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The Cross River Gorillas: A Distinct Subspecies, *Gorilla gorilla diehli* Matschie 1904

ESTEBAN E. SARMIENTO[1] AND JOHN F. OATES[2]

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[1] Research Associate, Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History.
[2] Professor, Department of Anthropology, Hunter College of the City University of New York, New York, NY 10021.

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ABSTRACT

This study presents the results of a new set of measurements made on museum specimens of gorilla skeletons from the Cross River headwaters. It provides a review of the taxonomy of Cross River gorillas and describes their distribution and related aspects of their natural history. Considering their distinctiveness and geographic isolation, Cross River gorillas are best regarded as a distinct subspecies, *G. g. diehli*. Compared to other western gorilla populations, Cross River gorillas have smaller dentitions, smaller palates, smaller cranial vaults, and shorter skulls. Although Cross River gorillas do not seem to differ from other western gorillas in either body size or limb long bone lengths, measurements from a single male suggest that they may have shorter hands and feet and a larger opposability index than other western gorillas. Marked variation in the habitats of Cross River gorillas and insufficient data on behavior frustrate attempts to directly associate morphology with ecology. Many of their distinguishing characters, however, are parts of an adaptive complex that in most primates is characteristic of increasing terrestriality. A subspecific designation for Cross River gorillas correlates with other biogeographic patterns, since many primate species and subspecies inhabiting the Cross River area are distinct from their counterparts further south where other western gorillas occur.

INTRODUCTION

In 1904, Matschie described a new species of gorilla, *Gorilla diehli*, based on eight specimens collected by Diehl in low montane forests on the northern watershed of the Cross River in western Cameroon, close to the Nigerian border. Matschie (1904) designated a male skull from Dakbe (ZMBU 12789) as the holotype of *G. diehli*, citing a short molar row and skull, a low and broad nuchal plane, and distinctive palatal morphology as species-distinguishing characters. Matschie supported a specific designation for these animals by claiming they were sympatric with *G. gorilla*. Subsequent taxonomic revisions by Rothschild (1904, 1906) and Elliot (1912) recognized this population as only a separate subspecies, *G. g. diehli*. Elliot, however, concluded that there were not enough specimens in museums to test for the validity of all the gorilla species and subspecies that had been proposed since the discovery of gorillas by the Western world (Savage and Wyman, 1848). Later, Coolidge (1929) simplified gorilla taxonomy by sinking all of the proposed species (11 at that time) into a single species. He denied *G. g. diehli* a subspecific status, assigning all of the gorilla populations of West Africa to *G. g. gorilla* and those along the Western Rift to *G. g. beringei*. Groves (1970), following Coolidge, supported the single species taxonomy of *Gorilla*, but emphasized the morphological distinctiveness of Virunga gorillas, granting them a unique subspecific status (as *G. g. beringei*). He resurrected *graueri* (Matschie, 1914) as a subspecies nomen to include the other Western Rift gorilla populations and those in the eastern Congo lowlands. Groves described *G. g. graueri* as a central link in a cline extending from the Virungas to the Cross River at either extreme. Although mean squared generalized distances computed from cranial measurements showed that *G. g. diehli* was the most distinctive of the West African gorilla populations, Groves reasoned that the relatively narrow cline exhibited by West African gorillas did not merit subspecific distinction for any one western population.

Recent analyses of mitochondrial DNA among western gorillas and observations on the behavior, ecology, and anatomy of Western Rift gorilla populations suggest that there is more diversity among gorillas than can be accommodated in Groves' (1970) single species taxonomy (Morell, 1994; Ruvolo et al., 1994; Sarmiento, et al., 1995, 1996; Groves, 1996; Sarmiento and Butynski, 1996). Because Groves' generalized distances between eastern and western gorillas may be more consistent with specific differences (Ruano, 1992; Ruvolo, 1994; Sarmiento and Butynski, 1996: Uchida, 1996, 1998), the question of the subspecific status of the Cross River gorillas is reopened.

Species and subspecies differences between the forest catarrhines of western equatorial Africa and those in western Cameroon (Oates, 1988), and the inclusion of non-Cross River gorillas in the revisions that initially sunk Matschie's taxon, warrant a reinvestigation of *G. g. diehli*.

BACKGROUND

Distribution

Cross River gorillas are restricted to semi-deciduous and montane forests between 5°55′–6°25′N and 8°48′–9°38′E on the border of Nigeria and Cameroon, 200 km northeast of the Gulf of Guinea. They are distributed in and around a set of escarpments whose peaks rise above the low-lying coastal forests and reach maximum elevations of 1600–1900 m (figs. 1 and 2). Today these gorillas are concentrated in four separate areas: (1) the Afi mountains of Nigeria, (2) the Mbe mountains of Nigeria, (3) the Boshi Extension forests of the Okwangwo division of Nigeria's Cross River National Park (CRNP), and (4) the Takamanda Forest Reserve of Cameroon and adjacent areas of CRNP along the Cameroon border (fig. 1; Oates, 1998a, 1998b). Both Sanderson (1940) and Thomas (1988) also indicated that these gorillas may inhabit forests southeast of Takamanda, that is the Mone Forest Reserve in Cameroon. The Cross River gorillas are said to have ranged into the relic montane forests of the Obudu plateau (1500–1700 m elev.) in the recent past (Harcourt et al., 1989).

The Cross River gorillas have the most northern and western distribution of all gorilla populations[3] and are isolated by a considerable distance from the other West African gorillas. Bafia and Sakbayeme (Zakbayeme), which lie on the right (north) and left (south) banks of the Sanaga River, respectively, and approximately 260 km southeast of Basho, are the closest recorded and verified gorilla collecting localities to the Cross River area (fig. 2). Both of these localities are outposts of the western equatorial African forest that forms a continuous cover over southern Cameroon, Gabon, Equatorial Guinea, northern Republic of Congo and southwestern Central African Republic, and provides the habitat of all non-Cross River western gorillas (fig. 2). Interspersed between the Cross River area and Bafia and Sakbayeme are the grasslands and fragmented forests of the Cameroon highlands, and the relatively densely settled lowlands of western Cameroon, which effectively isolate the Cross River gorillas from the other West African gorilla populations.

Taxonomic History

Matschie: In 1904, Matschie described *Gorilla diehli* based on eight skulls collected by Diehl in the vicinity of Dakbe, Oboni, and Basho, in the northern watershed of the Cross River, Cameroon. Matschie designated a male skull from Dakbe (ZMBU 12789; table 1, figs. 3, 4) as the holotype of *G. diehli* and the remaining seven specimens (supposedly 3 males and 4 females) as paratypes (figs. 4–7).

According to Matschie, (1) short skull length, (2) short molar row length, (3) palatal morphology, and (4) broad and low nuchal plane distinguished *G. diehli* from southern Cameroon gorillas (*G. gorilla*). To quantify the broad and low nuchal plane of *G. diehli*, he calculated the ratio of the maximum breadth of the back of the skull as percent of the length from basion (intercondylar notch) to the external occipital protuberance. In those specimens with a damaged skull base, Matschie took the (sagittal) midpoint of the line connecting the two mastoids in lieu of basion and corrected for the different reference point by subtracting 10 mm in males and adding 5 mm in females to the final length. He showed the ratios in his *G. diehli* (♂ 0.6–0.64, ♀ 0.51–0.58) to be outside the range of those of 34 males and 10 females of *G. gorilla* (♂ 0.73–0.81, ♀ 0.61–0.67), and of a single male Virunga gorilla (0.77; probably ZMBU 13254) when comparing respective sexes.

In support of a specific designation for *G.*

[3] A *G. g. gorilla* skull (MRAC 5885) from the Royal African Museum Tervuren collected by Bal in 1914 and labeled Ganga, Kamerun, may prove to have a more northern origin. The Cameroon gazetteer (U.S. Board of Geographic Names) provides the coordinates 7°22′N, 13°59′E for Mt. Ganga. German Kamerun, however, extended into what is present day Central African Republic and more than likely this locality refers to Ganga CAR at 4°59′N 16°52′E, since Mt. Ganga is well outside the equatorial evergreen forest zone that is the known habitat of western lowland gorillas.

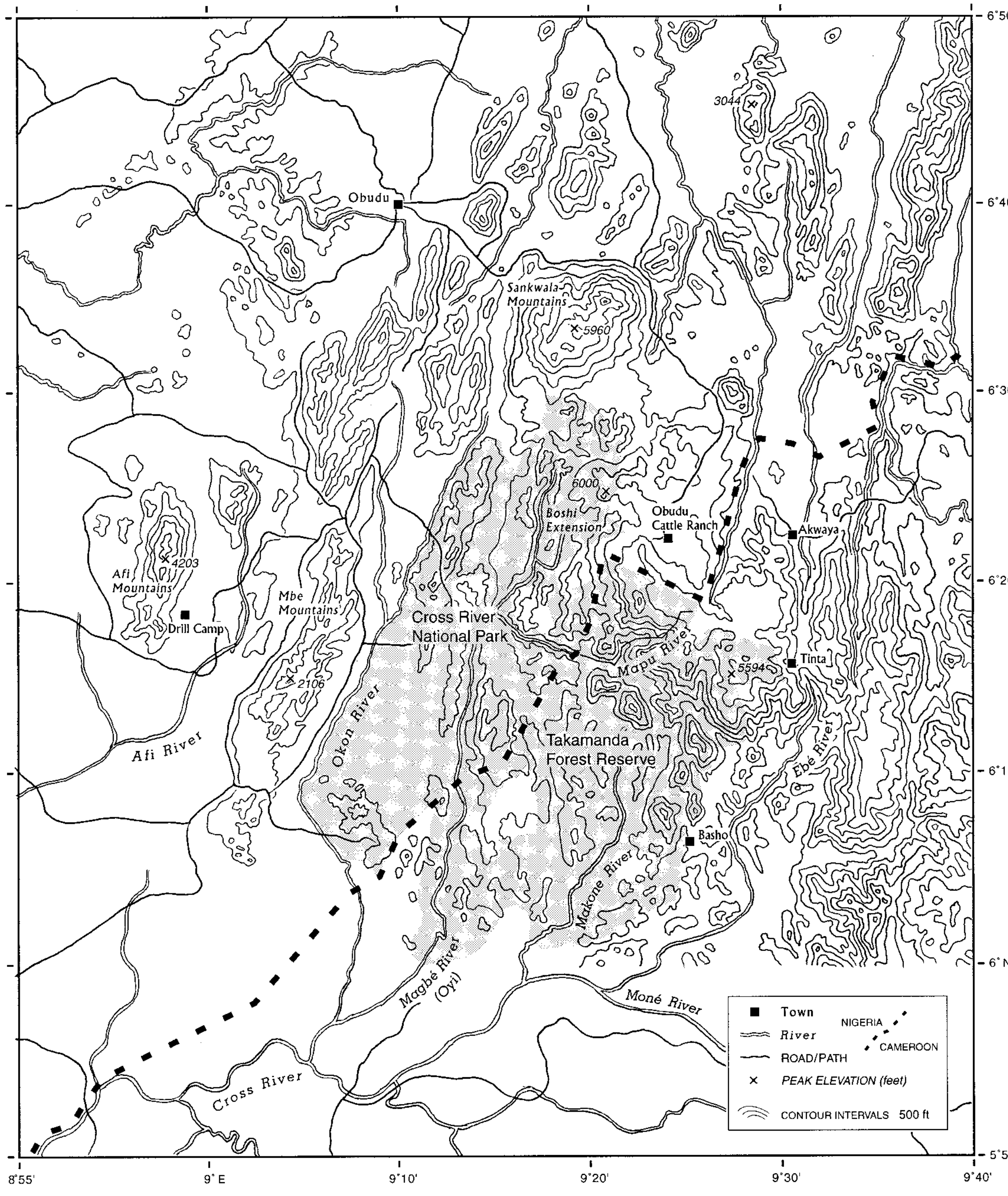

Fig. 1. Map of Cross River watershed showing national parks or forest reserves and the four separate areas inhabited by the Cross River gorillas.

diehli, Matschie drew attention to an additional female skull also collected by Diehl from Basho (ZBMU 12799). According to Matschie, this skull was indistinguishable from Southern Cameroon gorillas and showed that *G. gorilla* and *G. diehli* had overlapping geographic distributions. However, he did not present a nuchal ratio for this female skull or otherwise compare it to the eight specimens of *G. diehli*.

TABLE 1
Locality, Museum Number, Sex, and Age Class of Cross River Gorilla Specimens[a] in this Study

Locality	Museum	Number
Basho	ZMBU	12793 (♂juv)[b], 12794 (♀)[b], 12795 (♂)[b], 12799 (♀)[c], 48173 (♂), 83525 (♀), 83527 (♂), 83553 (♂)
Dakbe	ZMBU	12789 (♂)[d], 12792 (♂)[b]
Oboni	ZMBU	12790 (♂)[b], 12791 (♂)[b], 12796 (♂juv.)[b]
Ossidinge	ZMBU	83519 (♂), 83522 (♂), 83526 (♀), 83531 (♀), 83532 (♂juv), 83533 (♀), 83534 (♂), 83535 (♀), 83536 (♀), 83538 (♀), 83539 (♀), 83540 (♂), 83541 (♀), 83542 (♂juv), 83554 (♂), 83549 (♀), 83552 (♂), 83554 (♀), 83555 (♀), 83557 (♀), 83559 (♀), 83565 (♂), 83569 (♂), 83579 (♂), 83583 (♀), 85829 (♂), 85833 (♂), 85836 (♂), 85837 (♂), 85840 (♂), 85841 (♀), 85842 (♂juv)
	RCS	G165.3 (♀)
Ikom	BMNH	1913.2.2.1 (♂), 1913.2.2.2 (♂)
M'tene	BMNH	1948.437 (inf), 1948.435 (♀)
Obudu	BMNH	1935.3.19.1 (♂), 1935.3.19.2 (♀juv)
Okuni district	BMNH	1907.1.8.2 (♂), 1907.1.8.1 (♂), 1907.1.8.2 (♂), 1907.1.8.3 (♀), 1907.1.8.4 (♀), 1907.1.8.5 (♀), 1907.1.8.6 (♀), 1907.1.8.7 (♀)
Okwa, Ikom	BMNH	1910.11.27.1 (♀juv)
Tinta	BMNH	1948.436 (♂)
Afi Mts	AFI	1000 (♀)
Unknown[e]	ZMBU	41870 (♂)
	AMNH	L267 (♀)
	BMNH	1936.7.14.1 (♂), 1939.913 (♂), 1939.3408, G8 (♂)

[a] With the exception of ZMBU 12791 (a male skull and mixed male and female long bones), BMNH 1939.3408 G8, (a mounted skin), BMNH 1948–436 (a skin, skull and skeleton), and AFI 1000 (a skull and partial skeleton) all Cross River gorilla specimens consist of the skull only. All specimens are adults unless (juv) or (inf), —denoting juvennile and infant respectively—follows museum number.
Key to collection abbreviations in text.
[b] Paratypes.
[c] Assigned by Matschie (1904) to *G. gorilla* despite a Cross River locality.
[d] Holotype.
[e] Skulls with equivocal locality. Both BMNH specimens have a locality specified only as North Cameroon. ZMBU 41870 is labeled as originating from Tinto, a locality outside the known gorilla range. AMNH L-267 has the *G. g. diehli* morphotype but is of unknown provenance.

Notably, Matschie's nuchal ratio failed to distinguish males of *G. diehli* from Slack's (1862) *G. castaniceps*, a junior synonym of *G. gorilla* (Rothschild, 1906; Coolidge, 1929). Casting further doubts as to the diagnostic usefulness of the ratio, examination of the paratypes reveals that three of the supposed females (ZMBU 12793,[4] 12796, and 12795), are actually two juvenile males and an adult male, respectively. When the adult male is included in Matschie's sample, the average nuchal ratio values in *G. diehli* males are decreased (especially when considering differences in correction for a damaged skull). Although this further separates them from other male gorillas, the resulting small sample size for females (N=1) suggests that the ratio is unlikely to be diagnostic for larger samples.

ROTHSCHILD: Rothschild's (1904) subsequent review of great ape taxonomy recognized *G. g. diehli* as a subspecies of *G. gorilla*, but did not offer any morphological evidence to support this claim. In a later publication (Rothschild, 1906), he justified his numerous subspecific divisions by noting that gorillas probably cannot swim and are thus isolated by large rivers, and he provided

[4] ZMBU 12793 is a juvenile with a partially deciduous dentition including milk canines. The crown of the adult canine that is partially visible (fig. 6D) and the dimensions of the paired maxillary swellings overlying the canine crypts suggest that this animal is probably a male.

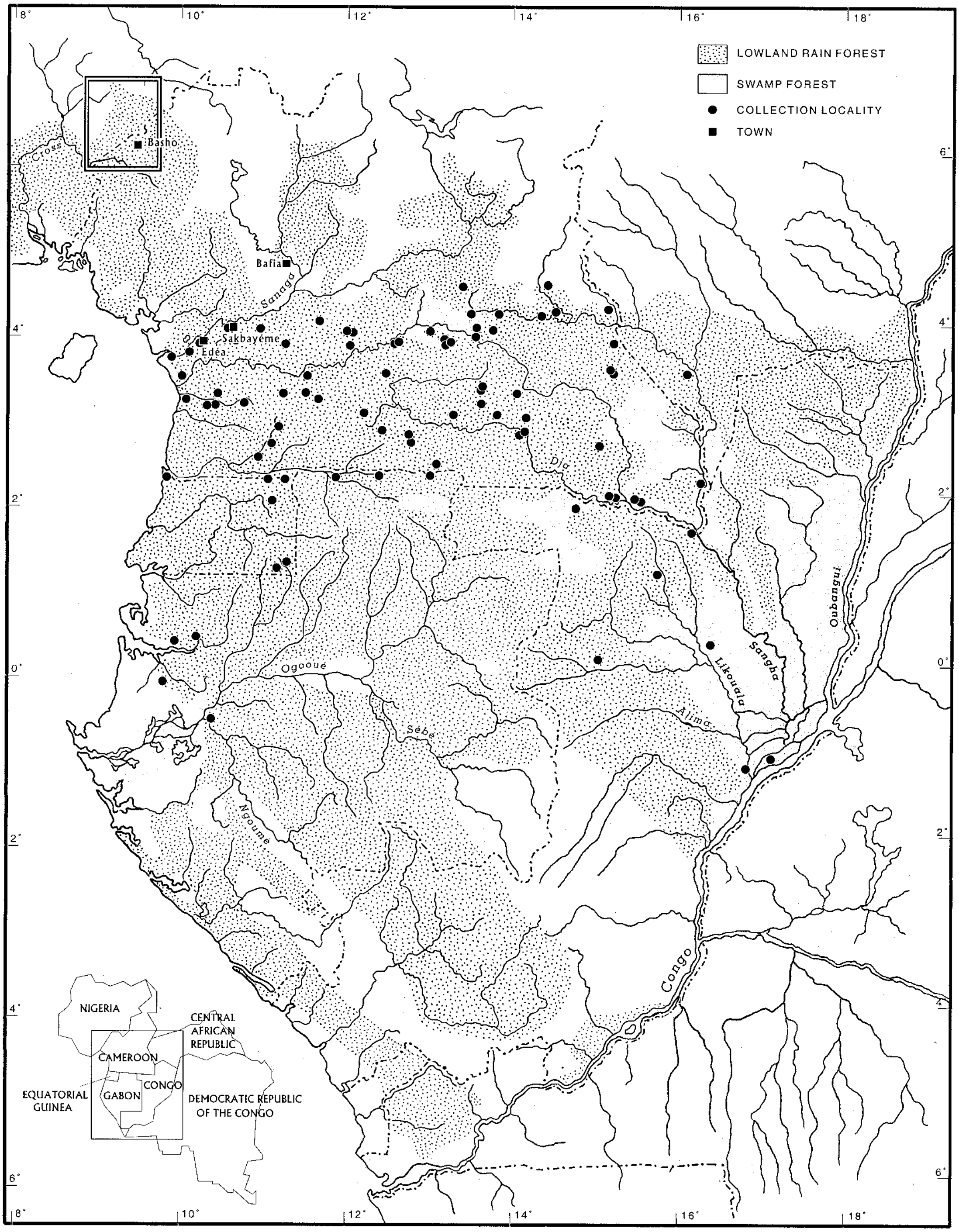

Fig. 2. Distribution map of western gorillas showing the western equatorial forest and the allopatry of *G. g. diehli* and *G. g. gorilla*. Bounded area represents Cross-River watershed mapped in fig. 1. All collecting localities for non-Cross-River western gorillas considered are marked by dots with the exception of Bamba Mayombe, which yielded a single specimen and is not marked. *G. g. gorilla* is

the first description of a *G. g. diehli* skin. Rothschild (1906) noted that *G. g. diehli* had a relatively long and thick black beard, and was all black save for a few brown hairs on the forehead, and an ash-gray back, belly, and chest. He noted that the skin exhibited an especially intense black color on the arms and shoulders. Rothschild (1906, 1908), however, failed to note the animal's sex and approximate age, and did not provide a specific collecting locality. The mounted skin, now in the British Museum (BMNH 1939.3408, G8), is of a male that may not be fully mature and is labeled only as originating from North Cameroon. Unfortunately, none of the ten skulls in the Tring collection, which Rothschild studied (see Rothschild, 1908), could be associated with the skin in order to estimate age. Moreover, as for the skin, museum records for these skulls only specify an origin from North Cameroon. Because gorillas in eastern Cameroon (east of the Sanaga) range into latitudes almost as far north as those inhabited by *G. g. diehli*, there is considerable uncertainty as to which of the specimens studied by Rothschild can be correctly referred to as *G. g. diehli*. Notwithstanding the known variation in pelage color, this uncertainty is further magnified by the presence of orange or rufous hair on the crown of the only adult male skin with a definite Cross River locality (BMNH 1948.436), and on those animals photographed or reported on (Sanderson, 1940; and this study). Despite his emphasis on biogeographic barriers, Rothschild (1904, 1906, 1908) did not provide a specific distribution for *G. g. diehli* or elaborate on the barrier that isolated Matschie's Cross River gorillas and whether this barrier grouped other northern Cameroon gorillas with the Cross River population.

ELLIOT: Concurring with Rothschild, Elliot (1912) recognized *G. g. diehli* as a subspecies of *G. gorilla*. Inexplicably, Elliot specified the type locality only as northern Cameroon, and listed its distribution as Oboni, northern Cameroon and Mokbe (Mboke?). The latter, according to Elliot, is a locality in southern Cameroon, adjacent to the border with French Congo (The Cameroon gazetteer of 1962, places Mboke south of the Sanaga River, see appendix 1). Elliot noted that the type skull of *G. g. diehli* is broader and shorter, with a smaller braincase, a broader face, a shorter rostrum, smaller teeth, and a much shorter and narrower palate than that of *G. beringei* (Virunga gorillas were the only known Western Rift gorilla at the time of Elliot's study). In further reference to *G. g. diehli* skulls, Elliot (1912: 219) noted: ''the flat expansions at sides and back of the brain case are very wide, and the posterior outline is rounded curving inwards in the center.''Elliot corrected Rothschild's description of the skin, (BMNH 1939.3408,G8) by noting that the rump, lower part of the back and outer sides of the thigh are iron gray; the chest, belly, inner thighs, and legs below the knees black, and the crown speckled with red. Like Rothschild, he failed to note the sex or estimate the age of the described skin. The skull measurements he provided for *G. g. diehli* are either at the extreme end of variation or out of the range of those measurements for *G. g. diehli* arrived at in this study. Elliot made no attempt to explain Matschie's claims that *G. g. diehli* and *G. g. gorilla* are sympatric.

