Terrestrial Traits in the Hands and Feet of Gorillas

ESTEBAN E. SARMIENTO[1]

CONTENTS

[1] Research Associate, Department of Mammology, American Museum of Natural History; Department of General Anatomy, University of the Witwatersrand, South Africa.

ABSTRACT

Although it is well documented that gorillas are mainly terrestrial quadrupeds, traditionally their morphology has been interpreted as arboreal. Comparison of the anatomy and use of the hands and feet of gorillas with those of chimpanzees and humans enables their terrestrial features to be understood. Both the feet and hands of gorillas show proportional, muscular, and osseous specializations which can be related to their use in terrestrial behaviors. Although some of these features are shown to some degree in chimpanzees and serve both terrestrial and arboreal behaviors, among the great apes, most are unique to gorillas. Gorillas, however, share with humans many of their unique terrestrial features. Current dogma functionally assigns these terrestrial features in human hands and feet to tool use and bipedal behaviors, respectively. That many of these features are better developed in the more terrestrial mountain gorilla than in lowland gorillas argues against this interpretation. The appearance of these features in the human and gorilla is much more likely to have been associated with terrestrial quadrupedal behaviors. Whether the features shared by humans and gorillas are the result of parallelism or of a uniquely shared evolutionary history cannot be convincingly resolved without further anatomical and biochemical evidence.

INTRODUCTION

Locomotor specializations among living and fossil hominoids have traditionally been interpreted within a dichotomy of arboreal vs. terrestrial behaviors (Gregory, 1934; Keith, 1934; Avis, 1962; Tuttle, 1974; Lovejoy, 1981; Stern and Susman, 1983; Rose, 1984; Susman et al., 1984). According to these interpretations, bipedalism is argued to account for the most committed terrestrial specializations and brachiation for the most committed arboreal ones. Further studies on free-ranging behavior, however, have led to the realization that living hominoids practice a wide range of locomotor behaviors in which bipedalism, quadrupedalism, quadrumanous climbing, brachiation, leaping, and other types of behaviors all form part of the locomotor repertoire (Schaller, 1963, 1965; Reynolds and Reynolds, 1965; Rodman, 1973, 1984; Mackinnon, 1974; Fleagle, 1976; Rijksen, 1978; Susman et al., 1980, 1984; Dixson, 1981; Fossey, 1983; Sarmiento, 1985; Hunt, 1989). It is the frequency with which each of the behaviors is practiced, not the types of behaviors, which in part distinguishes the locomotor repertoires of each of the hominoid genera (Napier and Napier, 1967; Rose, 1984). Nevertheless, vertical climbing has shaped the hominoid musculoskeletal structure as a result of either its frequency in the locomotor repertoire or limiting selection during a shared evolutionary history (Kortlandt, 1968; Fleagle et al., 1981; Sarmiento, 1985, in press). Vertical climbing has been shown to be preadaptive to the most morphologically committed locomotor special-izations exhibited in hominoids, namely bipedalism and brachiation (Fleagle et al., 1981; Jungers and Stern, 1984; Cartmill, 1985).

Although it is well documented that gorillas are mainly terrestrial quadrupeds (Schaller, 1963; Kortlandt, 1968; Jones and Sabater Pi, 1971; Dixson, 1981; Fossey, 1983; Webber and Vedder, 1983; Tutin and Fernandez, 1984; Watts, 1983; Vedder, 1984), it is not surprising, given their hominoid ancestry, that their morphology is traditionally interpreted as arboreal (Huxley, 1863; Morton, 1922, 1924; Lewis, 1969, 1980a, 1980b). Gorillas must possess structural features that reflect their terrestrial quadrupedality. However, those terrestrial quadrupedal adaptations that arose after the divergence of gorillas from a common hominoid stock may not be so easy to discern. Because (a) quadrupedalism has had a long evolutionary influence on the mammalian hind limb and forelimb structure (Romer and Parsons, 1977), (b) it is a widespread behavior among all living mammals including hominoids (Hrdlicka, 1931; Oxnard, 1983; Nowack, 1991), (c) all primates have more or less retained the generalized upper and lower limb skeleton of the ancestral mammals (Le Gros Clark, 1971), and (d) the quadrupedal traits of gorillas are superimposed upon the distinctive hominoid morphology (Sarmiento, 1985, 1988), such difficulty in distinguishing the newly acquired quadrupedal adaptations from the ancestral primate and mammalian ones may be expected. Functional analysis of the cheiridial adaptations of gorillas (including those of the

TABLE 1
African Apes Observed in Captivity

Sex and age	Hours observed	Facility
Pan troglodytes		
2F, M, 2 juv.	20	PZG[a]
F	4	SFZG
F, M, 2 juv.	10	PrZ
Gorilla gorilla		
M, F, 2 juv.	20	NYZP
2M, 2F, 2 juv.	12	SFZG[a]
M, 2F	8	PrZ[a]

Abbreviations: PrZ = Pretoria Zoo, South Africa; PZG = Philadelphia Zoological Gardens; SFZG = San Francisco Zoological Gardens.

[a] Trees or supports of varying orientation and diameter were present in the enclosure at the time of observation.

TABLE 2
Hands and Feet of African Apes and Humans Dissected

Sex	Hands	Feet	Origin
Pan troglodytes			
M(C)	1	1	NYU
M(C)	1	1	NYU
Gorilla gorilla gorilla			
M(C)	1	1	AMNH
M(C)	1	1	AMNH
F(C)	1		PMNH
Gorilla gorilla beringei			
F		1	AMNH
Homo sapiens			
6M	6	6	DGWU
6F	6	6	DGWU

Abbreviations: (C) = captive specimen; AMNH = American Museum of Natural History; PMNH = Peabody Museum of Natural History, Yale; NYU = New York University; DGWU = Department of General Anatomy, University of the Witwatersrand.

more terrestrial mountain gorilla), contrasted to those of humans and chimpanzees, can be used clarify what quadrupedal terrestrial adaptations, if any, they possess. Because the cheiridia directly interact with the environment, their morphology can be expected directly to reflect environmental constraints.

MATERIALS AND METHODS

In order to associate anatomy with function, both morphological and behavioral data must be considered (Fleagle, 1976; Sarmiento, 1985). In the case of the cheiridia, their use and the range of movement and posture that their joints are maintained in during such use are necessary for relating them to anatomy (Prost, 1965; Rose, 1974; Sarmiento, 1985, 1988). Through mechanical analyses, described anatomical differences can be tested to see if they correspond to, or are beneficial for, observed behaviors (Sarmiento, 1985, 1988).

Descriptions of the use and posture of the wrist joint in gorillas and chimpanzees comes from observations of captive specimens. Photographs of cheiridial postures were recorded on 35 mm photographic film (Sarmiento, 1988). The observation time spent viewing gorilla and chimpanzee cheiridial use and postures and the institutions at which each was observed are summarized in table 1. Given the captive environments in zoos,

it was impossible to distinguish with certainty differences in the use of the cheiridia in highland and lowland gorillas. Therefore, the described behavior applies to the genus *Gorilla*.

Anatomical features of the hands and feet of African apes and humans were determined from dissections of the specimens listed in table 2. Dissections concentrated on unique muscular features of gorillas (Huxley, 1864; Straus, 1930; Raven, 1950; Kohlbrugge, 1897; Pira, 1914; Sommer, 1907; Bischoff, 1880). If variation exists in muscular features, approximate frequency of occurrence for each trait as surveyed from the literature is provided. Results of muscular dissections are summarized in table 3.

Skeletal differences in the hands and feet were quantified to reflect mechanical concerns. In the foot, these include the orientation of joint surfaces, maximum length of the metatarsals, the length of the main pedal lever arms (Schultz, 1963), and the contribution by the various foot segments to these lever arm lengths. Lengths of the pedal lever arms and of the various foot segments which contributed to them are given in figures 1 and 2. Lever arms are analyzed bivariately relative to metatarsal foot length (figs. 3–15). A

goniometer was used to measure talar torsion, torsion of the first metatarsal, and the relative orientation of the articular surfaces of the entocuneiform. Methods for measurements of torsion and of pedal lever arms lengths are given in figure 1 and the results are summarized in tables 4, 6, 7 and 8. The angles of the cuboid were measured through triangulation. Measurements used to arrive at cuboid joint orientation are given in figure 2 and the results are summarized in table 5.

Hand measurements considered in discussion include lever arm lengths of the flexor carpi ulnaris, relative weight of the carpal bones, and the maximum length of the metacarpals. These data and methods for measurements are described in Sarmiento (1985, 1988). Relative length of the 1st metacarpal was analyzed bivariately relative to 3rd metacarpal length (see fig. 16 and table 9). Weight of the trapezoid and pisiform are presented as a proportion of the total carpal weight (table 10).

Slope and y intercept applying a least squares linear regression were calculated for all bivariate plots using a SAS statistical package (figs. 3–16). All bivariate comparisons were also formulated into indices for which mean, range of variation, and standard deviation are given in tables 6–9.

Osseous preparations of the hands and feet were also examined for unique anatomy. In the case of fusion of the radial sesamoid, these data are presented as a frequency of occurrence for the considered groups (tables 11, 12) with T-scores gauging range of error in the mean. In the other cases, only descriptive differences of the relevant morphology are provided. Metric quantification of these traits or a survey of their occurrence awaits further studies.

In addition to skeletal measurements and observations, absolute dimensions of the hands and feet and the body weight of male and female great apes and humans were also considered. These included the length of the hand and foot, the proximal extent of the cleft of the big toe, and the distal extent of the sole of the foot. Because a representative number of specimens for some groups was lacking, the author relies partly on data from the literature. The distal extent of the cleft of the foot, however, was measured in 30 humans

and 2 chimpanzees (table 13) after methods described in Schultz (1929). Natural log-on-log graphs of hand and foot length and the F14 vs. the body weight were plotted for great apes and humans. Considering hominoid dimorphism in body weight, males and females were plotted separately. These data are summarized in table 14 and figures 17–19.

Discussion and mechanical analyses focused mainly on the observed differences between humans, gorillas, and chimpanzees. The discussion is aimed at relating observed differences to hand and foot use in both an arboreal and terrestrial context.

TERRESTRIAL BEHAVIOR

HAND

Gorillas are mainly quadrupedal when moving on the ground. The hand is used in the knuckle-walking postures characteristic of African apes (Tuttle, 1967, 1969). However, gorilla knuckle-walking differs from that of chimpanzees in a number of respects. Unlike chimpanzees, the metacarpophalangeal joints of gorillas are hyperextended, so that the dorsum of the proximal phalanges approximates a right angle to the metacarpals. The dorsal surfaces of the middle phalanges of digits 2–5 all contact the substrate and transmit weight to it (Sarmiento, 1985; Inouye, 1992). Additionally, the volar surface of the hand is directed posteriorly so that the mediolateral axis of the wrist joint is approximately perpendicular to the direction of forward motion. This approximation is variable; some gorillas show a more anterior projection of the radial side of the hand than others, but none show the sagittal orientation of the wrist joint's mediolateral axis seen in chimpanzees. Because the elbow joint of gorillas is usually carried with the olecranon process facing posterolaterally during knuckle-walking (Tuttle et al., 1983), these variations in wrist posture result from varying degrees of forearm pronation. As in all knuckle-walking, the wrist is in a neutral position of flexion-extension and abduction-adduction. The long axes of the metacarpals and forearm are all parallel and nearly collinear.

In gorillas there is apparently very little movement of the wrist joint during knuckle-walking. The forearm becomes maximally

TABLE 3

Unique Muscular Features, Hands and Feet of African Apes and Humans as Reported from Dissections and Surveyed from the Literature[a]

	P. troglodytes	*G. gorilla*	*H. sapiens*
Hand			
1) Palmaris longus[b]			
a) Absent	0 (1.5)	0 (7)	1
b) Present	2 (15.5)	2 (4)	11
2) Flexor pollicus longus tendon			
a) Fully absent	(14)	(5)	
Originating from:			
b) FDP	2 (22)	1 (4)	0
c) Wrist or distal radius	0 (10)	2 (7)	0
d) Its own muscular bundle in forearm			12
3) Extensor pollicis brevis[c]			
a) Absent	2 (10)	2 (8)	0
b) Inserts into proximal pollical phalanx & extensor expansion	0	1 (9)	12
4) Palmaris brevis			
a) Absent	2 (2)	0 (2)	0
b) Present	0 (7)	2 (7)	12
5) Contrahentes			
a) Absent	(?)	2 (7)	12
b) To digits IV & V	1 (7)	0	0
6) 1st palmar interossei			
a) Absent	2 (5)	2 (10)	2
b) Present	(2)	(1)	10
Foot			
7) Peroneus tertius			
a) Absent	2 (7)	2 (13)	0
b) Present[d]	0 (1)	1 (6)	12
8) Plantaris longus[e]			
a) Absent	0 (32)	3 (25)	0
b) Present	2 (24)		12
9) Flexor fibularis, distribution of tendons to digits,			
a) I, III, IV	2 (13)	3 (7)	
b) I, III, IV, V		(1)	
c) I, II, III, IV		(1)	
d) I, II, III, IV, V		(1)	1
e) I, II, III			6
f) I, II			5
g) I, IV	(1)		
h) I, V		(1)	
10) Flexor tibilais, distribution of tendons to digits,			
a) II, V	2 (10)	3 (8)	
b) V		(1)	
c) II, III, IV, V	(2)	(4)	10

TABLE 3—(*Continued*)

	P. troglodytes	G. gorilla	H. sapiens
d) I, II, III, IV		(1)	
e) I, II, III, IV, V		(1)	2
f) II, III, IV	(2)		
11) Plantar aponeurosis			
a) Weakly developed	2 (8)		
b) Well developed		3 (10)	12
12) Flexor digitorum brevis, distribution of tendons from superficial head,			
a) II, III	(9)	1 (12)	
b) II, III, IV	2 (2)	2 (2)	4
c) III			
d) II, III, IV, V			8
distribution of tendons from deep head,			
a) IV, V	1 (4)	(9)	3
b) III, IV	(2)	3 (2)	
c) III, IV, V	1 (5)	(2)	
d) II, IV	(1)		
13) Ossi metatarsi quinti			
a) Absent	(?)	(6)	10
b) Present[d]	2 (5)	3 (5)	1
14) Quadratus plantae[f]			
a) Absent	1 (7)	2 (8)	
b) Present	1 (7)	1 (5)	12
15) Adductor hallucis transversus,			
a) Absent as a separate muscle	2 (3)		
Originating from digit:			
b) II–III	(3)	(3)	
c) II–IV	(1)	2 (5)	
d) II–V		1 (2)	12
e) III–V		(1)	
16) Contrahentes,			
a) To digit V	2 (6)	1 (2?)	2
b) Fully absent[d]	(?)	2 (9)	10
17) Interossei adduction–abduction axis through,			
a) 3rd digit	2 (9)	(4)	
b) 2nd digit[d]	(1)	3 (8)	12

All the other muscles with origins and/or insertions on the hands and feet not included in this table showed no consistent gross differences between humans, gorillas, and chimpanzees.

[a] Number of specimens in this study exhibiting condition are placed in column below their respective taxon. Number of specimens from literature survey exhibiting condition appear in parentheses.

[b] In a literature survey Keith (1899) found it present in 4 out of 11 gorillas, and 9 out of 12 chimpanzees.

[c] Keith (1899) found it present in 1 out of 20 chimpanzees and 4 out of 9 gorillas.

[d] Character was consistently present in all mountain gorillas.

[e] Keith (1899) found it present in 12 out of 12 gorillas and 25 out of 32 chimpanzees.

[f] Keith (1899) found it present in 6 out of 10 gorillas and 6 out of 11 chimpanzees.

Notes

(1) Kohlbrugge, 1897; Raven, 1950.

(2) Straus, 1942.

pronated as it enters the maximum weight-bearing part of the stance phase. Slight adduction and some flexion of the wrist joint occurs at the beginning of the swing phase. In this regard, gorillas lack the adduction-abduction movement of the wrist seen in chimpanzees.

Occasionally gorilla knuckle-walking involves a wider range of forearm pronation and supination. For instance, when the weight-bearing shoulder joint is locked or braced, the arm is rotated laterally and the forearm is markedly pronated. Moreover, when running quadrupedally, gorillas may pivot around the stationary hand and radius, abruptly changing or reversing their direction of travel. However, the forces that are applied at the wrist joint during such pivoting behaviors are limited by the frictional force between the digital pads and substrate (Sarmiento, 1988).

FOOT

During terrestrial behaviors, either bipedal or quadrupedal gorillas employ plantigrade foot postures. The sole of the foot underlying the tarsals, metatarsal, and phalangeal bones comes into contact with the substrate. The tibiotalar joint is markedly dorsiflexed so that the tibia may form an acute angle ($<90°$) with the dorsum of the foot, in contrast to this joint position in semidigitigrade or fully digitigrade animals. Because gorillas lack a fixed longitudinal arch, the midtarsus makes contact with the substrate in the region of the anterior plantar surface of the calcaneus, the cuboid, and the base of the 5th metatarsal on the lateral side, and the navicular tuberosity, the 1st cuneiform and the base of the 1st metatarsal on the medial side. The central portion of the sole underlying the 2nd and 3rd cuneiforms and the base of the 2nd and 3rd metatarsals does not consistently come into contact with the substrate. This was verified by footprints made by wet feet on a dry cement floor. In this regard, gorillas show some formation of the transverse tarsal arch. Although lacking a fixed longitudinal arch, gorillas, in contrast to chimpanzees, show very little dorsiflexion at the distal tarsal joint or

---

←

(3) Bischoff, 1870; Champneys, 1872; Duvernoy, 1855; Fick, 1925; Hartmann, 1886; Hepburn, 1892; Humphrey, 1867; Huxley, 1964; Langer, 1879; Michaelis, 1903.

(4) Bischoff, 1870; Champneys, 1872; Deniker, 1885; Duvernoy, 1855; Fick, 1925; Hepburn, 1892; Hofer, 1892; Michaelis, 1903; Pira, 1914; Raven, 1950; Sommer, 1907; Sonntag, 1923; Vrolik, 1841; Wilder, 1862; Wyman, 1855.

(5) Bischoff, 1870, 1880; Deniker, 1885; Fick, 1925; Forster, 1917; Hartmann, 1886; Hepburn, 1892; Lessertiseur, 1958; Pira, 1914; Raven, 1950; Sommer, 1907; Sonntag, 1923.

(6) Bischoff, 1870, 1880; Chapman, 1879; Deniker, 1885; Duvernoy, 1855; Fick, 1925; Forster, 1917; Hartmann, 1886; Hepburn, 1892; Huxley, 1864; Lewis, 1965; Macalister, 1874; Pira, 1914; Raven, 1950; Sommer, 1907; Sonntag, 1923; Symington, 1889.

(7) Bischoff, 1870; Hecker, 1922; Hepburn, 1892; Humphrey, 1867; Michaelis, 1903; Raven, 1950; Sonntag, 1923; Straus, 1930; Sutton, 1889.

(8) Loth, 1931.

(9 & 10) Kohlbrugge, 1897; Straus, 1930.

(11) Bischoff, 1870, 1880; Champneys, 1872; Duvernoy, 1855; Gratiolet and Alix, 1866; Hartmann, 1886; Hepburn, 1892; Huxley, 1864; Pira, 1914; Raven, 1950; Sommer, 1907; Sonntag, 1923, 1924; Straus, 1930; Symington, 1889.

(12) Kohlbrugge, 1897; Straus, 1930.

(13) Bischoff, 1870, 1880; Hartmann, 1886; Hepburn, 1892; Huxley, 1864; Kohlbrugge, 1897; Raven, 1950; Straus, 1930.

(14) Lewis, 1962; Raven, 1950; Straus, 1930.

(15) Bischoff, 1870, 1880; Deniker, 1885; Duvernoy, 1855; Fick, 1925; Hepburn, 1892; Huxley, 1864; Macalister, 1871, 1874; Michaelis, 1903; Pira, 1914; Raven, 1950; Sommer, 1907; Sonntag, 1923; Straus, 1930; Sutton, 1889; Traill, 1821.

(16) Bischoff, 1870; Champneys, 1872; Gratiolet and Alix, 1866; Hartmann, 1886; Hepburn, 1892; Macalister 1871, 1874; Raven, 1950; Sommer, 1907; Sonntag, 1923; Straus, 1930.

(17) Bischoff, 1870, 1880; Champneys, 1872; Gratoliet and Alix, 1866; Hartmann, 1886; Hepburn, 1892; Humphrey, 1867; Sonntag, 1923; Straus, 1930; Sutton, 1889.
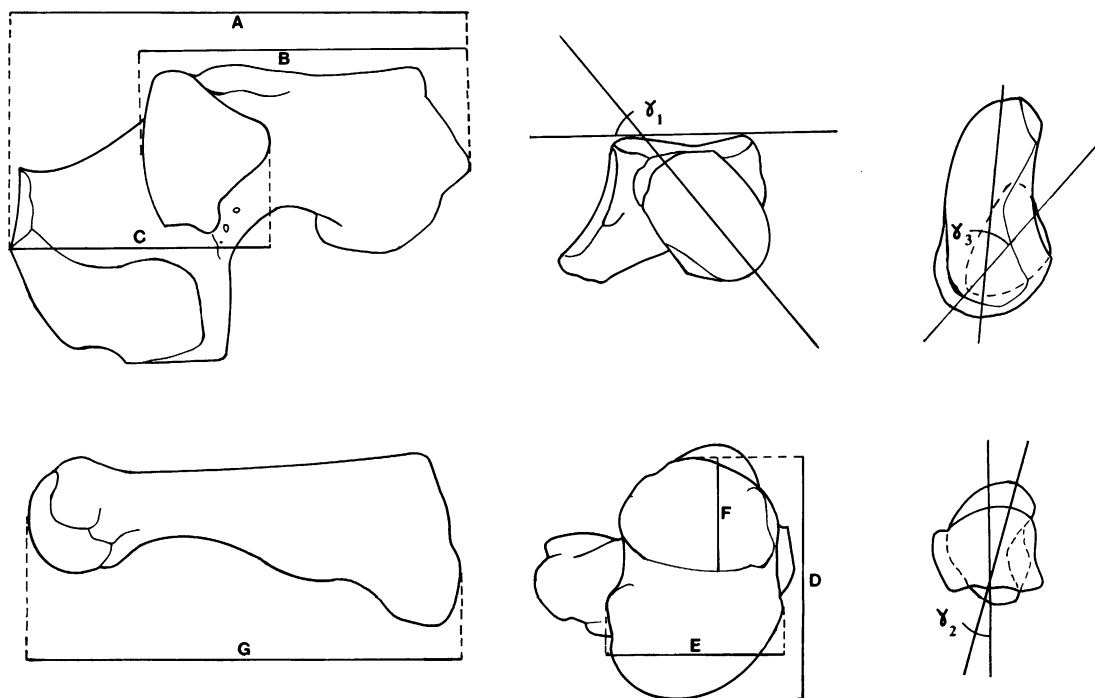
Fig. 1. Linear and angular measurements taken on calcaneus, talus, entocuneiform, and metatarsals. (A) maximum length of calcaneus, (B) distance from tuber to most distal (anterior) point on posterior talocalcaneal articulation, (C) distance from cuboid articulation to most proximal (posterior) point on posterior talocalcaneal articulation, (D) maximum dorsoplantar length of tuber calcaneus (TCPD), (E) maximum mediolateral width of tuber calcaneus (TCML), (F) distance from superior point on tuber calcaneus to most inferior point of insertion of triceps surae tendon (TSTH), (G) maximum length of metatarsal and metacarpals as illustrated on a gorilla 1st metatarsal (1st metatarsal length = MT1L, 3rd metatarsal length = MT3L, 1st metacarpal length = MC1L, 3rd metacarpal length = MC3L). γ_1 = angle of talar torsion, γ_2 = angle of 1st metatarsal torsion, γ_3 = angle of entocuneiform torsion.

The following formulas, $(A + B - C)/2$ and $(A + C - B)/2$, were used to calculate the lever length of the triceps surae (TRIL) and the length of that part of the calcaneus anterior to the posterior talocalcaneal joint axis (CALCL), respectively. The addition of CALCL to Ca4thmt (see fig. 2) was used to arrive at the anterior tarsal length (ANTARS). Metatarsal foot length (F14) was arrived at through the addition of the maximum lengths of the calcaneus (A) and the 4th metatarsal, and the Ca4thmt.

Axes for talar head, base of 1st metatarsal, and proximal and distal articular surfaces of entocuneiform were arrived at by bisecting their respective articular surfaces. Axis for 1st metatarsal head represents main plane of movement of metatarsophalangeal joint as could be judged by notched articular surface. For talar trochlea, axis is in frontal plane and rested on most superior points of trochlea's medial and lateral borders.

at the tarsometatarsal joints. Nevertheless, at midstance, the sole overlying the plantar tubercle of the calcaneus is off the substrate while the midtarsus apparently still contacts the substrate.

During the stance phase the metatarsophalangeal joints 2 to 5 are held in the neutral position, but during toe-off the proximal phalanges are dorsiflexed on the metatarsus. The long axes of the lateral four toes are set so as to deviate laterally from the long axis of the foot. The degree of lateral deviation of the toes is offset somewhat by a slight degree of flexion of the interphalangeal joints, and a rotated set to the metatarsophalangeal joint, so that the plantar surface of the toes faces somewhat medially. The degree of medial orientation of the lateral toes' plantar surface increases progressively, from the 2nd to the 5th toe. The hallux is somewhat abducted

TABLE 4
Mean ($\bar{x}$), Range of Variation, and Standard Deviation of Talar Head Torsion (THT), 1st Metatarsal Torsion (1MTT), and Angle Between Entocuneiform's Navicular and Distal Facets (AENT)[a]

	THT	1MTT	AENT
Pan troglodytes (N = 21)			
$\bar{x}$	22.4	35.9	60.1
Range of variation	7–31	20–50	42–75
Standard error	5.9	9.0	8.2
Gorilla g. gorilla (N = 18)			
$\bar{x}$	19.4	31.3	61.5
Range of variation	7–34	12–43	79–40
Standard error	7.5	8.11	11.1
Gorilla g. beringei (N = 11)			
$\bar{x}$	29.9	—	—
Range of variation	22–36	—	—
Standard error	4.6	—	—
Homo sapiens (N = 30)			
$\bar{x}$	35.8	9.2	45.9
Range of variation	48–20	20–0	62–30
Standard deviation	7.6	5.8	8.1

[a] Numbers (N) of individual specimens measured in parentheses.

and rotated so that its plantar surface faces laterally. As for the lateral four toes, the metatarsophalangeal and interphalangeal joints may be held slightly flexed.

During terrestrial behaviors the long axis of the foot is held more or less along the direction of travel, although at the beginning of the stance phase it deviates laterally and the foot is somewhat supinated. Toward the end of the stance phase, extension at the knee and medial rotation of the leg pronates the foot and orients it so its long axis is medial to the direction of movement. At this time, the metatarsophalangeal and interphalangeal joints become maximally extended and the plantar surfaces and digital pads of the lateral four toes make contact with the substrate. None of the gorillas observed exhibited the curled under toe postures characteristic of chimpanzees and Bornean orangutans, in which the dorsum of the middle and distal phalanges of the lateral four toes contacts the substrate (MacKinnon, 1974; Sarmiento, 1985). Although the rotated set of the 4th and 5th toes of gorillas causes the corresponding phalanges to make contact on their lateral surface, the interphalangeal joints of these toes were always held more or less extended—the long bone axes of the proximal, middle, and distal phalanges nearly aligned. Similarly, the rotated set of the gorilla hallux causes the medial surface of its metatarsal and proximal phalanges to make contact with the substrate. However, pronation of the foot, culminating at toe-off, together with considerable hyperextension of the metatarsophalangeal joint places the big toe's distal digital pad in full contact with the substrate. The metatarsophalangeal joints of the lateral four toes do not undergo as marked a degree of extension as does that of the hallux. In this regard, the metatarsophalangeal joint of the 5th toe exhibits very little extension at toe-off and that of the 2nd the most extension.

