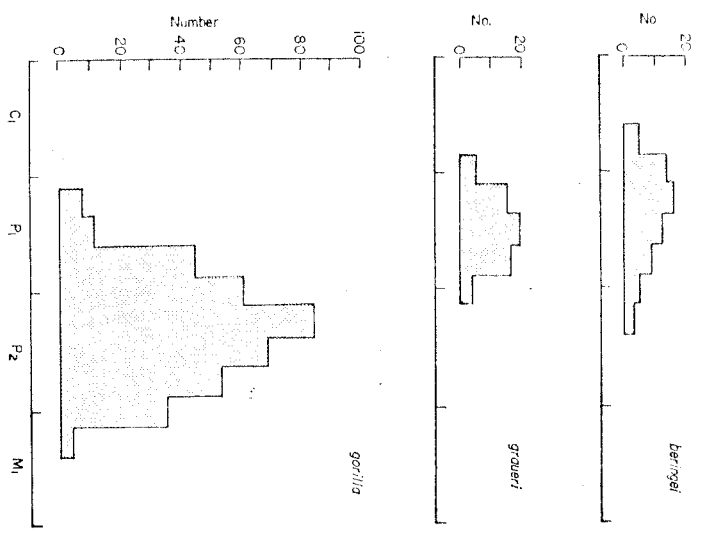


Fig. 3. Position of largest opening of mental foramen in the three subspecies of gorilla.

gorillas of Utu, the Tshiaberimu and Mwenga-Fizi groups from west of the Great Lakes, and finally to the easternmost group in the Virunga Volcanoes. The groups comprising this cline, however, are not, in the morphological sense, equally spaced, the squared generalized distance between the westerly group of "Mountain" gorillas, on the one hand, and both the Virunga group of true Mountain gorillas together with the entire complex of Lowland forms, on the other hand, being much bigger than the distances between any of the geographical subdivisions of this latter. *A priori*, therefore, it might seem appropriate to regard the westerly "Mountain" gorillas as a new and distinct subspecies, restricting the name *beringei* to the Virunga Volcanoes form. In order to test this view still further, data were accumulated on a number of meristic

open drawn to some of these by previous authors (Schultz, 1934; Vogel, 1961) in the process of defining the Mountain gorilla.

The meristic features, together with contrasts in their frequency of occurrence, are listed in Table II. This shows a progressive change in the frequency of occurrence of Multiple mental foramina, Multiple infraorbital foramina, Bliff mandibular condyles and Incomplete posterior part of palate, as progressive samples are taken from west to east across the gorilla's range. A further analysis showed that, in the case of the intermediate eastern group, in contrast to the other forms, a significant proportion of individuals had four, five or even six openings to the mental foramen. As shown in Fig. 3, it was also found that the biggest aperture of the mental foramen lies on average progressively more anterior in the west-to-east series.

Study of the postcranial skeleton also confirmed the distinctive nature of the geographic-ally intermediate group of the "Mountain" gorilla. Five morphological indices used by Schultz (1934) in his study of this form were calculated, the results being summarized in Table III. In the case of the brachial index and the relative lengths of clavicle and humerus, there is again a morphological west-to-east cline, while in the case of the intermembral index and the relative lengths of femur and humerus, the geographically intermediate group shows values somewhat bigger than obtained in the areas to the east or west of it. From a study of 17 specimens (none included in Schultz's (1934) analysis) it was found that the length of the great toe, relative to the foot as a whole, was as small in the intermediate group (with the exception of two specimens from Mt. Tshaberimu) as in the western (lowland) complex. This extends Schultz's own finding of a contrast between the two taxa recognized by him. Lowland and Mountain, it having been ascertained that Schultz's "Mountain gorilla" specimens, used for all the indices in his 1934 paper, were from the Virunga Volcanoes or else from Mt. Kahuzi, and thus not from any of the geographically "intermediate" areas specially studied in the present paper.