COOLIDGE: Coolidge's (1929) revision attempted to simplify gorilla taxonomy by sinking all of the described species of gorillas (11 at the time of his study) into a single species. The Western Rift gorillas were placed in the subspecies *G. g. beringei* and the western lowland gorillas in the subspecies *G. g. gorilla*, thus denying *G. g. diehli* a subspecific status. Coolidge claimed to base his study mainly on linear measures of male skulls and gave the following reasons for not including female specimens:

1) female skulls are relatively rare in museum collections;

←

confined within the western equatorial forest (including both rain and swamp forest) with no apparent discontinuity in distribution within the forest. [See Tutin and Fernandez (1984) for distribution of gorillas within Gabon and Fay and Agnagna (1991) for distribution in eastern Congo (Brazzaville)]. Extent and boundaries for the western equatorial forest are after Malbrant and Maclatchy 1949, and White 1983.

Fig. 3. The skull of ZMUB 12789, the male holotype of *G. diehli* (Matschie, 1904) in A dorsal, B ventral, C anterior and D posterior views. Note the large wide and flat zygoma, the superoinferiorly wide zygomatic arch with only a mild mediolateral curvature, the perpendicular set of the zygoma relative to the zygomatic arch, the pronounced malar tubercles, and the inferomedial concavity of the zygoma circumscribing the infraorbital foramen (see also male paratypes in fig. 6).

2) female skulls are of little value in classification, since they are very similar to, and difficult to distinguish from, young or semiadult skulls, and the latter are well known to have limited use in classification;
3) male ape skulls show the extreme range of variation for most characters and thus males are more likely to exhibit the contrasting morphology diagnostic of any one species or subspecies.

As noted by Haddow and Ross (1950), however, Coolidge (1929) did include juveniles and females in varying proportions in average measurements for most of his gorilla groups, and his measurements and tabulations are fraught with errors.[5] Thus, there is no support for Coolidge's claim that the wide range of morphological variation exhibited in gorilla skulls invalidates all the diagnostic specific characters cited by past taxonomists.

Of the 213 skulls measured by Coolidge, 22 male skulls are labeled as originating

[5] Haddow and Ross (1950) noted that Coolidge's measurements for outside alveolar width in two western Cameroon samples (#119, and #120 in Coolidge's table of skull measures corresponding to BMNH 1913.2.2.2 and 1913.2.2.1 from the Daryell collection) are typographical errors, but failed to mention the same error in a third specimen (#118, BMNH 1907.1.8.1), probably because it is not fully adult. More than likely the measurements provided by Coolidge for these three specimens are for inside alveolar width. In Coolidge's table of measurements, skull #139 with an origin from Gabon is classified as *G. diehli*. This is clearly a mistake.

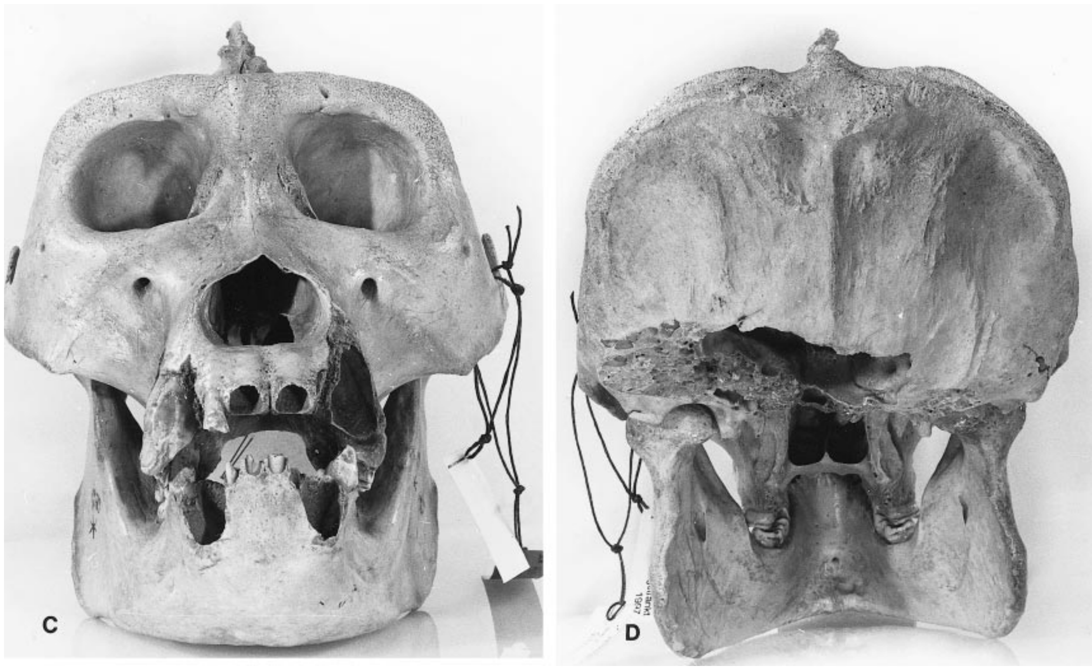

Fig. 3. Continued.

from West Cameroon, which he defined as a limited area around the Cross River and the localities of Mamfe and Dakbe. As verified from specimen numbers, Coolidge's sample includes only the holotype and one of the paratypes on which the description of *G. diehli* was based. Moreover, many of the specimens in Coolidge's sample are not from West Cameroon or the Cross River localities (table 2). Of the 12 skulls that yielded full sets of measurements, five originated from the Cross River area, four came from the vicinity or south of the Sanaga River, and three lacked precise locality data and probably originated from eastern or southern Cameroon. None of the specimens from the Royal College of Surgeons in Coolidge's West Cameroon sample still exist, but collection records show that, except for two individuals, all the specimens were Cross River gorillas. Due to the incomplete set of measurements from the Tring, RCS, and BMNH specimens (three of which were subadults) 10 of 28 average cranial measurements presented by Coolidge are based solely on the seven Berlin specimens. Given equivocal localities for many of the measured specimens, his data can not support claims of distinguishing metric characters in western Cameroon gorillas, especially regarding shortest palate and shortest height of ascending ramus. Coolidge, however, based his taxonomy largely on biogeographic distribution and not on measurements. In this regard, Coolidge did not recognize that the Cross River gorillas are isolated from the other western gorilla populations.

GROVES: As noted, Groves (1970) supported a single species taxonomy of *Gorilla*. Emphasizing the morphological distinctiveness of the Virunga gorillas, he granted them a unique subspecific status, but did not consider Cross River gorillas sufficiently distinct to merit subspecies recognition. Groves (1970) considered a total of 747 skulls. Of these, 230 skulls with West African localities were included in the multivariate analysis, 14 of which had accurate Cross River localities (which he referred to as ''Nigerian''). For purposes of comparison, he artificially divided into 14 subpopulations what was most likely (until very recently), a continuous western gorilla population southeast of the Sanaga river (fig. 2). These subpopulations

Fig. 4. Lateral views of ZMUB 12789 (A) and of the lone female paratype of *G. diehli* (Matschie 1904) ZMUB 12794 (B). The photograph shows the left side of ZMUB 12794 reversed for comparison. Note the strong concavity at the nasal bridge (especially in the female) and the inferior position of the mastoid relative to the external acoustic meatus. In the male the mastoid inflation is within the suboccipital plane, with only a very slight inferior protrusion. The development of the sagittal crest in the holotype is not characteristic of *G. g. diehli* males.

were either based on specimens from single collecting localities or from a group of localities supposedly within restricted areas of less than 100 square miles (259 km^2). Not all subpopulation samples included female specimens. Moreover, as can be calculated from the locality coordinates, one of Groves' ''subpopulations'' comes from an area encompassing 3108 km^2 (1200 square miles) and on average these ''subpopulations'' en-

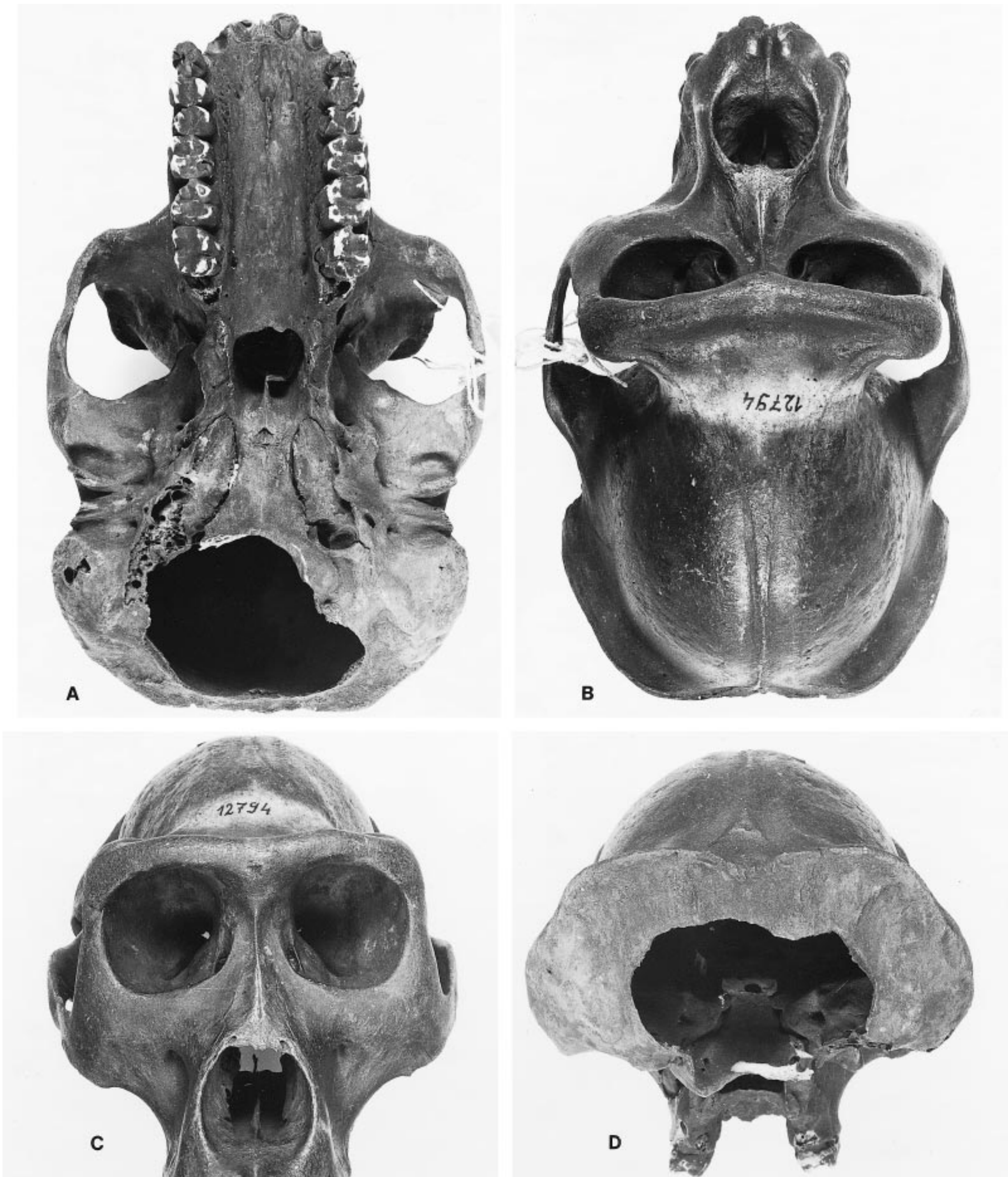

Fig. 5. The calvarium of ZMUB 12794: A dorsal, B ventral, C anterior, D posterior views. Note the well-developed torus along the midnasal suture, the perpendicular set of the zygomatic arch relative to the zygoma, the strong development of the postglenoid and entoglenoid processes, and the waisting of the nuchal crest.

compassed areas of approximately 1554 km^2 (600 square miles) without correcting for hilly terrain.

Comparing individuals segregated by sex in a multivariate analysis on 45 skull measurements, Groves arrived at mean squared generalized distances between gorilla groups (populations and subpopulations). He found the Nigerian (Cross River) gorilla population to be closest to the subpopulation at Metet, just south of the Ngong River in Cameroon, and all the western lowland gorilla groups to assort into four geographic clusters: Nigerian (Cross River), Cameroon plateau (including Metet), Sangha, and Coast. Comparing these four clusters he found Nigerian gorillas to be closest to the Sangha cluster; the differences in the relative distance between Nigeria and Sangha, and Nigeria and Cameroon plateau clusters were not marked. Although in both comparisons the mean squared generalized distances showed that *G. g. diehli* was the most distinctive of the western lowland gorilla populations, Groves (1970) reasoned that the relatively moderate clinal differences exhibited by western lowland gorillas did not merit subspecific distinction for any one western lowland population. He did not test Matschie's claim that *G. g. gorilla* was sympatric with *G. g. diehli*, or specifically consider Cross River gorillas as a geographical isolate. Instead, he pointed out that all four western lowland groups exhibited significant contrasts.

Stumpf et al. (1998) reported a canonical reanalysis of 19 measurements from Groves' raw data. Although they confused geographic groups with populations and subpopulations, their pairwise comparison of 19 ''geographic populations'' found that Nigerian (i.e., Cross River) male gorillas differed significantly from all other groups, and that Cross River female gorillas differed significantly in 92% of the comparisons. Furthermore, when comparing males, they found the Mahalanobis distances between Cross River gorillas and the non-Cross-River West African gorillas to rival those distances between Virunga gorillas and all the non-Virunga eastern gorilla groups.

NATURAL HISTORY

Apart from listing the collection localities, Matschie's (1904) original description of *G. g. diehli* contained no ecological information. The specimen localities of Dakbe [=Takpe?], Oboni [= Obonyi], and Basho are villages within, or close to, today's Takamanda Forest Reserve in southwestern Cameroon (fig. 1, appendix 1).

The first published account of the natural history of Cross River gorillas, including field sightings, is that by Allen (1932), who described a visit in 1930 to the forests above Umaji [= Bumaji] in Obudu District, Nigeria. Allen's report was followed by a set of notes published anonymously by F. S. Collier, Nigeria's Chief Conservator of Forests; Collier's notes (Anon., 1934) appear to be a combination of first-hand field observations (though Collier never saw a wild gorilla) and second-hand accounts. By this time, former German Kamerun was under British mandate and was administered from Nigeria. Collier was therefore the senior official responsible for the protection of both the Cameroon and Nigeria populations of Cross River gorillas. In 1932–33, I. T. Sanderson spent almost a year collecting animals in the forests near Mamfe in southwest Cameroon and in adjacent parts of Nigeria. He collected four gorillas (BMNH 1948.435–1948.437 and Cambridge Museum of Zoology E.7126.I) and published some anecdotal information on their behavior (Sanderson, 1940).

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Fig. 6. Dorsal and ventral views of the male paratypes of Matschie's *G. diehli*. **A** ZMUB 12790, **B** ZMUB 12791, **C** ZMUB 12792, **D** ZMUB 12793, **E** ZMUB 12795. Note absence of a palatal spine; large and anteriorly protruding glabella; large entoglenoid, postglenoid, and eustachian processes; markedly inflated mastoids and glenoids both extending laterally considerably past the external acoustic meatus; the posteriorly disposed union of the temporal lines (posterior to bregma) forming a keel rather than a crest (see fig. 3), and the large nuchal crest with the typically waisted profile (ZMBU 12790 and 12792). The large premaxillary nasal process is visible in the juvenile ZMBU 12793.

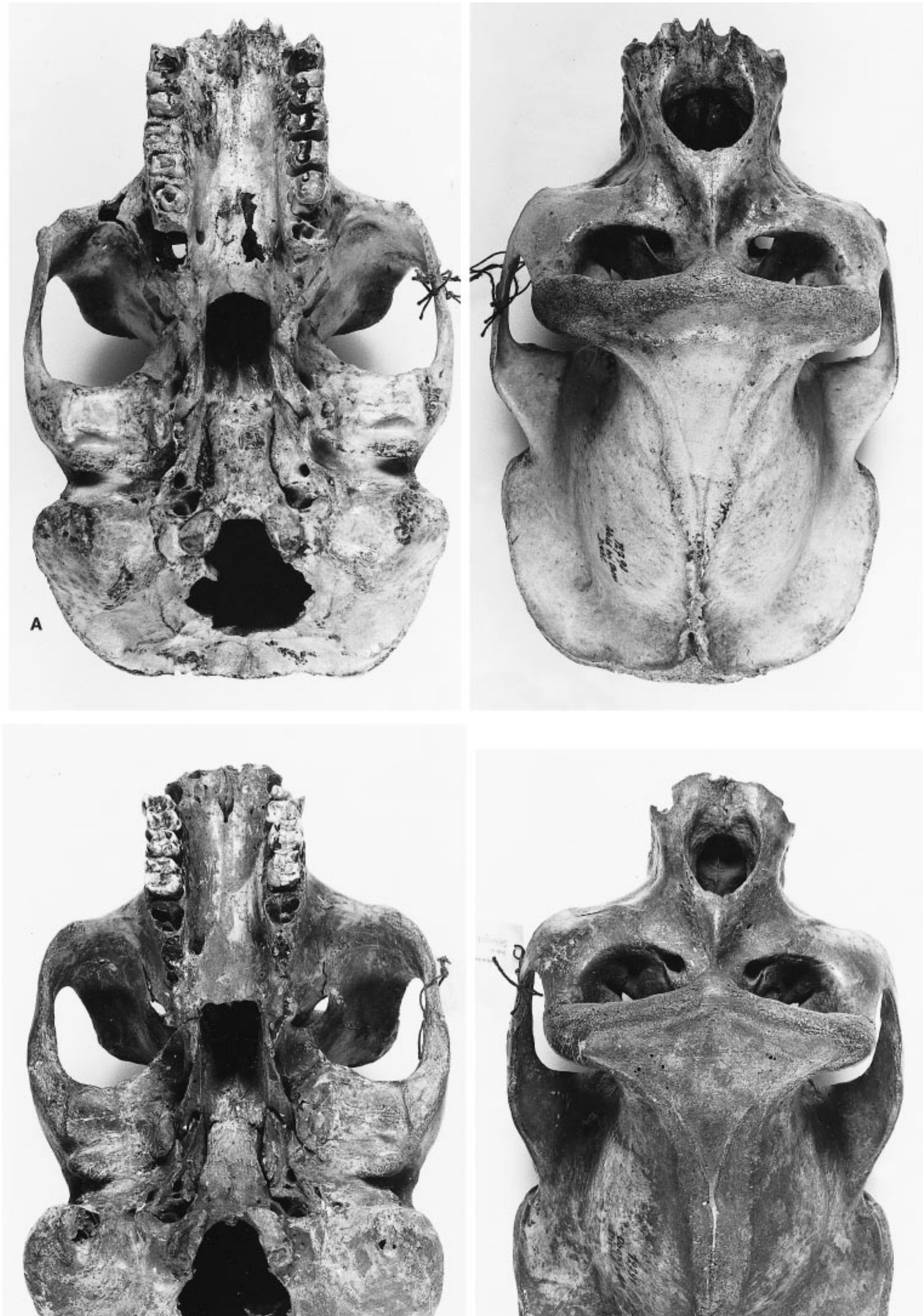
A
B

Fig. 6. Continued.

Fig. 6. Continued.

There were no further publications about the natural history of the Cross River gorillas until that of March (1957), Chief Conservator of Forests for Eastern Nigeria. March reported on a survey in 1955 and 1956 of the population inhabiting the forests southwest of the Obudu Plateau, the same population visited by Allen 25 years previously.

In December 1966, Struhsaker (1967) saw gorilla nests between Ejengi and Matene villages near Takamanda (Struhsaker, 1967). A subsequent survey of Takamanda by Critchley (1968) also extended into the Nigerian forests below the Obudu Plateau.

By 1978 it was assumed that gorillas were extinct in Nigeria (Cousins, 1978), but in 1982 C. Ebin of the Wildlife Conservation Unit of the Cross River State Forestry Department, Nigeria, obtained evidence of a gorilla population surviving in the Mbe Mountains (Ebin, 1983; Oates et al., 1990). His report led to several further surveys in Nigeria and in the Takamanda Forest Reserve between 1986 and 1990, and these established the currently known distribution of Cross River gorillas (Fay, 1987; Thomas, 1988: Harcourt et al., 1989; Oates et al., 1990).

The first long-term field study of the Cross River gorillas, by K. McFarland, commenced in the mountains of Nigeria's Afi River Forest Reserve in 1996 (Oates, 1998b).

MATERIALS AND METHODS

Table 1 lists the locality, sex, age class, and museum number and collection of the Cross River gorilla specimens considered in this study. Figure 2 summarizes localities of origin for non-Cross River western gorillas used in comparisons. All gorilla specimens reported on come from the following collections: Afi Mountain base camp, Afi Mts, Nigeria (AFI), American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); Insti-

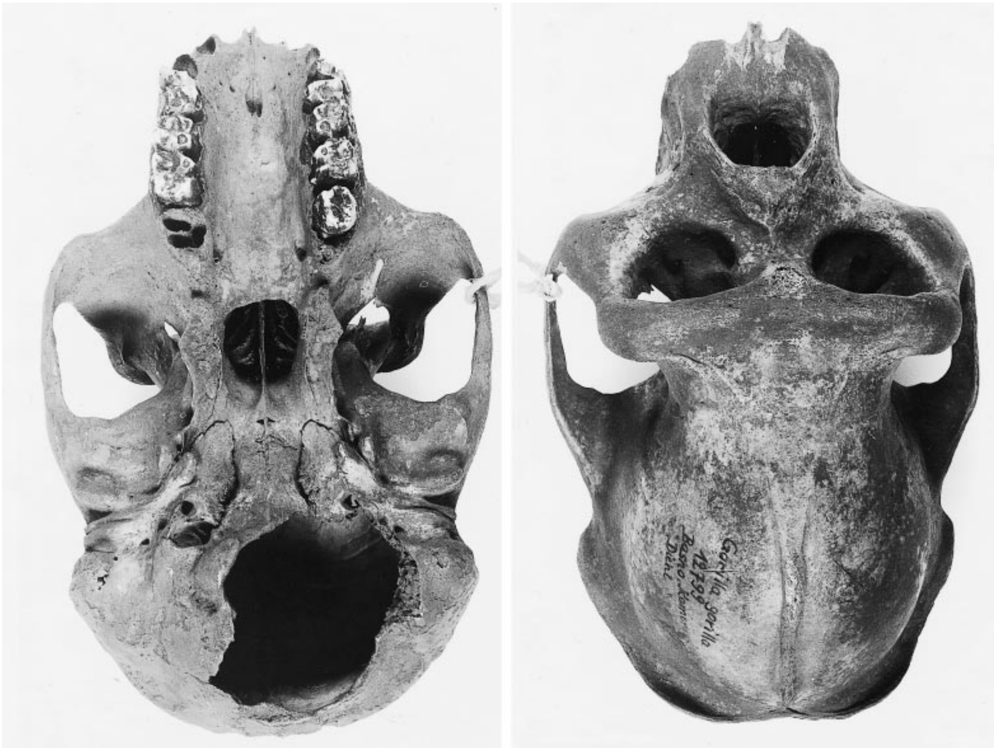

Fig. 7. Dorsal and ventral views of the calvaria of ZMBU 12799 from Basho, assigned by Matschie (1904) to *G. g. gorilla*. Note many of the characters typical of *G. g. diehli* (table 10). Multivariate analyses showed this specimen to group with the Cross River female gorillas.

tut Royal des Science Naturelles de Belgique, Brussels, Belgium (IRSN); Kenya National Museum, Nairobi (KNM); Museum of Comparative Zoology Harvard University (MCZ); Musee Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); National Museum of Natural History, Smithsonian Institute, Washington DC. (NMNH); Natural History Museum, London (BMNH); Philadelphia Academy of Natural Sciences, Philadelphia PA (PANS); Paleoanthropological research unit and Dart Collection University of the Witwatersrand, Johannesburg (PARU); Powell Cotton Museum, Birchington, England (PCM); Odontological Museum, Royal College of Surgeons, London (RCS); Swedish Museum of Natural History, Stockholm Sweden (SMNH); Zoologisches Museum der Humboldt Universitat, Berlin (ZMUB). Latitude and longitude coordinates for Cross River and other localities mentioned are provided in appendix 1.