TABLE 5
Mean ($\bar{x}$), Range, and Standard Deviation (SD) of Angles of Cuboid
Abbreviations as in fig. 2[a]

	PM		DL		DM		PL	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Pan troglodytes (N = 22)	64.0	3.51	88.1	6.47	87.5	5.70	120	9.92
Range of variation	59.4–76.8		74.7–105.1		73.8–95.3		104–147	
G. g. gorilla (N = 18)	61.5	2.34	80.5	6.14	87.5	5.17	131	8.05
Range of variation	58.0–65.9		67.5–91.4		77.5–94.4		120–154	
G. g. beringei (N = 3)	63.9	0.384	86.0	2.12	84.7	0.277	125	2.73
Range of variation	63.3–64.2		83.0–88.0		84.4–85.0		123–129	
Homo sapiens (N = 31)	68.0	3.99	99.4	6.22	80.0	4.33	112	6.59
Range of variation	61.0–75.8		86.6–116.6		70.3–90.5		100–129	

[a] Numbers (N) of individual specimens measured in parentheses.
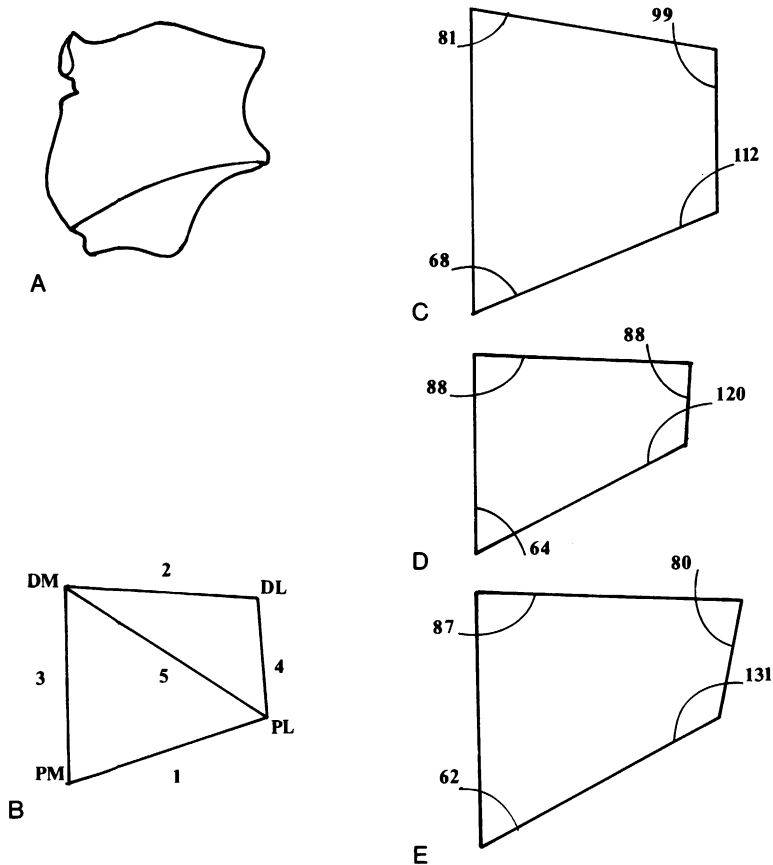
Fig. 2. Five linear measurements used to arrive at angles of cuboid (**B**) as illustrated on chimpanzee cuboid (**A**) and proportional representation of average values of these measurements and corresponding angles in humans (**C**), chimpanzees (**D**), and gorillas (**E**). 1 = maximum width of calcaneal articulation, 2 = maximum width of cuboid's distal articulation, 3 = distance from most medial point of calcaneal articulation to most medial point of distal articulation (abbreviated ca4thmt in text), 4 = distance from most lateral point of calcaneal articulation to most lateral point on distal articulation, 5 = distance from most lateral point of calcaneal articulation to most medial point of distal articulation. PL = proximolateral angle, PM = proximomedial angle, DL = distolateral angle, and DM = distomedial angle. Pythagorean theory was used to calculate angles (see Sarmiento, 1985, 1988).

ARBOREAL BEHAVIOR

HAND

Adult gorillas climb trees less frequently than do other great apes (Schaller, 1963; Reynolds and Reynolds, 1965; MacKinnon, 1974; Hunt, 1989; Rodman, 1984). Less arboreal than lowland gorillas, mountain gorillas tend to inhabit areas without trees where climbing is not a possibility (Schaller, 1963; Jones and Sabater Pi, 1971; Fossey, 1983; Watts, 1983; Vedder, 1984). When gorillas do climb trees, their size restricts them to supports of relatively large diameters (Schaller, 1963). None of the adult males observed were seen in trees, although females and some juveniles did occasionally climb trees. In all observed cases of arboreal behavior, captive gorillas occupied the large lateral branches close to the main trunk of the tree. Although gorillas may use phalangeal hook grasps when they pull branches toward them in foraging, this grasp was not used in hanging below horizontal supports. On these supports, the wrist is flexed, so that the palm of the hand can wrap around the opposite side of the support.
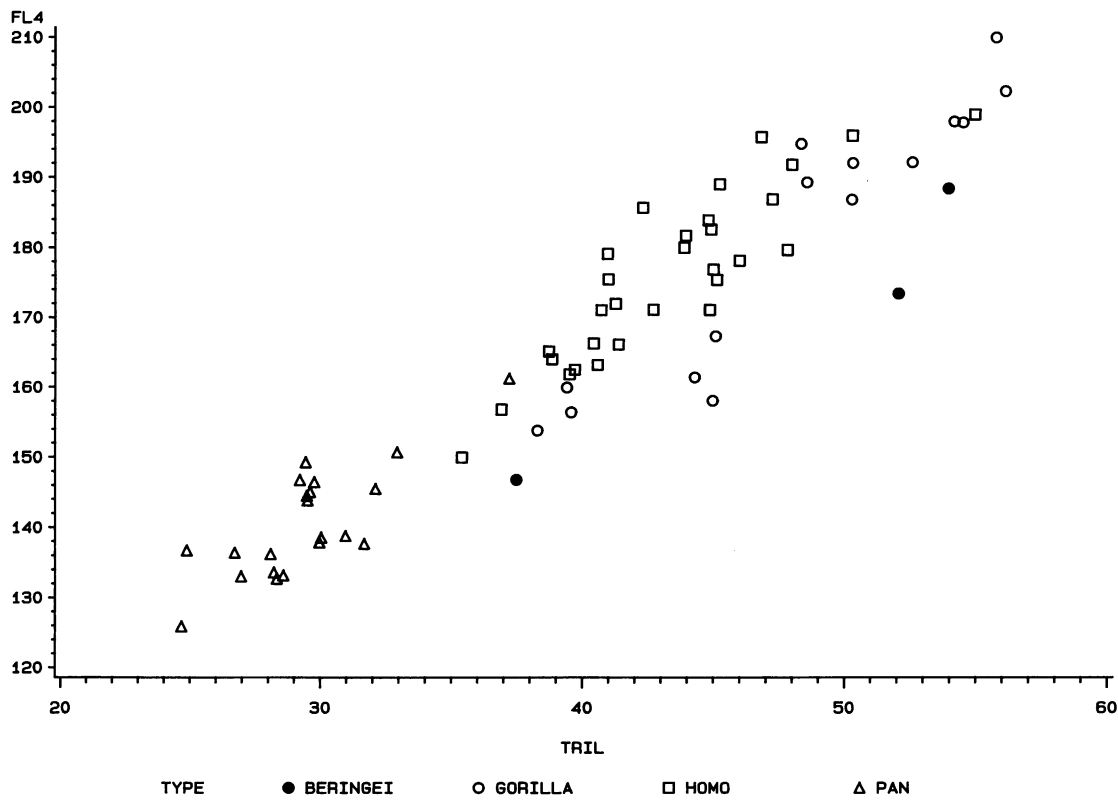
Fig. 3. The lever length of triceps surae (TRIL) vs. metatarsal foot length (FL4) in lowland gorillas (GORILLA, slope = 3.03, y intcpt. = 35.4, r^2 = 0.89), mountain gorillas (BERINGEI, slope = 2.26, y intcpt. = 61.6, adj. r^2 = 0.87), humans (HOMO, slope = 2.59, y intcpt. = 63.5, r^2 = 0.79), and chimpanzees (PAN, slope = 2.30, y intcpt. = 73.0, adj. r^2 = 0.63). Length in millimeters; see table 6 for number of specimens sampled.

The thumb is held adjacent to the fingers and is not used in opposition. Usually, given the size of the supports used, there is very little flexion of the metacarpophalangeal and interphalangeal joints.

When the animal climbs large vertical supports, the wrist joints are usually slightly flexed. Together with the other joints of the hand, they form an arc that coincides with the curvature of the support. On smaller-diameter vertical supports—those that the upper limbs can wrap fully around—the wrist may be flexed more, so that the hand can wrap around the opposite side of the support. Since the forearm is held with its long axis nearly perpendicular to the length of the support, there is only a slight degree of wrist adduction. Because supports climbed are usually of considerable diameter, the forearm is held in varying degrees of supination.

FOOT

Although gorillas may use a hook or opposable toe grasp to hold or manipulate objects with their feet, these grasps were never used for hanging below supports. In fact, no adult or juvenile gorilla observed used the foot for suspension. In this regard, when moving in trees the grasping capabilities of the foot are mostly employed in vertical climbing or walking along and between branches.

Gorillas vary the orientation of the foot's long axis, contacting the support with either the entire sole of the foot or with just that part distal to the tarsus, depending on the size of vertical supports climbed. On large-diameter supports, the long axis of the foot is oriented horizontally around the support's circumference. Dorsiflexion of the subtalar
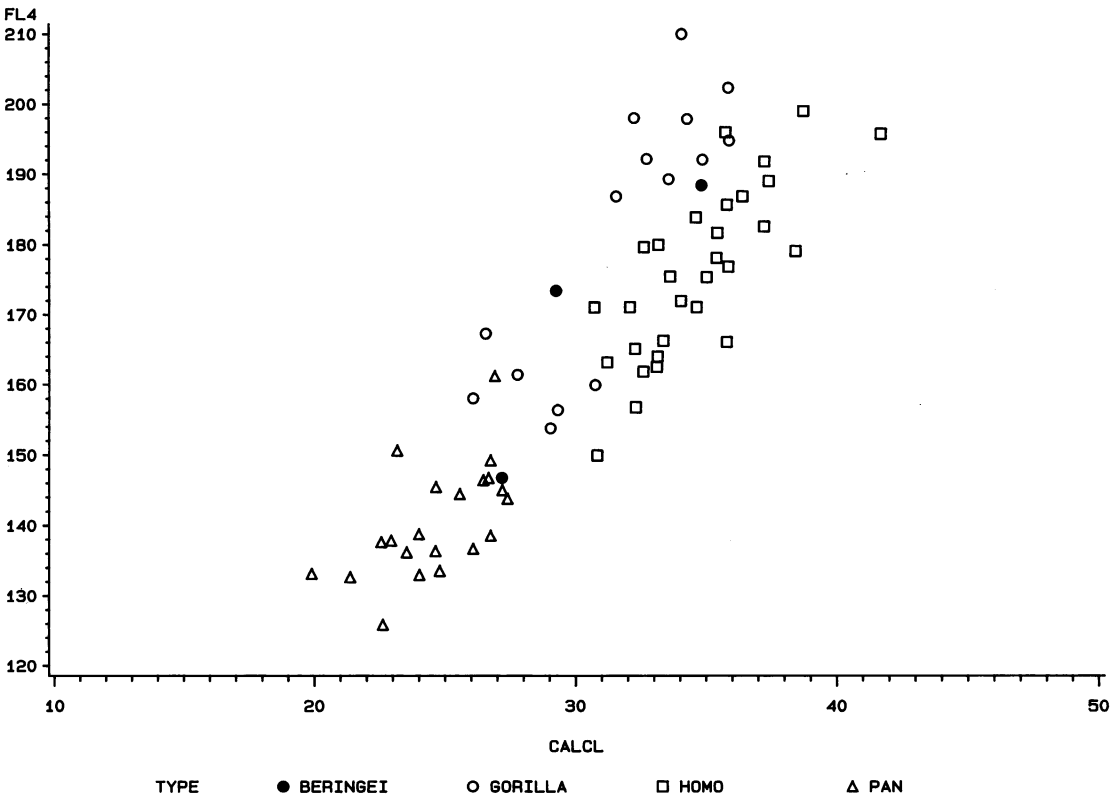
Fig. 4. The anterior lever arm of calcaneus (CALCL) vs. metatarsal foot length (FL4) in lowland gorillas (GORILLA, slope = 5.06, y intcpt. = 21.3, r^2 = 0.73), mountain gorillas (BERINGEI, slope = 4.87, y intcpt. = 21.4, adj. r^2 = 0.67), humans (HOMO, slope = 3.71, y intcpt. = 47.5, r^2 = 0.62), and chimpanzees (PAN, slope = 2.27, y intcpt. = 84.6, r^2 = 0.36). Length in millimeters; see table 6 for number of specimens sampled.

joint and plantar flexion of the other pedal joints conforms the sole of the foot to the curvature of the support. Because the supports climbed by gorillas are usually large relative to their foot size, there is very little flexion of the metatarsophalangeal and interphalangeal joints. With decreases in the radius of curvature of vertical supports, the foot's long axis progressively deviates from a horizontal to a vertical alignment relative to the support's circumference. Such changes in orientation with changes in support diameter present the foot's long axis with a more or less constant degree of support curvature through a wide range of support diameters. The preferred curvature which gorilla's pedal joints maintain is probably one which places them in a position optimal for applying a normal force. On support diameters larger than 20 cm, the big toe is always held alongside the lateral toes and is not op-

posed. On support diameters less than 10 cm, on the other hand, the toe is always held in opposition. When the animal climbs vertically on such small support diameters, the heel of the foot is held away from the support, and only that portion of the sole anterior to the tibiotalar joint makes contact.

Regardless of the size of supports climbed, at the beginning of the stance phase the ankle joint is dorsiflexed. The big toe or second toe is the most superior contact point of the foot. At the end of the stance phase the ankle joint becomes somewhat plantarflexed and supinated, since the leg approaches a parallel to the vertical support. At this time the toe is positioned inferior to the ankle joint. On support diameters smaller than 20 cm the sole of the foot overlying the tarsus and metatarsus is always pulled away from the support, especially toward the end of the stance phase. On such small support diameters, when using
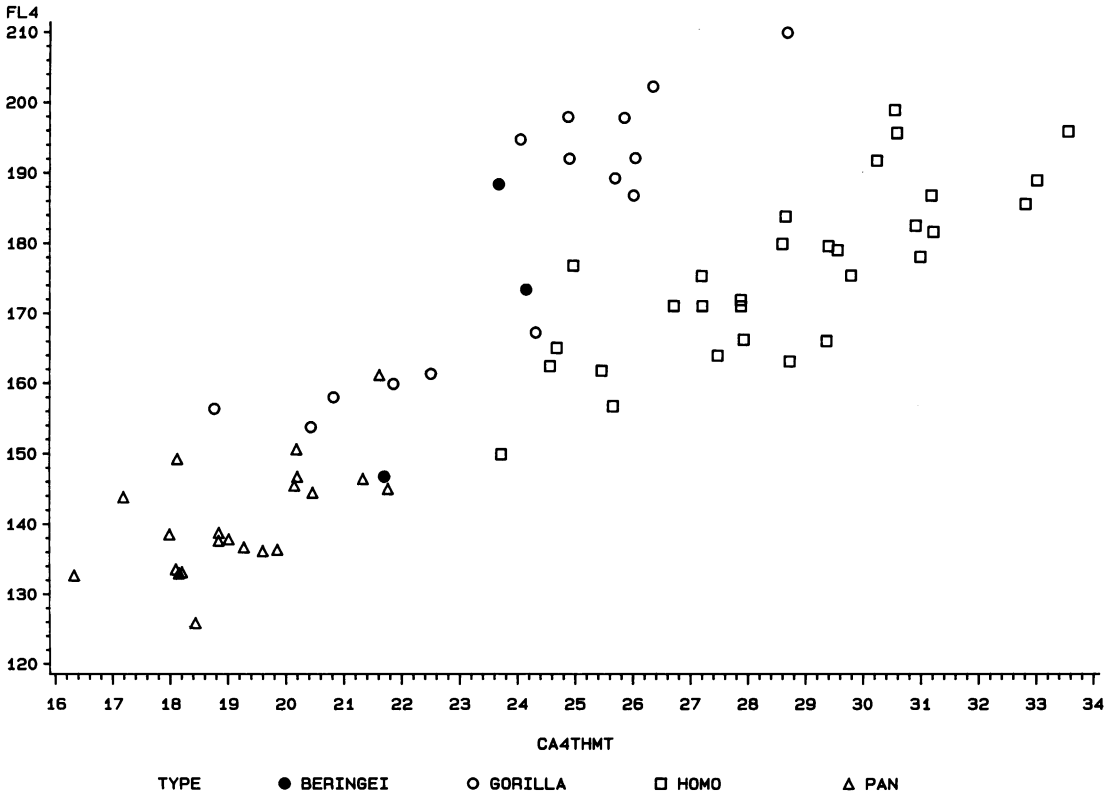
Fig. 5. The proximodistal length of medial side of the cuboid (CA4THMT) vs. metatarsal foot length (FL4) in lowland gorillas (GORILLA, slope = 6.56, y intcpt. = 23.4, r^2 = 0.81), mountain gorillas (BERINGEI, slope = 13.8, y intcpt. = −151, adj. r^2 = 0.46), humans (HOMO, slope = 3.71, y intcpt. = 69.5, r^2 = 0.63), and chimpanzees (PAN, slope = 3.41, y intcpt. = 75.0, r^2 = 0.38). Length in millimeters; see table 6 for number of specimens sampled.

an opposable toe grasp, the metatarsophalangeal joints of the 2nd and 1st toes become extended at the end of the stance phase.

When walking along horizontal branches, gorillas consistently use an opposable toe grasp. The degree of flexion of the pedal joints and the degree of hallucial opposability depend on the diameter of the support. On very large support diameters there is very little flexion of the metatarsophalangeal and interphalangeal joints and there is little functional opposability of the toe. With decrease in support diameter there is a greater degree of opposability and flexion of the toe joints. Only on relatively small support diameters is the big toe diametrically opposed to the other toes. Although opposable toe postures are maintained, the effectiveness of a grasp subtending a small central angle as seen on support diameters large enough or larger than that needed to hold the gorilla's weight

steadily is questionable (Sarmiento, 1985). In all other respects, foot orientation and joint postures throughout the stance phase when gorillas walk along horizontal supports are similar to those exhibited in terrestrial behaviors. Gorillas never show the splayed-out foot and wrap-around toe postures of chimpanzees (Tuttle, 1970) or orangutans (Sarmiento, 1985) when walking along horizontal supports.

MUSCULATURE

HAND

Extensor pollicis brevis muscle (EPB), abductor pollicis longus muscle (APL), and radial sesamoid

As summarized in table 3 there are a number of muscular similarities in the hands of gorillas and humans not seen in other hom-
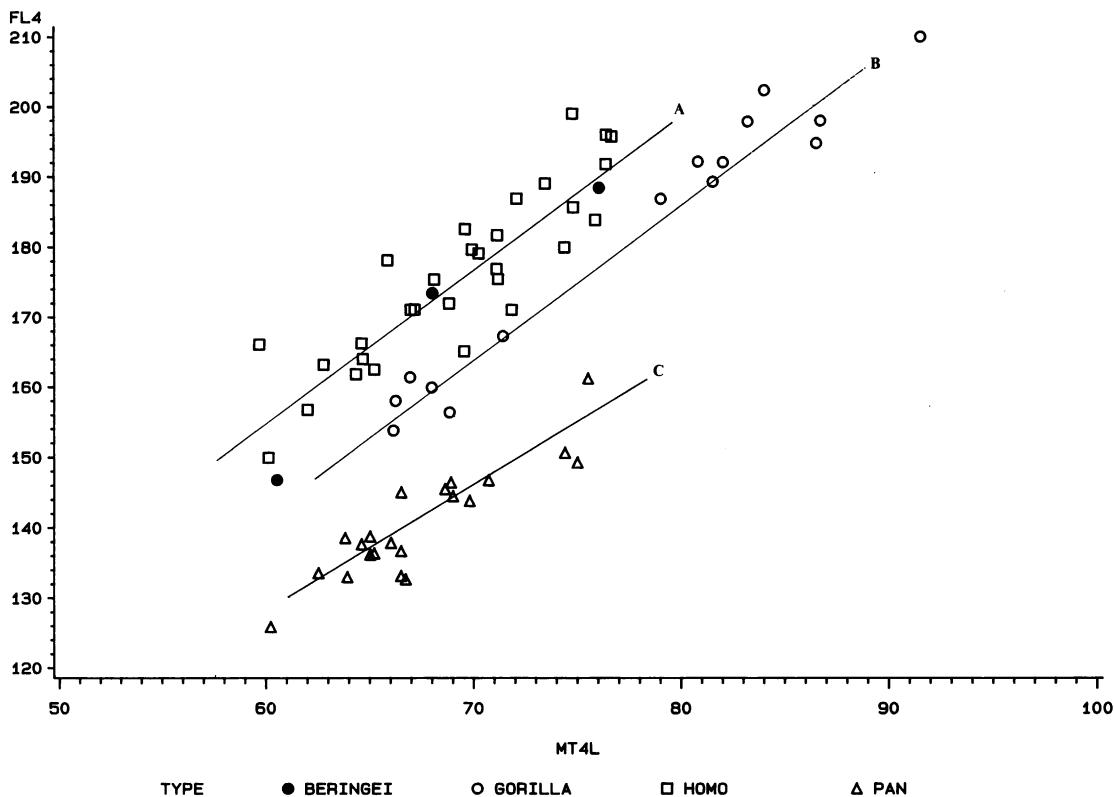
Fig. 6. Length of 4th metatarsal (MT41) vs. metatarsal foot length (FL4) in lowland gorillas (GO-RILLA B, slope = 2.19, y intcpt. = 11.3, r^2 = 0.96), mountain gorillas (BERINGEI, slope = 2.68, y intcpt. = −12.9, adj. r^2 = 0.94), humans (HOMO A, slope = 2.17, y intcpt. = 25.4, r^2 = 0.78), and chimpanzees (PAN C, slope = 1.77, y intcpt. = 21.8, r^2 = 0.80). Length in millimeters; see table 6 for number of specimens sampled.

inoids. One of these is the trend among go-rillas to differentiate the distal fibers of the APL into an EPB and hence approximate the human condition. In gorillas the differenti-ation of an EPB may be related to using the APL as a flexor of the carpal joint. Separation of the two muscles allows abduction and ex-tension of the pollex to occur separately from abduction (radial deviation) and flexion of the wrist (Sarmiento, 1985). Because of the orientation of the sellar articular axis of the trapezoid metacarpal joint in relation to the plane of the palm (fig. 20; see also Napier, 1961), flexion of the wrist joint occurs in a different plane than abduction of the pollex and/or extension of its phalangeal joints. Sep-aration of the muscle is probably necessary to achieve an effective degree of pollical ab-duction and phalangeal extension. The same

applies to humans where, partly because the carpal tunnel is shallow radially, the trape-zoid-carpal joint is less medially or ulnarly rotated than in orangutans or chimpanzees (fig. 20; also Napier, 1961). As has been noted for humans (Johnson, 1970), contraction of the APL in gorillas probably both flexes and abducts the joint.

With marked medially rotated position of the trapezoid metacarpal joint, the dorsum of the thumb is directed laterally. Flexion of the carpus, abduction of the carpometacarpal joint, and extension of the pollical phalanges occur almost along the same plane. In this case, a separate EPB is not necessary to insure an effective degree of pollical abduction or extension. A separate EPB is absent in orang-utans and in chimpanzees (Huxley, 1864; Bischoff, 1870; Chapman, 1879, 1880; Fick,
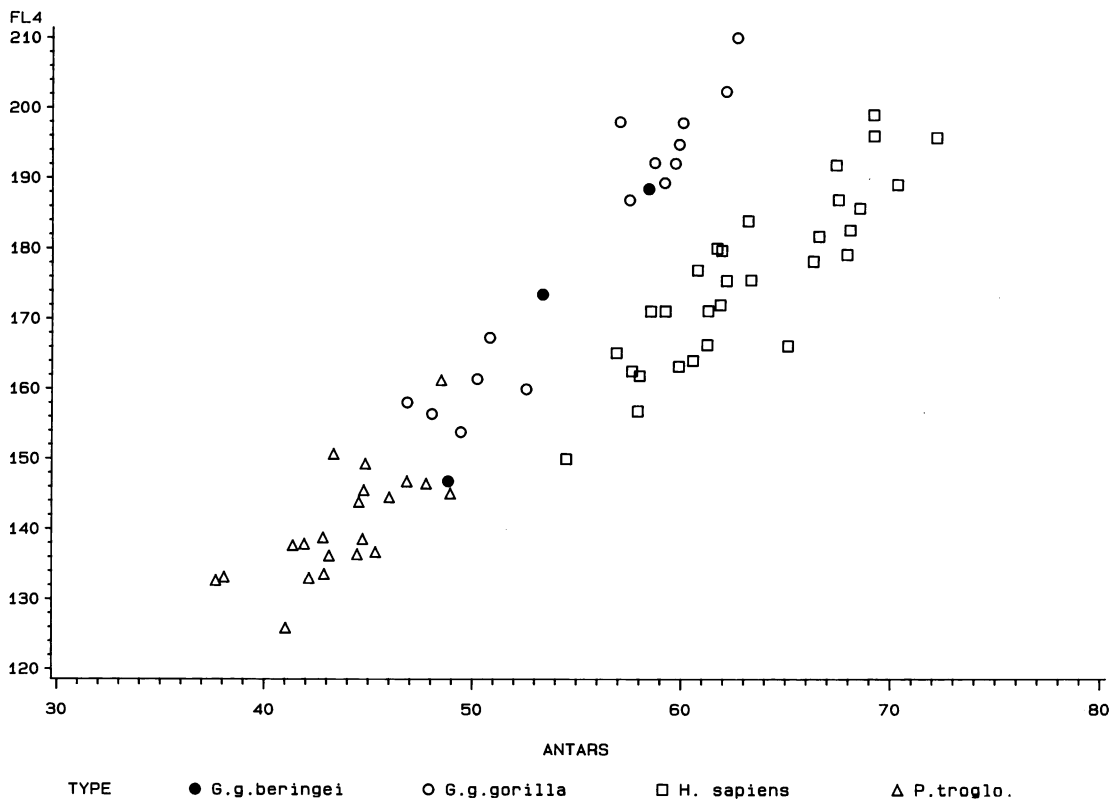
Fig. 7. Length of tarsus anterior to posterior talocalcaneal joint axis (antars) vs. metatarsal foot length (FL4) in lowland gorillas (*G. g. gorilla,* slope = 3.45, y intcpt. = −10.6, r^2 = 0.92), mountain gorillas (*G. g. beringei,* slope = −60.6, y intcpt. = 4.30, adj. r^2 = 0.92), humans (*H. sapiens,* slope = 2.32, y intcpt. = 29.3, r^2 = 0.77), and chimpanzees (*Pan troglo.,* slope = 1.91, y intcpt. = 56.8, r^2 = 0.51). Length in millimeters; see table 6 for number of specimens sampled.