In his 1934 paper, Schultz also described a feature of the scapula as diagnostic of Mountain gorillas (*beringei*): the vertebral border is sinuous, being somewhat pulled outwards near or at the root of the scapular spine. In Lowland gorillas, on the other hand, the vertebral border was said to be straight as in man. In the present study, numerous scapulae were examined from all parts of the gorilla's range; out of 26 of western (lowland) gorillas, only two showed the slightest trace of a sinuous border, whereas all from the Virunga Volcanoes and from Mt. Kahuzi showed at least some sinuosity, this characteristic being very marked in 10 out of 12 from Virunga and three out of four from Kahuzi. Schultz's distinction is thus confirmed; there is hardly any overlap. In the case of gorillas from the intermediate area, the vertebral border was found to be as straight as it is in western gorillas, with no trace of sinuosity in any out of 24 individuals examined from Mwenga-Fizi, in seven out of eight from Ulu, or in nine out of ten from Tshaberimu: making just two exceptions in 42 skeletons of the intermediate form.

The precise functional meaning of this scapular form is unclear; it is possible that, as Schultz himself suggested, it reflects a different attachment of certain muscles, such as *M. rhomboideus* or *M. serratus anterior*. If this is so, then it might be a response to the broader chest (as seen in the clavicle-humerus index) of the true Mountain gorillas, to assist in respiration in the thin atmosphere at high altitudes.

In all instances these contrasts, in meristic and postcranial features, are bigger between

the three principal groups of gorilla defined in this study than obtains between the sub-groups of the western (lowland) form or between those of the intermediate eastern group. The overall findings, and especially the observation that the overlap displayed by the combination of cranial measures is less than 10%, thus supports the conclusion that three subspecies of *Gorilla gorilla* should be recognized, rather than the two that have characterized almost all treatments since Coolidge's (1929) revision of the genus. The name *beringei* must therefore be restricted to the true Mountain gorilla from the region of the Virunga

TABLE III
(1) Indices of postcranial skeleton: means and standard errors

	Femur-humerus	Brachial	Clavicle-humerus	Intermembral
(1) Western	115.8	77.8	37.3	115.3
Nigeria	(1)	(1)	(1)	(1)
Coast Plateau	117.4 ± 0.5 (25)	80.2 ± 0.5 (24)	38.0 ± 0.5 (22)	116.5 ± 1.5 (24)
Sangha	114.2 ± 0.9 (6)	79.8 ± 1.2 (6)	36.3 ± 0.6 (6)	115.4 ± 1.2 (6)
(2) Intermediate eastern				
Ulu	117.1 ± 1.3 (3)	76.6 ± 1.2 (3)	38.9 ± 1.3 (5)	116.5 ± 1.8 (6)
Mwenga-Fizi	116.4 ± 0.4 (8)	78.6 ± 0.5 (7)	37.6 ± 0.4 (19)	117.3 ± 0.4 (15)
Tshaberimu	118.3 ± 0.8 (7)	78.3 ± 0.9 (6)	38.7 ± 1.0 (6)	116.8 ± 1.0 (6)
(3) Extreme eastern	113.0 ± 1.1 (7)	82.8 ± 1.2 (7)	42.1 ± 0.5 (13)	115.3 ± 1.0 (11)
Virunga	(7)	(7)	(13)	(11)
(4) Others	114.6	80.8 ± 1.0 (3)	40.8 ± 1.1 (4)	115.5 ± 0.5 (3)
Kahuzi	(2)	(3)	(4)	(3)

The following differences were found to be significant at the 5% level of Student's *t*-test.

- (1) Femur-humerus: Extreme eastern from all others except Sangha; Intermediate eastern from Sangha; Coast Plateau from Sangha.
- (2) Brachial: Virunga from all other samples except Kahuzi.
- (3) Clavicle-humerus: Virunga from all others except Kahuzi; Kahuzi from all others except Virunga, Tshaberimu and Ulu: at 10% in latter two cases.
- (4) Intermembral: only Virunga from Mwenga-Fizi.

(2) Great toe to foot index (as in Schultz, 1934)

	Schultz (1934)	New data
Western	84.1-86.6 (4)	84.5 ± 0.6 (4)
Intermediate eastern		
Mwenga-Fizi		83.7 ± 0.6 (7)
Tshaberimu		89.3 (2)
Extreme eastern		
Virunga, Kahuzi	88.6-88.9 (2)	88.9 ± 0.6 (4)

The difference between Extreme eastern and Mwenga-Fizi/Western is fully significant at the 5% level by Student's *t*-test.

ade" region) must take the name *graueri* Matschie, 1914. A formal definition of the three subspecies of the gorilla appears in the Appendix.