Skeletal lengths of the clavicle, os coxa, humerus, radius, femur, and tibia were measured to the nearest 0.5 mm using an osteometric board. Cranial, dental, vertebral, and foot and hand measurements were recorded to the nearest 0.1 mm using a digital vernier caliper and collected directly into a Lotus spreadsheet. All measurements were taken on the right side of the body except in those few cases where only the left skeletal elements were present. Length measurements used in indices were always from the same side of the body. Methods for postcranial measurements are reported in Sarmiento (1985, 1994), Sarmiento et al. (1996), and in figure 8. Figure 9 summarizes the cranial and dental measurements considered in this study. All skeletal measurements are from adult individuals with epiphyseal fusion of long bones. As a result of damage or missing teeth and/or skeletal elements, not all specimens yielded a full set of data.

TABLE 2
Locality and Population Group of Specimens in Coolidge (1929) West Cameroon Sample
Key to collection abbreviations in text, locality coordinates in appendix 1.

Museum no.	Locality	Population
ZMUB		
12789	Dakbe	Cross River
12790	Oboni	Cross River
17658	Momie	Cameroon Plateau
17963	Nola	Cameroon Plateau
6309	Cameroon	?
all6092	Between Kadei & Bange	Cameroon Plateau
18515	Uber Edea	Cameroon Plateau
BMNH		
1907.1.8.1	Okuni dist.	Cross River
1913.2.2.1	Ikom	Cross River
1913.2.2.2	Obudu, Ogoja Prov.	Cross River
BMNH (Tring)		
A40 1939.915 [a]	N. Cameroon	?
A34 1939.916	N. Cameroon	?
RCS		
23.22	Ossidinge division	Cross River
23.23	Ossidinge division	Cross River
23.24	Ossidinge division	Cross River
23.25	Ossidinge division	Cross River
23.26	Ossidinge division	Cross River
23.27	Ossidinge division	Cross River
23.28	Ossidinge division	Cross River
23.29	Ossidinge division	Cross River
25.5	No data	
570.22.3	No data	

Length measurements of long bones were formulated into the following indices: brachial (100 × radius/humerus); intermembral [100 × (humerus+radius)/(femur+tibia)]; crural (100 × tibia/femur); clavicular(100 × clavicle/humerus); coxa-humeral(100 × os coxae/humerus); and humero-femoral(100 × humerus/femur). In addition, the following length ratios were also considered: 1st manual ray length as a percent of 2nd manual ray length, 5th manual ray length as a percent of 3rd manual ray length, 3rd manual ray length as a percent of upperlimb length, 1st pedal ray length as a percent of foot length, foot length as a percent of lower limb length, and foot lever length as a percent of lower limb length. Molar and premolar dimensions were used to estimate cheek tooth surface area using the formula P3(bucolingual length × mesiodistal length)+ P4(BL × MD) + M1(BL × MD) + M2(BL × MD)+ M3(BL × MD). The product of biparietal width, skull vault height (bregma-basion), and vault length (inion-glabella) is reported as the vault volume and may be used as an estimate of cranial capacity. Tables 3–6 summarize the length measurements and indices for male and female Cross River gorillas and non-Cross River western gorillas. Probabilities of t for pairwise male and female comparisons of Cross River gorillas to non-Cross River western gorillas are given in table 7.

All indices were also considered as bivariate plots computed using the SAS statistical package (figs. 10–23). To test Matschie's claim of a unique nuchal ratio in Cross River gorillas, the maximum bimastoid width was plotted against inion-basion length in those

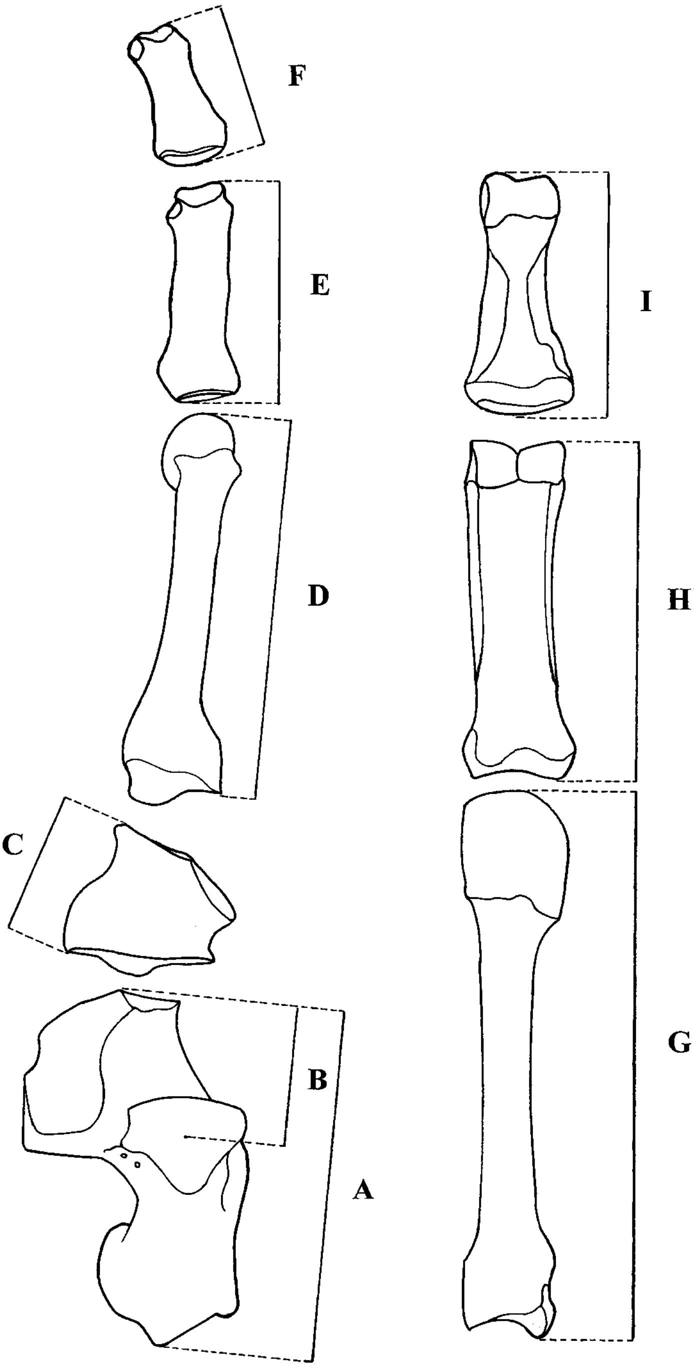

Fig. 8. Dorsal and ventral views of right foot and hand segments respectively showing measurements taken: A = calcaneal length, B = calcaneal outlever length, C = cuboid length, D = fourth metatarsal length, E = fourth proximal pedal phalanx length, F = fourth middle pedal phalanx length, G = third metacarpal length, H = third proximal phalanx length, I = third middle phalanx length. Calcaneal outlever length (B) was calculated from linear measures of the calcaneus as reported in Sarmiento (1994). A+C+D+E+F and B+C+D+E+F were taken as approximations of foot length and foot outlever

specimens with an intact foramen magnum (fig. 24). Additionally, two ratios that were distinctive in past studies of *G. g. diehli* were also considered as bivariate plots: incisor width in percent of premolar-molar row length, and bimastoid width in percent of skull length.

Length measurements of vertebral bodies as described and figured in Sarmiento et al. (1996) were used to calculate an approximate volume for the vertebral body of each of the last four thoracolumbar vertebrae. The sums of the four vertebral body volumes were plotted against the known body weight of individual wild caught gorillas to arrive at body weight estimates for the Cross River gorilla skeletons (table 8).

Cheek tooth occlusal surface areas of a number of eastern gorilla populations (table 9) were used to contrast the degree of differences in the two widely recognized eastern gorilla subspecies (i.e., *G. g. graueri* vs. *G. g. beringei*) with those differences separating Cross River gorillas from the non-Cross River western gorillas. Because they are less responsive to environmental forces than bony dimensions (Sarmiento, 1985), cheek tooth surface areas may be expected to more closely reflect inherited differences between populations and downplay the potentially confusing contribution to systematics of developmental or physiologically acquired characters.

The skulls of Cross River gorillas were also compared to those of non-Cross River western gorillas for non-metric differences (table 10). A more complete quantitative assessment of non-metric skull characters of Cross River gorillas is in preparation.

Stepwise discriminant analysis was undertaken to arrive at measurements that would best discriminate between Cross River gorillas and other western gorillas. The female skull (ZMBU 12799) noted by Matschie to be *G. gorilla*, and four skulls with uncertain locality data were included (table 1). Stepwise discrimination arrived at 11 measurements that were subsequently used in the multivariate discriminant analysis summarized in figure 25. This analysis included a four-group comparison of each sex for each of the two subspecies, and male and female pairwise comparisons of the two subspecies (fig. 25).

Descriptions of Cross River gorilla natural history have been gleaned from the literature and from notes accumulated during field surveys by JFO since 1990. More detailed studies on Cross River gorilla diet, ranging and grouping patterns are in progress (K. McFarland, personal commun.).

RESULTS

Ecology and Behavior

The Cross River gorillas inhabit an altitudinal range from below 200 m in the low-lying parts of Takamanda Forest Reserve, Cameroon, up to about 1500 m on the edge of the Obudu Plateau, Nigeria. The natural vegetation in the lower elevations throughout this area is moist semideciduous forest. Many human settlements occur around this habitat, and several settlements are enclaved within it. The forest has probably been disturbed by people for many generations, and should therefore be considered an old secondary forest. Much of the forest, however, has not been recently disturbed, and large trees are relatively abundant in the areas furthest from human settlement. Among the more common species of large trees are *Lophira alata*, *Cylicodiscus gabunensis*, *Piptadeniastrum africanum*, *Berlinia bracteosa*, *Brachystegia nigerica*, and *Terminalia* spp. (Thomas, 1988; Oates *et al.*, 1990). In younger forest, species such as *Pycnanthus angolensis* and *Musanga cecropioides* are common. The latter tree is found in secondary and disturbed forest throughout tropical Af-

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length, respectively. G+H+I was taken as an approximation of manual third ray length and an estimate of hand length. Corresponding measurements taken in the same manner were used to arrive at the lengths of the second and of the fifth manual ray. The lengths of the first manual and pedal rays were taken as sums of the first metacarpal and its corresponding proximal phalanx, and of the first metatarsal and its corresponding proximal phalanx, respectively.

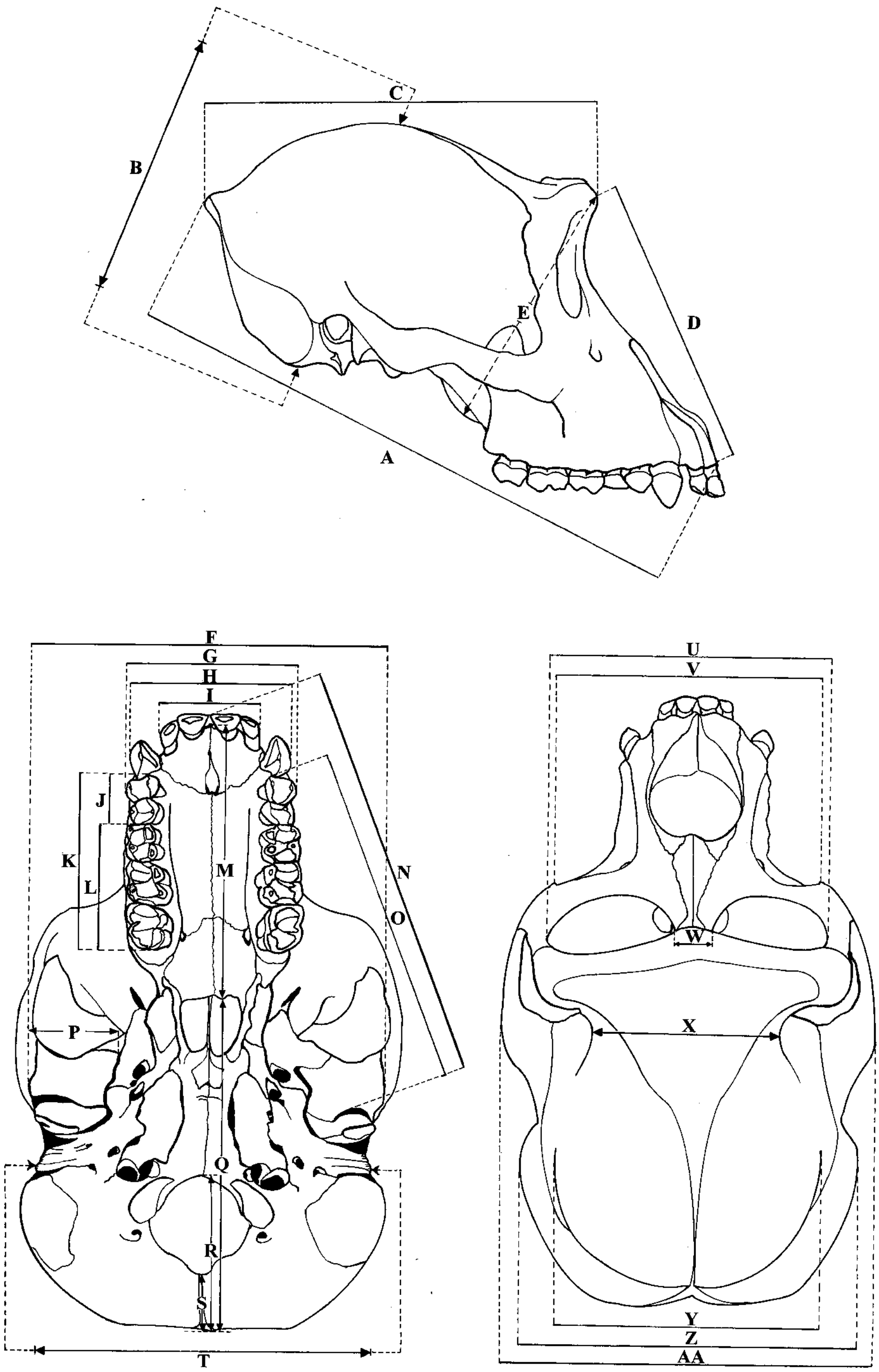

Fig. 9. Lateral, ventral, and dorsal views of an adult female gorilla skull showing the craniodental measures taken in this study. A = skull length, from prosthion to inion, B = vault height, from bregma to basion, C = vault length from glabella to inion, D = facial height from prosthion to glabella, E = postfacial height, from palatal spine to glabella, F= Maximum biglenoid width, G= biC1 diameter, H= maximum biP3 diameter, I= maximum incisor row length, J= premolar row length, K=cheek tooth row

rica and bears fruit commonly consumed by African apes and monkeys.

Above approximately 700 m the composition and height of the forest canopy change; at these intermediate altitudes large mahoganies and *Santiria trimera* are frequently seen. Above 1000 m there are distinctly montane elements in the flora, including *Cephaelis mannii* and *Podocarpus milanjianus*, and at the highest elevations (~1500 m) there is montane forest with smaller trees and abundant epiphytes. Much of the forest on the main Obudu Plateau (1500–1800 m) has been converted to grassland by a long period of human cultivation, burning, and cattle grazing.

The area inhabited by the Cross River gorillas has a complex topography and its climate changes both with altitude and with geographic locality; the most westerly part of the gorillas' range, in the Afi Mountains, has a drier climate than the southeastern parts of Takamanda. Reliable weather records, however, are hard to come by. Tables 11 and 12 present rainfall and temperature data for a number of localities circumscribing the gorilla habitat; the most notable feature of this climate is the prolonged dry season, with less than 50 mm of rain per month, typically falling in the November–March period. The amount of rainfall decreases with increasing latitude and decreasing elevation. The most northern area (i.e., the town of Obudu in the rainshadowed lowlands to the north of the escarpments and the gorilla range) receives the least rain (table 11). Annual rainfall is higher to the southwest of the gorilla range at Ikom (2465 mm, altitude 120 m), and very high on the Obudu Plateau (4300 mm; Keay, 1979; Hall, 1981). The Obudu Plateau has a three-month dry season and temperatures that range from a monthly minimum of 14–16°C to monthly maxima of 18–25°C (Hall, 1981, table 12). Hawkins and Brunt (1965) reported 1658 annual mean monthly hours of sunshine at Mamfe. This is a relatively low value amounting to approximately one-third of the maximum available at this latitude.

It is not obvious that the Cross River gorillas have strong habitat preferences within their present range. In Nigeria they currently live almost entirely in the most rugged terrain in the Afi and Mbe mountains and at the headwaters of the Asache and Mache rivers below the Obudu Plateau of Nigeria; in these areas the forest is often broken by sheer rock faces or rocky outcrops. In the Takamanda reserve in Cameroon their nests are found in high concentrations only in hilly areas (>400–700 m) close to the localities [i.e. Basho hills, Oboni hills, and Dakbe (Makone River)] where they were first collected by Diehl (Groves and Maisels, 1999). This distribution may be the consequence of long-term hunting pressure. The 1987 Takamanda survey found gorilla signs only in the Ma-

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length, L=molar row length, M= palate length from prosthion to palatal spine, N= incision to glenoid length, O= P3 to glenoid length, P= mediolateral glenoid width, Q= palatal spine to inion, R= bregma to inion, S= suboccipital plane length, from opisthion to inion, T= maximum biexternal acoustic meatus diameter, U= biorbital diameter, V= bimalar tubercle diameter, W= minimum interorbital diameter, X= minimum postorbital constriction width, Y= maximum biparietal diameter, Z = maximum bimastoid diameter, AA= maximum bizygomatic diameter. BiM3 and BIM2 diameter was taken parallel to and in an analogous manner to BiP3 diameter. The largest of these three diameters was taken as the maximum palate width. Mesiodistal(MD) and bucolingual (BL) lengths of molars and premolars are from the right side and were taken parallel and perpendicular to the tooth row, respectively.

In specimens with obliterated interparietal and frontoparietal sutures the midline and the slight depression that marks the obliterated frontoparietal suture was used to locate bregma. In specimens with a sagittal crest bregma was taken as a point to the right of the crest. For those specimens with heavy incisor wear or absence of incisors, the incisor row length was taken as the diameter between the lateral borders of the right and left I2 sockets. In specimens without a palatine spine, the corresponding point was taken as the most posterior point on the interpalatine suture. The points defining vault height (B) and postfacial height (E) cannot be depicted in any single view, so that the arrows point in the vicinity of bregma and the palatal spine. Lengths of incision to glenoid length and incision to P3 were taken on the right side, but depicted on the left for clarity.

TABLE 3
Long Bone, and Hand and Foot Segment Lengths (mm) in Adult Male and Female Western Lowland Gorillas *G. g. gorilla* and Cross River Gorillas *G. g. diehli*
Mean ± standard deviation and ranges; sample sizes in parentheses.

	G. g. gorilla		*G. g. diehli*	
	Males	Females	Males	Females
Humerus				
	437.6 ± 22.1 (45) 396.0–498.5	368.5 ± 14.4 (27) 343.0–395.0	445 ± 0 (2) 445	387.5 (1)
Radius				
	355.3 ± 19.0 (45) 316.0–390.0	295.6 ± 11.1 (24) 271.0–316.0	358 ± 17.0 (2) 346.0–370.0	305.4 (2) 303.3–310.5
Clavicle				
	163.3 ± 9.63 (42) 143.0–184.0	129.6 ± 10.50 (25) 93–150.0	176.6 —	146 —
Tibia				
	311.4 ± 16.0 (45) 281.0–340.0	257.6 ± 9.15 (27) 241.2–274.0	308 —	— —
Femur				
	372.2 ± 17.0 (45) 335.0–416.0	309.7 ± 11.21 (27) 291.0–332.0	377.5 ± 10.6 (2) 370.0–385.0	322 (1) —
Upperlimb				
	792.9 ± 40.3 (45) 717.0–888.5	664.8 ± 24.3 (26) 619.0–711.0	803.0 ± 17.0 (2) 791.0–815.0	698 (1) —
Lower limb				
	683.7 ± 30.8 (45) 627.4–742.0	567.2 ± 19.20 (27) 536.0–601.0	693 (1) —	— —
Os coxa				
	367.4 ± 15.79 (35) 331.0–401.0	306.76 ± 14.51 (25) 285.0–335.0	368 (1) —	332 (1) —
1st metacarpal				
	52.7 ± 3.61 (40) 59.5–46.2	44.4 ± 2.17 (22) 49.1–39.1	52.6 (1) —	— —
3rd metacarpal				
	52.7 ± 3.61 (40) 59.5–46.2	44.4 ± 2.17 (22) 49.1–39.1	52.6 (1) —-	— —
1st ray length manual				
	84.9 ± 5.26 (29) 92.9–73.5	70.43 ± 4.83 (13) 79.6–62.8	83.8 (1) —	— —
2nd ray length manual				
	194.3 ± 10.89 (29) 217.3–176.0	162.3 ± 12.68 (14) 174.1–124.6	184.3 (1)	—
3rd ray length manual				
	205.9 ± 11.64 (29) 230.4–185.0	173.6 ± 11.25 (14) 184.1–141.1	196.3 (1) —	— —
5th ray length manual				
	174.9 ± 11.28 (28) 196.9–146.5	146.4 ± 7.87 (13) 162.2–130.4	160.5 (1) —	— —

TABLE 3
Continued

	G. g. gorilla		*G. g. diehli*	
	Males	Females	Males	Females
1st metatarsal				
	66.58 ± 4.13 (36)	55.35 ± 3.42 (21)	61.39 (1)	—
	73.40–55.52	63.85–48.03	—	—
4th metatarsal				
	82.94 ± 4.51 (37)	69.57 ± 3.26 (22)	73.34 (1)	—
	91.69–72.01	75.55–62.97	—	—
1st pedal ray length				
	101.6 ± 6.16 (29)	83.145 ± 4.02 (19)	94.96 (1)	—
	110.7–85.7	93.6–74.7	—	—
4th pedal ray length				
	160.0 ± 9.05 (32)	134.0 ± 5.52 (18)	147.8 (1)	—
	176.2–141.3	144.7–123.9	—	—
Foot length				
	273.5 ± 14.61 (30)	224.9 ± 7.36 (18)	258.9 (1)	—
	295.3–236.1	236.1–212.6	—	—
Foot out lever length				
	210.2 ± 14.58 (30)	173.5 ± 10.60 (18)	201.3 (1)	—
	242.8–178.6	189.8–150.2	—	—

kone River valley in lowland interior of the forest, an area apparently less heavily hunted at that time than the northern more elevated areas of Takamanda (Fay, 1987; Thomas, 1988). Hunters who frequent the forests below the Obudu Plateau report that gorillas use higher elevations in the wet season and retreat to valley bottoms in the dry season (Oates et al., 1990).