1895; Kohlbrugge, 1897; Langer, 1879; Straus, 1941)—taxa with a markedly rotated trapezium (fig. 20, Napier, 1961). In these apes the fibers of the EPB are blended in with those of the APL (Testut, 1884; Straus, 1941) and find their insertion on the base of the first metacarpal. Although an EPB with a tendon and muscular belly separate from the abductor pollicis has been reported for an orangutan (Primrose, 1899), the muscle does not have the insertion on the base of the proximal phalanx characteristic of humans. In chimpanzees and orangutans the short extensor of the pollical phalanges when present is usually provided by an offshoot of the EPL tendon (Hepburn, 1892).

Associated with the muscular tendon of the APL at its attachment on the carpus is a radial sesamoid which articulates on the palmar as-

pect of the trapezium radial to the crest. To a varying degree in all great apes, the sesamoid may be fused to the trapezium, and/or to the scaphoid. In mountain gorillas *G. g. beringei,* a sesamoid fused to the trapezium occurred in all the 16 animals examined. In lowland gorillas, it occurs in about 40% of cases (table 11). Fusion to the scaphoid occurs less frequently and is more common in highland gorillas (table 12). Moreover, in all gorillas the radial sesamoid is extremely large and well developed. In both chimpanzees and orangutans it is most commonly unfused. Fusion in the specimen dissected by Gratiolet and Alix (1866) may account for its reported absence. Interestingly, in humans a radial sesamoid occurs in only 1–2% of the population. In this study, the single human specimen encountered with a radial sesamoid had
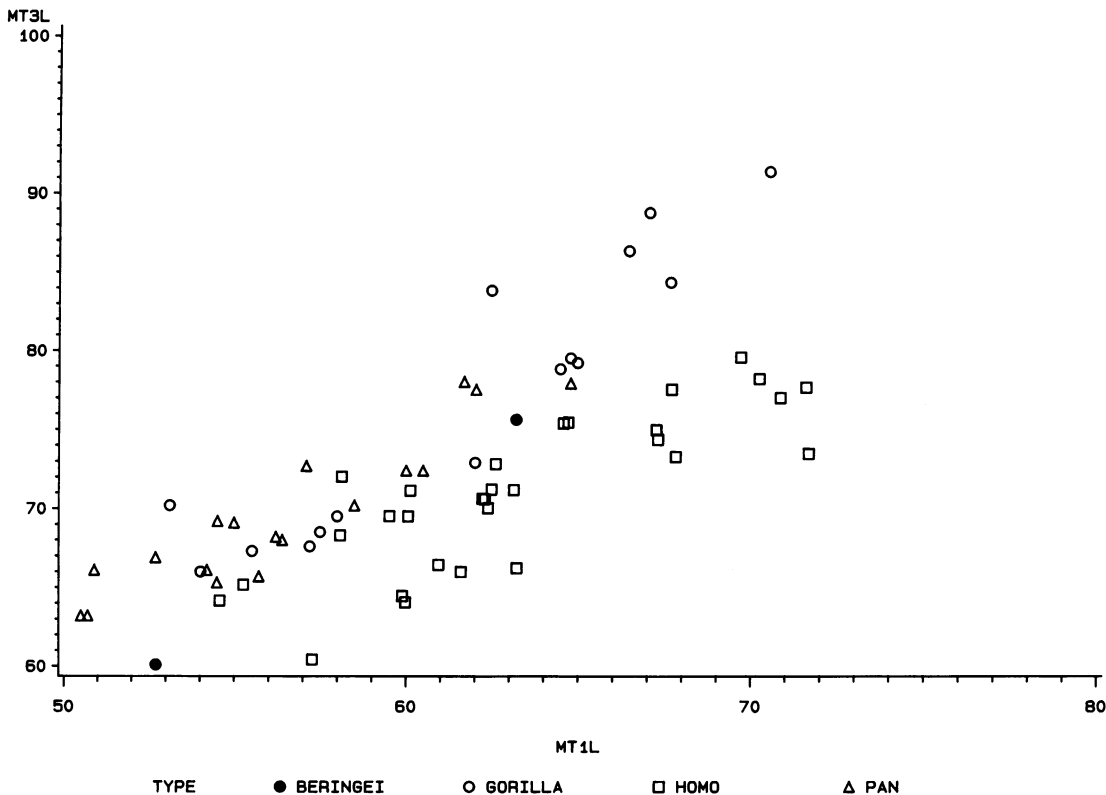
Fig. 8.   Length of 1st metatarsal (MT1L) vs. that of third (MT3L) in lowland gorillas (GORILLA, slope = 0.59, y intcpt. = 16.3 r^2 = 0.86), mountain gorillas (BERINGEI, slope = 0.68, y intcpt. = 11.9), humans (HOMO, slope = 0.81, y intcpt. = 5.74, r^2 = 0.68), and chimpanzees (PAN, slope = 0.81, y intcpt. = 0.087, r^2 = 0.86). Length in millimeters; see table 7 for number of specimens sampled.

a comparatively very small bone associated with a small carpal insertion of the APL.

Generally the size of the radial sesamoid corresponds with the size of the tendon of the APL inserting on the carpus. Moreover, a large carpal tendon and radial sesamoid as seen in gorillas is associated with fusion to the trapezium and/or to the tubercle of the scaphoid (Sarmiento, 1985) (fig. 21). The palmarly projected position of the radial sesamoid and of the supporting scaphoid tubercle in gorillas present a long lever arm to the APL for preventing extension or for flexing an extended wrist. A radially extended position of the sesamoid and the underlying scaphoid tubercle as seen to a marked degree in chimpanzees, and somewhat less so in orangutans, emphasizes abduction of the wrist (Sarmiento, 1988). The absence of the radial sesamoid in humans may reflect the comparatively reduced size of that portion of the APL tendon inserting into the trapezium. The gorilla condition is optimal for flexing and preventing extension of a wrist joint in quadrupedal behaviors and is associated with using the mediolateral axis of the hand perpendicular to forward movement.

Palmaris brevis muscle (PB)

Gorillas and humans both have well-developed PB (Raven, 1950; Gray, 1985). Although Hepburn (1892) and Wyman (1855) were unable to find this muscle in their dissected specimens, its presence in the gorilla has been confirmed in numerous studies (Duvernoy, 1855; Bischoff, 1880; Deniker, 1885; Hofer, 1892; Sommer, 1907; Pira, 1914; Raven, 1950). It has also been reported in chimpanzees by Sonntag (1923), Vrolik (1841),
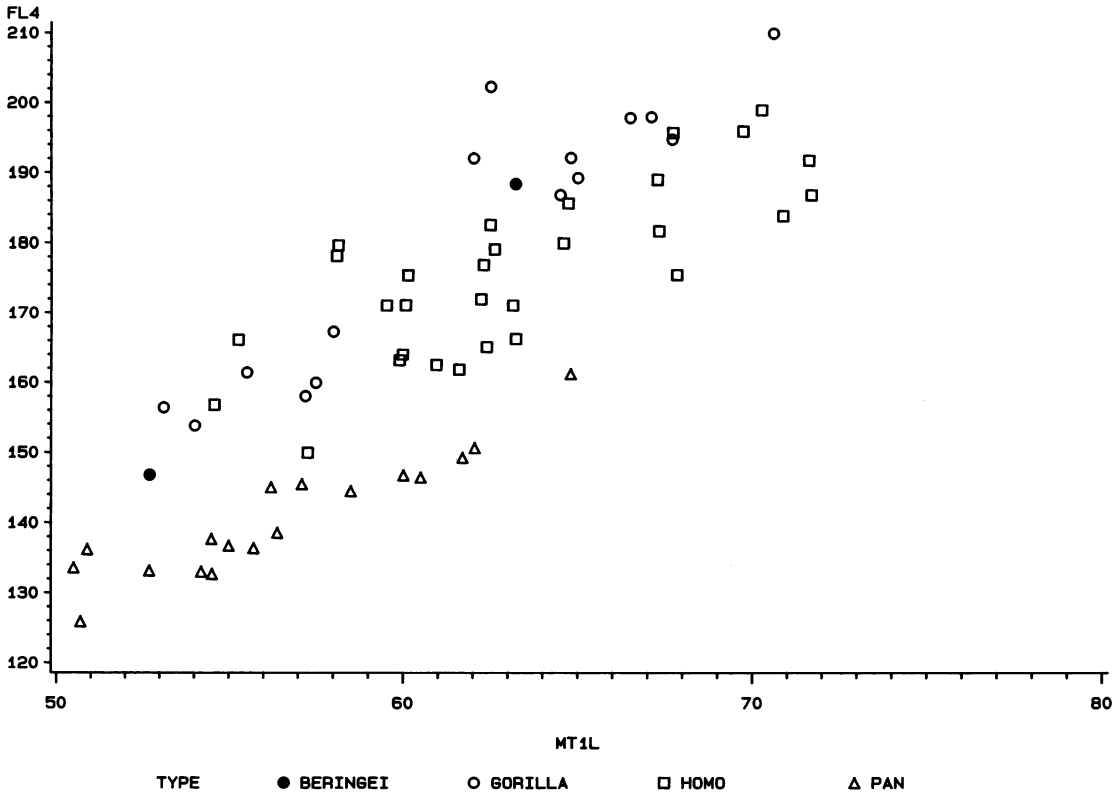
Fig. 9. Length of 1st metatarsal (MT1l) vs. metatarsal foot length (FL4) in lowland gorillas (GO-RILLA, slope = 3.1, y intcpt. = −19.3, r^2 = 0.83), mountain gorillas (BERINGEI, slope = 2.96, y intcpt. = −15.7), humans (HOMO, slope = 1.91, y intcpt. = 42.7, r^2 = 0.62), and chimpanzees (PAN, slope = 1.91, y intcpt. = 22.7, r^2 = 0.80). Length in millimeters; see table 7 for number of specimens sampled.

Champneys (1872), Michaelis (1903), and Fick (1925). The latter two authors noted that it is well developed in chimpanzees, although this study and most other studies note its weak development. In orangutans its presence was reported only by Westling (1884), Hofer (1892), and Fick (1895). When the muscle is present in orangutans, it is very weakly developed (table 3).

Supposedly, flexion of the PB in humans serves to deepen the hollow of the palm and protect the ulnar artery and nerve from pressure (Shrewsbury et al., 1972). Obviously this function is important in palmigrade and semidigitigrade quadrupeds. Therefore, its strong development in the cercopithecines and colobines is expected (Markze, 1971). However, its attachment to the palmar aponeurosis implies another important function. Unlike the palmaris longus, which gives

rise to the fibers of the palmar aponeurosis, the PB is able to act independently of the position of the radiocarpal joint. Such independent movement may also be the reason for its strong development in quadrupedal forms. Toward the end of the recovery phase of the stride, its actions would not be antagonistic to those of the wrist extensors. Nevertheless, since cautious climbers may also place pressure on the palm when grasping relatively large supports, development of this muscle may also reflect such a preference.

Contrahentes

Gorillas have a number of specializations of the intrinsic hand musculature which they share to a varying degree with all hominoids. Undoubtedly these specializations are related to a common arboreal heritage. As in humans
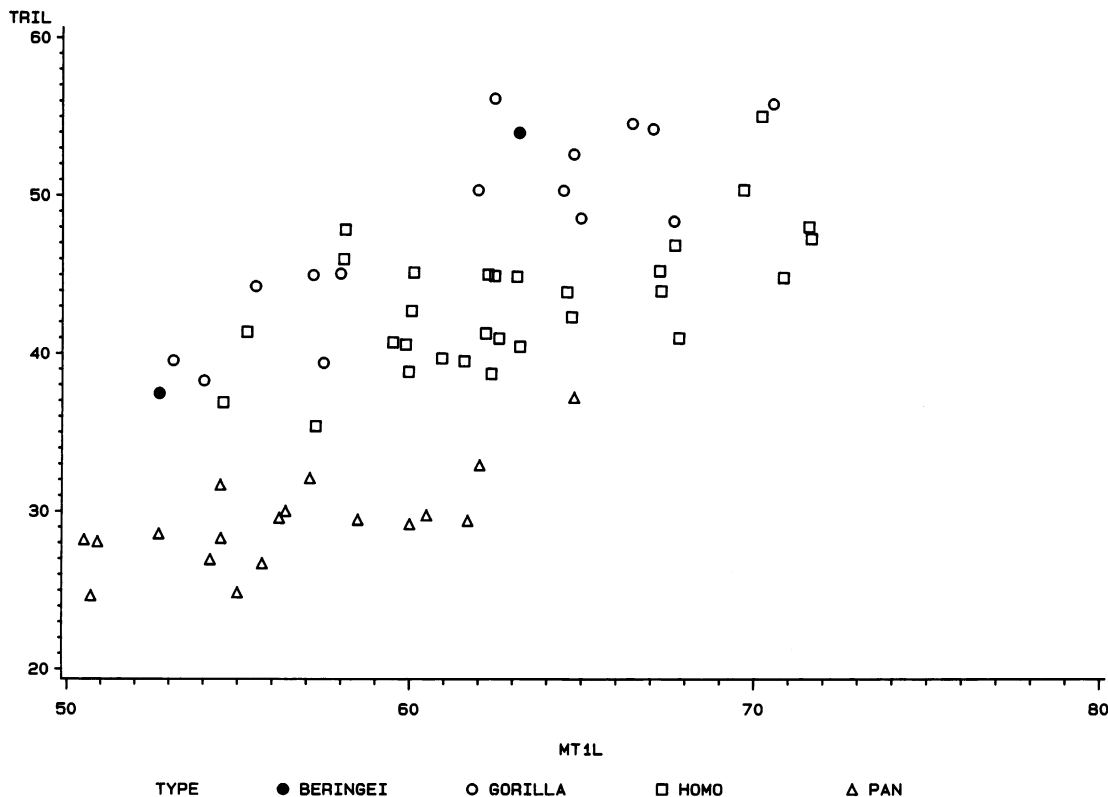
Fig. 10.   Length of 1st metatarsal (MT1l) vs. lever length of triceps surae (TRIL) in lowland gorillas (GORILLA, slope = 0.95, y intcpt. = −10.3, r^2 = 0.73), mountain gorillas (BERINGEI, slope = 1.57, y intcpt. = −45.3), humans (HOMO, slope = 0.54, y intcpt. = 9.32, r^2 = 0.38), and chimpanzees (PAN, slope = 0.50, y intcpt. = 1.36, r^2 = 0.48). Length in millimeters; see table 7 for number of specimens sampled.

and orangutans, gorillas have an anterior interossei fascia (deep palmar aponeurosis) in place of the contrahentes muscles to the 2nd, 4th, and 5th digit. The majority of chimpanzees and hylobatids exhibit contrahentes to either the 5th digit, the 2nd digit, or to both of these (Hepburn, 1892; Bischoff, 1870; Forster, 1917; Sonntag, 1924; Fick, 1925; Lessertisseur, 1958). As in most of the other nonhominoid primates, hylobatids, unlike chimpanzees, may occasionally exhibit the full set of contrahentes muscles (Kohlbrugge, 1890; Forster, 1917; Straus, 1942). In the hominoid hand the variability in the presence of contrahentes indicates an order of disappearance similar to that reported on by Straus (1930) for the primate foot. The contrahentes to the 4th digit is the one most commonly absent followed by that to the 2nd digit and

last by that to the 5th digit. The transverse and oblique heads of the adductor pollicis, which is continuous medially with the anterior interossei fascia, represent the contrahentes muscle to the 1st digit. This muscle is generally present in all hominoids. As implied by the name of the 1st contrahentes, the adductor pollicus, the contrahentes serve to adduct their respective digits toward the 3rd finger.

Jouffroy and Lessertisseur (1959, 1960) noted that loss of the contrahentes muscle is associated with the use of the hand as a hook during forelimb suspensory behaviors. In the nonhominoid primates, loss and/or feeble development of the contrahentes (usually contrahentes II and IV, those to the 2nd and to the 5th digit) are exhibited in the hands of *Colobus* (Bischoff, 1870; Kohlbrugge, 1897;
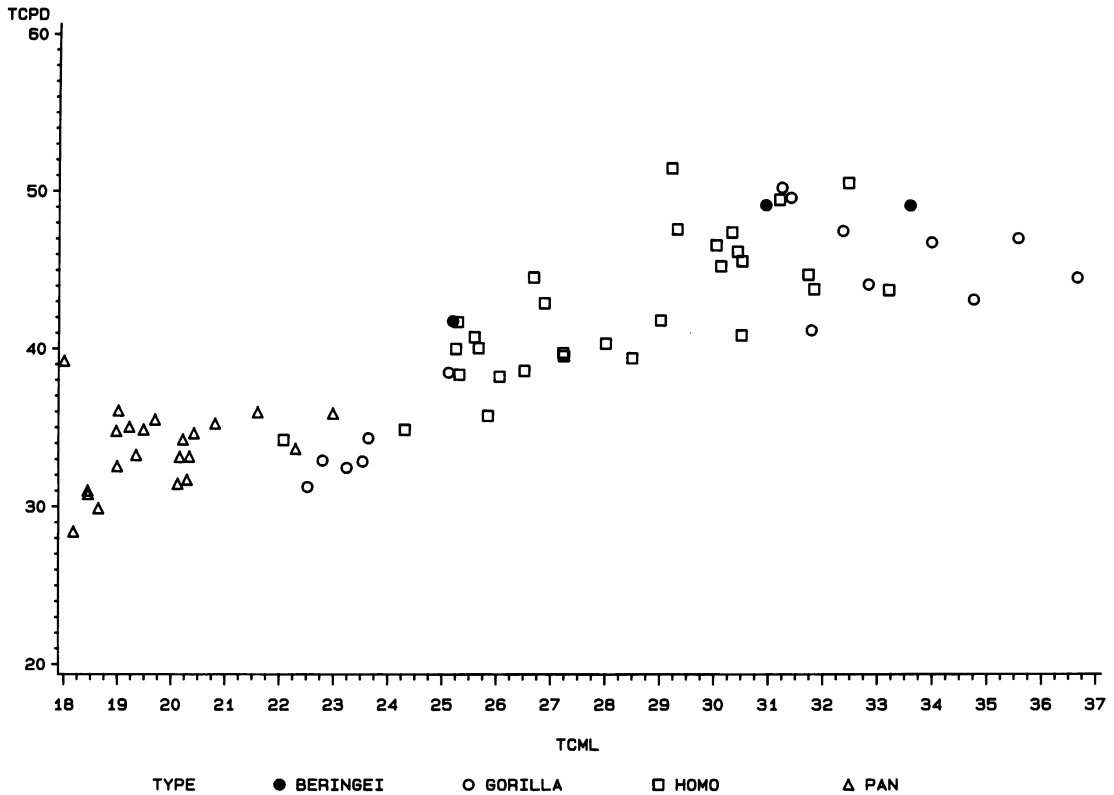
Fig. 11. Mediolateral width of tuber calcanei (TCML) vs. its dorsoplantar height (TCPD) in lowland gorillas (GORILLA, slope = 0.90, y intcpt. = 7.44, r^2 = 0.75), mountain gorillas (BERINGEI, slope = 1.07, y intcpt. = 20.1, adj. r^2 = 81.0), humans (HOMO, slope = 0.82, y intcpt. = 6.44, r^2 = 0.58), and chimpanzees (PAN, slope = 1.89, y intcpt. = 43.9, r^2 = 0.079). Length in millimeters; see table 8 for number of specimens sampled.

Polak, 1908; Straus, 1942; Jouffroy and Lessertisseur, 1959), atelines (Forster, 1917; Robertson, 1944; Hill, 1962), and alouattines (Sirena, 1876; Schon-Ybarra, 1966). Moreover, loss of the contrahentes is also exhibited in the feet of hominoids (Straus, 1930). The one function the hands and feet of the majority of these forms have in common is their use as hooks when grasping supports (Jouffroy and Lessertiseur, 1959, 1960; Napier and Napier, 1967; Tuttle, 1969, 1970; Jenkins, 1981; Sarmiento, 1983). As suggested by those adaptations common to the Hominoidea, it is likely that the ancestors of humans and gorillas also practiced such hand-and-foot grasping postures (Sarmiento, 1983, 1988). The absence of the contrahentes muscles in the hooklike cheiridia of three-toed and two-toed sloths (Makintosh, 1875; Meinke, 1911) provides additional evidence of the association between a hooklike cheiridial grasp (Mendel, 1981) and the loss of the contrahentes.

According to Jouffroy and Lessertisseur (1959, 1960), loss of the contrahentes and the associated formation of an aponeurosis enable suspensory forms to maintain cohesion at the metacarpophalangeal joint, with a minimum of energy expenditure. Unlike the muscular contrahentes layer, the aponeurosis is able to apply a constant passive force. The observation that considerable tensile forces may exist across the metacarpophalangeal joint during forelimb suspensory behaviors (Sarmiento, 1985, 1988) supports Jouffroy and Lessertisseur's interpretation.

However, the transformation of the contrahentes to an aponeurosis (the anterior in-
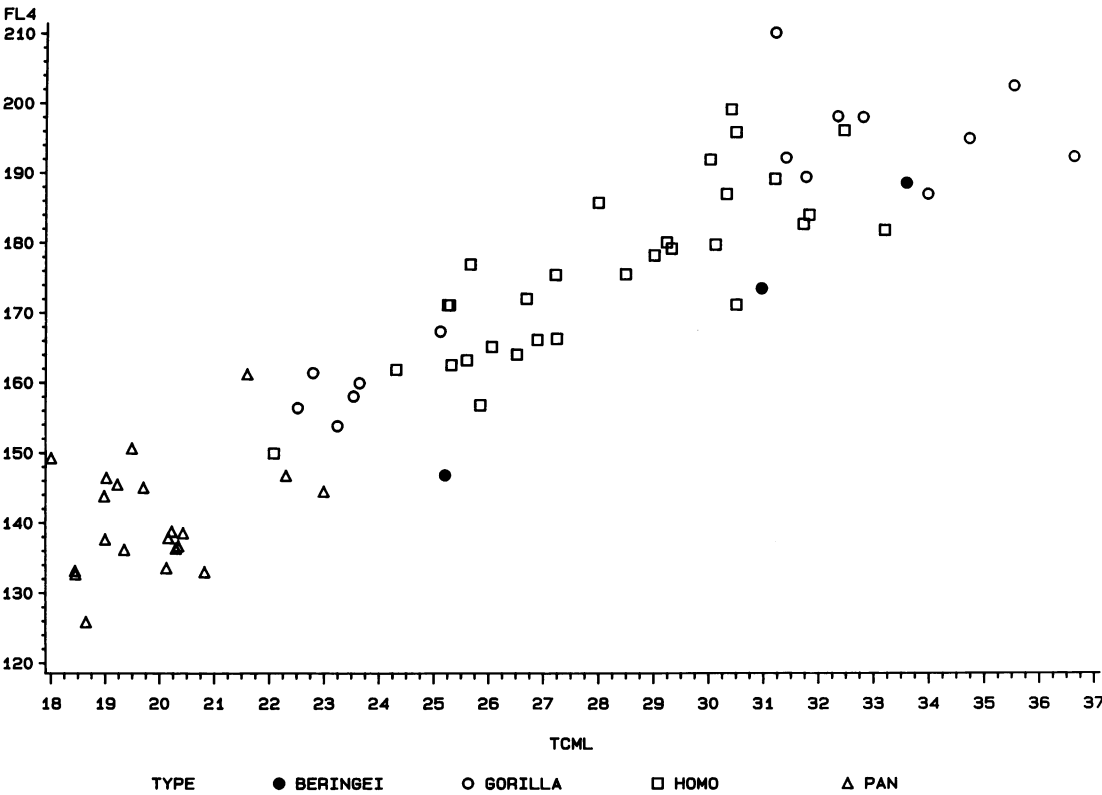
Fig. 12. Mediolateral width of tuber calcanei (TCML) vs. metatarsal foot length (FL4) in lowland gorillas (GORILLA, slope = 3.18, y intcpt. = 78.3, r^2 = 0.82), mountain gorillas (BERINGEI, slope = 3.71, y intcpt. = 46.8, adj. r^2 = 0.99), humans (HOMO, slope = 3.48, y intcpt. = 65.6, r^2 = 0.68), and chimpanzees (PAN, slope = 2.38, y intcpt. = 83.4, r^2 = 0.13). Length in millimeters; see table 8 for number of specimens sampled.

terossei fascia) is also a means of minimizing movements conjunct to flexion and extension at the metacarpophalangeal joint, thereby maximizing that percentage of tension in the short and long flexor employed in maintaining the hooklike cheiridial configuration. In theory, the most energy-efficient grasps are realized when all of the force generated by the digital flexors is used to maintain the digital joints in the hooklike configuration (Sarmiento, 1985). Therefore, tension in the tendons resulting in rotational and/or abductory and adductory forces at the metacarpophalangeal and interphalangeal joints must be minimized. Unlike the contrahentes muscle, the aponeurosis is able to do so, and maintain the most efficient joint positions (those which insure that the highest percentage of tendon tension is applied to maintain the hooklike

cheiridial postures), passively. The associated hingelike articulation at the metacarpophalangeal joint in suspensory forms complements the aponeurosis in passively checking inefficient movements.