Within the eastern segment of the gorilla's range, there are isolated populations on Mt. Kahuzi (west of Lake Kivu) and in the Kayonza forest (Kigezi district, Uganda), as well as in the specially studied areas here called Virunga, Tshaberimu, Mwenga-Fizi and Uru.

TABLE IV
Ecological data for gorilla habitats (from Schaller, 1963; *Natural Intelligence Handbook*, 1947; Blancou, 1951; Reichenow, 1920; Rohm & Christianson, 1963)

	Altitude (ft)	Mean temp. (°C)	Annual rainfall (in)	No. of in troop	% nests ground	Diet: % fruit, leaves etc.
<i>G. g. gorilla</i>						
Coast	100 (av.)	25.9	97.2	1 (?)	56 (?)	60 (?)
Plateau	2400	23.5	65.6	3-0	100 (?)	60 (?)
<i>G. g. graueri</i>						
Uru	2500	25.0	58.9	2-7	21.8	60.0
Mwenga-Fizi	7800	—	—	3 (?)	65.2	23.3 (?)
Tshaberimu	7400	17.8	70.0	—	32.9	19.5
<i>G. g. beringei</i>						
Kahuzi	6940	15.8	76.0	—	81.0	52.3
Virunga	10200	9.4	59.0 { Kisoro Kabara	2.3 6.2	45.3 97.1	24.5
Others:						
Kayonza	6700	13.4	41.0	1-8	53.5	55.5

In the study of postcranial features (above), gorillas from Mt. Kahuzi invariably assort with those from Virunga. In the cranial analysis, too few specimens from either Kahuzi or Kayonza were available for use in the primary analysis, and could only be fitted in afterwards: a procedure which may not be entirely satisfactory especially in the case of very restricted samples. The mean distances of the two isolates, based on the average squared generalized distances of one to four specimens from the four other eastern groups, are given below:

Distance from:	<i>Uru</i>	<i>Mwenga-Fizi</i>	<i>Tshaberimu</i>	<i>Virunga</i>
of: Kahuzi	6.52	3.93	3.44	7.34
Kayonza	5.62	3.17	6.18	3.56

No very marked differences are observable; Kahuzi is similar to the somewhat transitional Mwenga-Fizi and Tshaberimu groups, while Kayonza is fairly similar to Mwenga-Fizi and to Virunga, though not to Tshaberimu. A firm conclusion on both these two groups could only be derived from a study of further specimens, although in the case of Kahuzi the strong similarity with Virunga in postcranial features leaves little room for doubt that its true taxonomic position lies with *G. g. beringei*. Provisionally, the Kayonza forest gorillas may be placed under the subspecies *graueri*.

Although of no formal taxonomic significance, the contrasts that have emerged between

the subgroups *G. g. graueri* and *G. g. beringei* are of interest in that they can be correlated with ecological variations in the habitat (Table IV). Thus in phase with the changes in morphological patterns in each of the three subspecies, there are corresponding gradations in altitude, temperature and rainfall. Additionally, there appear to be contrasts in certain environmentally correlated behavioural traits, such as troop size (as shown by the number of females per group) and height of nesting sites. In this Table, the Nigeria and Sangha western groups are omitted for lack of data; only altitude is reported for the Cross River (Nigerian) region, which is said to live in hilly country at 1000 to over 5000 feet (Anon., 1934). The evidence of these subregional differences would appear to re-emphasize the biological reality of the clusterings within each subspecies adopted in this study, each of which can therefore justifiably be recognized as a deme.