Only a handful of direct sightings of Cross River gorillas have been made; almost all the information on their ecology and behavior derives from observations of sleeping nests, feeding trails, and reports by local hunters. Evidence from food remains and feces suggests that, as in other parts of West Africa, the Cross River gorillas feed heavily on fruit when it is abundant, and when fruit is scarce rely on terrestrial herbs such as *Aframomum*, *Costus*, *Palisota*, and species of Marantaceae (Anon, 1934; Fay, 1987; Oates et al., 1990; K. McFarland, personal commun.). Large patches of terrestrial herbaceous vegetation are not common in these forests, but preliminary observations suggest that they are more frequent in the Afi Mountains and on the Obudu Plateau than in the lowland forests.

Although, as at other sites, social group size of Cross River gorillas is variable, the great majority of nest clusters and sightings indicate groups of six or fewer individuals (Struhsaker, 1967; Critchley, 1968; Harris et al., 1987; Oates et al., 1990; Groves and Maisels, 1999). However, larger groups of at least 10 individuals (based on nest clusters) do occur, especially in the Afi Mountains (K. McFarland, personal commun.; Oates et al., 1990). As in other western gorilla populations, sleeping nests are made from ground level to heights of over 20 m, but surveys suggest that a large majority of nests are constructed on or close to the ground (fig. 26).

Dental and Skeletal Measurements

The volume of the lumbar vertebrae suggests that male Cross River gorillas are similar in body size and mass to other western gorillas, but female Cross River gorillas may be somewhat larger than other western females (table 8). Differences in lumbar ver-

TABLE 4
Long bone, Hand and Foot Indices in Adult Male and Female Western Lowland Gorillas, *G. g. gorilla*, and Cross River gorillas, *G. g. diehli*
Mean, ± standard deviation and range; sample sizes in parentheses.

	G. g. gorilla		*G. g. diehli*	
	Males	Females	Males	Females
Clavicular				
	37.68 ± 2.43 (38)	35.50 ± 1.80 (21)	37.76 (1)	37.61 (1)
	41.86–32.05	39.10–32.61	—	—
Brachial				
	81.21 ± 1.78 (41)	79.98 ± 1.75 (22)	81.18 ± 1.97 (2)	79.95 (1)
	85.61–76.98	85.13–77.14	83.15–79.20	—
Crural				
	84.18 ± 2.87 (41)	82.81 ± 1.90 (22)	80.0	—
	89.76–75.74	87.12–79.19	—	—
Intermembral				
	115.9 ± 2.45 (41)	116.8 ± 2.62 (22)	113.4	—
	125.9–111.7	121.4–111.2	—	—
Humerofemoral				
	118.0 ± 2.40 (41)	118.7 ± 2.89 (24)	117.3 ± 2.99 (2)	120.41 (1)
	123.7–112.2	124.2–109.5	120.3–114.3	—
Coxahumeral				
	83.85 ± 3.29 (38)	82.59 ± 3.20 (26)	82.70 (1)	85.63 (10
	91.07–76.31	88.14–74.67	—	—
100 × ray 3/upperlimb				
	26.09 ± 1.16 (27)	26.53 ± 0.897 (12)	24.82 (1)	—
	28.72–24.17	27.93–25.33	—	—
100 × manual ray 1/ray 2				
	43.69 ± 1.60 (29)	42.61 ± 2.07 (12)	45.45 (10)	—
	47.92–40.24	46.11–38.60	—	—
100 × manual ray 5/ray 3				
	85.17 ± 2.49 (27)	83.15 ± 2.59 (13)	81.75 (1)	—
	89.45–78.25	89.07–79.44	—	—
100 × 1st pedal ray length/foot length				
	37.02 ± 1.42 (29)	36.97 ± 1.14 (18)	36.67 (1)	—
	40.90–34.12	40.14–35.16	—	—
100 × foot/lowerlimb				
	40.32 ± 1.29 (28)	39.68 ± 1.17 (18)	37.36 (1)	—
	43.87–37.06	41.46–37.17	—	—
100 × lever/foot				
	77.03 ± 2.70 (28)	77.14 ± 3.74 (18)	77.77 (1)	—
	84.47–74.61	85.11–70.64		

tebral volume among females, however, may be largely the result of a small Cross River gorilla sample size and are not statistically significant.

Many of the skull measurements (i.e., skull length, vault length, cheek tooth surface area, incisor row width, BiM3 width, maximum palate width, premolar-molar row length, biglenoid diameter, and vault volume) have significantly smaller mean values in

TABLE 5

Cranial, Facial, and Dental Measurements (mm) in Male *G. g. gorilla* and *G. g. diehli*

Mean ± standard deviation and range; sample sizes in parentheses.

	G. g. gorilla Males	*G. g. diehli* Males
Skull length		
	291.7 ± 13.25 (55)	276.9 ± 13.83 (36)
	266.2–321.5	251.0–301.8
Vault length		
	192.0 ± 11.82 (56)	180.5 ± 11.45 (36)
	153.7–214.3	159.0–201.3
Cheek tooth area		
	1097.4 ± 102.3 (56)	961.3 ± 83.34 (30)
	935.5–1369.1	835.2–1158.7
Upper incisor row width		
	43.08 ± 2.83 (54)	39.15 ± 2.77 (32)
	35.65–47.95	33.79–44.68
Glenoid–incision		
	175.0 ± 8.30 (55)	169.44 ± 6.94 (36)
	153.7–190.6	155.5–188.5
Upper incisor row width		
	43.08 ± 2.83 (550	39.15 ± 2.77 (32)
	35.65–47.95	33.79–44.68
Molar–premolar row length		
	68.44 ± 3.19 (56)	63.74 ± 2.83 (36)
	62.78–75.04	59.65–71.28
Maximum palate width		
	75.67 ± 3.95 (49)	70.52 ± 2.73 (26)
	66.91–86.52	64.41–76.57
Palate length		
	111.2 ± 7.79 (55)	106.99 ± 6.44 (35)
	94.57–124.97	90.34–119.71
Bimastoid		
	160.7 ± 6.98 (42)	160.4 ± 8.25 (34)
	147.3–175.0	139.3–176.0
Biglenoid		
	151.39 ± 6.16 (54)	141.45 ± 5.85 (35)
	136.75–163.7	129.75–153.97
Bizygomatic		
	177.43 ± 8.04 (54)	174.44 ± 5.60 (32)
	155.4–192.1	162.5–185.8
Vault volume, mm^3		
	2221929 ± 252188 (55)	1969630 ± 218368 (27)
	1737283–2783581	1279490–2284481
Glabella–prosthion		
	131.80 ± 10.18 (43)	127.06 ± 8.25 (35)
	114.03–149.6	101.5–146.5
Minimum postorbital width		
	71.14 ± 4.25 (43)	70.63 ± 3.52 (36)
	60.70–79.12	63.61–77.06

Cross River gorillas than in other western gorillas, for both sexes (tables 5–7). Male Cross River gorillas additionally show significantly lower mean values for palate length, bizygomatic width, glenoid-incision length, and facial length (glabella-incision) when compared to other lowland gorillas (tables 5 and 7). Because the respective sexes of both groups appear to have similar body sizes, all distinctive skull measures are not just absolutely, but also probably relatively smaller in Cross River gorillas.

None of the remaining skull measurements, or the lengths of the long bones and hand and foot segments, exhibit significant differences between means for either sex (table 7). For some postcranial measurements, lack of significant differences may be the result of small sample size, since some segment lengths and proportions are at the extreme ends of the western lowland gorilla variation (tables 3, 4, figs. 16, 17, 18, 20, 21). In this regard, the single male Cross River gorilla measured has a relative length of the 5th manual ray at the lower range of variation of the other western gorillas (table 3, fig. 17) and an opposability index at the upper range of variation (table 4, fig. 16). In accord with a comparatively larger body size, the female Cross River gorilla has a clavicular and coxahumeral index, and absolute lengths of the clavicle and the os coxa, that are greater than the mean for other female western gorillas (table 4, figs. 10 and 12).

Qualitative Cranial Characters

In addition to significant differences in measured lengths, the unique skull morphology of Cross River gorillas is also exhibited in a combination of qualitative skull characters usually present in both sexes (table 10 and figs. 3–7). Although individually these characters exist as normal variation in non-Cross-River gorillas, their frequent occurrence and common association in Cross River gorillas results in a distinctive skull morphology.

Discriminant Analysis

Stepwise discrimination, of all skull measurements taken, determined 11 measure-

TABLE 6

Cranial, Facial, and Dental Measurements (mm) in Female *G. g. gorilla* and *G. g. diehli*

Mean ± standard deviation and range; sample sizes in parentheses.

	G. g. diehli Females	*G. g. gorilla* Females
Skull length		
	229.3 ± 10.54 (30)	220.9 ± 8.32 (25)
	211.3–251.0	199.4–236.3
Vault length		
	156.34 ± 8.65 (30)	149.1 ± 6.04 (25)
	141.98–175.0	137.0–159.9
Cheek tooth area		
	919.4 ± 63.21 (27)	832.0 ± 71.4 (16)
	774.8–1041.12	707.5–959.9
Upper incisor row		
	38.03 ± 2.69 (30)	35.70 ± 2.68 (24)
	31.8–42.19	29.11–43.5
Glenoid–incision		
	141.7 ± 7.23 (30)	141.0 ± 5.19 (25)
	128.6–155.0	125.5–149.6
Molar-premolar row length		
	61.87 ± 2.68 (30)	59.08 ± 3.25 (25)
	55.26–68.81	53.48–66.92
Maximum palate width		
	66.78 ± 2.81 (29)	63.79 ± 3.75 (20)
	60.0–72.25	59.83–70.37
Palate length		
	90.01 ± 5.63 (30)	88.52 ± 4.72 (27)
	79.51–102.95	72.5–97.27
Bimastoid		
	131.67 ± 8.03 (19)	133.74 ± 5.12 (22)
	116.25–145.00	125.9–141.7
Biglenoid		
	129.9 ± 7.10 (30)	123.8 ± 4.21 (25)
	115.4–144.32	117.7–145.6
Bizygomatic		
	144.60 ± 6.31 (30)	145.24 ± 5.29 (23)
	130.3–158.4	135.7–152.8
Vault volume, mm^3		
	1584309 ± 185170 (30)	1446136 ± 122868 (23)
	1230153–1999976	1214144–1662237
Glabella-prosthion		
	109.96 ± 6.45 (19)	108.86 ± 4.99 (25)
	99.22–124.7	98.54–118.1
Postorbital		
	65.58 ± 6.12 (19)	66.76 ± 3.47 (25)
	54.67–79.30	60.00–73.01

ments that account for most of the differences between Cross River gorillas and other western gorillas for pairwise comparisons of males and females (fig. 25). Inclusion of additional measurements in the analysis failed to improve separation. Discriminant analysis based on the 11 measurements correctly assigned all female gorillas and all male Cross River gorillas to their respective populations. Two non-Cross-River western gorilla males, however, were assigned to the Cross River population. Visual inspection of these two skulls, one from Efulen, Cameroon (AMNH 167627), and the other from Bamba Mayombe, Congo (214109), also revealed a number of qualitative characters common to Cross River gorillas, i.e., a hollowed depression or biconcavity inferomedially on the anterior surface of the maxilla's zygomatic process, a planar and superoinferiorly broad zygoma set perpendicular to a superoinferiorly broad temporal process, a large malar tubercle, a barlike supraorbital torus with minimal midsagittal depression or orbital elevation, and a midline separation of the temporal lines with associated absence or poor development of a sagittal crest. The female gorilla collected by Diehl from Basho (ZMBU 12799, fig. 7) grouped well within the Cross River population despite the fact that Matschie (1904) claimed it to be indistinguishable from *G. gorilla* and excluded it as a paratype of *G. diehli*. In agreement with its visual appearance, the female gorilla skull of unknown locality (AMNH L267) also grouped with the Cross River population. All three of the male skulls with equivocal localities grouped with *G. g. gorilla*.

Gorilla Cheek Tooth Surface Area

Comparisons of cheek tooth surface area between eastern and western gorillas (tables 5, 6, 9) show Cross River gorillas to have the mean smallest cheek tooth surface area. Notably, differences in mean cheek tooth surface area between Virunga gorillas (*G. g. beringei*) and the other populations of eastern gorillas are not as marked (table 9) as those between Cross River gorillas and the other

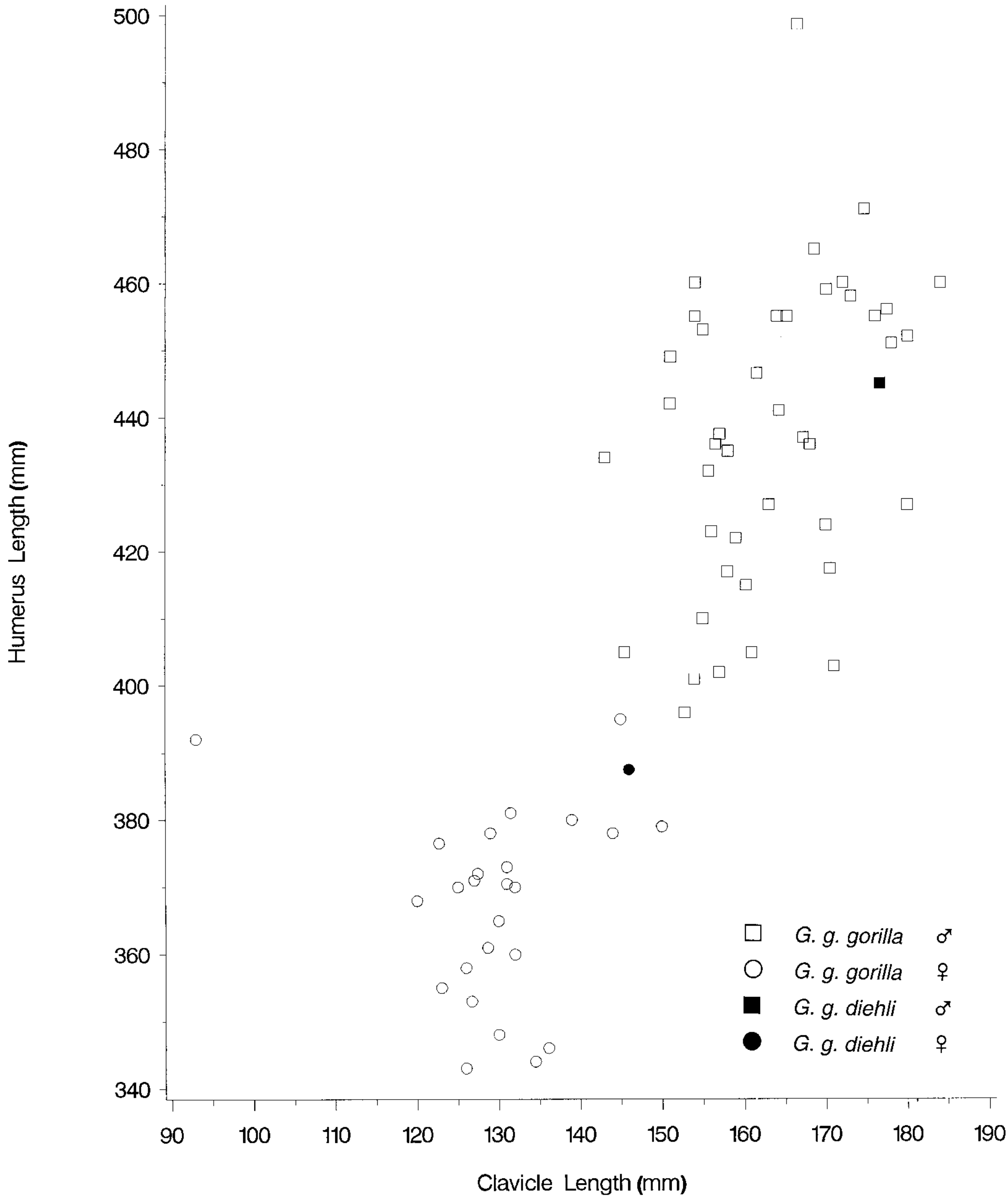

Fig. 10. Plot of humeral length vs. length of clavicle in Cross River gorillas (*G. g. diehli*) and in non-Cross-River western gorillas (*G. g. gorilla*). Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 1.485, y′ =186.2, adjusted R^2= 0.55.

western gorillas (table 7). Moreover, Virunga gorillas fail to show statistically significant differences in mean cheek tooth surface area in most pairwise comparisons with males and females of other eastern gorilla populations (table 9).

DISCUSSION

Morphology, Behavior, and Habitat

A necessary aspect of unravelling adaptation and arriving at biologically relevant taxonomies, association of the distinctive Cross

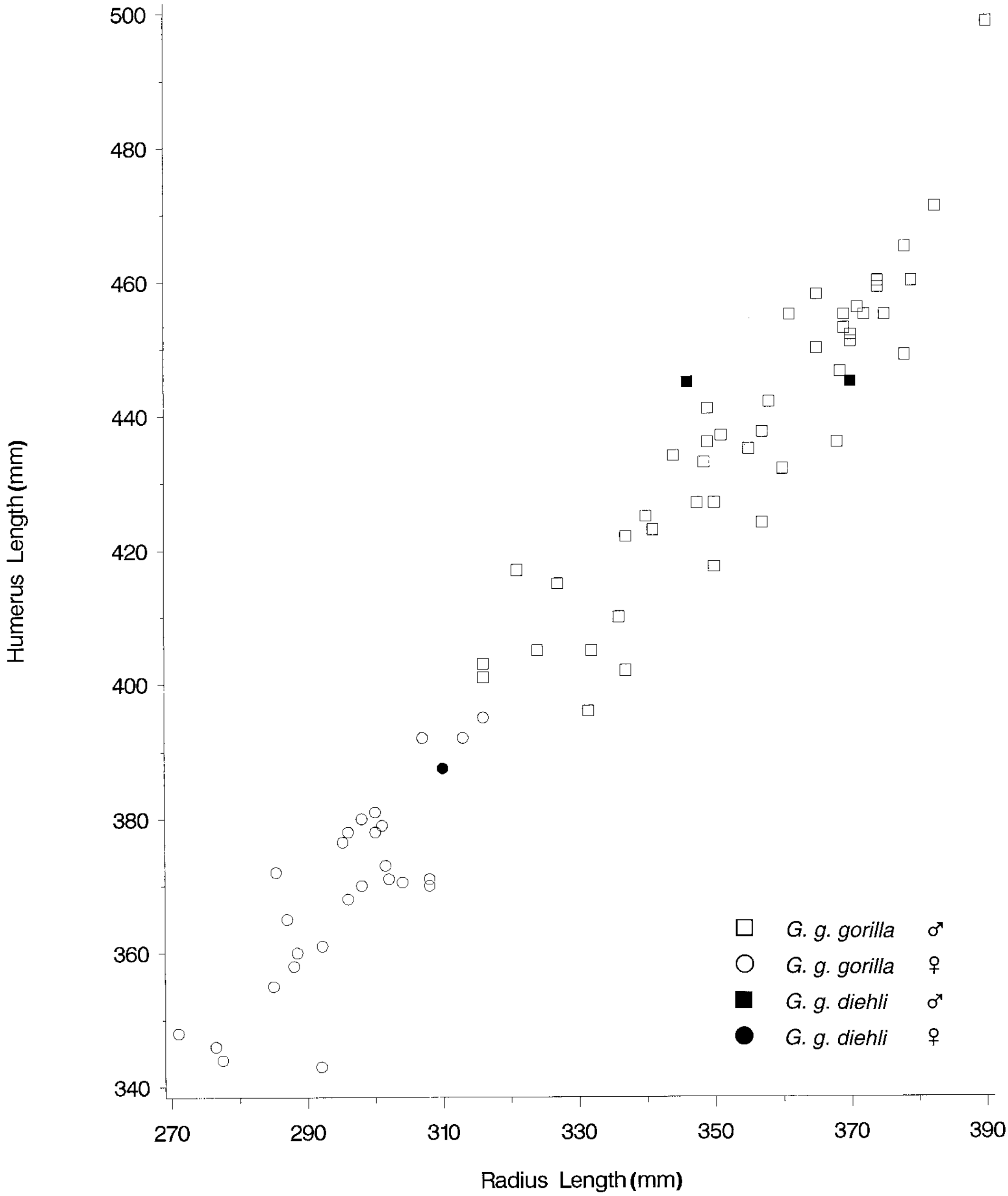

Fig. 11. Plot of humeral length vs. length of radius in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 1.131, y′ =35.07, adjusted R^2= 0.95.

River gorilla morphology with distinctive behaviors or habitat features, is not possible at present. Current understanding is confounded by considerable differences in the habitats occupied by the various Cross River gorilla populations and the scant information available on their diet and behavior.