Given the logarithmic relationship between a muscle's cross-sectional area and an animal's volume, large-bodied suspensory forms are under greater pressure to sacrifice the energy-requiring actions of the contrahentes for the passive forces applied by the aponeurosis. Therefore, the relatively reduced contrahentes muscular layer in pongids and hominids is to be expected. This is true despite the fact that hylobatids are probably more dependent on a hooklike grasp than are chimpanzees or gorillas (Reynolds and Reynolds, 1965; Tuttle, 1969, 1970, 1972a; Baldwin and Teleki, 1976; Fleagle, 1976; Sar-
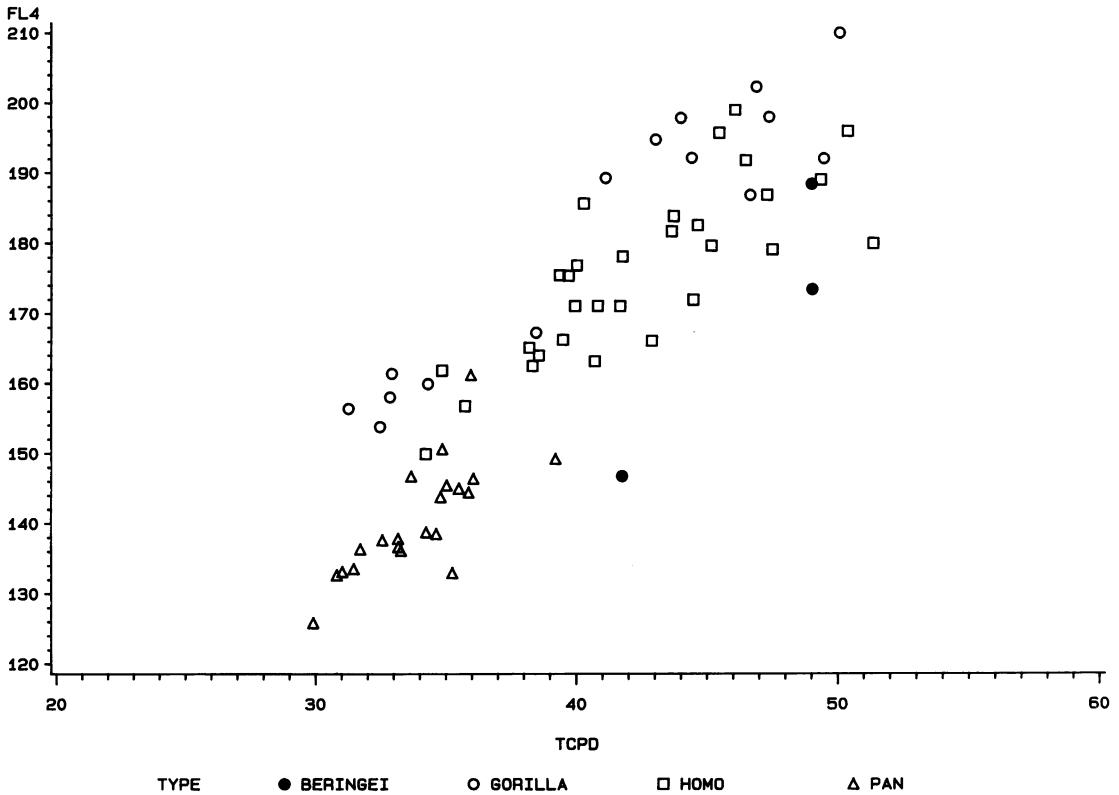
Fig. 13. Dorsoplantar length of tuber calcanei (TCPD) vs. metatarsal foot length (FL4) in lowland gorillas (GORILLA, slope = 2.71, y intcpt. = 70.0, r^2 = 0.89), mountain gorillas (BERINGEI, slope = 4.67, y intcpt. = -47.9, adj. r^2 = 0.75), humans (HOMO, slope = 2.18, y intcpt. = 83.4, r^2 = 0.64), and chimpanzees (PAN, slope = 2.70, y intcpt. = 49.0, r^2 = 0.56). Length in millimeters; see table 8 for number of specimens sampled.

miento, 1985, 1988). The total absence of the contrahentes in humans and gorillas could be taken as indicative of an arboreal, large bodied, common ancestor. Given the use of the hand as a propulsive lever for knuckle-walking behaviors, however, the further loss of the contrahentes in gorillas when compared to chimpanzees most likely reflects the need of a large-bodied great ape to apply a passive force that prevents dorsiflexion of the carpometacarpal joints.

Deep transverse metacarpal ligament (DTMCL)

In gorillas, humans, and chimpanzees, the anterior interossei fascia of the palm is thickened distally to form the DTMCL (Jouffroy and Lessertisseur, 1959, 1960; Marzke, 1971).

Regardless of the degree of loss of the contrahentes muscular layer, this thickening is absent in orangutans and hylobatids.

Marzke (1971) suggested that the DTMCL prevents dislocation at the metacarpophalangeal joint, which is likely to occur as a result of the downward thrust of the body on the extended joint. Undoubtedly this interpretation as to the function of the DTMCL is correct. However, Marzke goes further in relating the presence of this ligament solely to knuckle-walking and or fist-walking behaviors. The example she presents of the occurrence of an analogous ligament (the deep metatarsal transverse ligament) in the human foot clearly demonstrates that other behaviors such as semidigitigrade and digitigrade postures of the cheiridia also benefit from a deep transverse metapodial ligament. Re-
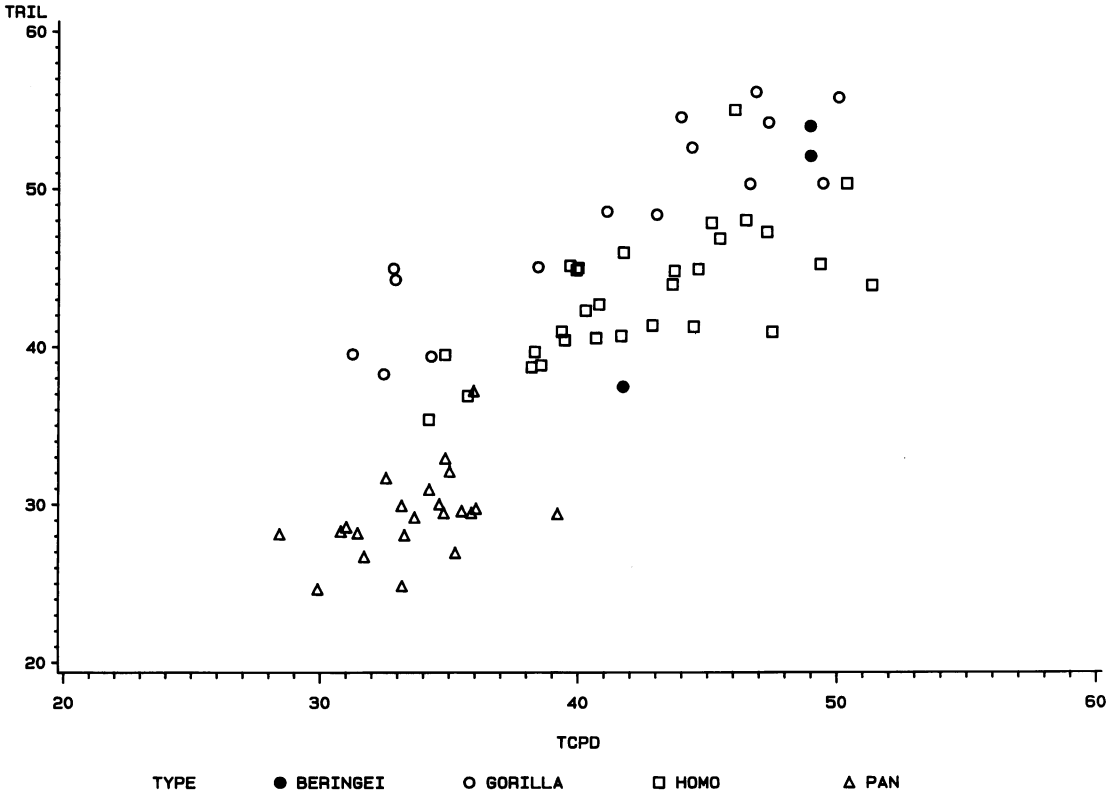
Fig. 14.   Plantodorsal height of tuber calcanei (TCPD) vs. lever length of the tricepes surae (TRIL) in lowland gorillas (GORILLA, slope = 1.00., y intcpt. = −7.37, r^2 = 0.80), mountain gorillas (BERINGEI, slope = 0.46, y intcpt. = 24.4, adj. r^2 = 0.98), humans (HOMO, slope = 0.74, y intcpt. = 10.3, r^2 = 0.48), and chimpanzees (PAN, slope = 0.51, y intcpt. = −4.82, r^2 = 0.54). Length in millimeters; see table 8 for number of specimens sampled.

gardless, the gorilla condition is associated with use of the hand in terrestrial quadrupedal behaviors.

Manual interossei

Of the seven palmar and four dorsal interossei of the generalized primate hand, gorillas have lost palmar interossei II, IV, V, and VII (these correspond to the III, V, VI, and VIII interossei of the primitive mammalian hand; see Lewis, 1965). More precisely, the gorilla's muscles have fused with the dorsal interossei (Lessertisseur, 1958; Lewis, 1965). A varying degree of fusion of the palmar interossei is exhibited in all hominoids (Bischoff, 1870, 1880; Hepburn, 1892; Lessertisseur, 1958; Lewis, 1965). Moreover, in all hominoids the homologs of the primate II, IV, V, and VII

palmar interossei may share a common insertion with the dorsal interossei (Landsmeer, 1955; Lewis, 1965).

Nevertheless, gorillas and humans differ from other hominoids in having proportionately less well-developed dorsal interossei. For example, orangutans and chimpanzees have extensive origins from the palmar aspects of the metacarpals for those parts of the dorsal interossei homologous to the IV, V, and VII palmar interossei (Hepburn, 1892; Lewis, 1965; Tuttle, 1969). Moreover, these well-developed dorsal interossei may receive additional fibers from the aponeurosis of the contrahentes (Primrose, 1899; Hepburn, 1892). Ratios of the weight of the dorsal and palmar interossei to that of the total palm musculature show that humans have relatively less-developed palmar than dorsal in-
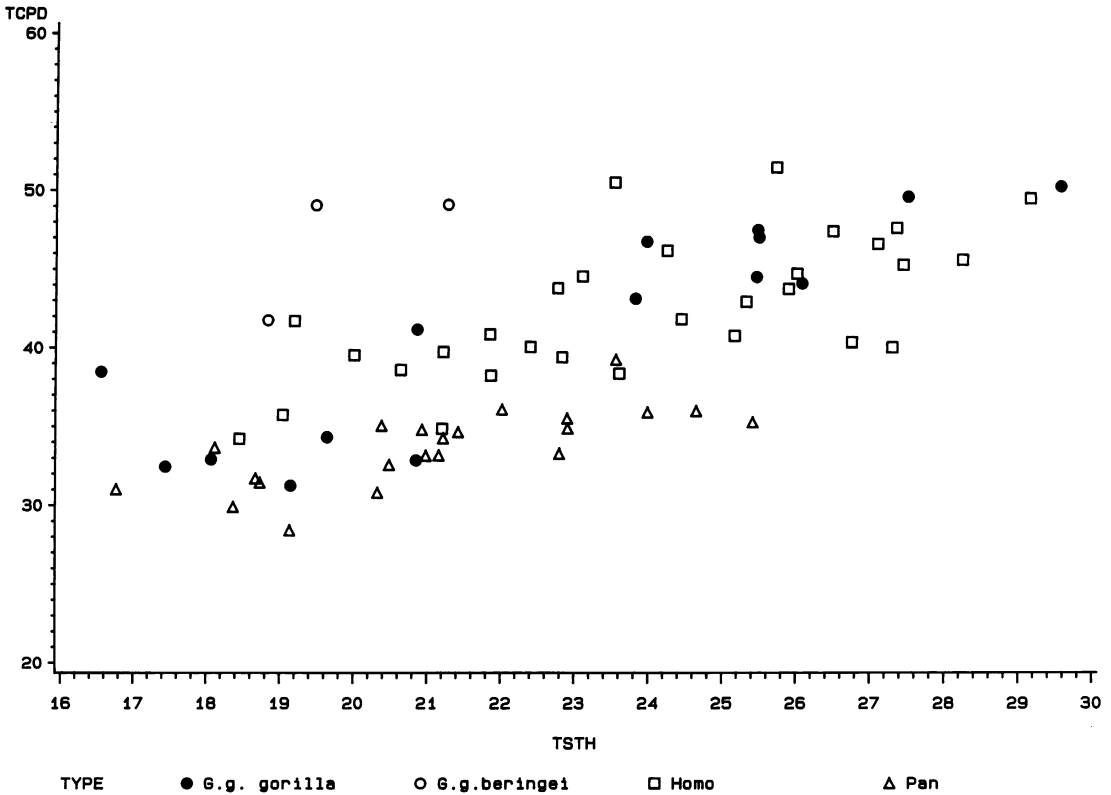
Fig. 15. Distance from the most superior point on tuber calcanei to most inferior point of attachment of triceps surae (TSTH) vs. mediolateral width of the tuber calcanei (TCML) in lowland gorillas (*G. g. gorilla,* slope = 1.50, y intcpt. = 7.05 r^2 = 0.79), mountain gorillas (*G. g. beringei,* slope = 2.34, y intcpt. = 0.13, adj. r^2 = 0.002), humans (*Homo,* slope = 1.02, y intcpt. = 17.95, r^2 = 0.46), and chimpanzees (*Pan,* slope = 0.80, y intcpt. = 16.8, r^2 = 0.55). Length in millimeters; see table 8 for number of specimens sampled.

terossei in comparison to chimpanzees and orangutans (Tuttle, 1969, 1972b). The relatively low ratio of palmar interossei to the total intrinsic hand musculature in humans shows that this difference is not due to the comparatively strong development of the palmar interossei in chimpanzees and orangutans. Unfortunately, there are no weight ratios available for the gorilla dorsal interossei that verify dissection reports (Raven, 1950; Preuschoft, 1965) of their weaker development relative to that of the other great apes.

There is considerable variability in the insertions of the palmar interossei among hominoids. Humans are classically described as having an insertion on the extensor hood (Landsmeer, 1955; Gray, 1985). On the other hand, great apes and hylobatids have been described as having double insertions on the base of the proximal phalanges and on the extensor hood (Kohlbrugge, 1890, 1897; Forster, 1917; Raven, 1950; Lessertisseur, 1958; Tuttle, 1970, 1972a). However, both patterns of insertions can occur in great apes and humans and may even vary according to the particular digit (Kohlbrugge, 1897; Primrose, 1899; Sommer, 1907; Forster, 1917; Kaplan, 1945, 1965; Haines, 1951; Landsmeer, 1955; Lessertisseur, 1958; Lewis, 1965). Nevertheless, it is interesting to note that in gorillas the palmar interossei often have a component inserting on the base of the phalanx (Raven, 1950; this study). Considering the hyperextended metacarpophalangeal joint in gorilla knuckle-walking hand postures, such an insertion would not be subject to the pro-
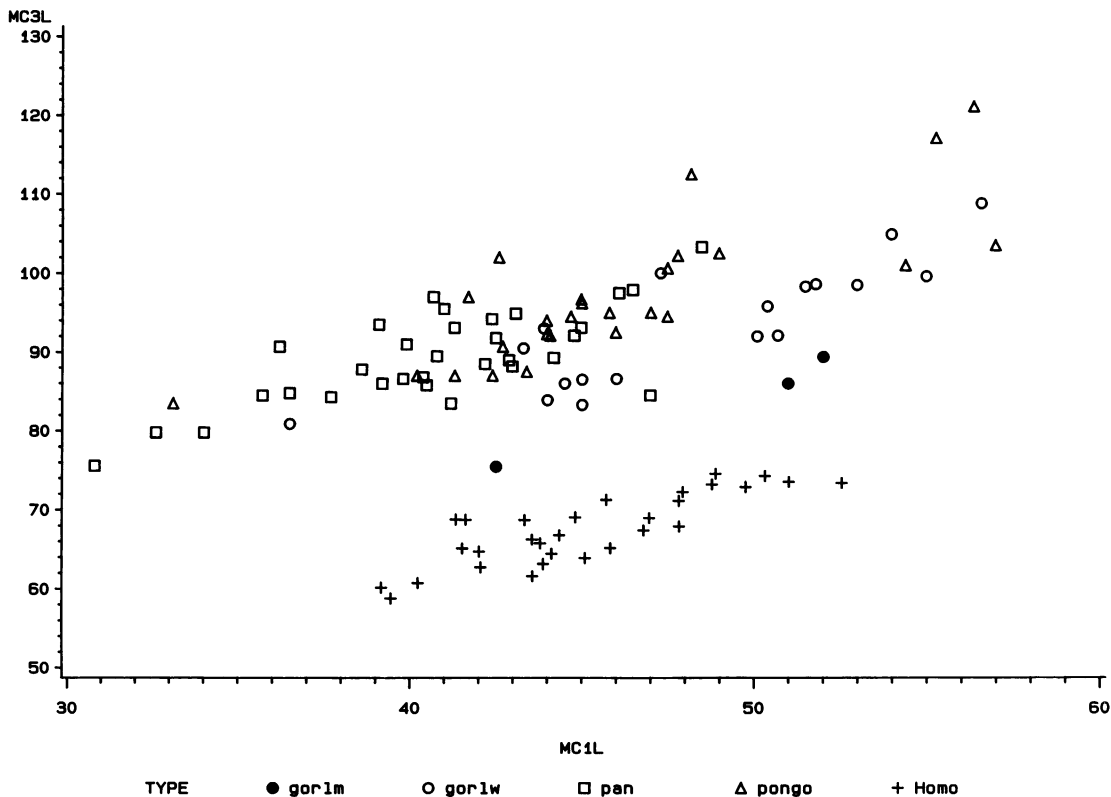
Fig. 16. Length of 1st metacarpal (MC1l) vs. that of 3rd metacarpal (MC3L) in lowland gorillas (gorlw, slope = 1.31, y intcpt. = 29.9, r^2 = 0.74), mountain gorillas (gorlm, slope = 1.37, y intcpt. = 17.0, adj. r^2 = 0.96), humans (Homo, slope = 1.07, y intcpt. = 19.3, r^2 = 69.8), chimpanzees (pan, slope = 1.05, y intcpt. = 46.4, r^2 = 0.53), and orangutans (pongo, slope = 1.38, y intcpt. = 33.6, r^2 = 0.64). Length in millimeters; see table 9 for number of specimens sampled.

nounced degree of tendon slackening that an extensor hood insertion would be. In this regard, the actions of the interossei could still be effective in hyperextended metacarpophalangeal postures. The insertion onto the base of the phalanx of the analogous plantar interossei in the human foot lends support to this interpretation. The metatarsophalangeal joints of the human foot achieve hyperextended postures analogous to those the metacarpophalangeal joints of gorillas are held in during knuckle-walking.

Marzke (1971) believes that, in humans, the substitution of the palmar interossei as adductors of digits in place of the contrahentes, and the transformation of the distal fibers of the latter into an aponeurotic sheet (the deep palmar fascia) are indicators of ancestral knuckle-walking or fist-walking be-

haviors. As noted, however, the association made by Marzke between loss of adductory ability and fist-walking, and/or knuckle-walking behaviors is not clear. Judging from the origin and insertion of the palmar interossei in the knuckle-walking and fist-walking great apes, these muscles have an adductory ability comparable to that of humans, and in the case of the gorilla probably even more than in humans. As noted, loss of the adductory-abductory components of motion at the metacarpophalangeal joint is best related to use of the cheiridia as hooks during suspensory behaviors. Although in the feet of hominoids the actions of the contrahentes may also be interpreted as having been substituted for by those of the interossei, it would be difficult to convincingly argue a knuckle-walking or fist-walking ancestry for hominoid

TABLE 6
Mean ($\bar{x}$) and Standard Deviation (SD) of Lengths of Segments Contributing to Lever Arms of Foot as a Percentage of Metatarsal Foot Length (fl4)
See text and fig. 1 for abbreviations[a]

Proportions	P. troglodytes (N = 21)		G. g. gorilla (N = 15)		G. g. beringei (N = 3)		H. sapiens (N = 30)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
tril/fl4	20.9	1.20	26.6	1.28	27.5	1.88	24.6	1.10
Range	18.2–23.1		24.6–28.6		25.5–30.0		22.8–27.6	
calcl/fl4	17.5	1.17	17.6	0.940	17.1	1.09	19.7	0.909
Range	14.9–19.3		16.2–19.2		15.9–18.5		17.9–21.5	
ca4thmt/fl4	13.7	0.790	13.1	0.566	14.4	0.359	16.3	0.877
Range	12.0–15.0		12.0–13.9		13.9–14.8		14.1–17.7	
mt4l/fl4	47.9	1.23	42.6	1.06	41.0	1.42	39.4	1.32
Range	45.9–50.3		40.3–44.4		39.2–42.7		35.9–42.7	
antars4/fl4	31.2	1.47	30.70	0.93	31.7	1.12	36.0	1.22
Range	28.4–33.7		28.8–32.9		30.8–33.3		34.2–39.2	

[a] Numbers of individuals measured in parentheses.

feet. While the formation of a deep transverse metacarpal ligament in the evolution of the human hand may be best explained by the interpolation of a terrestrial quadrupedal stage, the loss of the contrahentes is best explained by the interpolation of a suspensory stage. In this regard the palmar interossei of gorillas have not actually substituted for the contrahentes, but have persisted, due to the primary functions they subserve, when the metacarpophalangeal joint lost its abductory-adductory ability. With the reappearance of adductory-abductory movement, the palmar interossei resumed their secondary function of adduction, but hardly one that substitutes for the lost contrahentes.

FOOT

Flexor digitorum brevis muscle (FDB), plantar aponeurosis, and plantaris tendon

Great apes and humans have an FDB that originates from the plantar process of the tuber calcanei and supplies short tendons to at least the 2nd, 3rd, and partially to the 4th toe (Sarmiento, 1983). The deep head of the FDB,

TABLE 7
Average ($\bar{x}$) and Standard Deviation (SD) of Length of 1st Metatarsal (mtl1) as a Percentage of Length of 3rd Metatarsal (3mtl), Triceps Lever Arm (tril), and Metatarsal Foot Length (fl4) in Humans and African Apes

Proportions	P. troglodytes (N = 21)		G. g. gorilla (N = 15)		G. g. beringei (N = 2)		H. sapiens (N = 30)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
mtl1/mt3l[a]	81.2	2.81	80.5	3.41	85.6	2.12	89.1	3.84
Range	76.6–88.8		74.6–85.0		83.5–87.7		80.7–97.6	
mtl1/fl4	40.1	1.13	34.1	1.27	35.3	0.616	36.0	1.73
Range	37.4–41.3		30.9–36.1		34.7–35.9		32.3–38.7	
mtl1/tril	193	13.6	128	9.01	135	5.99	147	10.7
Range	172–221		111–146		129–141		122–166	

[a] For *P. troglodytes* N = 31.

TABLE 8

Average ($\bar{x}$) and Standard Deviation (SD) of Mediolateral Breadth of Tuber Calcaneus (tcml) as a Percentage of its Dorsoplantar Length (tcdp) and of Metatarsal Foot Length (f14), and Dorsoplantar Length of Tuber Calcanei as a Percentage of Triceps Lever Arm (tril) and of Metatarsal Foot Length

Proportions	P. troglodytes (N = 21)		G. g. gorilla (N = 15)		G. g. beringei (N = 3)		H. sapiens (N = 30)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
tcml/tcpd	59.1	4.51	72.0	5.44	62.9	2.02	66.7	4.47
Range	45.9–66.3		62.4–82.5		60.4–65.3		56.9–76.1	
tcml/f14	14.2	0.969	16.3	1.51	16.7	1.21	16.0	0.903
Range	12.1–15.9		14.1–19.1		15.0–17.9		14.5–18.3	
tcpd/f14	24.1	1.0	22.7	1.85	26.6	2.5	24.1	1.52
Range	22.3–26.5		20.0–26.0		23.0–28.4		21.5–28.6	
tcpd/tril	67.9	6.76	61.4	5.63	60.8	4.8	65.3	4.67
Range	58.1–81.8		51.5–71.9		55.7–67.3		55.4–75.6	
tsth/tcpd	107	11.1	77.0	9.54	69.8	3.68	81.7	6.53
Range	81.2–131		58.0–94.6		65.9–74.7		67.8–91.7	

which is usually lacking in humans (Gray, 1985), supplies the remaining portion of the short tendon to the 4th toe in the gorilla, and is the sole contributor to the short tendon of the 5th, when the latter tendon is present. Mountain gorillas exhibit a tendency for the superficial head to contribute the majority of the short tendon to the 4th digit, further approximating the human condition (Straus, 1930). In chimpanzees, the superficial head of the FDB only supplies tendons to the 2nd and 3rd toe, and on occasion makes a small contribution to the 4th toe. Moreover, the deep head of the FDB in chimpanzees may have a small contribution to the third toe and is always the main or sole contributor to the tendon of the 4th toe. The tendon to the 5th toe is not as commonly absent in humans, chimpanzees, and orangutans as it seems to be in gorillas (Straus, 1930).

Gorillas share with humans an origin of

TABLE 9

Average ($\bar{x}$) and Standard Deviation (SD) of Length of 1st Metacarpal (1mcl) as a Percentage of Length of 3rd Metacarpal (3mcl) × 100.

Species (N)	$\bar{x}$	SD	Range
P. troglodytes (31)	45.6	3.21	39.9–55.6
G. g. gorilla (18)	51.7	2.82	45.1–55.2
G. g. beringei (3)	57.9	1.24	56.3–59.3
H. sapiens (30)	66.8	2.80	60.1–71.6

TABLE 10

Mean ($\bar{x}$) and Standard Deviation (SD) of Weight of Trapezoid and Pisiform as a Percentage of Carpal Weight in some Haplorrhine Primates
(after Sarmiento, 1985)

	Trapezoid		Pisiform	
	$\bar{x}$	SD	$\bar{x}$	SD
Cebus (6)	4.1	0.72	11.5	2.8
Alouatta (4)	4.1	0.06	12.6	0.29
Ateles (3)	5.2	0.57	3.6	0.59
Lagothrix (3)	3.6	0.1	9.7	—
Macaca (1)	5.7	—	12.5	—
Papio (5)	5.6	0.74	10.7	2.88
Cercocebus (5)	5.9	0.88	11.6	0.61
C. aethiops (1)	4.3	—	14.1	—
C. patas (1)	6.4	—	13.2	—
Presbytis (1)	4.2	—	9.0	—
Nasalis (1)	6.8	—	6.8	—
Colobus (1)	4.8	—	12.6	—
Hylobates (4)	5.5	0.52	4.2	1.37
Hylobates (3)	5.1	0.31	3.9	0.65
Pongo (7)	5.6	0.27	4.9	0.50
Range	5.3--5.9		4.1--5.5	
Pan (8)	6.8	0.38	6.1	1.10
Range	6.3--7.3		4.8--7.3	
Gorilla (10)	7.8	0.70	6.3	0.47
Range	6.8--8.9		5.4--7.2	
Homo (11)	8.0	0.87	4.1	0.60
Range	6.7--9.6		3.3--5.1	

TABLE 11

Percent Frequency of Fusion of the Radial Sesamoid to the Trapezium in the Sampled Hominoids and the Predicted Range of Frequency (P) (±) as Arrived at from *t* Scores at 0.01 Level of Significance

	Right		Left		Bilateral	
	% (N)	P	% (N)	P	% (N)	P
Pongo						
Male	11.0 (18)	±19.1	11.0 (18)	±19.1	11.0 (18)	±19.1
Female	20.0 (25)	±20.6	16.0 (25)	±18.9	16.0 (25)	±19.1
Pan						
Male	0 (16)		7.1 (14)	±17.7	0 (12)	
Female	0 (19)		0 (19)		0 (18)	
G. g. gorilla						
Male	35.8 (53)	±17.0	37.7 (53)	±17.2	34.0 (46)	±18.0
Female	48.0 (31)	±23.0	44.0 (27)	±24.7	42.9 (21)	±27.8
G. g. beringei						
Male	100 (9)		100 (9)		100 (8)	
Female	100 (7)		100 (7)		100 (6)	

the FDB muscle from a strongly developed plantar aponeurosis (Sarmiento, 1983). In contrast, the plantar aponeurosis is not well developed in chimpanzees and is usually absent or very poorly developed in orangutans. In neither of these forms does the FDB take an origin from the plantar aponeurosis. Notably, among the great apes and humans the degree of development of the plantar aponeurosis correlates well with the degree of terrestriality. Humans, with the best developed aponeurosis and an aponeurotic FDB, are the most terrestrial and orangutans, with a very fleshy FDB and no plantar aponeurosis, the least terrestrial (Sarmiento, 1983). In all humans and great apes the plantaris tendon, when present, inserts in common with the triceps surae tendon on the tuber calcaneum. Therefore, it does not give an origin to the plantar aponeurosis or the FDB muscle.