Externally, there are differences between the three subspecies. *G. g. beringei* and *G. g. graueri* are jet-black in colour of both skin and hair; the adult male develops a silvery-white "saddle" on the back, in the short-haired region between shoulders and rump. The former subspecies however, is easily distinguished by its shorter arms, more stocky build, and much longer, silkier fur especially on the arms. In *G. g. gorilla* the hair is short like *graueri*, but more greyish or brownish; the male's "saddle" of whitish hair extends onto the thighs, and grades more into the body colour. Western gorillas are reported to have a prominent "lip" at the top of the nasal septum (Napier & Napier, 1967); this lip has been seen in living specimens by the present author, and its absence from individuals of the other two subspecies has been noted. Surprisingly little information is available on absolute size; what has been gathered from various sources indicates that *G. g. graueri* may be the largest subspecies, closely followed by *G. g. beringei*:

graueri, average height in male 175 cm, weight 360.3 lb (4)
beringei, average height in male 172.5 cm, weight 342.9 lb (6)
gorilla, average height in male 166.6 cm, weight 307.3 lb (32)

(data from Coolidge, 1936; Chagula, 1961; Du Chailu, 1861; Frechkop, 1943; Lorenz von Lburnau, 1917; Schaller, 1963; Powell-Cotton museum registration cards; L. G. Smith, pers. comm.).

Summary

A study has been made of quantitative features of 747 adult gorilla skulls, drawn from a total of 19 districts, encompassing some 100 individual localities, representing practically all parts of the range of *Gorilla gorilla*.

Analysis using the statistic of squared generalized distance (D^2) showed that in features of the skull and mandible the populations of gorillas fell into three clusters, between which the morphological contrasts were greater than those that obtained between the constituent populations of each.

The first of these clusters comprised groups from the western parts of the range, including Gabon, Cameroon, Congo (Brazzaville), Rio Muni and the Cross River district of Nigeria. This cluster corresponds to the nominate subspecies, *Gorilla gorilla gorilla* Savage & Wyman, 1847.

The second included only the gorillas of the Virunga Volcanoes. The prior name for this subspecies is *Gorilla gorilla beringei* Matschie, 1902.

Appendix
Diagnoses of subspecies of gorilla

- (1) Western or lowland gorilla. *Gorilla gorilla gorilla* Savage & Wyman, 1847. Synonymy: see Allen, 1939; to which must be added the following:
1903. *Gorilla gigas* Haeckel. *Anthropogene*, 5th ed., 1: 426, text-f., 243-244. Jaunde (Yaounde), Cameroon.

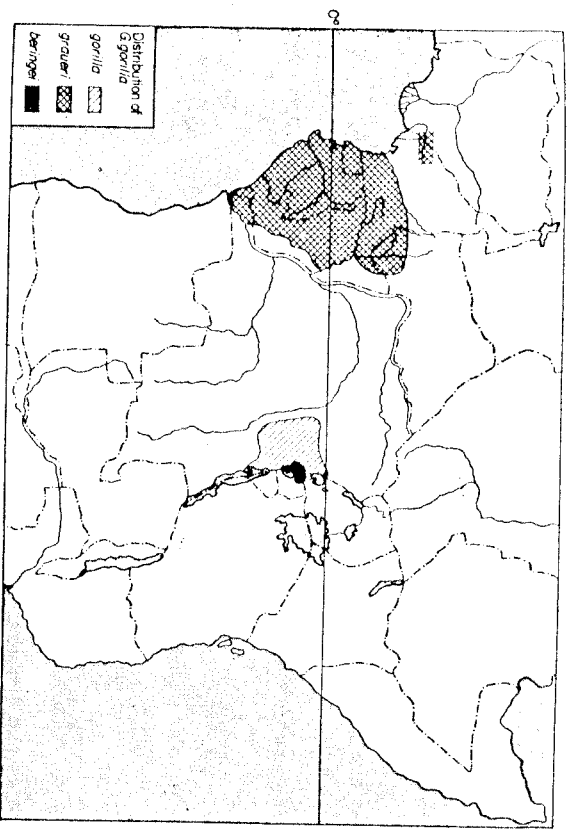


FIG. 4. Map of the central region of Africa to show distributions of the three subspecies of gorilla.