In theory, a small cheek tooth occlusal surface area compared to the other western gorillas, but a comparable body size in both

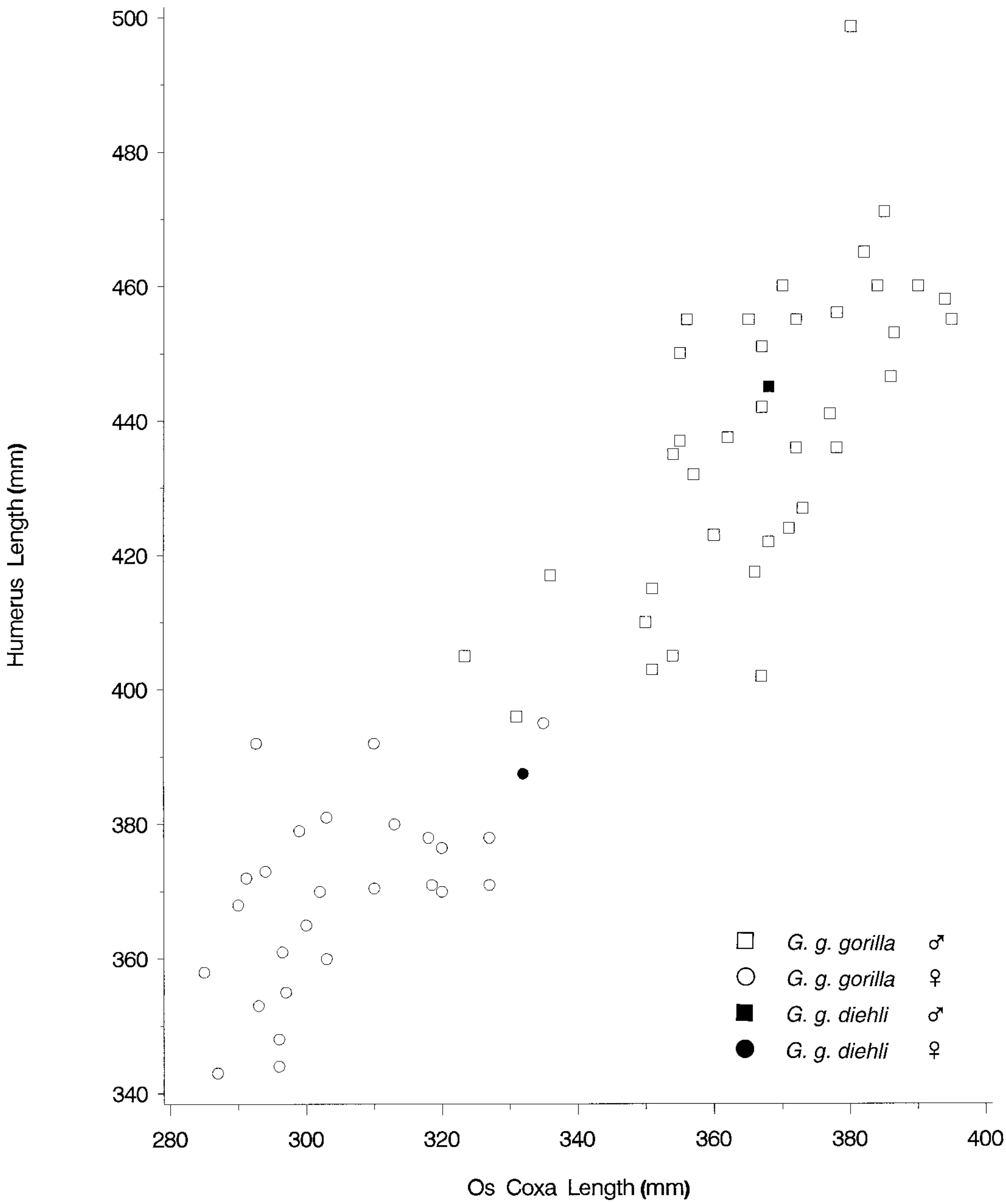

Fig. 12. Plot of humeral length vs. length of os coxa in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 1.003, y′ = 68.03, adjusted R^2= 0.83.

populations, could suggest that Cross River gorillas are suited to consume a less abrasive diet, lower in bulk, and requiring less dental processing per unit of caloric intake. The significantly shorter and narrower palate of Cross River males (table 5) also suggests less oral processing and a lower intake of bulk than in other western males.

A significantly smaller cheek tooth surface area may also suggest increased occlusal

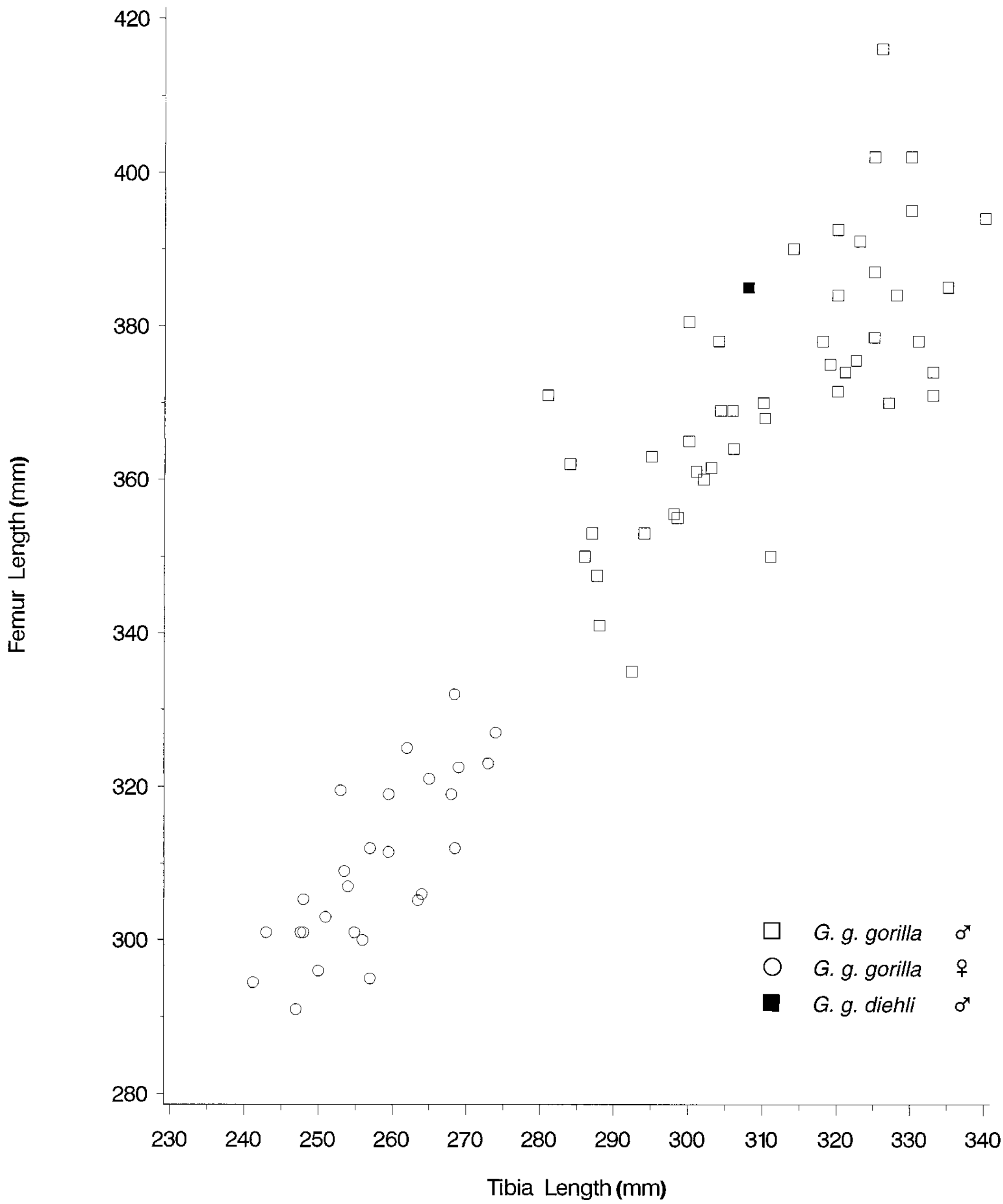

Fig. 13. Plot of femoral length vs. length of tibia in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 1.082, y′ =33.83, adjusted R^2= 0.89.

force per unit of tooth surface area (Sarmiento, 1995, 1998). Given comparable bizygomatic and postorbital widths (the latter dimensions reflecting a comparable cross-sectional area of the masticatory muscles), the smaller cheek tooth surface area suggests that Cross River females are able to generate a relatively greater occlusal force per unit area than western lowland females. Their comparatively narrower palate and the asso-

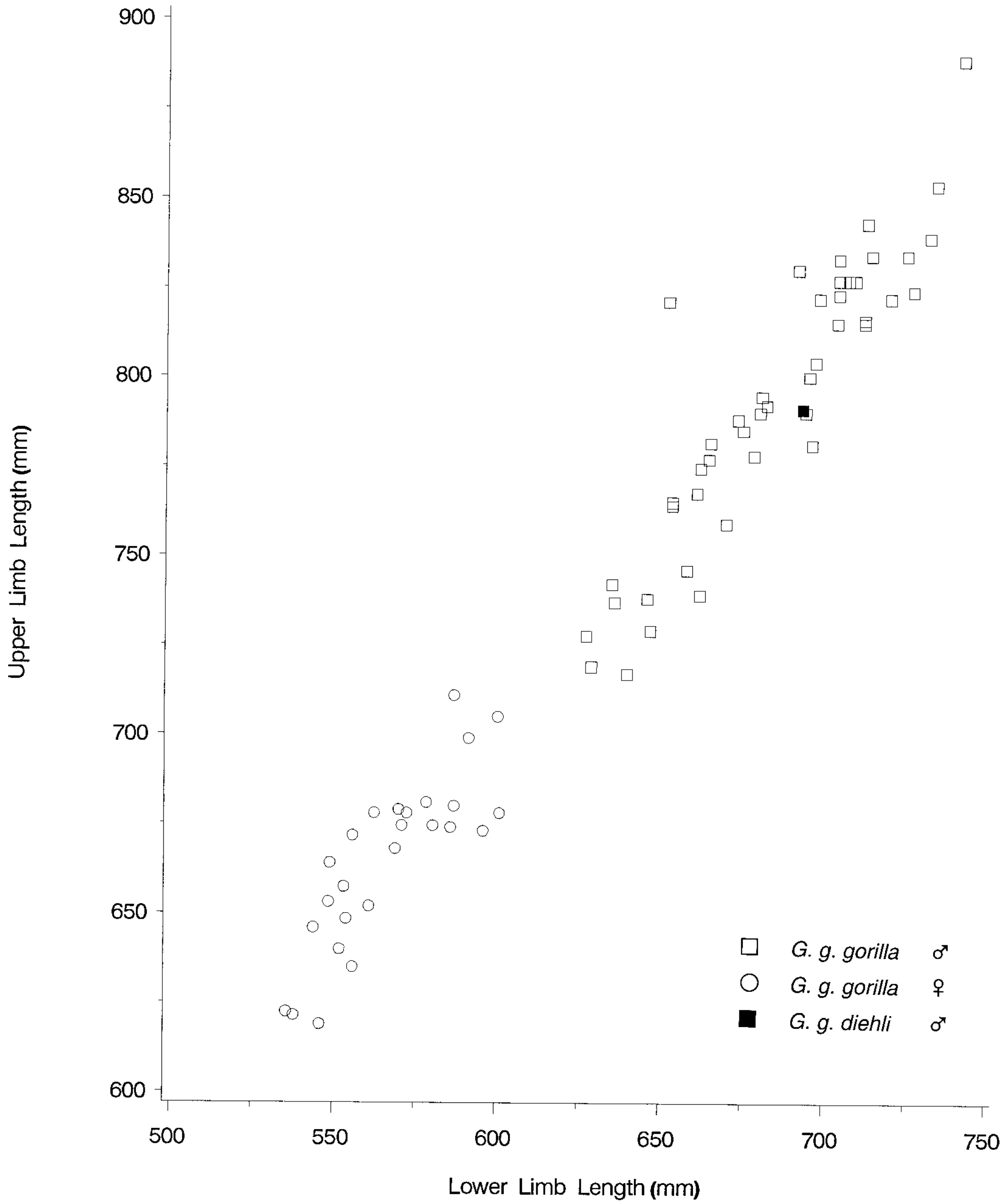

Fig. 14. Plot of upper limb length vs. lower limb length in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 1.109, y′ = 35.65, adjusted R^2= 0.95.

ciated greater magnitude of rotational masticatory forces in the frontal plane with increasing disparity between bizygomatic and palatal width (Marcus and Sarmiento, 1996; Sarmiento, 1995, 1998) further enhance the magnitude of occlusal force that female Cross River gorillas can generate. Although Cross River males do not show as much of a difference between bizygomatic and palate width as their female counterparts do, and

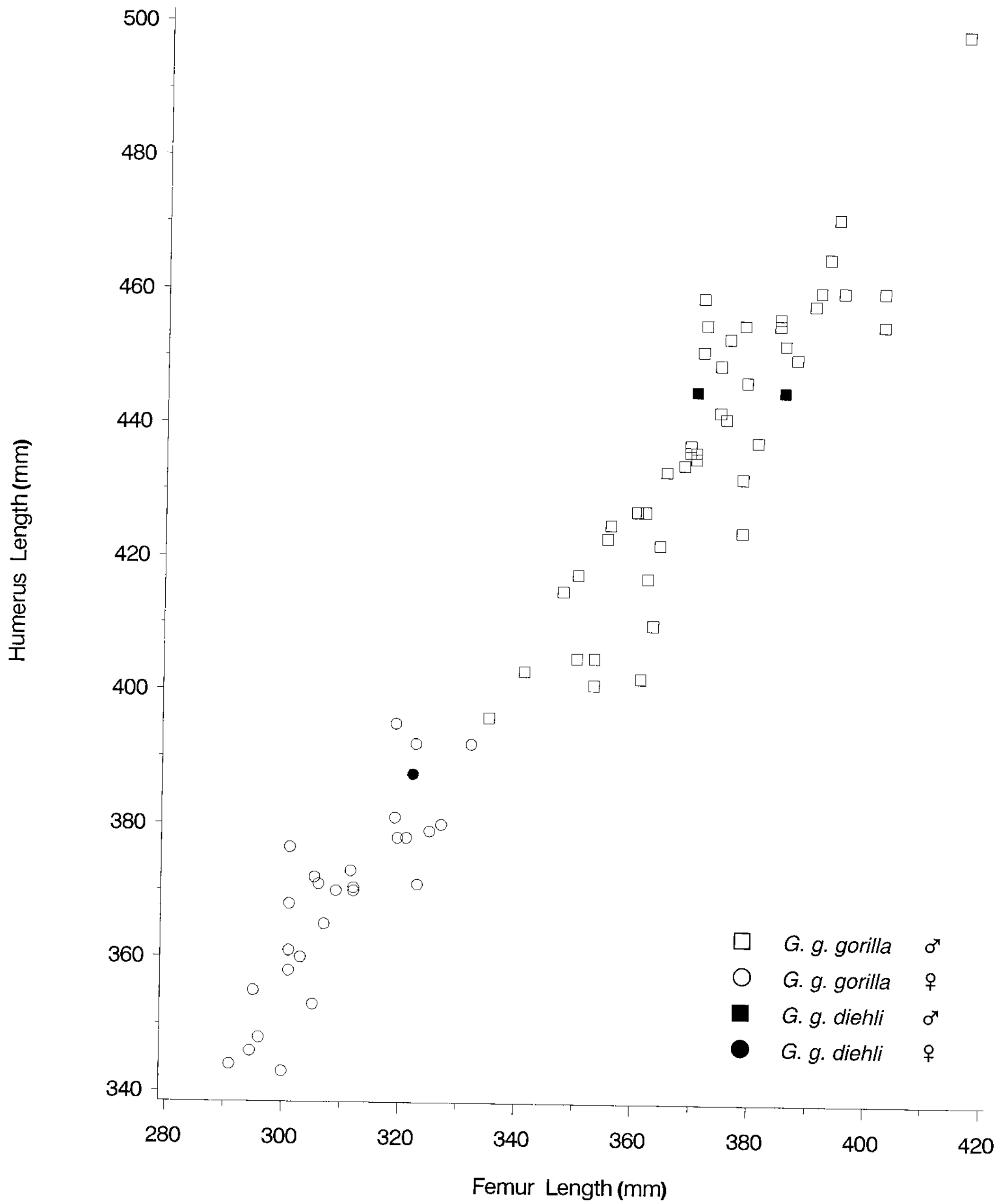

Fig. 15. Plot of humeral length vs. length of femur in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 1.113, y′ = 23.36, adjusted R^2= 0.95.

their bizygomatic width is significantly smaller than that of other male western gorillas (table 5, 6, and 7), a comparatively greater occlusal force per unit area is also implied by their small cheek tooth area. In this regard, many of the qualitative characters commonly exhibited by Cross River gorillas can be associated with lower jaw stabilization and the generation of greater magnitude of masticatory forces: a large malar

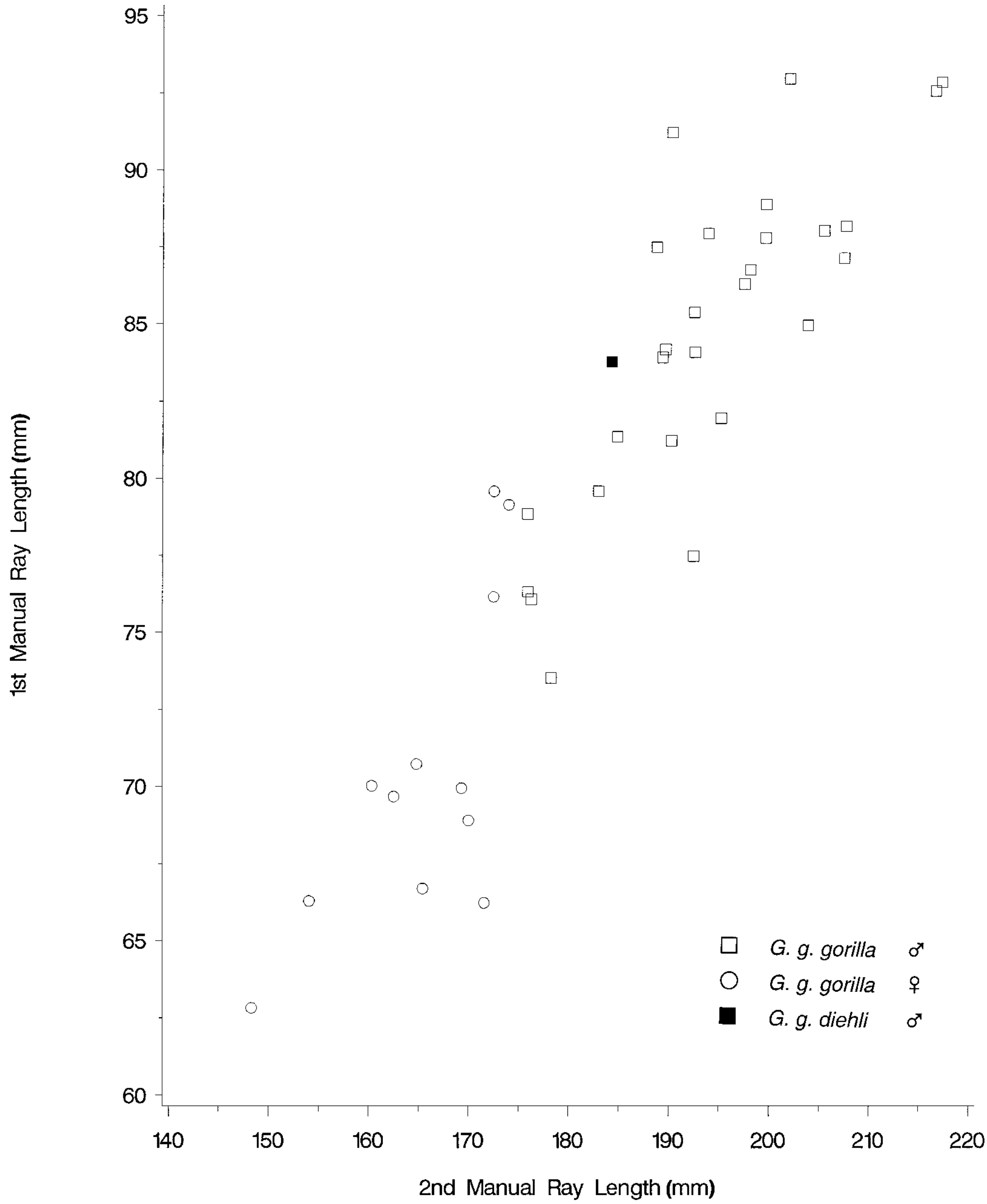

Fig. 16. Plot of 1st manual ray length vs. 2nd manual ray length in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 0.4635, y′ = −5.477, adjusted R^2= 0.84.

tubercle, strongly developed entoglenoid and postglenoid processes buttressing the glenoid joint, well-developed eustachian process, and superoinferiorly broad zygomas, and zygomatic arches.

The comparatively short face (glabella-incision), and short glenoid-incision length, in male Cross River gorillas (table 5) is associated with a narrower jaw gape than that of other western gorillas. This indicates that

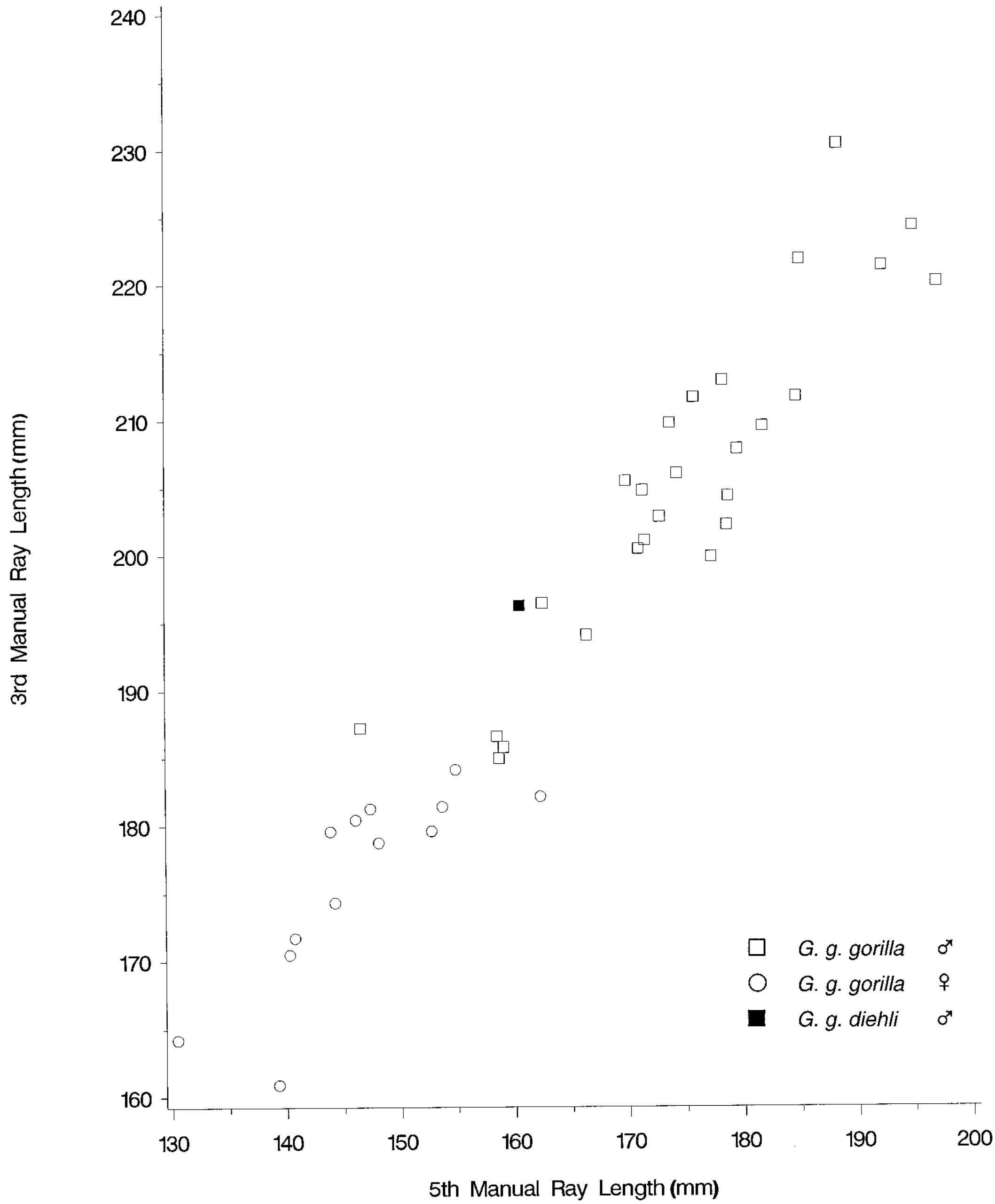

Fig. 17. Plot of 3rd manual ray length vs. length of 5th manual ray in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of non-Cross-river gorillas datum points fits a line with a slope = 0.9789, y′ = 33.78, adjusted R^2= 0.91.