In cercopithecoids, the plantar aponeurosis and the superficial head of the FDB both originate from the plantaris tendon (Sarmiento, 1983). The superficial head of the FDB muscle supplies the short flexor tendons only to the second digit; the remaining digits are supplied by the deep head of the FDB originating from the tendon of the flexor tibialis longus. Therefore, in Old World monkeys the FDB's actions are affected by the position of the ankle and knee joint, via the origin of the plantaris muscle from the lateral femoral condyle, and of the flexor tibialis from the tibia (Sarmiento, 1983).

TABLE 12

Percent Frequency of Fusion of the Radial Sesamoid to the Scaphoid in the Sampled Highland and Lowland Gorillas and the Predicted Range of Frequency in the Population (P) Using *t* Scores at 0.01 Level of Significance

	Right		Left		Bilateral	
	% (N)	P	% (N)	P	% (N)	P
G. g. gorilla						
Male	1.9 (53)	±4.8	3.8 (53)	±6.8	2.2 (46)	±5.5
Female	0 (7)		0 (6)		0 (6)	
G. g. beringei						
Male	33.3 (9)	±40.5	22.2 (9)	±35.8	25.0 (8)	±39.5
Female	0 (7)		0 (6)		0 (6)	

TABLE 13

Distance from Heel of the Foot to Cleft of Big Toe in Percentage of Total Foot Length in Great Apes and Humans

	%	SD
P. troglodytes (2)	48.7	—
Range		45.0–52.3
G. g. gorilla	63	—
G. g. beringei	75	—
H. sapiens (30)	82	1.9
Range		80.0–85.8

Gorilla percentages after Schultz (1934).

Passive maintenance of the longitudinal arch, which necessitates the strong development of connective tissue anchoring the tuber calcanei to the ball of the foot, explains the human condition of the FDB. Although gorillas lack a longitudinal arch, the morphology of the FDB probably attests to the rigidity of the midtarsal joint and the use of the foot as a propulsive lever. The ancestral pongid FDB probably arose as an arboreal adaptation that allows the foot a strong grasp independent of ankle joint position (Sarmiento, 1983). In this regard, the human and gorilla conditions are terrestrial modifications of the characteristic pongid condition.

Pedal interossei

Both gorillas and humans also share an interossei arrangement that adducts the toes toward an axis passing through the 2nd digit (Bischoff, 1880; Deniker, 1885; Symington, 1889; Hepburn, 1892; Keith, 1899; Leche, 1900; Sommer, 1907; Pira, 1914; Straus, 1930; Raven, 1950). Although this arrangement is also seen occasionally in chimpanzees (Hepburn, 1892; Michaelis, 1903) and orangutans (Fick, 1895; Michaelis, 1903), these apes most often have an interossei arrangement with an adduction axis through the 3rd digit, as do other anthropoids (Kohlbrugge, 1897; Bischoff, 1870; Straus, 1930). The usual anthropoid condition is only reported occasionally in lowland gorillas (Duvernoy, 1855; Macalister, 1874) and may also occur as variation in humans (Manter, 1945).

As noted by Hepburn (1892), the interossei arrangement in African apes, particularly gorillas, is associated with an emphasis on ter-

TABLE 14

Average Body Weight, Hand and Foot Length, and Metatarsal Foot Length (fl4) in Males and Females of Great Apes and Humans

	Body weight (kg)	Hand length (mm)	Foot length (mm)	fl4 (mm)
P. pygmaeus				
Male	75 (12)	263	308	195 (19)
Female	38 (12)	233	273	175 (18)
G. g. beringei				
Male	165 (5)	—	—	181 (2)
Female	90 (3)	—	—	147 (1)
G. g. gorilla				
Male	140 (32)	239	281	196 (6)
Female	70 (15)	201	236	160 (9)
P. troglodytes				
Male	49 (14)	235	240	142 (14)
Female	39 (12)	223	227	138 (7)
H. sapiens				
Male	71 (20)	187	242	182 (15)
Female	59 (12)	169	219	174 (15)

Numbers in parentheses represent numbers sampled for each measurement. Weights of lowland gorillas after Groves and Stott (1979). Human, orangutan, and chimpanzee weights, and hand and foot length are after Schultz (1940, 1941, 1953, 1956). Weights of highland gorillas compiled from museum records of wild-shot individuals (Sarmiento, 1985).

restrial behaviors and a more fully plantigrade foot posture, as opposed to the inverted foot postures of orangutans. Among hominoids, it is clear that the tendency to migrate the axis of adduction from the 3rd to the 2nd digit is exhibited with increased terrestriality. More precisely, it reflects an emphasis on opposition between the hallux and the 2nd toe at the cost of the independent opposition of the 3rd, 4th, and 5th toes against the hallux. It is also associated with a redirection of the longitudinal axis of the foot and that of each of the lateral four toes toward the hallux.

Peroneus tertius muscle

Mountain gorillas as a rule, and lowland gorillas as variation, possess a peroneus tertius muscle. In lowland gorillas this muscle occurs in only about 30% of the specimens (Straus, 1930). On the other hand, it was bi-
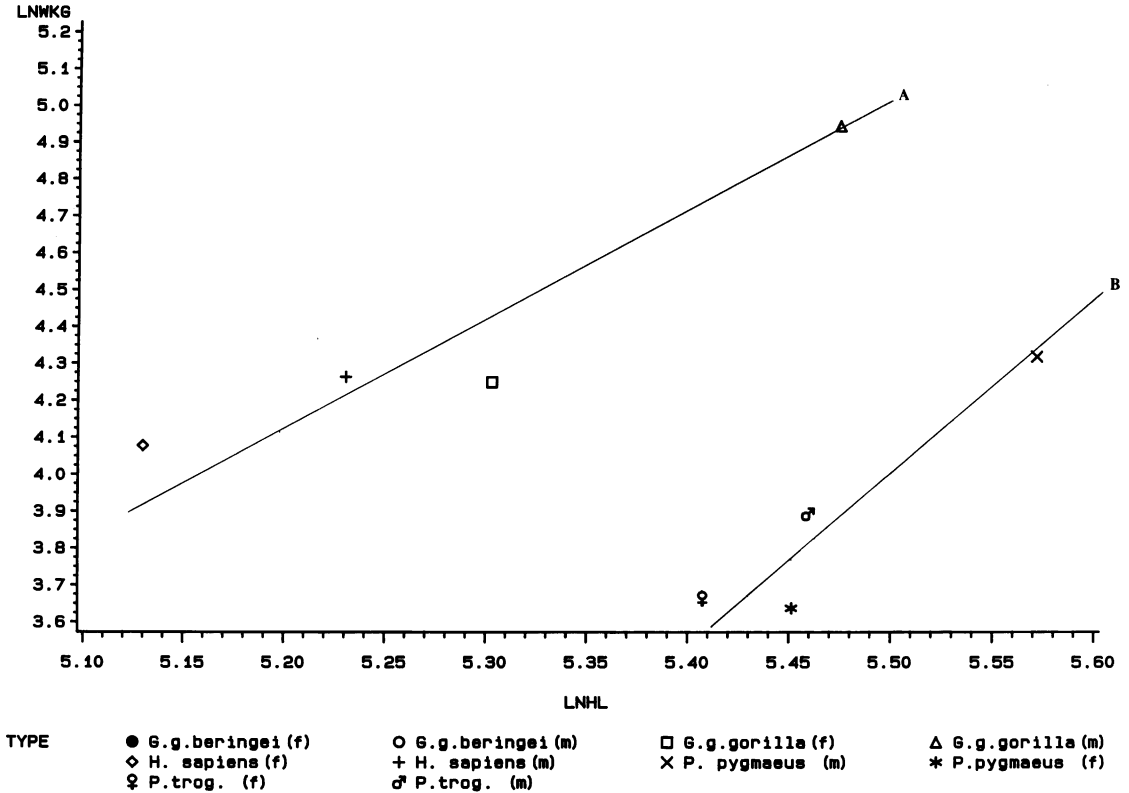
Fig. 17.   Natural log of average value of the body weight (LNWKG) vs. that of average hand length (LNHL) in male and female lowland gorillas, chimpanzees, orangutans, and humans. Linear regressions: **A**, for humans and lowland gorillas (slope = 0.362, y intcpt. = 3.70, adj. r^2 = 0.84), **B**, for orangutans and chimpanzees (slope = 0.211, y intcpt. = 4.65, adj. r^2 = 0.84).

laterally present in the single reported mountain gorilla (Morton, 1924; Straus, 1930) and present in the single foot of the female mountain gorilla dissected in this study. In humans it has a 90% incidence (Le Double, 1897; Krause, 1879). In chimpanzees it has only been reported once (Hecker, 1922). According to Straus (1930) it does not occur in any other primate. The literature reviewed in this study and the specimens dissected support Straus's contention, with the exception of a reported anomalous occurrence in the chacma baboon (Wells, 1935). Among hominoids, the frequency of occurrence of this muscle seems to increase with terrestriality. The peroneus tertius everts and dorsiflexes the foot. It is important at the beginning and end of the swing phase to insure that the foot clears the ground and its sole is placed flat on the ground, respectively (Smith, 1882). A similar mechanical requirement for planti-

grade terrestrial quadrupedalism may explain the presence of this muscle in the gorilla foot.

Long flexor tendons of toes

Gorillas approximate the human condition in the arrangement of the long flexor tendon of the toes. In humans the ancestral mammalian flexor fibularis has been transformed to the flexor hallucis, and is usually the sole contributor to the long flexor tendon of the hallux (Weidenreich, 1922; Lewis, 1962). As a rule, it also contributes secondary fibers to the 2nd and 3rd long flexor tendons and less commonly to the long tendon of the 4th toe (Schulze, 1867; Turner, 1867). Although not as well developed as in humans, the long flexor tendon of the big toe in gorillas originates solely from the flexor fibularis muscle. In contrast to humans, however, the flexor fi-
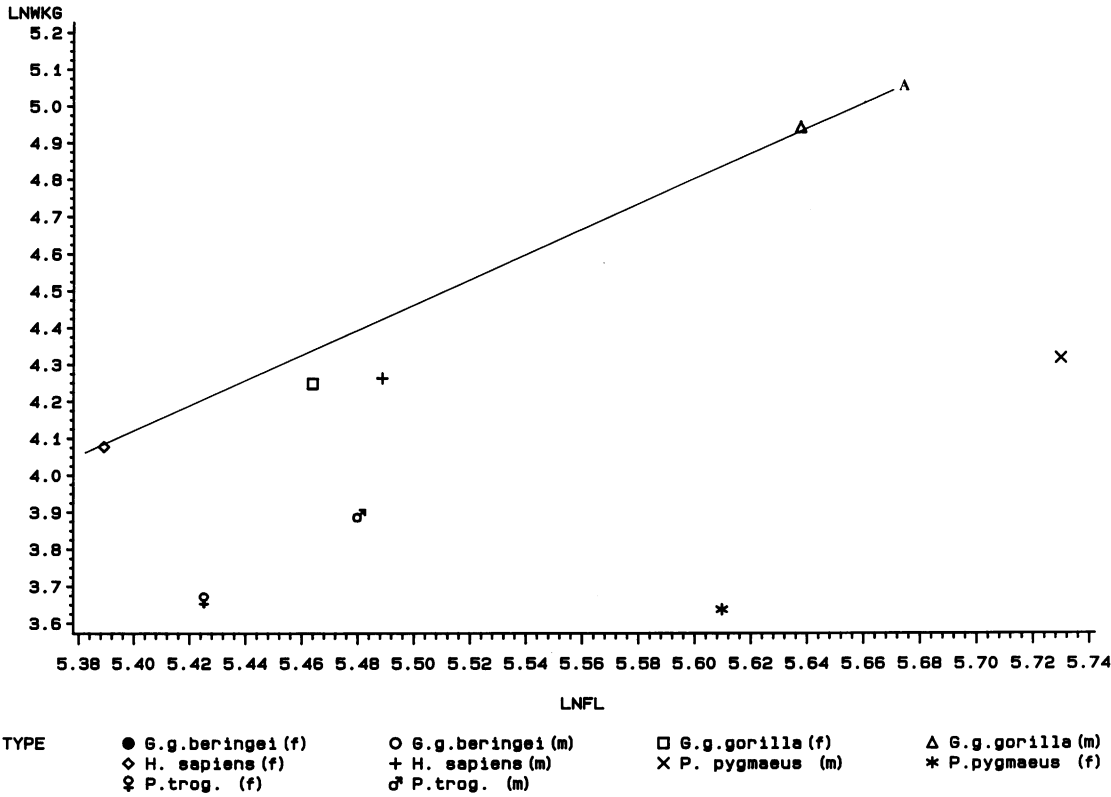
Fig. 18. Natural log of average body weight (LNWKG) vs. that of average foot length (LNFL) in male and female lowland gorillas, chimpanzees, orangutans, and humans (A, linear regression for humans and lowland gorillas, slope = 0.361, y intcpt. = 3.18, adj. r^2 = 0.98).

bularis only very rarely contributes a tendon to the 2nd toe (Straus, 1930). The majority of this tendon always comes from the flexor tibialis. A similar condition is seen in chimpanzees, and both chimpanzees and gorillas may show on occasion the condition common to humans. Orangutans also have an arrangement similar to that of gorillas and chimpanzees, but usually lack the long flexor tendon to the big toe. In all of the other catarrhines including gibbons, the hallucial tendon is also derived partially or largely from the flexor tibialis. The gorilla condition is associated with the independent use of the big toe from the lateral toes for propulsion in terrestrial plantigrade foot postures.

Transverse head of adductor hallucis muscle and pedal contrahentes

As in humans, gorillas commonly exhibit a separate transverse head of the adductor

hallucis muscle. The gorilla muscle, however, has a more restricted origin than that of humans (Straus, 1930) and is occasionally fused to its oblique head (Sommer, 1907; Pira, 1914). In gorillas the transverse head originates from the 2nd to 4th metatarsal heads and the associated metatarsal aponeurosis (Duvernoy, 1855; Huxley, 1864; Macalister, 1874; Hepburn, 1892), while in humans it originates from the deep transverse metatarsal ligament around the heads of the 2nd, 3rd, 4th, and 5th metatarsals (Wood-Jones, 1929). The origin of the muscle in chimpanzees extends out only to 2nd and 3rd metatarsal heads. Only rarely do chimpanzees show a division of the adductor hallucis into two heads or an origin for the transverse head that extends out to the 4th metatarsal (Kohlbrugge, 1897; Hepburn, 1892). In orangutans the muscle is always composed of a single head and takes a similar origin as in chimpanzees (table 3).
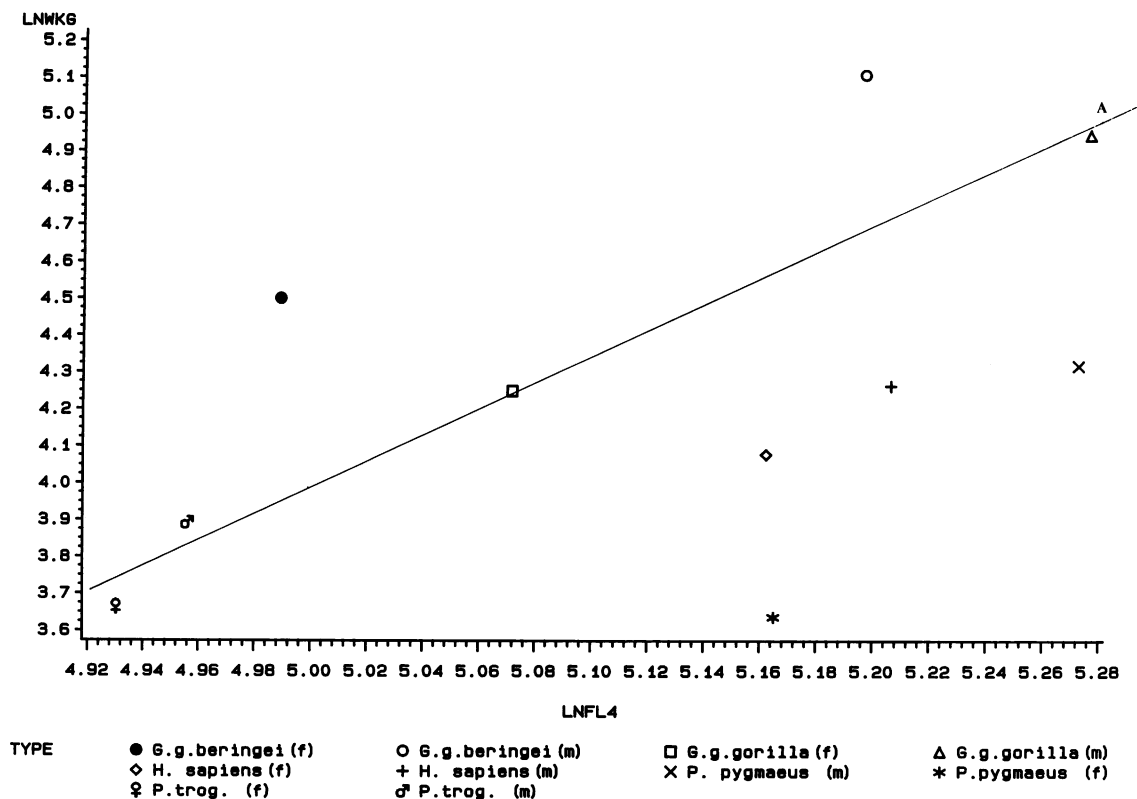
Fig. 19. Natural log of average values of body weight (LNWKG) vs. that of the average FL4 in male and female lowland and highland gorillas, chimpanzees, orangutans, and humans (A, linear regression for chimpanzees and lowland gorillas, slope = 0.282, y intcpt. = 3.88, adj. r^2 = 0.98).

Both humans and great apes possess a tendinous raphe that provides the origin for the transverse head of the adductor hallucis whenever the muscle is present. The raphe, probably a remnant of the contrahentes to the II, IV, and V digit (Rugge, 1878; Straus, 1930), reflects the common loss of these muscles among hominoids. The adductor hallucis, the homolog of the 1st contrahentes muscle, is the only pedal contrahentes retained by all hominoids. Nevertheless, gorillas most closely resemble humans in having completely lost the three lateral contrahentes muscles. Straus (1930) found only one report by Macalister (1874) as to the probable presence of a contrahentes in the gorilla, that to the 5th toe. However, Macalister (1874) does not present an illustration of this muscle. There is no information as to the division of this adductor from the flexor of the little toe and hence its identity as a contrahentes is by no means certain. As noted by Keith (1899) the

2nd to 4th contrahentes muscles are always more developed in chimpanzees than in gorillas. They are also present in orangutans and gibbons, although in both these forms as in chimpanzees, they are attenuated. Usually it is the 4th contrahentes muscle to the 5th digit that is most commonly seen among the hominoids (Kohlbrugge, 1897).

Mechanically, the transverse head of the adductor hallucis of humans acts as a contractile tie for the heads of the metatarsals, complementing the passive force applied by the deep transverse metatarsal ligament. Prior to the toe-off, the actions of the muscle and the force applied by the ligament insure that the load is distributed evenly and sequentially over the ball of the foot. In this regard, the less developed transverse head of the adductor hallucis in great apes attests to a relatively lighter load on the foot—specifically on the metatarsal heads. From among the apes, its strong development in gorillas
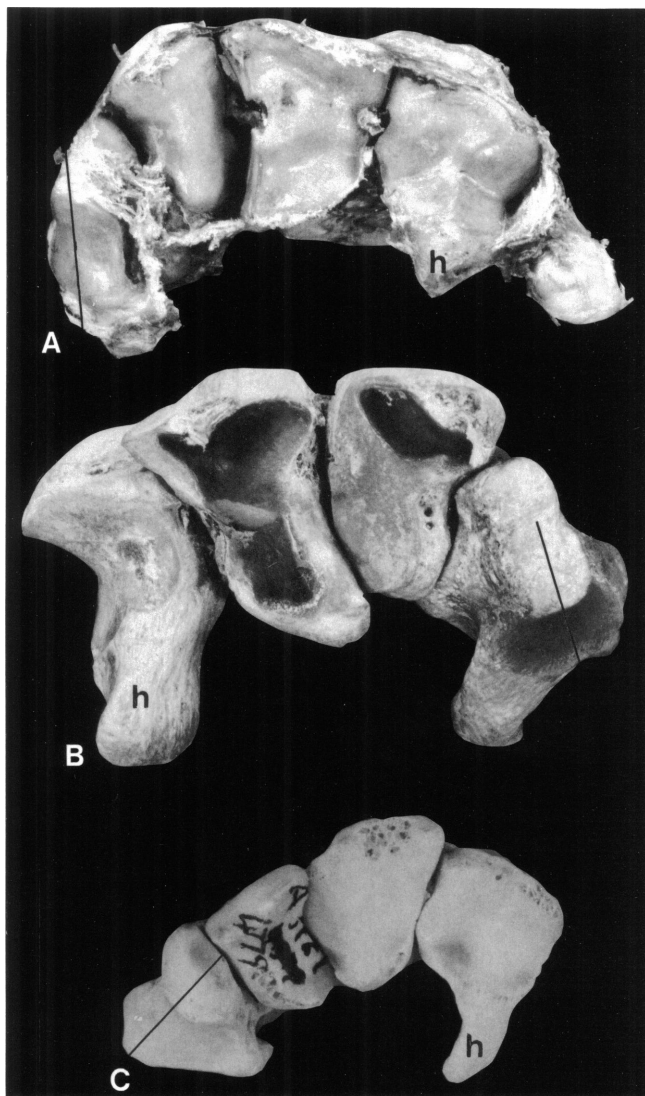
Fig. 20.   Proximal articular surfaces of carpometacarpal joints in closed packed position in chimpanzee (**A**, left side), highland gorilla (**B**, right side), and human (**C**, left side). Note difference in orientation of axis of 1st carpometacarpal joint. Gorillas show an orientation intermediate between chimpanzees and humans. The human and gorilla trapezoid is larger (table 10), mediolaterally broader palmarly,and not as wedge shaped as in chimpanzees. Hence, the trapezium does not exhibit as rotated a set as in chimpanzees. Also note the relatively marked palmar extension of the hamulus (h) in both gorillas and humans accentuating the palmar arch, ulnarly.

in part reflects their size, and also the similar mechanical requisites on the foot in bipedal and quadrupedal terrestriality. In this regard, the loss of the contrahentes and the development of a tendinous raphe reflect the use of the foot as a rigid lever and merit a similar explanation in both humans and gorillas as the full loss of the manual contrahentes.

PROPORTIONS AND STRUCTURAL FEATURES

HAND

Ulnocarpal joint

As in humans, the gorilla wrist has fully incorporated the semilunar meniscus into the

triangular articular disc, and is the only great ape that does so (Lewis, 1969; Sarmiento, 1988). Fusion of these structures fully excludes the ulnar styloid process from the proximal carpal joint. This specialization allows the ulnar head, housed in its own synovial cavity, to unload weight through the triangular articular disc onto the carpals (Corrucinni, 1978; Sarmiento, 1985, 1988). The triangular disc acts as a bearing surface allowing pronation and supination of the forearm during weight support (MacConaill, 1941; Sarmiento, 1985, 1988). As a result of its exclusion from the ulnocarpal joint, the gorilla's ulna practically lacks a styloid process.

Curvature of carpal rows and angles of hamate

Gorillas, like humans, have a larger radius of curvature for the carpal rows than do any of the other great apes. The radius of curvature is reflected in the angles of the hamate, which are similar to those of humans and the terrestrial cercopithecoids (Sarmiento, 1985, 1988). A large radius of curvature of the carpal row is functionally associated with restricted mediolateral deviations of the hand (Sarmiento, 1988). The angle values of the hamate, however, are also indicative of the inclination and length of the ulnar and distal sides of the bone. Hence they are representative of the ability of the ulnar head to transmit weight through the triquetrum to the hamate. With very large proximal angles and disproportionately long distal articulations, the triquetral articulation is nearly parallel to the articulation for the 4th and 5th metacarpals. As exhibited in gorillas, such an orientation is advantageous for weight support.

Gorillas, like humans, chimpanzees, and cercopithecoids all have a shelflike ulnar extension of the triquetral articular surface referred to by Lewis (1974) as a "spiral" triquetral articulation, that allows the triquetrum to more effectively transfer weight to the hamate (Jenkins and Fleagle, 1975). This articular configuration effectively increases the curvature of the carpal row and the surface area perpendicular to weight-bearing loads. It also probably serves to check mediolateral movements at the midcarpal row

when the wrist is in extended postures (Lewis, 1977). Associated with carpal curvature the facet no doubt reflects the hands' use as a weight-bearing organ (Sarmiento, 1985).

Hamulus of the hamate and pisiform

A relatively large and long hamulus of the hamate, and a palmarly protruding pisiform are other characteristics that are shared by African apes and humans (Sarmiento, 1988), but are nonetheless best expressed in gorillas (fig. 20). The pisiform, which is bound to the hamulus by the piso-hamate ligament, acts as the lever arm of the flexor carpi ulnaris. A palmarly protruding hamulus and pisiform are beneficial when flexing an extended wrist or preventing further extension of an extended wrist (Sarmiento, 1988). In habitually arboreal forms, on the other hand, the pisiform is usually positioned and directed distally (Sarmiento, 1985, 1988). This position improves the lever arm of the flexor carpi ulnaris for ulnar adduction of the wrist and flexion of a flexed wrist. Although humans and African apes have the distal migration of the pisiform characteristic of an arboreal ancestry (Sarmiento, 1985, 1988), the pisiform is directed palmarly. Specifically in gorillas, the lever arm of the flexor carpi ulnaris muscle for wrist flexion is greater in extended than in flexed wrist postures. Furthermore, owing to its length and probably also to the size of the flexor carpi ulnaris muscle, the gorilla pisiform forms a greater percentage of the weight of the carpus than it does in the other hominoids (table 10). When compared to that of chimpanzees, the gorilla's hamulus is also much better developed, and presents a more palmar orientation (fig. 20). This provides the intrinsic muscle of the hypothenar eminence with an advantageous lever for flexion and preventing extension of an extended 5th carpometacarpal joint. As in other terrestrial quadrupeds, the long, large and palmarly protruding pisiform is associated with use of the hand in propulsive efforts (Sarmiento, 1985, 1988). The large palmarly directed hamulus of gorillas and humans, a trait not commonly seen in other terrestrial anthropoids, probably reflects the need to stabilize the mobile midcarpal and 5th car-
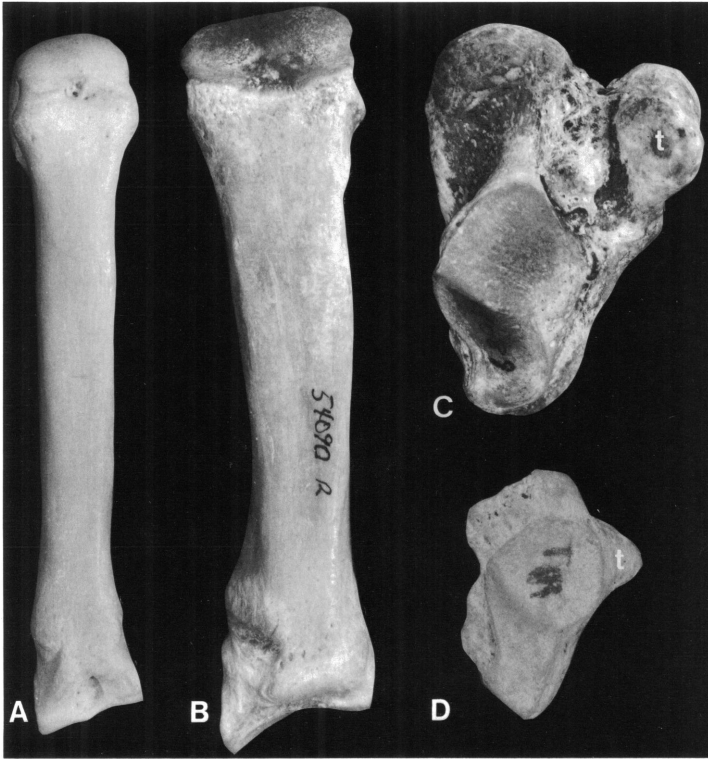
Fig. 21. Dorsal view of 3rd left metacarpal in male chimpanzee (**A**) and male mountain gorilla (**B**), and proximal view of right trapezium in male mountain gorilla (**C**) and South African black male (**D**). Note in the mountain gorilla, the large tubercle (t) resulting from fusion of the radial sesamoid of the abductor pollicis longus to the trapezium, and the poor development of a corresponding tubercle in humans. 3rd metatarsal in the gorilla has a well-developed styloid process on its base which is absent in chimpanzees, although both animals show an ulnar inclination of their proximal articular surface.

pometacarpal joint characteristic of hominoids.