1943. *Gorilla (Pseudogorilla) ellioti* Frechokop. *Explor. Parc natn. Albert Miss. S. Frechokop No. 1: 13*. New name for *Pseudogorilla manyema* Elliot (Fernan Vaz, Gabon), not *Gorilla manyema* Alix & Bouvier.
- West African portion of range: also a small area near Bondo, Uele River (at least until 1908). Smallest; fairly broad face, small jaws and teeth, short palate; toothrow about 60-70 mm long; a single mental foramen on each side, under P₃ or P₄; jaw condyle without cleft; palate often incomplete behind; vertebral border of scapula straight; humerus long compared to radius, femur and clavicle; great toe short, rather divergent; lighter, greyer colour with short fur; "saddle" of adult male extends to thighs; "tip" on nasal septum.
- (2) Eastern lowland gorilla. *G. g. graueri* Matschie, 1914. Synonymy:
1908. *Gorilla gorilla manyema* Rothschild. *Novit. Zool.* 15: 392. "South Congo region"; by inference, the province of Manyema, Congo-Kinshasa. Lapsus for *manyema* Alix & Bouvier (Corbet, 1967).

the west of Lakes Tanganyika and Edward ... eastern Congo lowlands and the mountains under *beringei*, it is submitted that this group should be separated previously generally included the name *Gorilla gorilla graueri* Matschie, 1914. This view is supported by the examination of (a) quantitative features of the postcranial skeleton, (b) meristic features of the skull, (c) external characteristics such as pelage.

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The taxonomic status of British Water voles, genus *Arvicola*

G. B. CORBET

British Museum (Natural History), London

JANET CUMMINGS*

Department of Zoology, University of Durham

S. R. HEDGEC†

British Museum (Natural History), London

AND

W. K. RZANOWSKI

Rothamsted Experimental Station

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(With 5 figures in the text)

Samples of skulls of *Arvicola* were studied from several regions of Britain to test the hypothesis that more than one species of the genus might be present. Analysis of cranial measurements and of quasi-discriminuous variants of the skull provides no grounds for recognizing more than a single species, and comparison with samples from continental Europe supports the view that all the British samples represent *A. terrestris* rather than *A. sapidus*. The analysis of epigenetic variants confirms the difference between *A. terrestris* and *A. sapidus*. None of the characters studied shows much regional variation within the Britain mainland, but further data are provided on the characters of an insular population on Eilean Gannha, Argyll.

Contents

Introduction	302
Analysis of measurements	303
Material	303
Methods	303
Variation within Britain	303
Size	303
Nasals	305
Incisors	305
Length of tail	305
The form on Eilean Gannha	306
Comparison of British and Continental <i>Arvicola</i>	306

* Present address: Dept. of Biology, University of Sussex, Brighton.
 † Present address: Science Unit, B. B. C., London, W. 1.

1914. *Gorilla granivi* Matschie. *Sber. Ges. naturf. Freunde Berl.* 1914: 324. West shore of L Tanganyika, 80 km north-west of Boko, Wabembe country.
 1927. *Gorilla gorilla rex-pyngaeronum* Schwarz. *Rev. Zool. Bot. Afr.* 14: 333, pl. 11-13. Luofu, west of L. Edward (Mt. Tshiaberimu).
 Ulu lowlands of eastern Congo: Iombwe and Tshiaberimu highlands: perhaps Kayonza forest. Largest: high, narrow face, larger jaws and teeth, longer palate; toothrow about 67-75 mm; mental foramen often multiple, under P₃; jaw condyle often cleft; palate nearly always complete behind; vertebral border of scapula straight; humerus long; great toe usually short, divergent; black colour, short fur; "saddle" of adult male restricted to back; no "lip" on nasal septum.
 (3) Mountain gorilla, *G. g. beringei* Matschie, 1903.
 Synonymy:
 1903. *Gorilla beringei* Matschie. *Sber. Ges. naturf. Freunde Berl.* 1903: 257. Mt. Sabino, Virunga Volcanoes.
 1917. *Gorilla beringei mikenensis* Lönnerberg, K. Svenska Vet.-Akad. *Handl.* (2) 58, no. 2: 7, pl. 1-4. Mt. Mikeno, Virunga Volcanoes.
 Virunga Volcanoes; Mt. Kahuzi (including Mts Nakalongi and Biega).
 Rather larger, low, broad face; very big jaws and teeth, very long palate; toothrow length 70-78 mm; mental foramen multiple, under C or P₃; jaw condyle usually cleft; palate always complete behind; vertebral border of scapula sinuous; humerus short; great toe long, parallel to other toes; black colour, very long silky fur; "saddle" of adult male restricted to back; no "lip" on nasal septum.