Cross River males cannot dentally process objects as large as those processed by other western males. The usual absence, or relatively poor development, of the sagittal crest in many male Cross River gorillas (fig. 6, table 10), reflecting a shorter temporal muscle with shorter contractile length, also indicates a comparatively small gape. Female

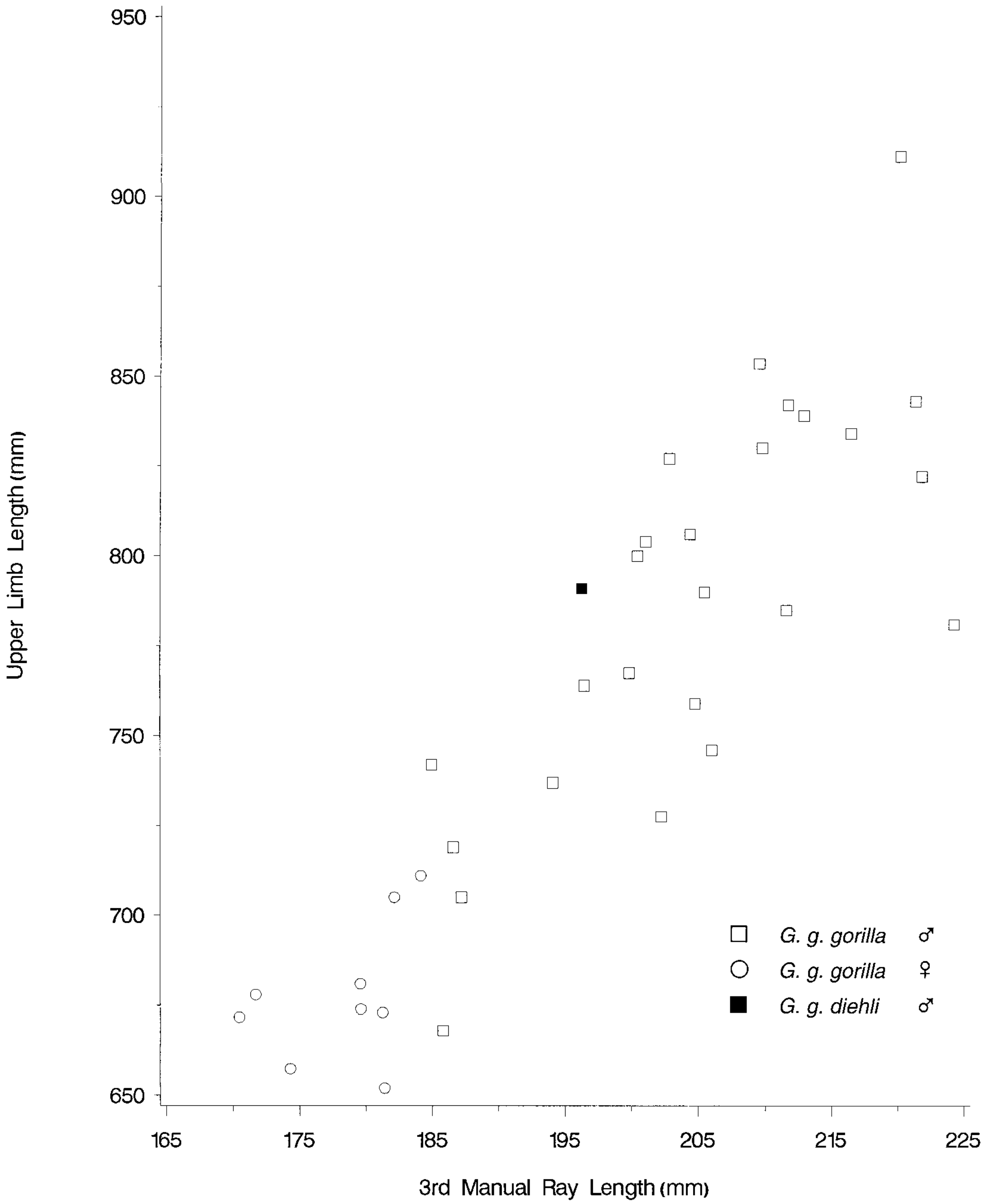

Fig. 18. Plot of upper limb length vs. 3rd manual ray length in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 3.799, y′ = 3.630, adjusted R^2 = 0.79.

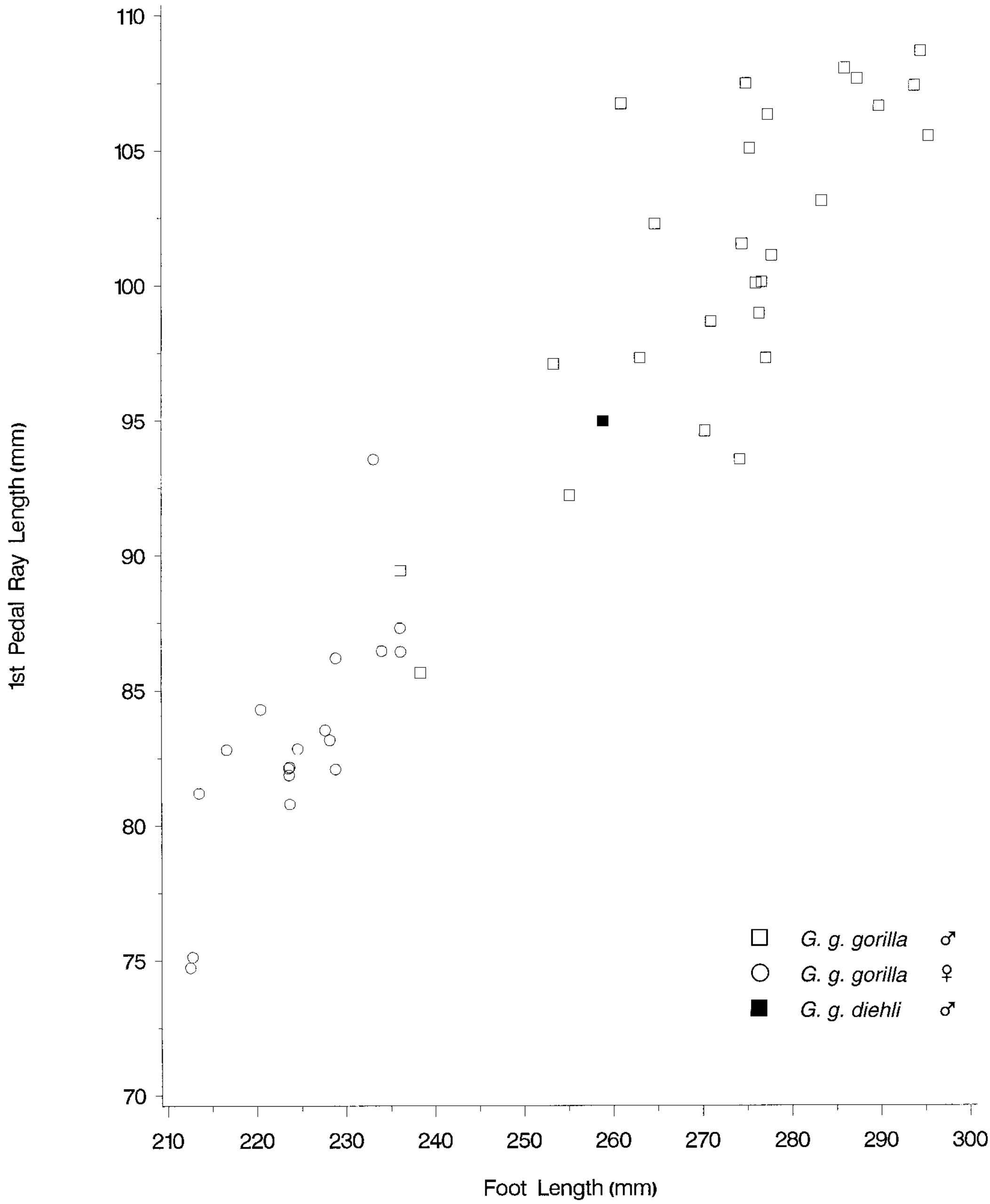

Fig. 19. Plot of 1st pedal ray length vs. foot length in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 0.366, y′ = 1.025, adjusted R^2= 0.89.

Cross River gorillas probably have a gape similar to that of other western females, considering similar glenoid-incision and face lengths (table 6). There is less of a difference, therefore, between the size of objects that the two sexes of Cross River gorillas can dentally process than there is for the two sexes of other western gorillas.

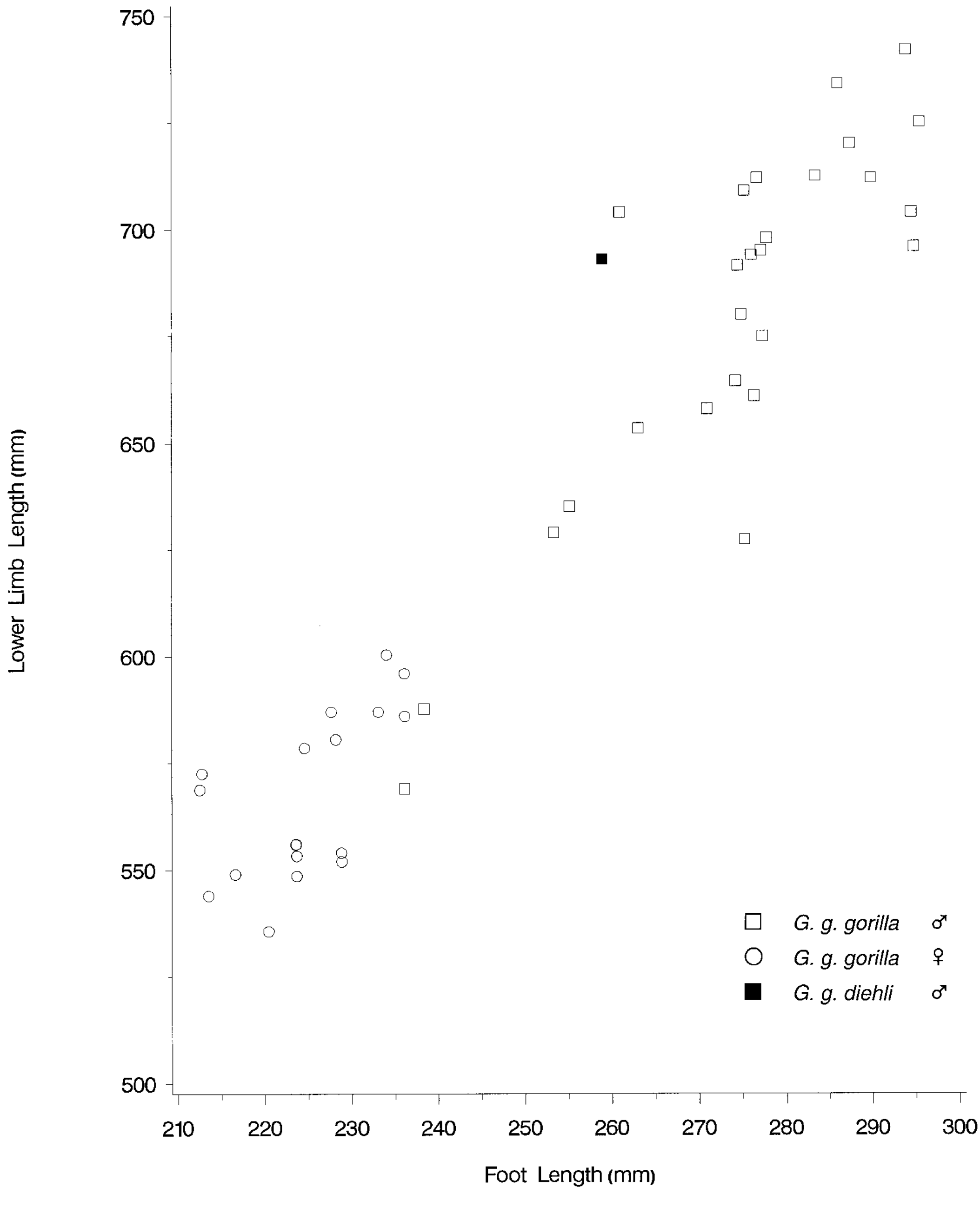

Fig. 20. Plot of lower limb length vs. foot length in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 2.286, y′ =53.48, adjusted R^2 = 0.91.

The comparatively small incisor-row diameter in Cross River gorillas (tables 5, 6, and 7) is another indication—along with the short and narrow palate and small cheek tooth surface area—that these animals are consuming foods that require less dental processing per unit of caloric intake than those consumed by other western gorillas. Strongly

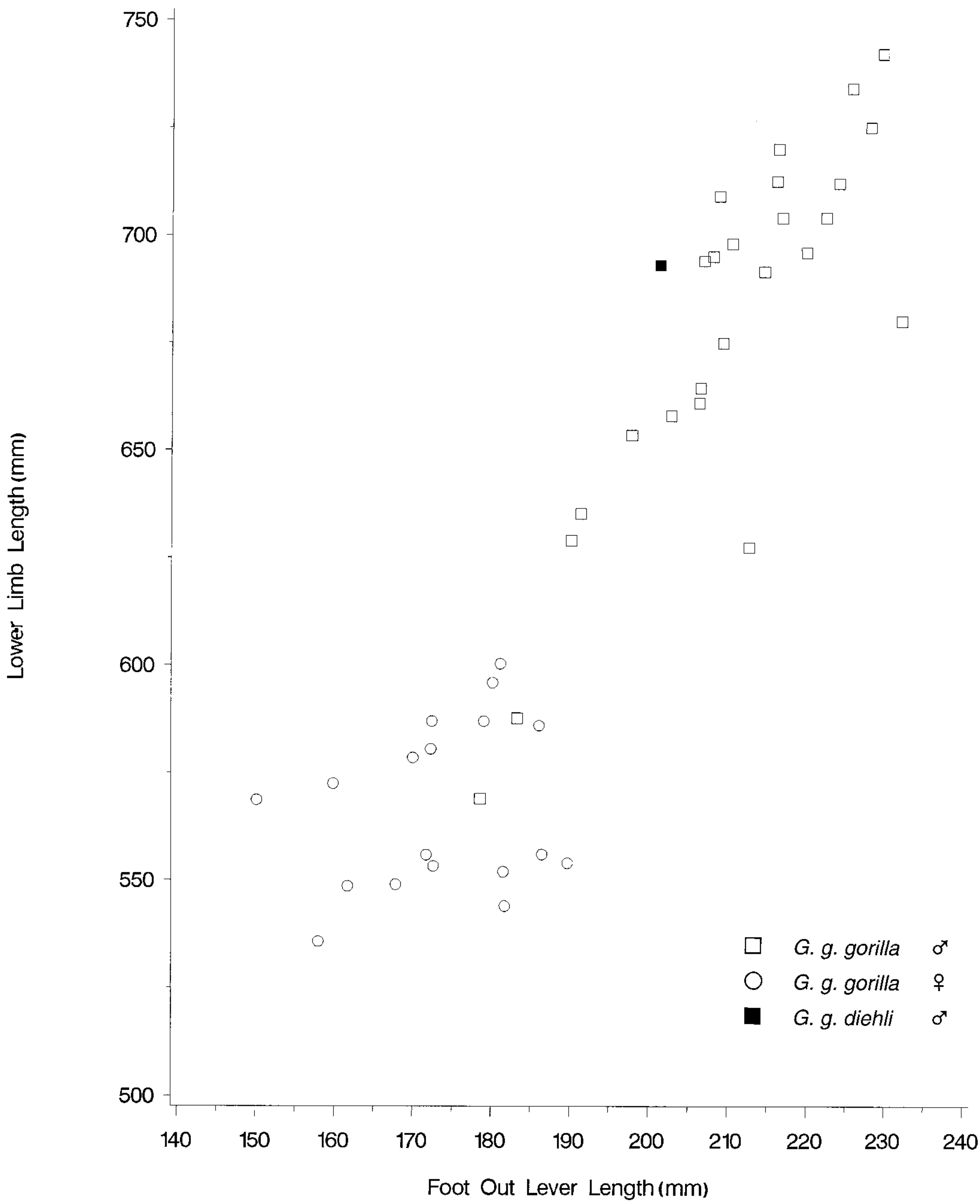

Fig. 21. Plot of lower limb length vs. foot outlever length in Cross River gorillas and in non-Cross-River western gorillas. Least square regression of the non-Cross-River gorilla datum points fits a line with a slope = 2.617, y′ = 121.97, adjusted R^2= 0.82.

bent incisor roots relative to the incisor blade (table 10) and characteristically heavy incisor wear, on the other hand, suggest relatively more incisive preparation than is common in other western gorillas. Moreover, Cross River gorillas may generate a greater incisor occlusal force, especially the males with their shorter glenoid-incision length and an in-

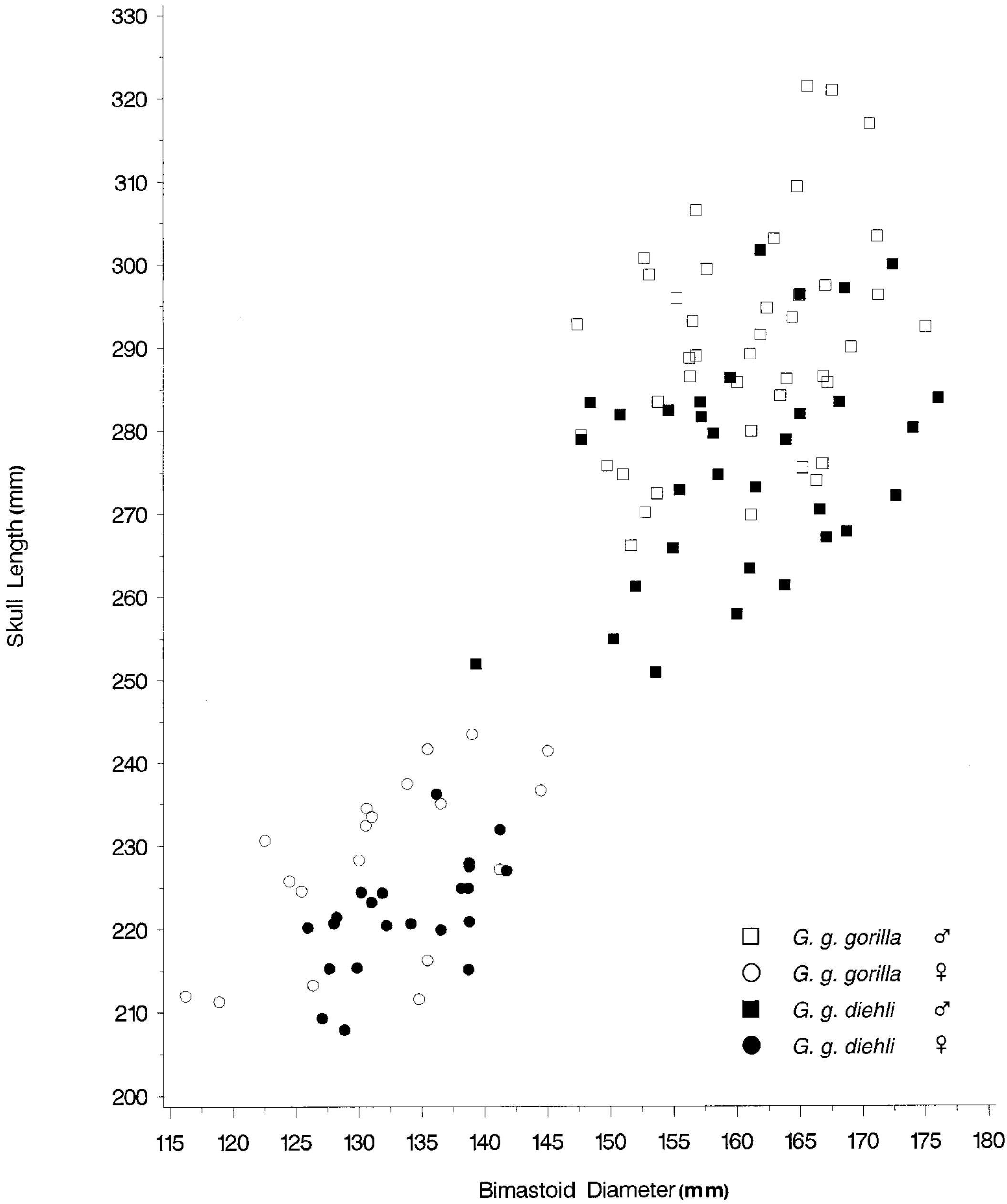

Fig. 22. Plot of skull length vs. bimastoid diameter in Cross River gorillas and in non-Cross-River western gorillas. *G. g. gorilla*, slope = 1.830, y′ = −6.458, adjusted R^2 = 0.790, *G. g. diehli*, slope = 1.710, y′ = −1.820, adjusted R^2 = 0.790.

ferred shorter outlever for the muscles of mastication. In this regard, the small incisors are more likely correlates of an overall small dentition and palate, and do not necessarily imply reduced incisor function.