Relative weight of trapezoid

In percentage of total carpal weight, gorillas and humans have the heaviest trapezoid of all of the measured haplorrhines (table 10). Compared to chimpanzees, the weight of the gorilla trapezoid reflects the use of the 2nd metacarpal for weight support. Chimpanzees characteristically orient the mediolateral axis of the hand along the plane of upper-limb movement and rarely contact the substrate with the phalanges of the second digit (Tuttle, 1970). The body weight distributed to the 2nd metacarpal in gorillas may account for a relatively larger trapezoid.

Owing to its relatively large size the trapezoid of gorillas is relatively broader mediolaterally on its palmar surface (fig. 20), variably exhibiting a palmar articulation with the base of the 3rd metatarsal and with the palmar beak of the capitate. When compared to chimpanzees, the palmar breadth of the gorilla's trapezoid is associated with a less palmarly rotated set to the trapezium (fig. 20). Both the morphology and the relative mass of the gorilla trapezoid reflect loading of the four lateral digits and are a corollary of committed terrestriality. The relatively heavy trapezoid in patas monkeys and baboons, both terrestrial quadrupeds, further supports this association.

Os centrale

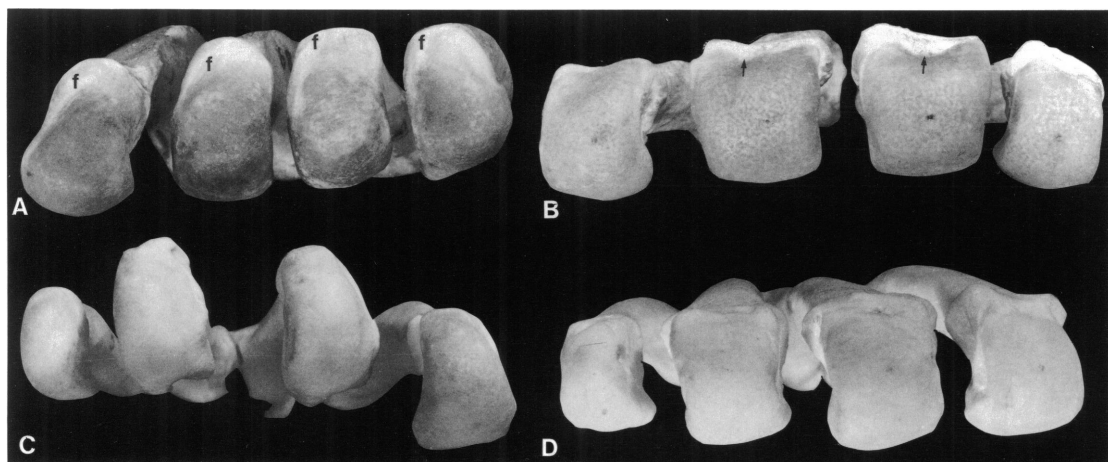Gorillas share with humans and chimpanzees the fusion of the os centrale to the scaph-

Fig. 22. Distal view of 2nd through 5th metatarsal and metacarpal heads of male highland gorilla (**A & B**, left side) and male chimpanzee (**C & D**, right side). Note in gorillas the greater mediolateral width of metacarpal heads relative to their dorsoplantar breadth, the notched dorsal edge of the articular surface on the 3rd and 4th metacarpal heads (marked by arrows), and the relatively large 5th metacarpal head. Relative to chimpanzees, the mediolateral width of the metatarsal heads in gorillas do not vary as much from the palmar to the dorsal aspect of the articular surface. Also note the well-developed dorsal flanges (f) of the gorilla's metatarsal heads, testimony to their hyperextended metatarsophalangeal postures.

oid (Mivart, 1867; Virchow, 1929; Weinert, 1932; Schultz, 1968). Interestingly, fusion of the os centrale is seen earliest in life in humans (3rd fetal month: Leboucq, 1884) followed by chimpanzees, and then gorillas (at birth and in infancy respectively, Schultz, 1968). As a rule, in all of the other anthropoids the os centrale is free from the scaphoid. However, there is considerable variability in this trait. Complete fusion of the os centrale is occasionally seen in all of the other species of hominoids in late adult life (Schultz, 1940, 1941, 1944, 1956). It also occurs rarely in various genera of anthropoids (Sarmiento, 1985). In indrids (*Indri* and *Avahi*), the os centrale is always fused to the scaphoid (Mivart, 1867). This fusion probably reflects the preference for weighing the radial side of the hand during vertical climbing and quadrupedal behaviors, and an associated radial position of the midcarpal joint axis (Sarmiento, 1985). Because an unfused os centrale provides movement between the midcarpal joint and the scaphoid, it compensates for the eccentric movements of the joint relative to the scaphoid. The proximity of the midcarpal joint's fulcrum to the scaphoid minimizes these eccentric movements. Hence, the additional mobility afforded by a separate os centrale is not necessary. Among the African apes the tendency for loading the radial side of the carpus which leads to fusion can also be seen in the relatively heavier weight of the capitate and trapezium in proportion to the total weight of the carpal bones (Sarmiento, 1985). A separate os centrale does occur occasionally in African apes and humans. Its fusion in chimpanzees and gorillas contrasted to its presence in orangutans is probably due to the use of the hand for weight-bearing during terrestrial behaviors.

Relative length of pollical metacarpal

The pollical metacarpal of African apes and humans has more or less the same absolute length. Gorillas, however, have pollical metacarpals that, relative to the length of the 3rd metacarpal, are longer than in chimpanzees, but shorter than in humans. Highland gorillas exhibit pollical metacarpals that are relatively longer and more closely approximate the human condition than those of lowland gorillas (table 9, fig. 16). In this regard,
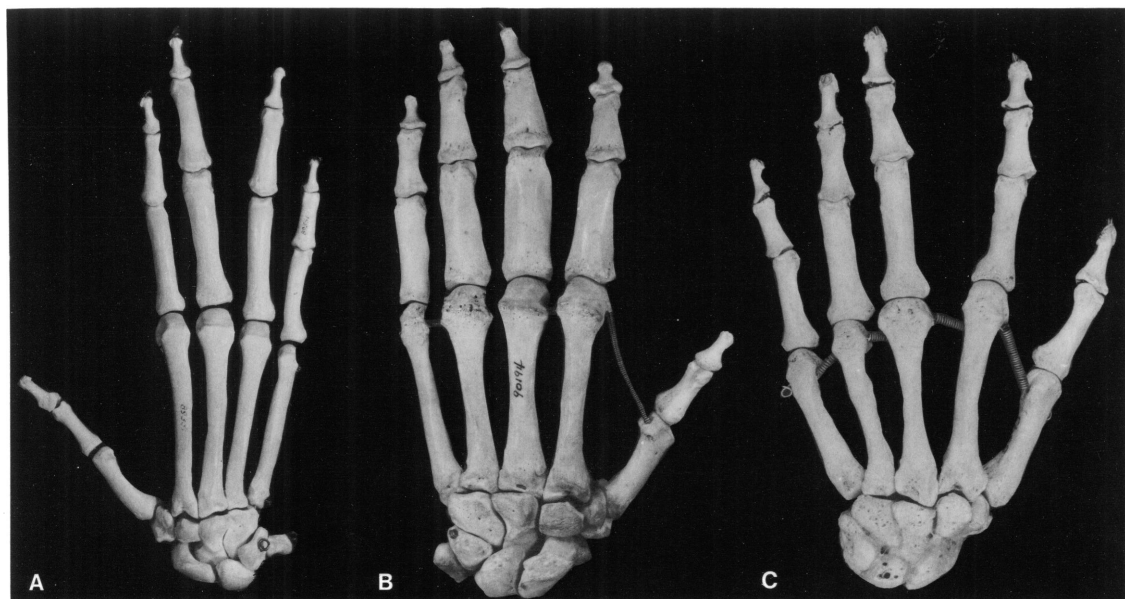
Fig. 23.   Right hand of male chimpanzee (A) and left hands of male lowland gorilla (B) and South African black male (C) all reduced to the same size. Note the longer rays and relatively short and narrow carpus of the chimpanzee when compared to that of the human and gorilla. The human and gorilla have much more robust metacarpals and phalanges, with articular surfaces that are wide relative to their length. Gorillas, however, have proximal phalanges with mediolaterally broad shafts owing to the well-developed flanges for the flexor sheath. Also note the similarities in the length of the gorilla metacarpals in contrast to the progressive increase in length from the 5th to the 2nd metacarpal in the human. Additionally, the gorilla thumb is not as long as that of the human.

it could be argued that the relative length of the pollical metacarpal is the result of the decreased length of the remaining metacarpals. Short metacarpal length is a correlate of terrestrial quadrupedality (Jolly, 1965, 1972; Etter, 1974; Sarmiento, 1985).

Styloid process on base of third metacarpal

The presence of the styloid process on the 3rd metacarpal is a trait which has been cited as peculiar to humans. (Marzke, 1983, 1986; Marzke and Marzke, 1987). A strongly formed styloid process, however, is also common in gorillas (fig. 21). The length of the styloid process is associated with a proximodistally long dorsal contact facet between the 2nd and 3rd metacarpal and a respectively short and proximally oriented contact facet between the capitate and 2nd metacarpal. Because the palmar border of this facet serves as an attachment area for intermetacarpal ligaments, an increase in styloid length indicates a sec-

ond metacarpal that is more strongly bound to the 3rd metacarpal. On the other hand, the larger contact and greater attachment area between the 2nd and 3rd metacarpal sacrifice the attachment between the 2nd metacarpal and the capitate. Strong ligaments anchoring the 2nd metacarpal to the carpus are important in suspensory forms where tensile forces tend to pull the two apart (Sarmiento, 1985, 1988). The strong attachment of the 2nd and 3rd metacarpal provides more stability of the metacarpals relative to each other during weight bearing. Additionally, a well-developed styloid stabilizes against rotation of the 2nd and 3rd metacarpals relative to the carpus and impedes palmar displacement of the metacarpal and hyperextension at the carpometacarpal joint. In this regard, the presence of the styloid in gorillas and its absence in chimpanzees may be associated with their differences in loading of the 2nd metacarpal during knuckle-walking. A styloid process, however, may also be beneficial to other hand postures which stress the carpometacarpal

joint in the same manner, i.e., digitigrade or semidigitigrade hand postures. Furthermore, since the relative development of the styloid is also associated with the inclination of the 3rd metacarpal's proximal articular surface and the related inclination of the long axis of the 3rd metacarpal relative to the carpus (fig. 21), this process in gorillas and humans also reflects their relatively shorter and broader hands. Although Marzke (1986) has suggested that the styloid is associated with the use of the hand for throwing and other manipulative behaviors, it is unclear how it actually augments them. Even if it is beneficial for these behaviors, this does not explain the presence of a styloid in gorillas.

Dorsal phalangeal digital pads and dorsal flanges on metacarpal heads

As noted by Tuttle (1967, 1969), the African apes exhibit digital pads on the dorsal surface of the middle phalanges of all four fingers. Additionally, they also exhibit dorsal flanges on their metacarpal heads. Because the metacarpophalangeal joint is held in hyperextended postures, the metacarpal head of gorillas is notched dorsally (fig. 22), a feature that is absent in chimpanzees. Gorillas also differ from chimpanzees in having relatively larger 2nd and 5th metacarpal heads, and articular condyles on the proximal phalanges that are best defined palmarly. In gorillas these features reflect respectively the weighing of the 2nd and 5th metacarpal and the markedly flexed posture of their proximal interphalangeal joint during knuckle-walking (Sarmiento, 1988; Inouye, 1992).

Relative length of hand and robusticity and curvature of phalanges

The hands of gorillas are extremely broad in relation to their length, which approximates the proportions of human hands (fig. 23; Schultz, 1956). The more terrestrial mountain gorilla has a relatively broader hand than does the lowland gorilla (Schultz, 1934). The ratio of hand breadth to length in gorillas is in large part a function of their relatively short hands (fig. 17). Lowland gorillas have short hands that relative to body weight scale similarly to those of humans, while chimpanzees and orangutans have relatively lon-

ger hands. Gorilla metacarpals and fingers are relatively shorter than those of the other great apes and considerably more robust, either when compared to the diameter of their articular surfaces or to that of their midshafts (Stern and Susman, 1983; Susman et al., 1984). Given this length and robusticity coupled with the markedly extended postures at the metacarpophalangeal joint (Sarmiento, 1985) the gorilla phalanges are less curved than those of chimpanzees, approximating the curvature seen in humans (Susman et al., 1984). Gorilla behavior associates their manual proportions and phalangeal curvatures with terrestrial quadrupedal hand use.

FOOT

Pedal lever arms

In proportions of the main segments of the foot, gorillas approximate humans more closely than do any other great ape (Schultz, 1936, 1963, 1968). When these proportions are analyzed in light of the lever arms they determine, gorillas are hard to distinguish from humans, while both are easily separable from chimpanzees (tables 6, 7; figs. 3–7). There is a large range of overlap between humans and gorillas in the values of the lever arm of the triceps surae when compared to the 4th metatarsal foot length (fig. 3). Lowland gorillas show slightly higher values for this ratio than do humans, but highland gorillas show approximately the same values as humans. Although this proportion scales linearly within the African apes and humans, chimpanzees have only a small overlapping range with either gorillas or humans (table 6). A logarithmic comparison of the length of the FL4 to body weight, however, shows that lowland gorillas and chimpanzees fit more or less the same regression (fig. 19). In contrast, highland gorillas have shorter feet and humans have longer feet relative to weight. Humans are unique in having a relatively long tarsus distal to the axis of the subtalar joint, and metatarsals that are short relative to metatarsal foot length (figs. 6, 7). In this case, mountain gorillas have values that widely overlap those of humans and approximate them more closely. This is best shown when the proximodistal length of the cuboid is compared to metatarsal foot length

(fig. 5). The long distal tarsus of humans is associated to the longitudinal arch and the need to increase the lever arm of the tibial and peroneal musculature (Sarmiento, in prep.).

Comparison of the length of the hallucal metatarsal to metatarsal foot length shows that gorillas generally have a proportionately shorter hallucal metatarsal than do chimpanzees or humans, but have values overlapping those of humans (table 7). The hallucal metatarsal of lowland gorillas, when taken as a proportion of the length of the lever arm of the triceps surae, is also relatively shorter than those of humans and chimpanzees. The gorilla's 1st metatarsal is likewise generally shorter than that of humans, but similar in length to that of chimpanzees when compared relative to the length of the third metatarsal. With regards to this proportion, mountain gorillas approximate humans more closely than do other African apes (fig. 8).

That gorillas show a very low value of the 1st metatarsal length relative to the lever arm of the triceps surae may be related to their body weight and the propulsive use of the hallux in plantigrady. Considering that muscular strength proportionately decreases with increase in size, gorillas should have a relatively longer triceps surae lever arm than a hallucal outlever, if they are to apply a proportionately equivalent force at toe-off as that applied by the smaller-bodied chimpanzees. When the triceps lever length, metatarsal foot length, or 3rd metatarsal length are plotted against the length of the 1st metatarsal, gorillas, humans, and chimpanzees all show a proportional decrease in these ratios with an absolute increase in 1st metatarsal length (figs. 8–10), lending support to the above interpretation. All of the gorilla lever arms can be associated with the use of a plantigrade foot in terrestrial quadrupedal behaviors.

Tuber calcanei

The tuber calcanei of lowland gorillas tends to be broader mediolaterally relative to its dorsoplantar height than that of humans or chimpanzees (table 8). Mountain gorillas, however, possess a relatively narrower tuber calcanei than most humans, but are well within the human range. The lowland gorilla

ratio is as much a result of having a mediolaterally broad tuber calcanei as it is of having a plantodorsally short tuber. When the mediolateral breadth of the tuber calcanei is compared to the metatarsal foot length, it is seen to scale more or less linearly within African apes and humans (fig. 12). The exceptions are mountain gorillas, which tend to show a somewhat broader tuber calcanei in relation to metatarsal foot length than the other African apes and humans. When the dorsoplantar height of the tuber calcanei is compared to that of metatarsal foot length, lowland gorillas are seen to have a relatively much shorter tuber calcanei than humans and highland gorillas (fig. 13). Relative to metatarsal foot length, highland gorillas have the greatest dorsoplantar height of the tuber calcanei from among humans and the African apes. This height gives their broad tuber a narrow appearance.

The wide tuber calcanei of gorillas no doubt reflects the wide area of insertion associated to a large triceps surae muscle. The proportionate increase in the relative breadth of the tuber calcanei with increasing metatarsal foot length reflects the proportionately larger muscle in gorillas, and the scaling effects of size on muscular strength.

The dorsoplantarly short tuber of lowland gorillas, however, merits a different explanation. It suggests that the actual lever length of the triceps surae would be severely compromised toward the end of the range of joint motion especially in dorsiflexion. In analogy to a cam, a dorsoplantarly long tuber relative to triceps lever length, insures the muscle a constant lever arm throughout a wide range of movement at the tibiotalar and subtalar joints. Such a situation applies to the proportions exhibited in chimpanzees in which the height of the tuber is greater than the length of the lever arm (fig. 24), so that regardless of the position of the ankle joints the triceps surae maintains a consistent length for its lever arm. Comparison of calcanei (fig. 24) shows that gorillas have a reduced dorsoplantar length of that part of the tuber superior to the calcaneal body. This morphology suggests that the triceps surae of gorillas is unable to act powerfully in dorsiflexed postures of the foot. The close values of the triceps lever length and dorsoplantar tuber
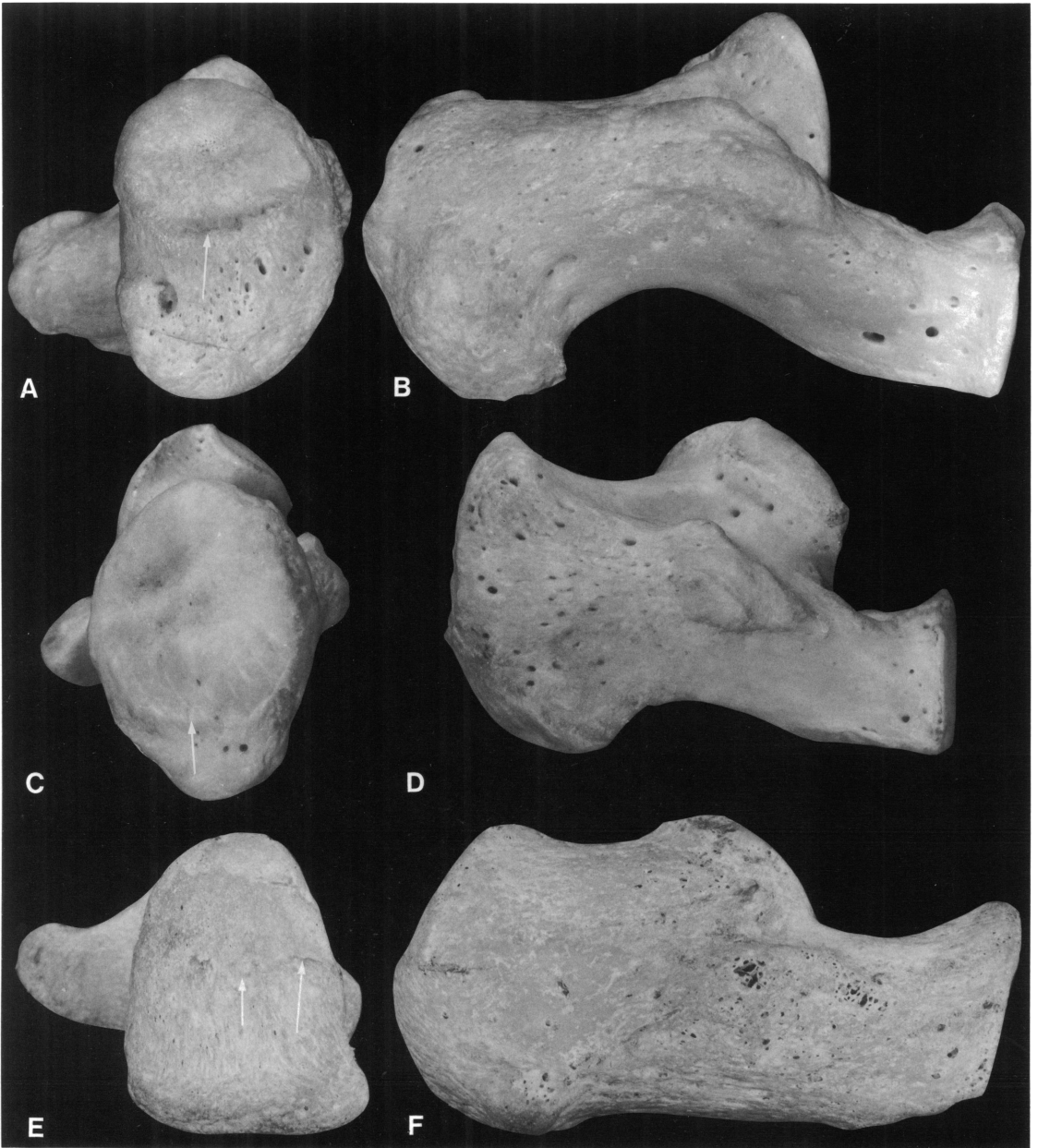
Fig. 24.   Posterior and lateral views of the calcanei of a lowland female gorilla (**A, B**), a male chimpanzee (**C, D**), and a female bushman (**E, F**). The insertion of the triceps surae tendon (marked by arrow) is proximally disposed in gorillas and humans and distally disposed in chimpanzees. The tuber of chimpanzees is analogous to a cam. Hence, the triceps surae tendon maintains a constant lever arm length throughout a wide range of dorsi and plantar flexion of the ankle joint. In humans and gorillas on the other hand, the higher insertion suggests the triceps surae acts effectively through a smaller range of ankle joint movement. Additionally, the gorilla tuber has plantarflexed set relative to the calcaneal body so as to provide a longer lever arm in plantarflexed postures of the ankle joint. In this regard, note the relatively more superior position of the posterior talocalcaneal joint in gorillas. Also note the progressive increase in the plantar inclination of the cuboid facet from chimpanzees to gorillas to humans.
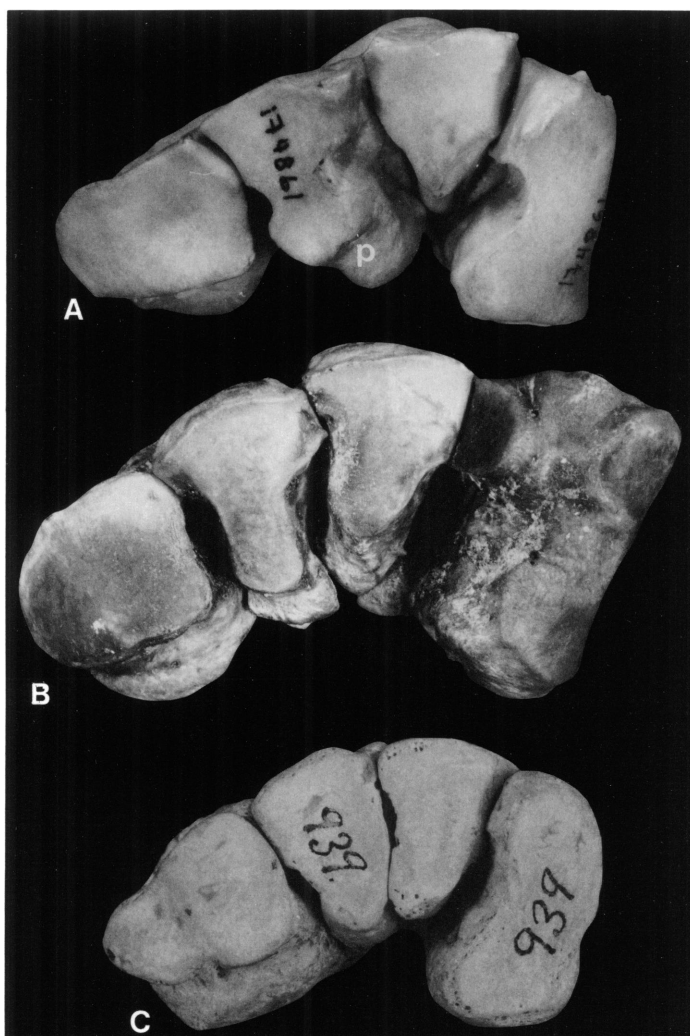
Fig. 25.   Proximal articular surface of the tarsometatarsal joint in the closed pack position in a male chimpanzee (**A**), male highland gorilla (**B**), and female bushman (**C**), depicting the height of the transverse tarsal arch. Note how much higher the arch is in gorillas and humans relative to chimpanzees. Chimpanzees consistently have a well-formed plantar tubercle (p) on the ectocuneiform, for contacting the substrate. This tubercle is variably developed in gorillas and absent in humans.

height in most humans and mountain gorillas (fig. 14) suggest that an optimum lever length of the triceps surae is maintained throughout the range of joint motion.

When the dorsoplantar height of insertion of the triceps surae tendon is compared to the dorsoplantar height of the tuber, gorillas have a higher insertion point on the tuber than do chimpanzees and humans (table 8). The higher insertion in gorillas also reflects the limited range of motion the gorilla triceps

surae acts through, relative to that of chimpanzees and humans.

Weight-bearing tubercles of tarsus and talocalcaneonavicular joint

In gorillas, because the sole overlying the distal tarsus makes contact with the substrate during weight support, the underlying bones exhibit weight-bearing tubercles on their plantar surfaces. The entocuneiform, the ectocuneiform, the navicular, and the cuboid

all have such weight-bearing processes variably developed. Gorillas additionally exhibit a well-developed anterior plantar tubercle on the calcaneus. Chimpanzees also possess all of these tubercles, usually relatively better developed than in gorillas (fig. 25). Humans lack weight-support tubercles on the plantar surfaces of the distal tarsal bones due to the longitudinal and transverse arches.