Considered as a whole, the Cross River gorilla skull and gnathic characters indicate consumption of food items that (compared to those consumed by other western gorillas) are smaller, require less dental processing,

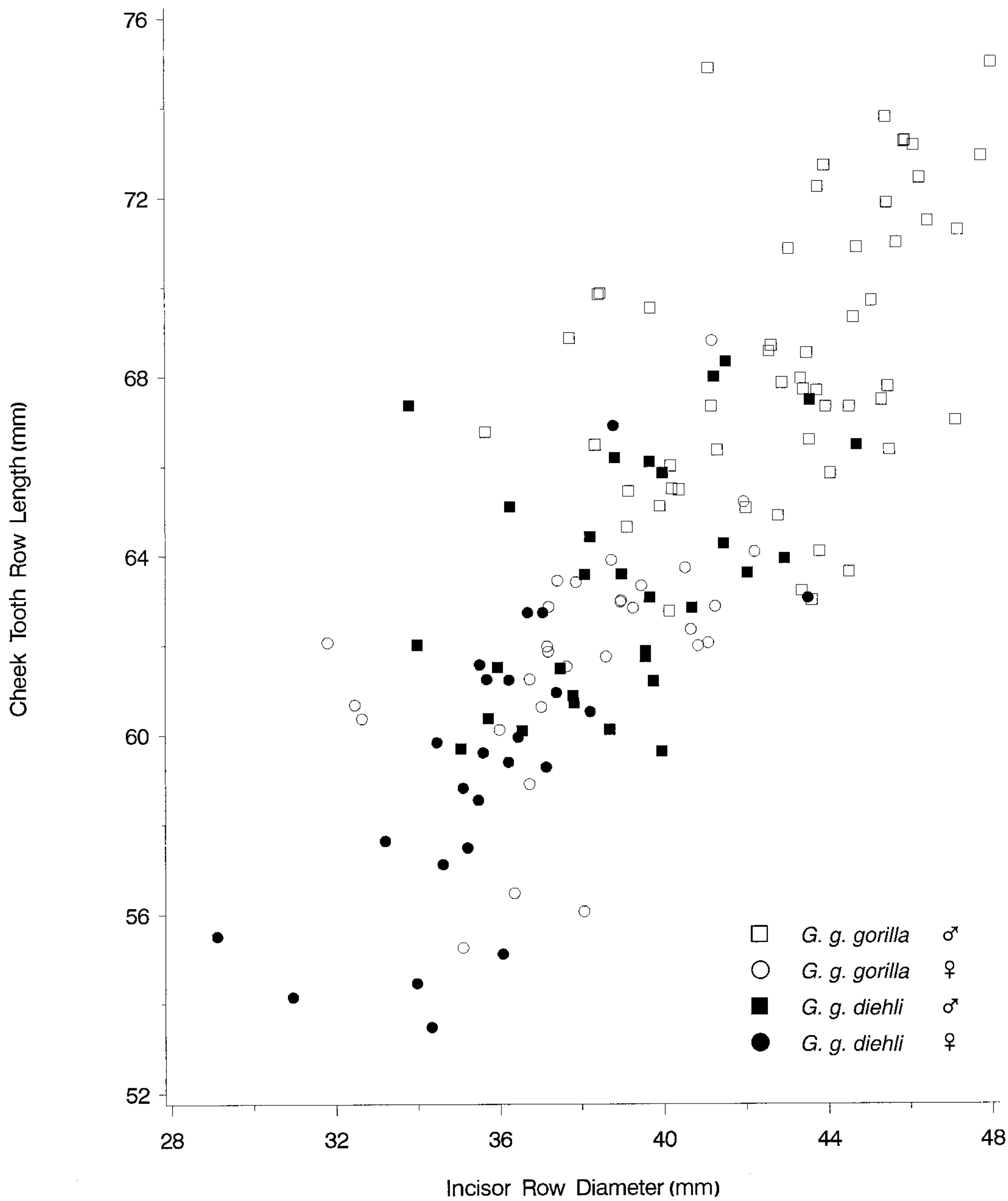

Fig. 23. Plot of cheek tooth row length vs. incisor row length in Cross River gorillas and in non-Cross-River western gorillas. *G. g. gorilla*, slope = 0.858, y′ = −30.69, Adjusted. R^2 = 0.51, *G. g. diehli*, slope =0.790, y′ = −31.90, adjusted R^2 = 0.47.

and may be somewhat harder. This implies that Cross River gorillas spend less time chewing than do other western gorillas. Incisive preparation, however, is no doubt an important component of feeding in Cross River gorillas, and possibly makes up a greater percentage of the feeding time, or includes harder and more abrasive foods, than in other western gorillas.

The relatively and absolutely shorter foot

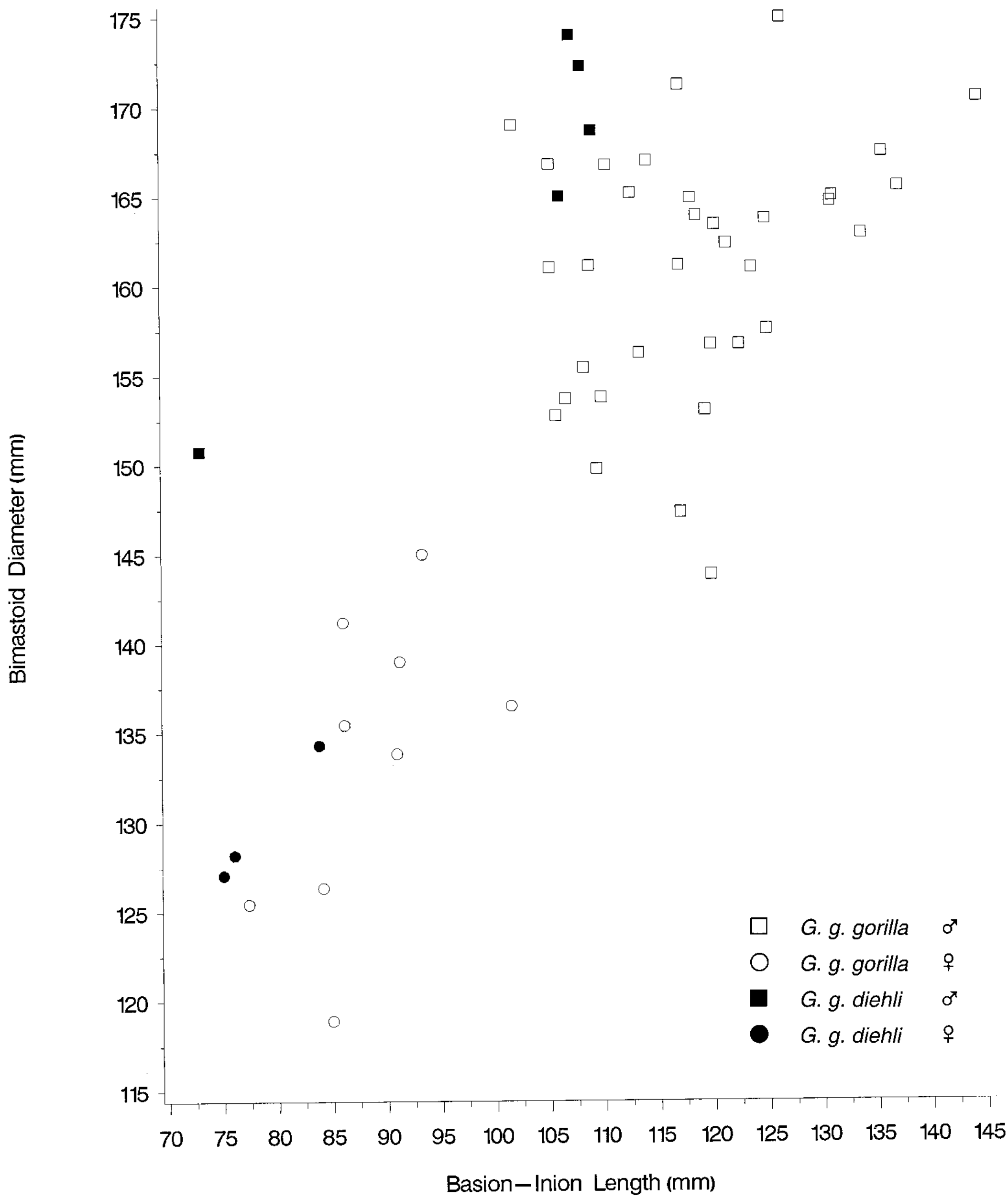

Fig. 24. Plot of bimastoid diameter vs. basion-inion length in Cross River gorillas and in non-Cross-River western gorillas. *G. g. gorilla*, slope = 0.669, y′ = −80.15, adjusted R^2 = 0.60, *G. g. diehli*, slope =1.079, y′ = −53.05, adjusted R^2 = 0.76.

length, foot lever length, and manual ray length (tables 3 and 4; figs. 18, 20, and 21) and the higher opposability index of the Cross River male gorilla (table 4, fig. 16) all suggest a greater commitment to terrestrial behaviors than seen in other western lowland gorillas (Sarmiento, 1994; Sarmiento et al., 1996).

The distinguishing postcranial and gnathic characters exhibited by Cross River gorillas

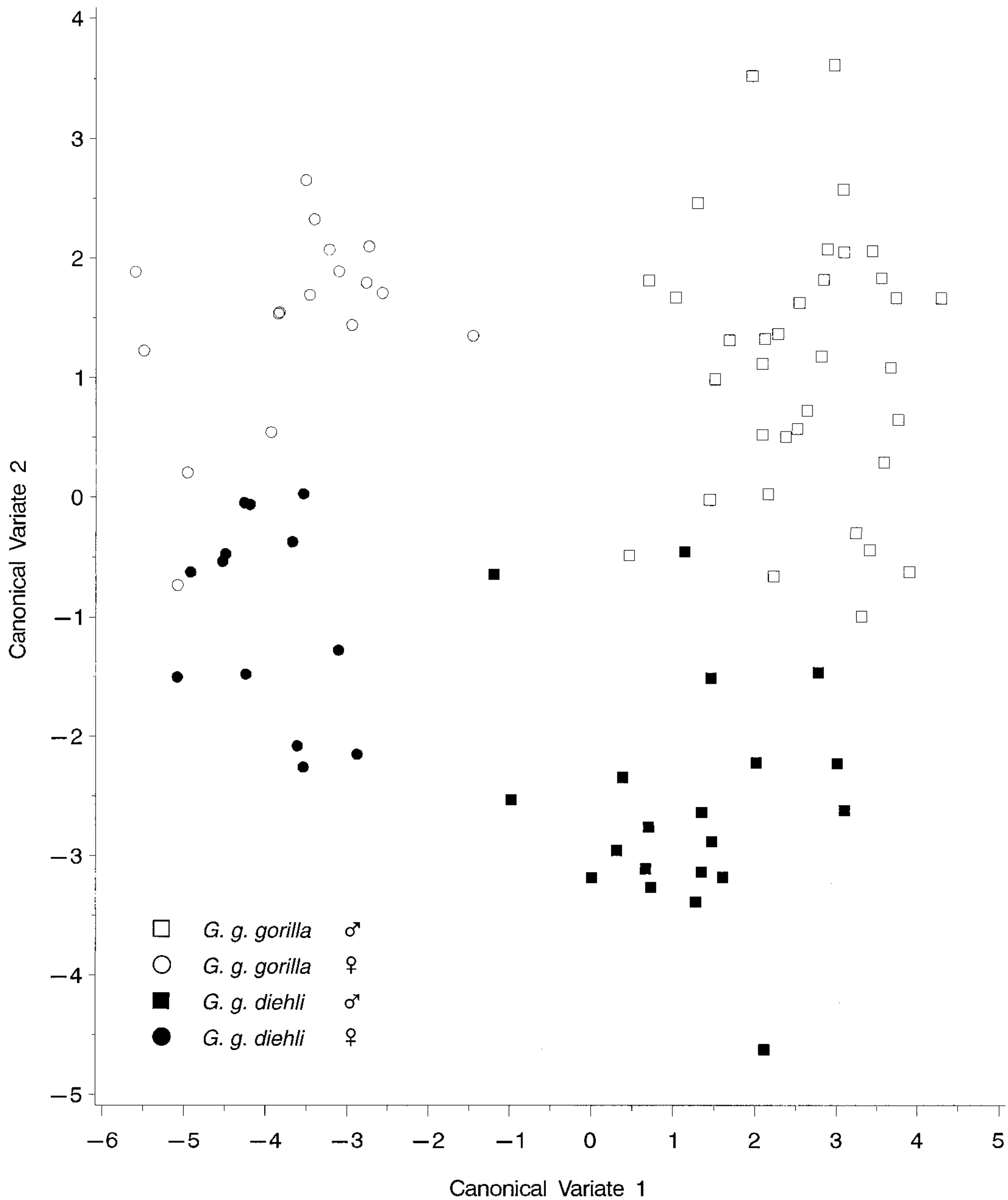

Fig. 25. Canonical variate analysis summarizing craniodental differences between *G. g. diehli* males (n = 20), *G. g. diehli* females (n = 13), *G. g. gorilla* males (n = 35) and *G. g. gorilla* females (n = 17) based on 11 measurements: (1)incisor row diameter, (2) bimastoid diameter, (3) bizygomatic diameter, (4) biglenoid diameter, (5) interparietal diameter, (6) M1 mesiodistal length, (7) biorbital diameter, (8) skull vault length, (9) cheek tooth row length, (10) P3 mesiodistal length, and (11) maximum palate width listed in decreasing order of discriminating ability. According to a stepwise discrimination analysis these measurements best summarize the measured differences between groups. Mahalanobis generalized squared distances (D^2) are 15.52 between the two male means; 6.85 between the two female means; 29.61 between the male and female means for *G.g. diehli*, 39.09 between male and female means of *G. g. gorilla*, 47.94 between *G. g. diehli* females and *G. g. gorilla* males, and 39.44 between *G. g. gorilla* females and *G. g. diehli* males.

TABLE 7

Probability Values of t for Differences in Mean Measurements of *G. g. gorilla* vs. *G. g. diehli* for Male to Male and Female to Female Comparisons[a]

	Male	Female
Skull length	0.0000	0.0021
Vault length	0.0000	0.0009
Cheek tooth area	0.0000	0.0001
Glenoid incision	0.0013	0.6833
Upper incisor row width	0.0000	0.0027
Molar premolar row length	0.0000	0.0010
Maximum palate width	0.0000	0.0005
Palate length	0.0023	0.2972
Bimastoid	0.8771	0.3253
Biglenoid	0.0000	0.0004
Bizygomatic	0.0462	0.6980
Vault volume	0.0000	0.0032
Minimum postorbital width	0.5707	0.4213
Glabella-prosthion	0.0291	0.5310
BiM3	0.0000	0.0020
Palate-glabella length	0.2211	0.8705
Humerus	0.4697	0.2054
Radius	0.8598	0.2495
Clavicle	0.1909	0.1378
Tibia	0.8336	—
Femur	0.6670	0.2879
Upperlimb	0.7272	0.1983
Lower limb	0.7654	—
Os coxa	0.9663	0.0629
1st metacarpal	0.9336	—
3rd metacarpal	0.3111	—
1st ray length manual	0.8654	—
2nd ray length manual	0.3951	—
3rd ray length manual	0.4413	—
5th ray length manual	0.3857	—
1st metatarsal	0.3296	—
4th metatarsal	0.1377	—
1st ray length pedal	0.3101	—
3rd ray length pedal	0.2520	—
4th ray length pedal	0.2097	—
Foot length	0.3396	—
Foot out lever length	0.5553	—

[a] Differences in the means are considered significant when probability values are less than 0.05.

have been associated in other anthropoid primates with shifts to more open habitats (Hall, 1965; Jolly, 1970; Sarmiento, 1998). In the Cross River gorillas, these characters could also be associated with lower fruit abundance in habitats at high elevations, or with long dry seasons (Sarmiento et al., 1996; Sarmiento, 1998).

It is unclear, however, how the distinctive gnathic morphology of Cross River gorillas relates to the habitat they presently occupy. Comparisons of known gorilla food plants to the list of plants growing in the Takamanda Reserve show that a large variety of potential foods, including many fruits that must be harvested arboreally, are available to the Cross River gorillas (table 13). Most of these food plants are available throughout a wide range of elevations in the different Cross River gorilla habitats. It is unlikely, therefore, that Cross River gorillas at present have a diet with a species composition that differs markedly from that of other western gorillas, or that they would emphasize terrestrial behaviors at the expense of arboreal ones (fig. 26). The frequency with which different plant types or parts are consumed will probably be the only difference in the diets of Cross River gorillas and of the other western gorillas. A large number of fruit-eating competitors (Sanderson, 1940; Thomas, 1988), a single but long dry season, and a long rainy season suggest that fruit may be even less reliably available to gorillas in the Cross River habitat than they are in other western gorilla habitats.

Possibly the present habitats occupied by Cross River gorillas do not represent the habitats in which they originally differentiated and/or to which they are best suited. In this regard the Obudu Plateau and other areas of the Bamenda Highlands, which once supported an extensive and unique montane forest ecosystem (Keay, 1979), may be a better representation of the habitat in which they evolved.

Regardless of their origin, the distinctive Cross River gorilla characters have important taxonomic implications. Because Cross River gorillas are allopatric relative to the other western gorillas, and differences between the two reflect differences in an adaptive complex associated with increasing terrestriality, it is best to refer Cross River gorillas to a separate subspecies, *G. g. diehli*. Considering that ZMBU 12799 was indistinguishable from *G. g. diehli* in discriminant analysis, Matschie's (1904) contention that Cross River gorillas are a separate species, referable to *G. diehli* (since ZMBU 12799 was in his view *G. gorilla*) is not supported.

When striving to maintain consistency in

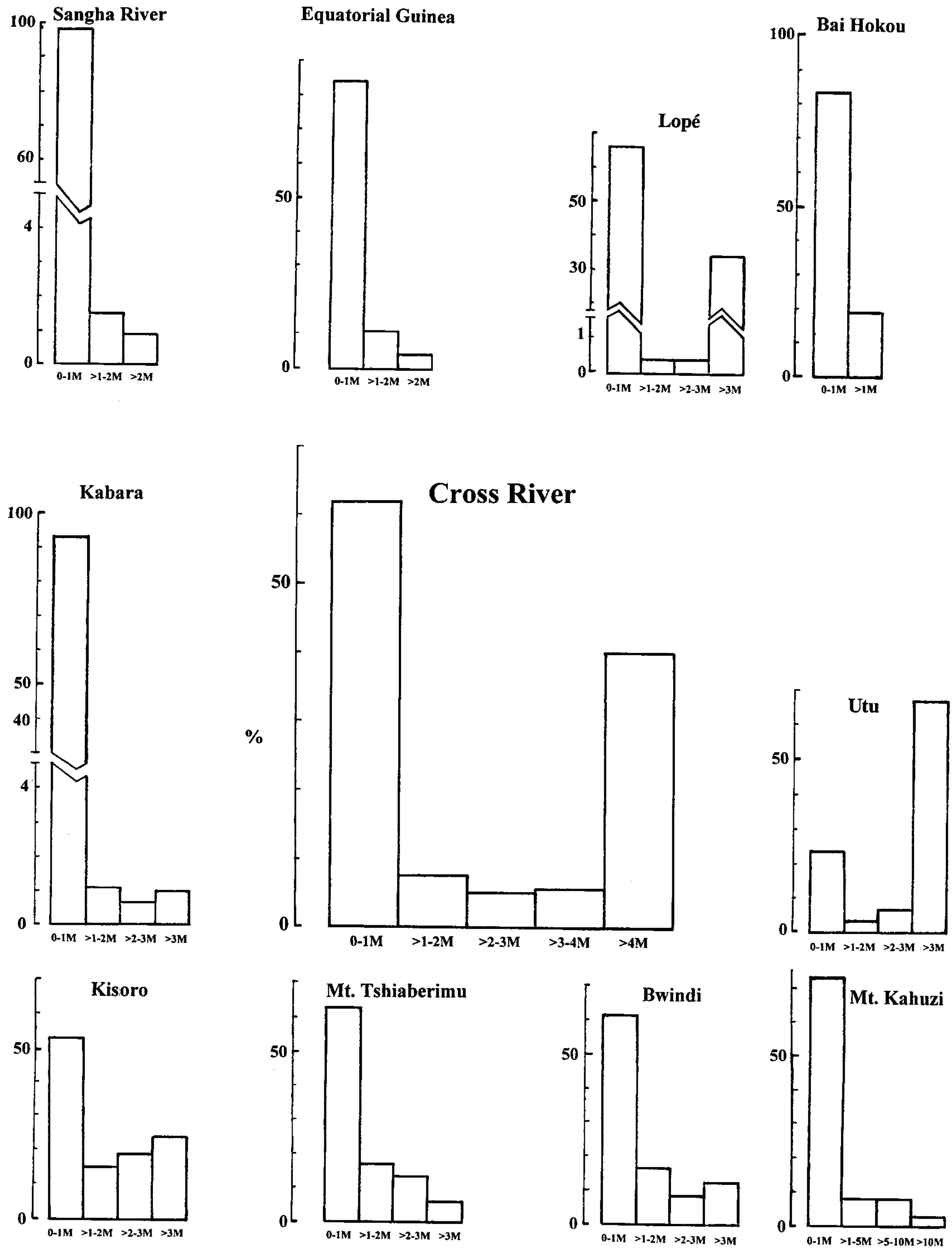

Fig. 26. Percentage distribution of Cross River gorilla nests grouped at 1 meter height intervals and compared to nest height distributions reported for other gorilla populations. Although eastern gorillas are reputed to be more terrestrial than western gorillas, there does not seem to be a direct relationship between arboreal behavior and the percentage distribution of nest heights. Western gorillas build nests

the magnitude of differences assigned to the same taxonomic levels within the genus *Gorilla* (Simpson, 1961; Mayr, 1969), it is relevant that Cross River gorillas show significant differences in cheek tooth surface area when compared to other western gorillas (Tables 5, 6, and 7), but that Virunga gorillas (*G. g. beringei*) fail to show such difference when compared to different populations of *G. g. graueri* (table 9). Significantly, tooth morphology is less likely to reflect developmental and/or physiological plasticity than is bone morphology, suggesting that *G. g. diehli*'s distinctiveness is at least partially a result of genetic differences probably greater than those separating *G. g. beringei* from *G. g. graueri*. Such relative differences in cheek tooth area, therefore, support a taxonomic distinction for *G. g. diehli* among western gorillas as great or greater than that accorded to Virunga gorillas among eastern gorillas.

PRIMATE BIOGEOGRAPHY

Our conclusion that the gorilla populations at the headwaters of the Cross River merit recognition as a distinct subspecies is not surprising when viewed in light of the affinities and distribution of other primates living in the region straddling the Nigerian-Cameroonian border. At least six other catarrhine species or subspecies appear to be unique to this area (including Bioko Island): *Procolobus badius preussi*, *Mandrillus leucophaeus*, *Cercopithecus erythrotis*, *C. nictitans martini*, *C. pogonias pogonias*, and *C. preussi* (Gartlan and Struhsaker, 1972; Gartlan, 1975; Oates, 1988). Gonder et al. (1997) argued, based on DNA analysis, that chimpanzee populations in this area are also unique and should be referred to the subspecies *Pan troglodytes vellerosus*. The taxonomy of African prosimians is currently in a state of flux, but at least two prosimian species also seem to be restricted to this area: *Arctocebus calabarensis* and *Euoticus pallidus* (Oates, 1996). The historical causes of this endemism are uncertain, but may be related to the presence of a Pleistocene forest refuge in this region (Booth, 1958; Oates, 1988).

Although past forest refuge or refuges in the vicinity of the Cameroon Highlands might explain the past differentiation of primate taxa in this region, barriers limiting the spread of these primates subsequent to isolation are less clear. Specialized ecological requirements may have limited the dispersal of *C. preussi* (restricted to the Cameroon Highlands and Bioko Island) and *P. b. preussi* (restricted to lowlands in the far southwestern corner of Cameroon and the adjacent part of Nigeria). Likewise, it is possible that some features of the habitat in the hill country at the Cross River headwaters allow gorillas to survive there, but not elsewhere in the immediate region.

One potentially important dispersal barrier in the region is the Sanaga River (Booth, 1958; Gartlan, 1975; Oates, 1988). The southern limit of many of the forest primates endemic to the Nigerian-Cameroonian border region appears to be in the vicinity of the Sanaga River. This river also serves as the northern limit of several primates that are typical of the West Equatorial forest region (table 14).