Additionally, gorillas and chimpanzees possess a large plantar-weight-bearing tubercle on the navicular bone associated in part with the insertion of the tibialis posterior (fig. 26). The gorilla tubercle, however, is much larger than that of the chimpanzee, and is associated superiorly with a proximally extended articular surface for the talar head. As a result of this extension, the navicular's talar articulation subtends a larger central angle in gorillas than in chimpanzees. When articulated with its corresponding facet on the sustentaculum tali, the navicular and sustentaculum of gorillas form the entire articular surface for the talar head. There is no articular surface on the gorilla's talar head corresponding to the plantar calcaneonavicular or spring ligament as exhibited in both humans and chimpanzees. Moreover, chimpanzees and humans usually lack a defined articular surface between the navicular and sustentaculum (fig. 26). Given the condition in gorillas, the tibialis posterior does not support the head of the talus. Considering the energy-storing function of the spring ligament and underlying tibialis posterior during footfall (Kerr et al., 1987; Alexander, 1989) the gorilla foot is probably less elastic than that of humans and hence unable to store as much energy.

Transverse arch

Gorillas, especially the mountain variety, show some development of a transverse arch when the distal tarsus is articulated in a closed-packed position (fig. 25) despite having plantar weight-bearing tubercles on the distal tarsus. The less developed plantar tubercle on the ectocuneiform relative to chimpanzees reflects the stronger development of this arch in gorillas. Its presence is also reflected in the less developed groove for the tendon of the peroneus longus on the ectocuneiform and

on the medial aspect of the plantar surface of the cuboid. Given a strong development of the transverse arch, the peroneus longus tendon bow strings and does not strongly groove the plantar surface of the tarsus. In this regard, gorillas approximate the human condition. In humans the ectocuneiform lacks a plantar weight-bearing tubercle or a groove for the peroneus longus tendon. Considering that gorillas use the foot as a lever during propulsion, the development of a transverse arch and the shape it positions the foot into would increase its ability to withstand bending moments along a sagittal plane as in humans. In analogy to humans and gorillas, baboons also show a strongly developed transverse arch and similarly use the foot as a lever for propulsion (Rose, in press).

Cuboid angles

The gorilla cuboid also differs from that of humans and chimpanzees in the angles that define the orientation of its proximal and distal articulation and the relative length of its four sides (fig. 2, table 5). Gorillas have the highest average value for the cuboid's proximolateral angle and the lowest average value for the cuboid's proximomedial and distolateral angle when compared to humans and chimpanzees. Therefore, the gorilla cuboid has relatively the longest distal side, and the shortest lateral and medial side. Nevertheless, in gorillas the average inclination of the proximal articulation relative to the distal one does not differ from that of humans and differs only slightly from that of chimpanzees. Gorillas and humans show a distal articulation that diverges laterally from the proximal articulation an average of 32° and chimpanzees show one that on the average diverges 28°. In chimpanzees the angle between the articular surfaces reflects the lateral divergence of the 4th and 5th ray from the long axis of the foot. In humans, due to the transverse arch and the associated medially rotated posture of the cuboid, these angles reflect the plantar orientation imparted to the 5th metatarsal, and hence the cuboid's role as the keystone of the lateral longitudinal arch. Due to the less developed transverse arch in gorillas, the angle formed by the two articulations reflects both the laterally divergent
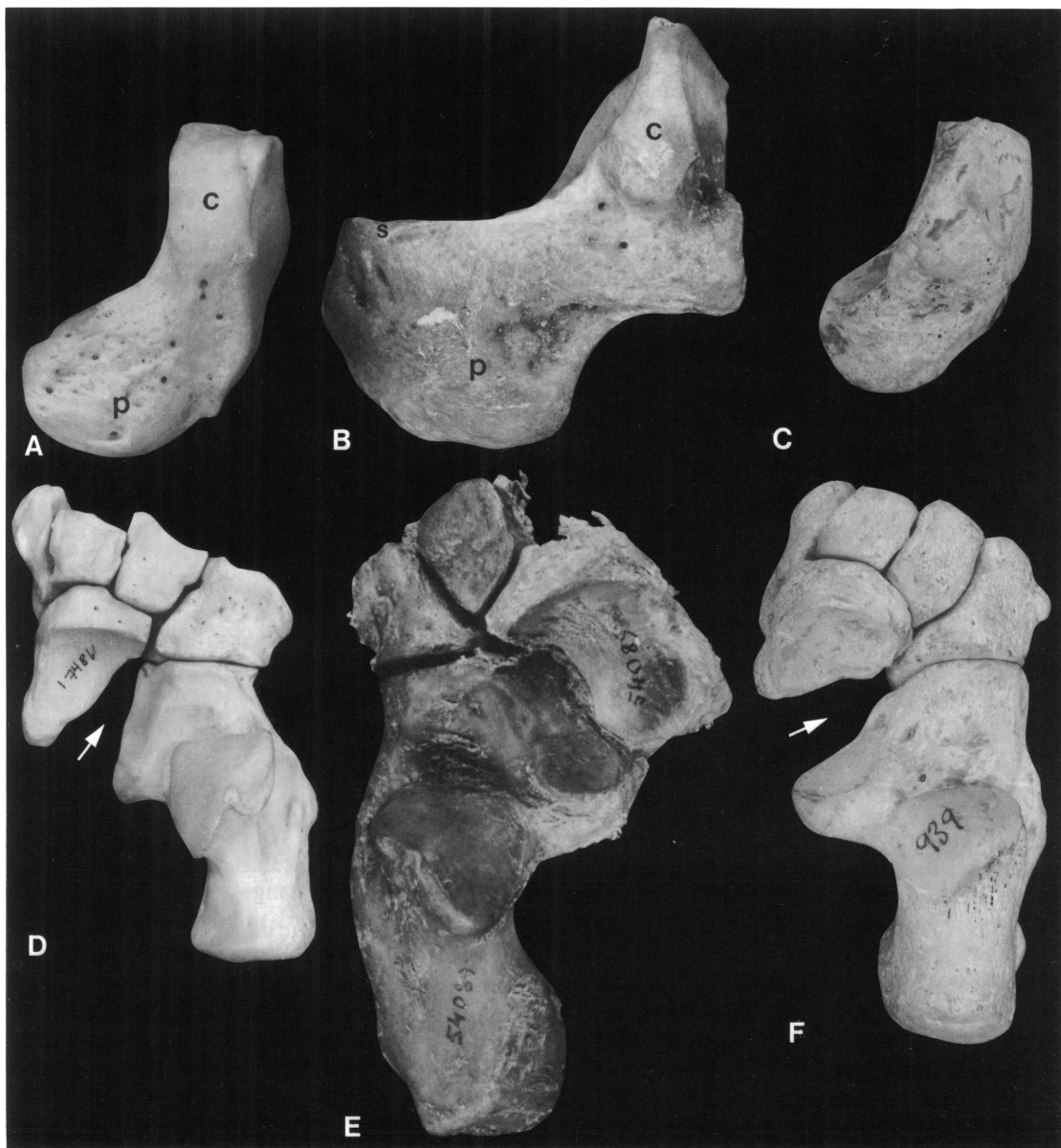
Fig. 26. Medial view of right navicular in male chimpanzee (A), male highland gorilla (B), and female bushman (C); corresponding dorsal view of the tarsus with the talus removed in the chimpanzee (D, right side), gorilla (E, left side), and human (F, right side). Note the large radius of curvature subtended by the navicular's talar facet and the large plantar tubercle in the gorilla (p). Both gorillas and chimpanzees consistently exhibit a facet for the cuboid (c). However, gorillas may also show a small sustentacular facet proximally (s), on the medial edge of the navicular's talar facet. When articular, the calcaneus and the navicular of gorillas form the complete articular surface for the head of the talus. In humans and chimpanzees, on the other hand, there is an intervening space between the sustentaculum and navicular that is closed off by the calcaneonavicular or spring ligament and reinforced inferiorly by the tendon of the tibialis posterior.

4th and 5th metatarsal and a slight plantar inclination of the articulation of the 5th metatarsal.

Calcanean process of cuboid

When compared to chimpanzees and humans, gorillas show a remarkably poor development of the calcanean process of the cuboid (fig. 27). It is especially poorly developed in large males while the smaller females show a better development. According to Lewis (1980a) and Rose (1988) the calcanean process of chimpanzees and orangutans functions as an odontoid process enabling rotation of the cuboid relative to the calcaneus while helping to maintain joint stability. The absence of this process in some male gorillas suggests that they lack this stability and may not rotate the cuboid and hence markedly supinate the calcaneocuboid joint. In this regards, the better development of the calcanean process in female gorillas may actually reflect a greater foot mobility associated with smaller body size. Humans, on the other hand, also have a strong development of the odontoid process, but do not show marked rotation at the calcaneocuboid joint. The strong development of the human process may be necessary to stabilize the calcaneus on the cuboid when weight is shifted along the lateral arch from the heel to the balls of the foot. In this regard, its absence in gorillas also means that the anterior plantar tubercle of the calcaneus contacts the substrate and the cuboid need not impart such stability.

First metatarsal torsion

Gorillas approximate humans in the degree of torsion of the 1st metatarsal, both sharing an overlapping range of values (table 4). Gorillas exhibit considerably less torsion of the 1st metatarsal than do chimpanzees. In humans, the degree of torsion of the 1st metatarsal is related to adducted hallucal postures and the loss of opposability. These features, necessary for the formation of the medial longitudinal arch (fig. 28), are achieved through (a) reorientation of the 1st cuneiform's proximal articulation relative to its distal one, (b) talar head torsion, and (c) the associated plantodorsal realignment of the long axis of the navicular and 1st cuneiform (table 4). As
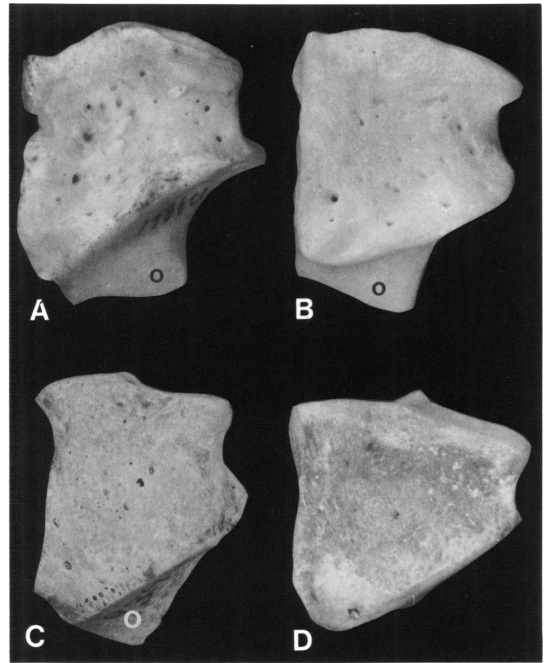

Fig. 27. Dorsal view of the right cuboids of a male chimpanzee (**A**), a female lowland gorilla (**B**), a female bushman (**C**), and a male lowland gorilla (**D**). Note the total absence of a calcanean or odontoid process (O) in the male lowland gorilla and the well-formed processes in the chimpanzee and female gorilla.

such, the entocuneiform metatarsal joint is positioned with its long axis parallel to the gravity vector, so as to best resist the bending moments associated with weight bearing. The alignment of the plane of movement of the 1st metatarsophalangeal joint with the plane of movement of the foot and along the plane of bending moments is a necessity for effective propulsion, and hence is associated with the low torsion values of the 1st human metatarsal. The torsion value of the gorilla 1st metatarsal, similarly, reflects a hallux that is held close in line with the foot's long axis and a dorsoplantar plane of movement of the 1st metatarsophalangeal joint. These orientations enhance the big toe's role in propulsion at the expense of its role in opposition. Because gorillas lack a medial longitudinal arch, and hence have lower talar torsion values than do humans (table 4), the 1st metatarsal can exhibit higher torsion values, but can still be effectively oriented for propulsion. The
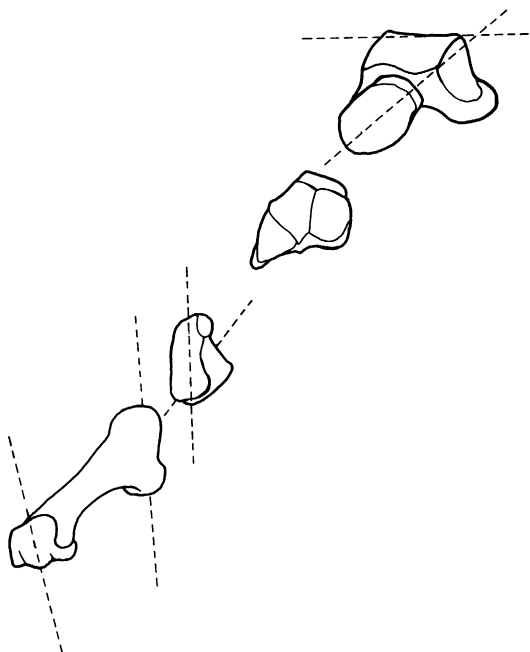
Fig. 28. The contributions of talar head torsion, 1st metatarsal torsion, and the relative orientation of the distal and proximal articular surfaces of the entocuneiform to the final orientation of the head of the 1st metatarsal as illustrated in a human. The angle in the frontal plane between the talar trochlear axis and the 1st metatarsal head is the sum of the three component angles. Decrease in talar head torsion is offset by an increase in metatarsal torsion or an increase in the angles between the distal and proximal articulations of the entocuneiform and vice versa.

high talar torsion values of mountain gorillas approximating those of humans reflect a talonavicular joint with its long axis positioned so as to best resist bending moments from loading. This orientation indicates that despite the weight-bearing tubercles of the distal tarsus and the absence of a longitudinal arch, the midtarsal joint of mountain gorillas is better able to resist dorsiflexion than those of lowland gorillas and chimpanzees.

Metatarsal heads

The heads of the metatarsals in gorillas project more superiorly above the metatarsal shaft than do those of chimpanzees (fig. 29). Additionally, the metatarsal heads of gorillas are not relatively as narrow dorsally as in

chimpanzees and exhibit a dorsal flange for limiting extension and presenting proximal displacement of the phalanges (fig. 22). This morphology is in accord with the terrestrial postures of gorillas, which show hyperextension of the metatarsophalangeal joint at toe-off, a posture not exhibited in chimpanzees.

Length and width of foot

The similarities to humans exhibited in the internal structure of the gorilla foot are also reflected externally. The foot of the more terrestrial mountain gorilla, which shows a closer approximation in muscular and osseous features to the foot of humans, also differs externally from that of lowland gorillas. Mountain gorillas have a broader foot than do lowland gorillas (Schultz, 1934; Groves and Stott, 1979). The gorilla foot is broader than that of humans, especially across the midtarsal joint (Schultz, 1956, 1968) owing to the less pronounced transverse tarsal arch and the less adducted postures of the hallux. As with their wide hands, the wide foot of gorillas in part reflects its short length relative to body weight and hence plantigrade terrestrial specializations. A natural log-on-log plot of foot length vs. body weight scales similarly in gorillas and humans. Although chimpanzee hands scale similar to those of orangutans, chimpanzee feet have lengths that scale midway between those of orangutans, and those of humans and gorillas, reflecting some degree of terrestrial commitment. This trend among hominoids to reduce foot length with increasing terrestriality clearly associates the length and breadth of the gorilla foot with marked terrestriality.

Distal extent of sole

The sole of the foot of mountain gorillas extends to the base or middle of the middle phalanges (table 13; Schultz, 1934; Groves and Stott, 1979). Mountain gorillas often exhibit a syndactylous condition in which the cleft between the lateral toes is absent. In the lowland gorillas the sole usually extends to the middle of the proximal phalanges as in humans. In chimpanzees, the sole extends up to the base of the proximal phalanges, as does the palmar surface of humans hands. Similarly, the cleft between the first and second
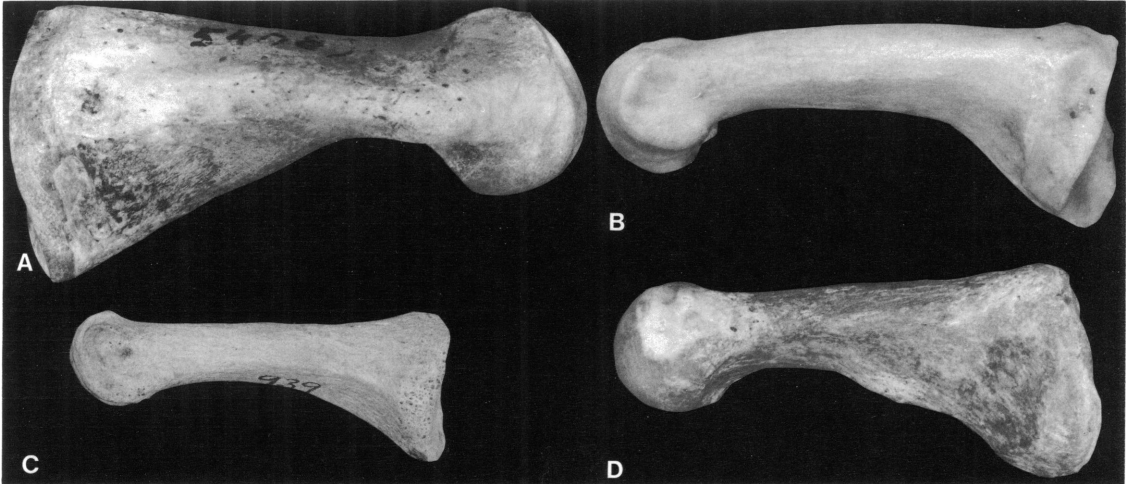
Fig. 29. Medial view of the 1st metatarsal of a highland male gorilla (**A**, left side), a chimpanzee (**B**, right side), and a bushman (**C**, right side), and lateral view of the same bone in a female highland gorilla (**D**, left side). Note the straight dorsal border of the metatarsal shaft and the dorsal extension of the head's articular surface in both gorillas and humans. Additionally, in gorillas, the shaft is markedly pyramidal in shape.

toe forms a smaller percentage of total foot length in highland than in lowland gorillas. According to Schultz (1934), and Groves and Stott (1979), the cleft comprises about 25% of foot length in highland gorillas and 37% in lowland gorillas. Measurements show that this cleft comprises between 16 and 18% of foot length in humans and between 42 and 52% of foot length in chimpanzees (table 13). The distal extent of the sole relative to the foot, is no doubt a terrestrial specialization. Strong cohesion between the phalanges provides better protection from sprains, and the toes' propulsive efforts can be kept along parallel planes. The more distal commencement of the cleft between the 1st and 2nd metatarsals in highland gorillas reflects an emphasis on the use of the hallux in propulsion at the expense of its use in opposition and merits a similar functional explanation as the distal extent of the sole.

CONCLUSIONS

When contrasted to humans and chimpanzees, the hand and foot morphology of gorillas clearly shows a large number of features that are associated with their quadrupedal terrestrial behaviors (table 15). In general, these features are always better developed in the mountain gorillas. The relatively short and wide hands and feet of gorillas are a requisite of terrestriality also exhibited in the other terrestrial primates (Jolly, 1965, 1967, 1972; Etter, 1973, 1974; Schultz, 1956; Napier and Napier, 1967). A number of features, also terrestrial in nature, are partly or wholly the result of these proportions, i.e., the large radius of curvature of the carpal row and the angles of the hamate, the relatively long pollex, the styloid process of the 3rd metacarpal, the relatively short outlever of the foot, and in highland gorillas the relatively long 1st metatarsal. Some features are directly related to the weight support functions of the hands and feet in quadrupedal behaviors and are also variably expressed by chimpanzees, i.e., the weight-bearing tubercles on the plantar surfaces of the distal tarsal bones, the digital pads on the dorsum of the middle phalanges, the relative weight of the trapezoid, the fused os centrale, the development of the triangular articular disc and the dorsal flanges on the heads of the metacarpals. Other features give mechanical advantage to movements important for quadrupedal motion and the postures associated with these movements. They include: the relative length of the lever arm of the triceps surae; the length, size, and orientation of the pisiform and the hamate's hamulus; the large and often fused radial ses-

TABLE 15
Terrestrial Characters in the Hands and Feet of Gorillas
A, Character seen in African apes and humans, B, Character usually exhibited in humans and gorillas, C, Character seen in chimpanzees and gorillas, D, Character unique to gorillas from among hominoids.

Character	Distri-bution	Functional interpretation in gorillas	Hypothesized primitive hominoid condition
1) A separate EPB muscle	B	Extension of pollical phalanx separate from pollical abduction	EPB & APL blended together
2) Fused radial sesamoid & associated large scaphoid tubercle	D	APL important flexor of extended wrist	Small unfused sesamoid, APL wrist abductor
3) Palmaris brevis muscle	B	Protection of ulnar artery during palmar weight bearing	Muscle absent
4) Complete absence of manual contrahentes[a]	B	Passive control of conjunct movements at metacarpophalangeal joint	Presence of poorly developed muscles to II & V digit
5) Deep transverse metacarpal ligament	A	Cohesion of metacarpophalangeal joint during loading	Absent
6) Palmar interossei with basal phalanx insertion	D	Hyperextended metacarpophalangeal joint postures	Palmar interossei with extensor hood insertion
7) Relatively poor development of dorsal interossei in hand	B	Emphasize stabilizing forces directed into palm, indicates D-P axis of hand aligned to direction of travel & hand grasp not used for weight support	Dorsal interossei well developed with large palmar components
8) Flexor digitorum brevis originating from well-developed plantar aponeurosis	A	Stabilize foot against dorsiflexion for use as rigid lever	Muscle fleshy, emphasizing II & III tendon
9) Strongly developed plantar aponeurosis	B	Strong cohesion of sole	Plantar aponeurosis absent
10) Pedal interossei adducting towards the second toe axis	B	Redirection of longitudinal axis of foot for propulsion at the expense of opposition	Interossei abduct toward III toe axis
11) Peroneus tertius	B	Eversion of foot to clear ground	Muscle absent
12) Segregation of the tendons of flexor fibularis and flexor tibialis[a]	A	Emphasize independent use of hallux for propulsion	Long flexor tendons derived from both muscles
13) Development of transverse head of adductor hallucis[a]	A	Loading of metatarsal heads during propulsion	Absent or poorly developed
14) Absence of pedal contrahentes & presence of tendinous raphe[a]	B	Passive cohesion of metatarsophalangeal joints during loading	Poorly developed muscle to II & V toe, absence of raphe
15) Large mediolateral radius of curvature of the carpal joints	B	Reduced carpal mobility, indicates weight-bearing hand	Tight radius of joint curvature
16) Large proximal hamate angle	B	Loading of IV & V metacarpals indicates weight-bearing hand	Angle small

TABLE 15—(*Continued*)

Character	Distri-bution	Functional interpretation in gorillas	Hypothesized primitive hominoid condition
17) Marked reduction of ulnar styloid process & triangular articular disc fully separating the ulna from the carpal joint	B	Loading of ulnar head in weight bearing	"Semilunar menicus" not fused to triangular disc, ulnar styloid protruding into carpal joint
18) Spiral triquetral facet	A	Control for midcarpal mobility, indicates possible locking mechanism during weight bearing	Absence of facet
19) Large, long and palmarly projected pisiform	A	Flex or check extension of extended wrist	Short distally directed pisiform
20) Large and palmarly projected hamulus	A	Flex or check extension of extended wrist & 5th carpometacarpal joint	Distally directed hamulus
21) Relatively large trapezoid with a mediolaterally expansive 2nd metacarpal articulation	B	Loading of 2nd metacarpal	Wedgelike trapezoid
22) Fused os centrale	A	Loading of radial side of wrist & radial position of midcarpal joint axis	Unfused bone
23) Relatively long pollical metacarpal[a]	B	Short II–V metacarpals, minimize bending moments during weight bearing	Conflicting data as to condition
24) Styloid process on the base of the 3rd metacarpal	B	Stabilize against rotation and extension of capitate 3rd metacarpal joint	Absence of styloid process
25) Digital pads on the dorsum of the phalanges	C	Weight bearing in knuckle-walking postures	No digital pads on dorsum of phalanges
26) Metacarpal heads with dorsal flanges	C	Stabilize metacarpophalangeal joint in hyperextended knuckle-walking postures	No flanges
27) Relatively short and broad hand[a]	B	Counteract & minimize bending moments, emphasize stability & surface area perpendicular to load, indicates hand used in weight bearing	Elongated hand
28) Relatively short and robust manual rays[a]	B	Counteract & minimize bending moments, indicates hand used in weight bearing	Long rays
29) Mild degree of phalangeal curvature compared to the other great apes[a]	B	Flexor tendons apply force in extended phalangeal postures, indicates grasping of relatively large supports or objects	Some degree of curvature
30) Large triceps lever arm relative to metatarsal foot length[a]	D	Use of foot as rigid lever for propulsion	Short lever arm
31) Relatively long hallucal metatarsal[a]	B	Use of foot as rigid lever for propulsion	Conflicting data as to condition

TABLE 15—(Continued)

Character	Distri-bution	Functional interpretation in gorillas	Hypothesized primitive hominoid condition
32) Relatively broad tuber cal-canei[a]	B	Use of foot as rigid lever for propulsion	Mediolaterally narrow tuber
33) Proximodistally short tuber calcanei	D	Triceps lever arm compro-mised by joint mobility, in-dicates restricted ankle mo-bility	Proximodistally tall tuber
34) Weight-bearing tubercles on tarsus	C	Use of tarsus for weight bear-ing in plantigrade foot	Tubercles absent on tarsoplan-tar surface
35) Absence of articular surface for spring ligament on talar head and associated enlarged navicular	D	Use of tarsus for weight bear-ing, compromised foot elas-ticity	Presence of surface and expan-sive ligament
36) Development of fixed trans-verse arch[a]	B	Rigidity of foot to dorsoplantar bending moments, indicates foot used as rigid lever for propulsion	Mobile transverse arch
37) Reduction or absence of cal-canean process of cuboid	D	Reduced ability for rotation at calcaneocuboid joint	Large calcanean process
38) Low 1st metatarsal torsion[a]	B	Alignment of the plane of movement of the foot with that of the metarsophalan-geal joint	Relatively high torsion
39) High talar torsion[a]	B	Alignment of long axis of talona-vicular joint with plane of foot movement	Relatively low torsion
40) Mediolaterally narrow and superiorly projected metatar-sal heads with dorsal flanges	D	Hyperextended postures at metatarsophalangeal joints	Metatarsal heads similar to metacarpal heads
41) Relatively short and broad foot[a]	B	Counteract and minimize bending moments. Empha-size stability & surface area perpendicular to load	Elongated foot
42) Reduced hallucal abduction[a]	B	Realignment of foot axis for propulsion	Fully abducted hallux
43) Distally extended sole[a]	B	Protection of toes during ter-restrial foot use	Sole reaching level of metatar-sophalangeal joint

[a] Character exhibits a morphological cline with increased terrestriality for chimpanzees, lowland gorillas, mountain gorillas, and humans in that order.

amoid and the associated palmarly projected scaphoid tubercle; the degree of torsion of the 1st metatarsal; the relative orientation of the entocuneiform's articular surfaces; talar tor-sion; the dimensions of the tuber calcanei; the transverse tarsal arch; the orientation and shape of the metatarsal heads; the distal ex-tent of the sole relative to the foot; and the proximal extent of the big toe's cleft.