Of the western Cameroonian catarrhines that are not obviously represented by different taxa on either side of the Sanaga, most

←

below 1 m as often or more often than eastern gorillas, and some eastern gorillas may build a greater percentage of their nests at heights above 3 m. Percentage distributions of nest heights are based on the following studies: Cross River gorilla (N=214), JFO field notes; Sangha river (N=547), Fay 1989; Equatorial Guinea, Jones and Sabater Pi (N=410), 1970; Lope (N=2,435), Tutin et al. 1995: Bai Hokou (N=1,123), Remis 1993; Kabara (N=2,488), Kisoro (N=106), Bwindi (N=179), and Utu (N=110), Schaller 1963; Mt. Tshiaberimu (N=195), Sarmiento and Butynski notes; Mt Kahusi (N=964), Casimir 1977. Intervals as reported in the literature have been modified to best enable comparisons. Data was combined for those studies separately reporting ground nests and nests built on vegetation at heights of 1 meter and below. Schaller's nest heights were reported in feet and converted into meters for comparisons. Casimir (1977) gave nest height intervals of 5 m. which are not comparable for nest heights above 1 meter.

TABLE 8

Cross-Sectional Volume of Four Last Thoracolumbar Vertebral Bodies in *G. g. gorilla* and *G. g. diehli* Males and Females

Mean ± standard deviation and range; sample sizes in parentheses.

	Males	Females
G. g. gorilla	246386 ± 39255 (31)	129787 ± 24644 (23)
	308768–168346	188189–80126
G. g. diehli	255057 (1)	154767 (1)
	—	—

In 15 lowland western gorillas with reported field weights a bivariate plot of x-sectional volume (mm^3) of the last 4 thoracolumbar vertebral bodies vs. body weight (kg) conforms to a linear equation with an adjusted $r^2 = 0.965$, slope = 0.725, and $y' = -19.26$. This regression predicts a body weight of 166 kg for the Cross River male gorilla and 93 kg for the Cross River female gorilla with ranges of 145–187 and 72–114 kg at 95% level of confidence.

are species either typical of savanna woodland or often found in gallery forest in the savanna zone (e.g., *Colobus guereza*, *Papio anubis*, *Cercopithecus aethiops*, and *C. mona*). The headwaters of the Sanaga are well inside the savanna zone (fig. 2), so it is not surprising that these taxa occur on either side of the river. The only forest catarrhines that do not appear to show taxonomic differentiation across the Sanaga are two mangabeys, *Cercocebus torquatus* and *Lophocebus albigena*. Elsewhere in Africa, mangabeys appear to have distribution patterns less influenced by rivers than the other forest monkeys; indeed, they are sometimes associated with swamp forest or riverine vegetation.

Along the lower course of the Sanaga, *G. g. gorilla* specimens are known from close to the southern bank of the river, but not from its northern bank.[6] The lower Sanaga, therefore, or something in its immediate vicinity, does seem to act as a dispersal barrier both to gorillas and to other catarrhines. On the other hand, this river is not an absolute barrier to forest catarrhines. *Cercopithecus erythrotis* has been recorded on the southern bank of the lower Sanaga, while *Miopithecus* has been observed on the northern bank (Gartlan and Struhsaker, 1972); higher up the river's course, where the Sanaga is smaller and crosses the forest-savanna boundary, *Mandrillus sphinx, Cercopithecus cephus, C. n. nictitans,* and *G. g. gorilla* occur in the

TABLE 9

Cheek Tooth Surface Area (mm^2) in Some Eastern Gorilla Populations

Mean ± standard deviation and range; sample sizes in parentheses.[a]

	Male	Female
Virunga		
	1269 ± 129.2 (29)	1088 ± 60.45 (23)
	1487–943.7	1198–956.4
Bwindi		
	1211 ± 126.1 (5)	971.7 ± 71.77 (3)
	1387–1034	1022–920.5
Itombwe		
	1278 ± 95.14 (9)	1106 ± 91.04 (8)
	1454–1108	1236–933.0
Walikale Itebero–Utu		
	1142 ± 106.1 (11)	1085 ± 60.42 (11)
	1323–998.0	1181–957.0
West Lake Edward		
	1306 ± 118.2 (14)	1178 ± 58.1 (16)
	1483–1125	1252–1063
Angumu		
	1211 ± 135.5 (5)	1131 ± 70.14 (7)
	1351–986.7	1225–998.8

[a] Male to male and female to female comparisons of the mean cheek tooth surface area of Virunga gorillas to those of the other eastern gorilla populations showed significant diference ($t \leq 0.05$) only with Walikale males and with Lake Edward females.

[6] At present there are no gorillas on the northern bank of the lower Sanaga River, but the words ''über Edea'' (Edea referring to a village on the south bank of the Sanaga River) on the label of three ZMBU specimens (18515, 18516, 18519) collected by Göpfert may indicate that their absence is a recent phenomenon. Considering that the Sanaga runs from a northeast to a southwest direction, the word ''über'' may refer to an area northeast of Edea but still south of the Sanaga River.

TABLE 10

Morphological Skull Characters of *G. g. diehli*[a]

a) Incisor roots and alveoli strongly bent almost perpendicular to the incisor blade.
b) Premaxillary–maxillary sutures outside pyriform aperture forming large nasal premaxillary processes flanking nasal bones inferolaterally.
c) Superoinferiorly short face, strongly concave at nasal bridge.
d) Protruding bony ridge or torus extending nearly the length of midnasal suture.
e) Mediolaterally narrow intermaxillary process of frontal bone with marked inferior prolongation between paired frontal processes of maxillae.
f) Large protruding glabella
g) Large, superoinferiorly wide and flat zygoma, set almost perpendicular to very broad (superoinferiorly) but nearly flat (lacking mediolateral curvature) zygomatic arch.
h) Males exhibit large jugal fossa variably circumscribing infraorbital foramina and continuous with inferomedial concavity of zygoma.
i) Pronounced, inferiorly elongated, and low set maxillary tubercle on zygoma.
j) Strong, stylar shaped eustachian process of entoglenoid.
k) Strongly pronounced and inflated temporal entoglenoid and postglenoid processes.
l) Exaggerated inflation of squamous temporal bone below glenoid and extending into zygomatic arch.
m) Mastoid processes large, protruding well below and well lateral to external acoustic meatus, and with pronounced inflation continuing posteriorly into nuchal crest.
n) Posterior (subnuchal) surface of mastoid shows little or no relief from suboccipital plane.
o) Nuchal flange or crest tapers at midline so that crest's profile in transverse plane appears waisted.
p) Temporal lines often fail to meet, forming a strong sagittal keel as opposed to a crest.
q) No palatal spine.

[a] See figures 3–6.

TABLE 11

Average Monthly and Yearly Rainfall (mm) for Localities[a] with Varying Altitude and Latitude in Cross River Catchment area

See appendix 1 for locality coordinates.

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Obudu town (alt. 396 m, yearly rainfall 1813 mm)[b]											
4.6	14.0	45.8	116.5	254.8	244.6	240.1	238.4	356.2	260.2	30.4	2.5
Obudu plateau (alt. 1585 m, yearly rainfall 4280 mm)											
Afi Base Camp (alt. 700 m, yearly rainfall 3346 mm)											
0.4	0.1	11.8	237.2	321.0	338.0	441.8	750.3	736.7	503.7	13.1	14.7
Drill Ranch Camp (alt. 150 m, yearly rainfall 3303 mm)											
14.7	0	78.8	220.4	293.4	462.4	449.4	697.6	482.5	544.0	55.5	5.1
Ikom (alt. 119 m, yearly rainfall 2465 mm)											
Mamfe (alt. 122 m, yearly rainfall 3424 mm)											
33	79	160	206	325	437	513	465	564	452	152	38
Dikome Balue, Rumpi hills (alt. 270 m, yearly rainfall 4933 mm)											
113	196	374	342	307	397	757	975	801	380	231	60

[a] Obudu town based on monthly averages from Jan ′78–Apr ′90 collected from town records by JFO; Obudu plateau after Hall (1981), only yearly averages available; Afi base camp based on monthly averages Apr ′96–Dec ′96, and Dec ′97–Dec ′98, data collected by K. McFarland (personal commun.); Drill Ranch Camp based on monthly averages from Jan ′97–Sep ′98 data collected by Pandrillus; Ikom after Keay (1979), only yearly average available; Mamfe based on monthly averages over a 32 year period after Hawkins and Brunt (1965); Dikome Balue, Rumpi hills based on monthly averages over two years after Tuegels et al. (1992).

[b] Keay (1979) reported yearly average rainfall of 1585 mm for Obudu town.

TABLE 12
Ambient Temperature (°C) for Three Localities[a] in Cross River Catchment Area
See appendix 1 for locality coordinates.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ikom (alt. 107 m, avg. yearly max 32.0)												
Max	32.4	32.8	33.7	33.1	32.6	32.1	30.6	30.0	31.1	31.6	32.1	31.5
Afi Base Camp (alt. 700 m, avg. yearly max 26.0, min 18.8)												
Max	25.9	28.0	28.6	28.2	27.7	26.3	24.6	23.5	23.6	24.6	25.9	25.4
Min	17.0	18.3	20.4	20.2	19.8	19.4	19.3	18.6	18.1	18.6	18.2	17.5
Drill Ranch Camp (alt. 150 m, avg. yearly max 33.5, min 21.9)												
Max	31.5	35.0	36.5	36.5	35.3	33.7	33.7	32.4	31.1	33.0	32.6	31.0
Min	18.5	18.5	21.5	23.5	23.5	23.0	23.0	22.9	22.9	23.0	23.0	19.0

Ikom based on records over a total of 9 years after Teugel et al. (1992); only maximum averages available; Afi Base camp based on daily averages from Apr ′96–Dec ′96, and Dec ′97–Dec ′98, data from K. McFarland (personal commun.); Drill Ranch camp based on daily averages, Jan ′97–Sep ′98, data from Pandrillus. Considering a decrease of 6.5° per 1000 m, the expected maximum and minimum yeraly average temperature at the Obudu Plateau (1600 m) are 20.2° and 13.0°C, respectively. Hall (1981) reported maximum and minimum temperatures of 18–25°C and 14–16°C, respectively, for the Obudu Plateau at 1585 m.

Bafia region to the northwest of the Sanaga (Oates, 1988; this study).

CONCLUSIONS

G. g. diehli may have differentiated from *G. g. gorilla* during an arid phase of the African Pleistocene in response to declining arboreal food sources and a greater emphasis on herbivory and terrestrial behaviors. During this dry phase, which was not necessarily the last glacial maximum, the ancestors of *G. g. diehli* were presumably isolated in forests near the Cross River headwaters and/or elsewhere in the Cameroon highlands. Cross River gorillas may not have spread far beyond this area since their isolation. The ancestors of *G. g. gorilla* differentiated somewhere to the south and/or east of the Sanaga and their subsequent northward dispersal has been limited by the lower reaches of that river and the highlands immediately west of the river. Contrary to Matschie's suggestion (1904), there is no evidence that *G. g. diehli* and *G. g. gorilla* were sympatric in recent times. At the moment, therefore, there is no reason to regard Cross River gorillas as a unique species, but the evidence we have presented strongly supports recognizing them as a separate subspecies, *G. g. diehli*.

Gorilla gorilla diehli Matschie 1904

HOLOTYPE: ZMBU 12789 (figs. 3 and 4) and adult male skull (including mandible) collected by Mr. S. Diehl in 1904 from Dakbe (fig. 1, appendix 1) near the Makone (Menome) River, northwestern Cameroon. The base of the skull around the foramen magnum is damaged, and the cortical bone covering the mastoid process on the left side abraded. Both upper central incisors and the left I2 and C1 are missing.

REFERRED SPECIMENS: Table 1 lists the referred specimens and the material each specimen is represented by.

DISTRIBUTION: Known from semideciduous montane forests at elevations of 150-1500 m in the Cross River watershed area 5°55′–6°25′N and 8°48′–9°38′E.

DIAGNOSIS: *G. g. diehli* is distinguished from *G. g. gorilla* in exhibiting significantly less cheek tooth occlusal surface area, smaller vault volume, narrower biglenoid diameter and narrower incisor row and palate width. *G. g. diehli* males are further distinguished in having significantly lower average palate lengths, bizygomatic widths, glenoid-incision lengths and facial lengths (glabella-incision) than *G. g. gorilla* males (tables 5 and 7). The combination of non-metric skull characters listed in table 10 is also diagnostic of *G. g.*

TABLE 13
Plant Foods Growing in Takamanda Reserve Consumed by Other Gorilla Populations[a]

Plant	Part eaten	Population
Anacardiaceae		
Antrocaryon klaineanum[b]	Fruit, leaves	EqGui, Gabon, Utu (sp)
Pseudospondias longifolia[b]	Fruit	Gabon, Lopé
Trichoscypha sp.	Fruit	Gabon, EqGui, Lopé (sp)
Annonaceae		
Uvariopsis dioica[b]	Fruit, leaves, pith	Utu
Xylopia africana[c]	Pith, bark, fruit	EqGui (sp), Gabon (sp)
Xylopia hylolampra[b]	Pith, bark, fruit, leaves	EqGui (sp), Gabon (sp) Ndoki (sp), Lopé
Apocynaceae		
Rauvolfia manni	Fruit, leaves	EqGui (sp)
Tabernaemontana pachysiphon[b]	Fruit, leaves	Ndoki (spp), Bwindi(sp)
Arecaceae		
Elaeis guineensis[b]	Fruit, pith	Utu, Lopé
Burseraceae		
Dacryodes edulis[b]	Fruit	EqGui (sp), Gabon (sp), Lopé (sp)
Santiria trimera[b,c]	Fruit	EqGui, Gabon, Ndoki
Caesalpiniaceae		
Anthonotha sp.[c]	Leaves	Utu (sp)
Dialium sp.[c]	Fruit	EqGui, Gabon, Utu (sp)
	Fruit, leaves	Ndoki, Lopé
Clusiaceae		
Garcinia sp.[c]	Fruit, leaves, roots	Utu (spp)
Symphonia globulifera[c]	Fruit, leaves, bark, roots	Utu, Bwindi
Commelinaceae		
Palisota sp.	Fruit, pith	EqGui, Gabon, Ndoki, Utu, N. Congo, Itombwe
	Leaves	Campo (spp)
Cyatheaceae		
Cyathea kameruniana	Shoots, pith	Utu (sp), Bwindi (sp), Kahusi (sp)
Ebenaceae		
Diospyros sp.	Fruit	Ndoki (sp)
	Leaves	Utu (spp)
	Fruit, leaves	Lopé (spp)
Euphorbiaceae		
Alchornea hirtella	Fruit, leaves	EqGui (spp), Utu (spp), Bwindi
Antidesma sp.	Fruit	Lopé
Macaranga sp.[c]	Pith	EqGui (sp), Gabon (sp), Ndoki (sp) Utu (sp), Bwindi
	Fruit, pith, bark	Mt. T
Maesobotrya duseni[b]	Leaves	Utu (sp)
Uapaca sp.[b]	Fruits	EqGui, Gabon, Ndoki, Lopé
	Fruit, pith, bark, leaves	Utu(spp)
Fabaceae		
Angylocalyx talboti	Fruits and leaves	Ndoki(spp)
Millettia sp.[b]	Leaves	Ndoki(sp)
Flacourtiaceae		
Caloncoba glauca[b]	Fruit	Ndoki, EqGui (sp)

Table 13
(Continued)

Plant	Part eaten	Population
Irvingiaceae		
Irvingia gabonensis[b]	Fruits	EqGui, Gabon, Ndoki, Lope
Klainedoxa gabonensis[b]	Fruits	Gabon, Utu, Ndoki, Lope, N. Congo
Meliaceae		
Guarea sp.[c]	Fruits	Gabon (sp)
Carapa procera[b]	Bark	Kahusi (sp)
Mimosaceae		
Newtonia sp.[c]	Bark	Bwindi
Parkia bicolor[b]	Fruit	Lopé
Piptadeniastrum africanum[b]	Leaves, bark	Utu
Tetrapleura tetraptera	Fruit	Campo
Moraceae		
Antiaris africana[b]	Leaves, bark	Utu
Ficus sp.	Leaves	N. Congo
	Fruit, leaves	Utu (spp), Lopé (spp), Ndoki (spp), Gabon (spp), EqGui (spp), Kahusi (spp)
Musanga cecropioides[b]	Fruit, leaves	EqGui, Gabon
	Flowers, pith	Ndoki, Utu, Bwindi, Campo
Myrianthus arboreus[c]	Fruit	Gabon, Ndoki, Lopé, Bwindi
	Fruit, leaves	Utu, Kahusi
	Bark, pith	Itombwe
Treculia obovoidea[b]	Fruit	Utu (spp), Ndoki (spp), Lopé (sp)
Myristicaceae		
Pycnanthus angolensis[b]	Fruit	EqGui, Gabon, Ndoki,
	Leaves, bark	Utu
Staudtia stipitata[b]	Fruits	Ndoki, Gabon (sp)
	Leaves, bark	Utu
Olacaceae		
Heisteria parvifolia[b]	Fruit	Gabon
Strombosia grandifolia[b]	Fruit	Gabon (sp)
Strombosiopsis tetrandra	Fruit	Ndoki
Polygalaceae		
Carpolobia lutea[b]	Leaves	EqGui (sp)
Rubiaceae		
Gardenia sp.[b]	Leaves, pith	EqGui (sp)
Nauclea diderrichii[b]	Fruit	Gabon, Lopé
Proterandia sp.	Leaves	Ndoki (sp)
	Fruit	Lopé
Psychotria sp.[b,c]	Leaves, pith	Utu
	Fruit	Lopé
Pavetta[b]	Leaves	Lopé
Rutaceae		
Fagara macrophylla[b]	Pith	EqGui (sp)
	Fruit, leaves	Utu (sp)
Sapotaceae		
Gambeya lacourtiana[b]	Fruit	EqGui, Gabon, Ndoki
Gambeya sp.	Fruit	EqGui (sp), Ndoki (sp), Lopé (sp)
Omphalocarpum procerum[b]	Fruit	EqGui (sp)
Sterculiaceae		
Cola sp.[b]	Fruit	Ndoki (spp)
Tiliaceae		
Duboscia virdiflora[b]	Fruit	Lopé (sp)

TABLE 13
(Continued)

Plant	Part eaten	Population
Verbenaceae		
Vitex doniana[b]	Fruit	Ndoki, Lopé
Violaceae		
Rinorea sp.	Fruit	Ndoki (sp)
	Leaves	Utu (sp)
Zingiberaceae		
Aframomum spp.[b]	Fruit, leaves, pith	EqGui, Gabon, N.Congo, Utu, Ndoki, Bwindi, Kahusi, Lopé, Itombwe, Campo

[a] Takamanda Reserve plant list from Thomas, 1988. Plant diet for gorilla populations based on the following: **Bwindi**, Sarmiento notes, Butynski personal commun., Schaller, 1963; **Campo**, Calvert, 1985; **EqGui** (Equatorial Guinea), Sabater Pi 1977; **Gabon**, Tutin and Fernandez 1985; **Itombwe**, Schaller 1963; **Kahusi**, Casmir, 1975, Goodall 1975, Schaller 1963; **Lopé**, Rogers et al. 1990; Williamson et al. 1990, Tutin et al., 1997; Ndoki, Nishihara, 1995, Remis, 1997; **N.Congo** (Northern Congo), Fay and Agnagna 1991; **Mt. T** (Mt. Tshiaberimu), Sarmiento and Butynski notes, Schaller 1963; Utu, Yamagiwa et al., 1994. Plants of the same genus but of a different species than those found in Takamanda are indicated by sp or spp in parentheses (when there is more than one species consumed) following the population known to consume it.

[b] Plants growing between 300 and 900 m.

[c] Plants growing between 900 and 1200 m.

diehli, although not all these characters may be present on any one given skull and *G. g. gorilla* may ocassionally show these characters independently. The pelage and postcrania are poorly known and no distinguishing differences were established.

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TABLE 14
Forest Primates of West Africa with Species or Subspecies Boundaries Roughly Coinciding with Sanaga River

	Distribution	
Genus	Northwest of Sanaga	Southeast of Sanaga
Galago	*G. alleni*	*G. gabonensis*
Arctocebus	*A. calabarensis*	*A. aureus*
Euoticus	*E. pallidus*	*E. elegantulus*
Colobus	—	*C. satanas*
Mandrillus	*M. leucophaeus*	*M. sphinx*
Miopithecus	—	*M. ougouensis*[a]
Cercopithecus	*C. erythrotis*	*C. cephus*
	—	*C. neglectus*
	C. nictitans martini	*C. n. nictitans*
	C. pogonias pogonias	*C. p. grayi*

[a] Nomen nudum used by Kingdon (1997).

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APPENDIX 1

Locality Coordinates

Afi mountains	6°20′N 9°3′E
Akwa	6°3′N 9°27′E
Assumbo	6°43′N 9°20′E
Ashunda	6°10′N 9°36′E
Badshama	6°10′N 9°31′E
Bafia	4°45′N 11°14′E
Bamba Mayombe	3°56′S 11°45′E
Bange	4°7′N 14°31′E
Basho	6°8′N 9°26′E
Boshi extension	6°25′N 9°20′E
Dakbe (=Takpe?)	6°6′N 9°20′E
Dikome Balue, (Rumpi hills)	4°55′N 9°25′E
Drill Ranch Camp	6°18′N 9°E
Edea	3°48′N 10°8′E
Efulen	2°49′N 10°39′E
Ikom	5°58′N 8°42′E
Ganga, CAR	4°59′N 16°52′E
Kadei	3°31′N 16°3′E
Kekpane hills	6°6′N 9°24′E
Makone river valley	6°5′ 9°20′E— 6°11′N 9°23′E
Mamfe	5°31′N 9°37′E
Matene	6°15′N 9°23′E
Mbe mountains	6°14′N 9°8′E
Mbilishi	6°7′N 9°25′E
Mbu	6°2′ 9°27′E
Metet	2°58′N 12°1′E
(=Mboke?)	4°19′N 12°37′E
Momie	5°36′N 14°13′E
Mone forest reserve	5°46′–6°3′N 9°22′–9°35′E
M’tene 853 m	6°15′N 9°1′E
Nola	3°30′N 16°5′E
Obonyi I	6°8′N 9°16′E
Obonyi II	6°7′N 9°11′E
Obonyi III	6°8′N 9°17′E
Obudu plateau	6°25′N 9°20′E
Obudu	6°37′N 9°8′E
Okuni district	7°N 9°E
Ossidinge[a]	5°55′N 9°5′E
Rumpi hills	4°45′–5°N 9°10′–9°25′E
Sakbayeme	4°02′N 10°34′E
Takpe[b] (=Dakbe?)	6°01′N 9°20′E
Takamanda	6°01′N 9°16′E
Takamanda forest reserve	5°59′N–6°26′N 9°11′–9°28′E
Tinta	6°17′N 9°30′E
Tinto	5°32′N 9°35′E
Umbaj [=Bumaji]	6°29′N 9°15′E

[a] Coordinates for Ossidinge taken from a map reproduced and printed by W. and A. K. Johnston limited, Edinburgh and London 1905, for the topographical section, General Staff, War Office.

[b] Takpe may represent the same locality as Dakbe.

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