However, many of the features that distin-guish gorillas from chimpanzees and that have been interpreted as terrestrial in nature can also be associated with the gorilla's larger body size. This applies to many of those features

that impart a mechanical advantage to quadrupedal propulsive efforts and to those proportional differences that are seen to scale more or less linearly within the African apes. Although it can be argued that these features are not terrestrial in nature, the noncompatibility of a large body size with arboreal behaviors out of necessity associates them with terrestriality. Given reports that juvenile and female gorillas spend more time in trees than do the larger males (Schaller, 1963, 1965; Jones and Sabater Pi, 1971; Dixson, 1981) and that Bornean male orangutans are more terrestrial than their smaller female counterparts (Mackinnon, 1974; Galadikas-Brindamour, 1979), such a scaling effect could be a built-in feature of a hominoid multipurpose structure endowed with the ability to produce the appropriate arboreal or terrestrial structure. In this regard, it would be of interest to document in chimpanzees if such increasing terrestriality is also seen with increasing body size.

Considering their quadrupedal behaviors, the hands and feet of gorillas (especially those of mountain gorillas) closely approximate the human morphology. In the foot, chimpanzees, lowland gorillas, mountain gorillas, and humans, in that order, form a morphological cline of increasing terrestrial characters, corresponding with an increasing emphasis on terrestrial behaviors (table 15). In this regard, many of those features of the feet that have been used to argue for bipedality i.e., transverse tarsal arch (Gomberg and Latimer, 1984), hallucal adduction (Latimer and Lovejoy, 1990a), the dimension of the plantar process (Latimer and Lovejoy, 1989), the orientation of longitudinal foot axis (Day and Napier, 1964; Latimer, 1991), the dorsiflexed set of the metatarsal heads (Latimer and Lovejoy, 1990b) relatively short metatarsals and phalanges (White and Suwa, 1987; Latimer, 1991) etc., may have originally evolved as the result of quadrupedal terrestriality. In fact, of those features described in this study, there are only a few in which gorillas do not closely approximate humans i.e., the contribution of cuboid length to metatarsal foot length, the strong formation of the cuboid's calcanean process, the absence of weight-bearing tubercles on the plantar process of the distal tarsal bones and a well-developed

two-headed quadratus plantae. Notably, all of the unique human features are associated with the longitudinal arch. Likewise, there is no reason to argue that the African apelike features in the foot of early hominids are necessarily indicative of arboreal behaviors (Lewis, 1980a, 1980b; Stern and Susman, 1983; Susman et al. 1984; Susman and Stern, 1991), since their approximation to gorillas (Sarmiento, 1991) argues strongly for terrestriality.

In trying to explain the large number of similarities in the hands of gorillas and humans which are interpreted as terrestrial features in this and other studies (Jolly, 1972; Etter, 1973, 1974; Sarmiento, 1985, 1988), a quadrupedal origin for many of the terrestrial features of the human foot gains additional support. Because tools are fashioned to fit the hand that makes them, it is difficult, if not illogical, to interpret the anatomical structure of the human hand as adaptive to tool use. It is likely that these structures, as in gorillas, evolved as a response to terrestrial quadrupedality.

Whether or not the similarities between humans and gorillas are indicative of a unique evolutionary history separate from chimpanzees is debatable. Huxley (1863, 1864) was the first to argue that similarities in the hands and feet of humans and gorillas did indicate such a heritage. Both biochemical as well as anatomical studies may find that the time it took for humans and African apes to diverge from each other is too short to convincingly resolve this trichotomy. The biochemistry and anatomy of chimpanzees, gorillas, and humans is so similar and the overlap shown by their variation so large that parallelisms in the relatively subtle differences that exist between them is not implausible. The hands and feet of humans and gorillas could have evolved in parallel in response to terrestrial behaviors. The principle of parsimony, however, argues for interpreting the cheiridial similarities as shared derived features. Additional anatomical data may show if such an interpretation stands.

ACKNOWLEDGMENTS

REFERENCES

Alexander, R. McN.
  1989. Elastic mechanisms in animal movement. New York: Cambridge Univ. Press.

Avis, V.
  1962. Brachiation: the crucial issue of man's ancestry. Southwestern J. Anthrop. 18: 119–148.

Baldwin, L. A., and G. Teleki
  1976. Patterns of gibbon behaviour on Hall's Island, Bermuda. In D. M. Rumbaugh (ed.), Gibbon and Siamang 4: 21–105. Basel: S. Karger.

Bischoff, Th. L. W.
  1870. Bietrage zur Anatomie des Hylobates leuciscus und zu einer Vergleichenden Anatomie der Muskeln der Affen und des Menschen. Abh. Konig. Bayer, Akad. Wiss. Munchen, Math.-Phys. Classe 10(3): 199–297.
  1880. Bietrage zur Anatomie des Gorilla. Abh. Konig. Bayer, Akad. Wiss. Munchen, Math.-Phys. Classe 13(3): 1–48.

Cartmill, M.
  1985. Climbing. In M. Hildebrand, D. M. Bramble, K. F. Leim, and D. B. Wake (eds.), Functional vertebrate morphology, pp. 73–88. Cambridge, MA. Belknapp Press.

Champneys, F.
  1872. On the muscles and nerves of a chimpanzee (Troglodytes niger) and a 'Cynocephalus anubis'. J. Anat. Phys. London 6: 176–211.

Chapman, H. C.
  1879. On the structure of the chimpanzee. Proc. Acad. Nat. Sci. Philadelphia, 52–63.
  1880. On the structure of the orang outang. Ibid., 160–175.

Corrucinni, R. S.
  1978. Comparative osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. J. Hum. Evol. 7: 307–321.

Day, M. H., and J. R. Napier
  1964. Fossil foot bones. Nature 201: 969–970.

Deniker, J.
  1885. Recherches anatomiques et embryologiques sur les singes anthropoides. Arch. Zool. Exp. Gen. Suppl. ser. III.

Dixson, A.
  1981. The natural history of the gorilla. New York: Columbia Univ. Press.

Duvernoy, G. L.
  1855. Des caracteres anatomiques des grands Singes psuedoanthropomorphes. Arch. Mus. Hist. Nat. 8: 1–248.

Embleton, D.
  1864. Notes on certain parts of the anatomy of a young chimpanzee. Nat. Hist. Rev. 4: 250–258.

Etter, H. F.
  1973. Terrestrial adaptations in the hands of the cercopithecinae. Folia Primatol. 20: 331–350.
  1974. Morphologisches und metrisches vergleichende Untersuchung am Handskelett rezenten Primaten. Gegenb. Morphol. Jahrb. 120: 153–171.

Fick, R.
  1895. Vergleichend anatomische studien an einem erwachsenen orang-utang. Arch. Anat. Physiol., Anat. Abt., pp. 1–96.
  1925. Beobachtungen an den Muskeln eineger Schimpansen. Arch. Anat. Physiol., Anat. Abt., pp. 1–100.

Fleagle, J. G.
  1976. Locomotion and posture of the Malayan Siamang and implications for hominid evolution. Folia Primatol. 26: 245–269.

Fleagle, J. G., J. T. Stern, W. L. Jungers, R. I. Susman, A. K. Vangor, and J. Wells
  1981. Climbing a biomechanical link with brachiation and bipedalism. Symp. Zool. Soc. London 48: 359–373.

Forster, A.
  1917. Die muscle contrahentes und interosei manus in der saugetierreihe und beim menschen. Arch. Anat. Phys., Anat. Abt., pp. 101–378.

Fossey, D.
  1983. Gorillas in the mist. Boston: Houghton Mifflin.

Galidikas-Brindamour, B. M. F.
　1979. Orangutan adaptation at Tanjong Pu-
　　　ting Reserve, mating and ecology. In D.
　　　Hamburg (ed.), Perspectives on human
　　　evolution 4: 194–233. New York: Ad-
　　　dison-Wesley.
Gomberg, D. N., and B. Latimer
　1984. Observations on the transverse tarsal
　　　joint of A. afarensis and some com-
　　　ments on the interpretation of behavior
　　　from morphology. Am. J. Phys. An-
　　　throp. (Abstract) 63: 164.
Gratiolet, L. P., and P. H. E. Alix
　1866. Recherches sur l'anatomie du Troglo-
　　　dytes aubryi. Nouv. Arch. Mus. Hist.
　　　Nat. Paris 2: 1–264.
Gray, H.
　1985. Anatomy of the human body, 33rd ed.
　　　Philadelphia: Lea and Felsiger.
Gregory, W. K.
　1934. Man's place among the anthropoids.
　　　Oxford: Clarendon Press.
Groves, C. P., and Stott, K. W., Jr.
　1979. Systematic relationship of gorillas from
　　　Kahuzi, Tshiberimer and Kayonza. Fo-
　　　lia Primatol. 32: 161–179.
Haines, R. W.
　1951. The extensor apparatus of the finger. J.
　　　Anat. London 85: 251–259.
Hartmann, R.
　1886. Anthropid apes. London: Keegan.
Hecker, P.
　1922. Formation di peronier anterieur chez un
　　　chimpanze. Arch. Anat. Hist. Embryol.
　　　1: 147–155.
Hepburn, D.
　1892. The comparative anatomy of the mus-
　　　cles and nerves of the superior and in-
　　　ferior extremities of the anthropoid apes.
　　　J. Anat. Phys. London 26: 149–185.
Hill, W. C. O.
　1962. Primates, comparative anatomy and
　　　taxonomy. V. Cebidae Part B. Edin-
　　　burgh: Edingburgh Univ. Press.
Hofer, W.
　1892. Vergleichend-anatomische Studien uber
　　　die Nerven des Armes und der Hand
　　　bei den Affen und dem Menschen.
　　　Munchener Med. Abhandl. 30(VII
　　　Reihe, Heft III): 1–106.
Horr, D. A.
　1977. Orangutan maturation, growing up in a
　　　female world. In S. Chevallier-Skolni-
　　　koff and F. E. Poirier (eds.), Primate
　　　bio-social development, biological so-
　　　cial and ecological determinants, pp.
　　　289–321. New York: Garland.
Hrdlicka, A.
　1931. Children who run on all fours, and other

animal-like behaviours in the human
　　　child. New York: McGraw Hill.
Humphry, G. M.
　1867. On some points in the anatomy of the
　　　chimpanzee. J. Anat. Physiol. London
　　　1: 254–268.
Hunt, K. D.
　1989. Positional behaviour in Pan troglodytes
　　　at the Mahale mountains and the Gombe
　　　Stream national parks, Tanzania. Ph.D.
　　　thesis, Univ. of Michigan.
Huxley, T. H.
　1863. Evidence as to man's place in nature.
　　　London: Williams and Norgate.
　1864. Lectures on the structure and classifi-
　　　cation of the Mammalia, vols. I and II.
　　　Medical Times and Gazette.
Inouye, S. E.
　1992. Ontogeny and allometry of African ape
　　　manual rays. J. Human Evol. 23: 107–
　　　138.
Jenkins, F. A.
　1981. Wrist rotation in primates, a critical ad-
　　　aptation for brachiators. Symp. Zool.
　　　Soc. London 48: 429–451.
Jenkins, F. A., and J. G. Fleagle
　1975. Knuckle-walking and the functional
　　　anatomy of the wrist in living apes. In
　　　R. H. Tuttle (ed.), Primate functional
　　　morphology and evolution, pp. 213–227.
　　　The Hague: Mouton.
Johnson, D. R.
　1970. An electromyographic study of extrinsic
　　　and intrinsic muscles of the thumb.
　　　M.Sc. thesis, Queen's Univ. Canada.
Jolly, C. J.
　1965. The origins and specializations of ba-
　　　boons. Ph.D. diss., Univ. of London.
　1967. Evolution of the baboons. In H. Vagt-
　　　borg (ed.), The baboon in medical re-
　　　search, pp. 323–338. Austin: Univ. Tex-
　　　as Press.
　1972. The classification and natural history of
　　　Theropithecus (Simnopithecus) ba-
　　　boons of the African Pleistocene. Bull.
　　　Br. Mus. Nat. Hist. Geol. series.
Jones, C., and J. Sabater Pi
　1971. Comparative ecology of Gorilla gorilla
　　　(Savage and Wyman) and Pan troglo-
　　　dytes (Blumenbach) in Rio Muni, West
　　　Africa. Bibl. Primatol. No. 13. Basel:
　　　Karger.
Jouffroy, F. K., and J. Lessertisseur
　1959. Reflexions sur les muscles contracteurs
　　　des doigts et des ortiels (Contrahentes
　　　digitorum) chez les primates. Ann. Sci.
　　　Nat. Zool. 12(1): 211–235.
　1960. Les specialisations anatomiques de la

main chez les singes a progression suspendue. Mammalia 24: 93–151.

Jungers, W. I., and J. T. Stern
1984. Kinesiological aspects of brachiation in lar gibbons. In H. Preuschoft, D. J. Chivers, W. Y. Brockleman, and N. Creel (eds.), The lesser apes evolutionary and behavioral biology, pp. 119–134. Edinburgh: Edinburgh Univ. Press.

Kaplan, E. B.
1945. Functional significance of the extensor communis digitorum in man. Anat. Rec. 92: 293.
1965. Functional and surgical anatomy of the hand, 4th ed. Philadelphia: Lippincott.

Keith, A.
1899. On the chimpanzees and their relationship to the gorilla. Proc. Zool. Soc. London 33: 296–312.
1934. The construction of man's family tree. London: Watts.

Kerr, R. F., M. B. Bennet, S. R. Bibby, R. C. Kester, and R. McN. Alexander
1987. The spring in the arch of the human foot. Nature 325: 147–149.

Kohlbrugge, J. H. F.
1890. Versuch einer anatomie des genus Hylobates. Zoologisches Ergebnisse einer Reise, Nederlandisch Ost-Indien 1: 211–354.
1897. Muskeln und Periphere Nerven der Primaten, mit besonderer Berucksichtigung ihrer Anomalien. Verhandel. d. Konikl. Akad. van Wetenschappen te Amsterdam. (Tweede Sectie), V, 6: 1–246.

Kortlandt, A.
1968. Handgebrauch bei Freilebenden Shimpansen. In B. Rensch (ed.), Handgebrauch und Verstandigung bei Affen und Fruhmenschen, pp. 59–102. Bern: Hans Huber.

Krause, W.
1879. Anatomischen Varietaten. Handbuch der Menschlichen Anatomie. Hannover.

Lamy, P.
1986. Settlement of the longitudinal plantar arch of some African Plio-pliestocene Hominids, a morphological study. J. Hum. Evol. 15: 31–46.

Landsmeer, J. M. F.
1955. Anatomical and functional investigations on the articulation of the human fingers. Acta Anat., suppl. 24.

Langer, C.
1879. Die Musculatur der Extremitaten des Orang als Grundlage einer vergleichend-myologischen Untersuchung. S.B. Math.-Naturwiss. Cl. Akad. Wiss. zu Wein 79: 177–122.

Latimer, B.
1991. The pedal skeleton of Australopithecus afarensis and the beginnings of bipedality. In B. Senut and Y. Coppens, (eds.), Origine de la bipedie chez les hominides Cahiers de Paleoanthropologie, pp. 169–176. Paris: CNRS.

Latimer, B., and C. O. Lovejoy
1989. The calcaneus of Australopithecus afarensis and its implication in the evolution of bipedality. Am. J. Phys. Anthrop. 78: 369–386.
1990a. Haluccal tarso-metatarsal joint in Australopithecus afarensis. Ibid., 82: 125–133.
1990b. Metatarsophalangeal joints of Australopithecus afarensis. Am. J. Phys. Anthrop. 83: 13–23.

Leboucq, H.
1884. Recherches su la morpholgie du carpe chez les mammiferes. Arch. Biol., Paris 5: 35–102.

Leche, W.
1900. Mammalia muskulature. In H. G. Bronn (ed.), Klassen und Ordnungen des Thier-Reichs 6(5): 649–919. Leipzig.

Le Double, A. F.
1897. Traite des variations du systeme musculaire de l'homme et de leur signification au point de vue de l'anthropologie zoologique. Paris: Schleicher Freres.

Le Gros Clark, W. E.
1971. The antecedents of man. New York: Quadrangle Press.

Lessertisseur, J.
1958. Doit-on distinguer deux plans de muscles interosseux a la main et au pied des primates? Ann. Sci. Nat. Zool. Biol. Anim., ser. 11 20: 77–103.

Lewis, O. J.
1962. The comparative morphology of the m. flexor accessorius and the associated long flexor tendons. J. Anat. London 96: 77–109.
1965. The evolution of the mm. interossei in the primate hand. Anat. Rec. 153: 275–287.
1969. The hominoid wrist joint. Am. J. Phys. Anthrop. 30: 251–267.
1974. The wrist articulations of the Anthropoidea. In F. A. Jenkins (ed.), Primate locomotion, pp. 143–169. New York: Academic Press.
1977. Joint remodelling and the evolution of the human hand. J. Anat. London 123: 157–201.
1980a. The joints of the evolving foot. Part II.

The intrinsic joints. J. Anat. 130: 833–857.

1980b. The joints of the evolving foot. Part III. The fossil evidence. Ibid., 275–298.

Loth, E.
1931. Anthropologies des parties molles (muscles, intestins, vaisseaux, nerfs). Paris: Masson.

Lovejoy, C. O.
1981. The origin of man. Science 211: 341–350.

Macalister, A.
1871. On some points of the chimpanzees and others of the primates. Ann. Mag. Nat. Hist. 8: 341.

1874. The muscular anatomy of the gorilla. Proc. R. Irish Acad. 1(2): 501–506.

MacConaill, M. A.
1941. The mechanical anatomy of the carpus and its bearing on some surgical problems. J. Anat. London 75: 166–175.

Mackinnon, J.
1974. The behaviour and ecology of wild orangutans (Pongo pygmaeus). Anim. Behav. 22: 3–74.

Makintosh, H. W.
1875. On the muscular anatomy of Choloepus didactylus. Proc. R. Irish Acad. (2): 66–78.

Manter, J. T.
1945. Variations of the interosseus muscles of the human foot. Anat. Rec. 93: 117–124.

Marzke, M. W.
1971. The origin of the human hand. Am. J. Phys. Anthrop. 34: 61–84.

1983. Joint function and grips of the Australopithecus afarensis hand, with special reference to the region of the capitate. J. Hum. Evol. 12: 197–211.

1986. Tool use and the evolution of human hands and bipedal ability. In J. G. Else and P. C. Lee (eds.), Primate evolution, pp. 203–209. Cambridge: Cambridge Univ. Press.

Marzke, M. W., and R. E. Marzke
1987. The third metacarpal styloid process in humans, origin and functions. Am. J. Phys. Anthrop. 73: 415–431.

Meinke, F.
1911. Morphologischen untersuchungen uber die myologie an den extremitaten bei Bradypus tridactylus. Morphol. Jahrb. 42: 309–360.

Mendel, F. C.
1981. Hand of two-toed sloth its anatomy and potential use relative to size of support. J. Morphol. 169(1): 1–19.

Michaelis, P.
1903. Beitrage zur vergleichenden myologie des Cynocephalus babuin, Simia satyrus, Troglodytes niger. Arch. Anat. Phys., Anat. Abt., 205–256.

Mivart, St. G. J.
1867. On the appendicular skeleton of the primates. Philos. Trans. R. Soc. London. 157: 299–429.

Morton, D. J.
1922. Evolution of the human foot. I. Am. J. Phys. Anthrop. 5: 305–336.

1924. Evolution of the human foot. II. Am. J. Phys. Anthrop. 7: 1–52.

Napier, J. R.
1961. Prehensility and opposability in the hands of primates. Symp. Zool. Soc., London 5: 115–132.

Napier, J. R., and P. H. Napier
1967. A handbook of living primates. New York: Academic Press.

Nowack, R. M.
1991. Walker's mammals of the world, 5th ed. Baltimore: Johns Hopkins Univ. Press.

Oxnard, C. E.
1983. The order of man. Hong Kong: Hong Kong Univ. Press.

Pira, A.
1914. Beitrage zur anatomie des gorilla, I. Das Extremitatenmuskelsystem. Morphol. Jahrb. 48: 167–238.

Polak, C.
1908. Die Anatomie des genus Colobus. Verh. Akad. Wet. Amsterdam, II Section 14: 1–247.

Preuschoft, H.
1965. Muskeln und gelenke der vorderextremitat des gorilla. (Gorilla gorilla Savage et Wyman, 1847). Morphol. Jahrb. 107(2): 99–183.

Primrose, A.
1899. The anatomy of the orang-utang (Simia satyrus). Trans. R. Soc. Can. Inst. 6: 507–598.

Prost, J. H.
1965. A definitional system for the classification of primate locomotion. Am. Anthrop. 67: 1198–1214.

Raven, H. C.
1950. Regional anatomy of the gorilla. In W. K. Gregory (ed.), The anatomy of the gorilla, pp. 15–188. New York: Columbia Univ. Press.

Reynolds, V., and F. Reynolds
1965. Chimpanzees of the Budongo Forest. In I. Devore (ed.), Primate behaviour, field studies of monkeys and apes, pp. 368–424. New York: Holt.

Rijksen, H. D.
   1978. A field study on Sumatran orangutans, ecology, behaviour and conservation. Netherlands: Wagenigen.
Robertson, D. F.
   1944. Anatomy of the South American woolly monkey (*Lagothrix*). Part I. The Forelimb. Zoologica 29: 169–192.
Rodman, P. S.
   1973. Population composition and adaptive organization among orang-utans of the Kutai reserve. *In* R. P. Michael and J. H. Crook (eds.), Comparative behaviour and ecology of primates, pp 171–209. New York: Academic Press.
   1984. Foraging and social systems of orang-utans and chimpanzees. *In* P. S. Rodman and J. H. G. Cant (eds.), Adaptations for foraging in non-human primates, pp. 134–160. New York: Columbia Univ. Press.
Romer, A. S., and T. S. Parsons
   1977. The vertebrate body, 5th ed. Philadelphia: Saunders.
Rose, M. D.
   1974. Postural adaptations in New and Old world monkeys. *In* F. A. Jenkins (ed.), Primate locomotion, pp. 201–222. New York: Academic Press.
   1984. Food acquisition and the evolution of positional behaviour, the case of bipedalism. *In* D. J. Chivers, B. A. Wood, and A. Bilsborough (eds.), Food acquisition and processing in primates, pp. 509–524. London: Plenum Press.
   1988. Functional anatomy of the cheiridia. *In* J. H. Schwartz (ed.), Orangutan biology, pp. 299–310. Oxford: Oxford Univ. Press.
   In press. Quadrupedalism in Miocene hominoids. J. Hum. Evol.
Rugge, G.
   1878. Entwicklungsvorgange an der Muskulatur des Menschlichen Fusses. Morphol. Jahrb. IV(Suppl.): 117–152.
Sarmiento, E. E.
   1983. The significance of the heel process in anthropoids. Int. J. Primatol. 4(2): 127–152.
   1985. Functional differences in the skeleton of wild and captive orang-utans and their adaptive significance. Ph.D. thesis, New York Univ.
   1988. Anatomy of the hominoid wrist joints, its evolutionary and functional implications. Int. J. Primatol. 9: 281–345.
   1991. Functional and phylogenetic implications of the differences in the pedal skeleton of australopithecines. Am. J. Phys. Anthrop., Suppl. 12: 157–158.
   In press. Cautious climbing and folivory: a model of hominoid differentiation. Human Evolution.
Schaller, G. B.
   1963. The mountain gorilla. Chicago: Univ. Chicago Press.
   1965. The behaviour of the mountain gorilla. *In* I. Devore (ed.), Primate behaviour, field studies of monkeys and apes, pp. 324–367. New York: Holt.
Schon-Ybarra, M. A.
   1966. The muscular system of the red howling monkey. Smithson. Inst. U. S. Natl. Mus. Bull. 273: 1–185.
Schultz, A. H.
   1929. The technique for measuring the outer body of human fetuses and of primates in general. Carnegie Inst. Washington Publ. 394. Contrib. Embryol. 20: 213–257.
   1934. Some distinguishing aspects of the mountain gorilla. J. Mammal. 15: 51–61.
   1936. Characters common to higher primates, and characters specific to man. Qt. Rev. Biol. 11: 259–283, 425–455.
   1940. Growth and development of the chimpanzee. Carnegie Inst. Washington Publ. 525. Contrib. Embryol. 29: 57–110.
   1941. Growth and development of the orangutan. Carnegie Inst. Washington Publ. 525. Contrib. Embryol. 29: 57–110.
   1944. Age changes and variability in gibbon. Am. J. Phys. Anthrop. 2: 1–129.
   1953. The relative thickness of the long bones and the vertebrae in primates. Am. J. Phys. Anthrop. 11: 277–311.
   1956. Postembryonic age changes. Primatologia 1: 887–964.
   1963. Relations between the lengths of the main part of the foot skeleton in primates. Folia Primatol 1: 150–171.
   1968. The recent hominoid primates. *In* S. L. Washburn and P. C. Jay (eds.), Perspectives on human evolution, pp. 122–195. New York: Holt.
Schulze, F. E.
   1867. Myologische Untersuchungen. I Die Sehenverbildung in der Planta des Menschen und die Saugethiere. Z. Wissensch. Zool. 17: 1–22.
Shrewsbury, M. A., R. K. Johnson, and D. R. Ousterhold
   1972. The palmaris brevis—a reconstruction of its anatomy and possible function. J. Bone Jt. Surg. 54(A): 344.

Sirena, S.
1876. Ricerche della miologia del *Mycetes fuscus*. Giorn. di Sc. Nat. ed. Econom. 7: 1–84.

Smith, W. S.
1882. The functions of the peroneus tertius muscle. Edinburgh Med. J. 28: 632–656.

Sommer, A.
1907. Das muskelsystem des gorilla. Jena Zr. Naturwiss. 42: 181–308.

Sonntag, C. F.
1923. On the anatomy, physiology and pathology of the chimpanzee. Proc. Zool. Soc. London 23: 323–429.
1924. The morphology and evolution of the apes and man. London: John Bale, Sons & Danielson.

Stern, J. T., and R. L. Susman
1983. The locomotor anatomy of *Australopithecus africanus*. Am. J. Phys. Anthrop. 60: 279–316.

Straus, W. L., Jr.
1930. The foot musculature of the highland gorilla (*G. g. beringei*). Qt. Rev. Biol. 5: 261–317.
1941. The phylogeny of the human forearm extensors. Human Biol. 13: 23–50, 203–238.
1942. Rudimentary digits in primates. Qt. Rev. Biol. 17(3): 228–243.

Susman, R. L.
1983. The evolution of the human foot: Evidence from plio-pliestocene hominids. Foot Ankle 3: 356–376.
1984. The locomotor behavior of *Pan paniscus* in the Lomako forest. *In* R. L. Susman (ed.), The pygmy chimpanzee: evolutionary biology and behavior, pp. 369–393. New York: Plenum Press.

Susman, R. L., N. L. Badrian, and A. J. Badrian
1980. Locomotor behaviour of *Pan paniscus* in Zaire. Amer. J. Phys. Anthrop. 53: 69–90.

Susman, R. L., and J. T. Stern, Jr.
1991. Origin and evolution of early hominid bipedality. *In* B. Senut and Y. Coppens (eds.), Origine de la bipedie chez les hominides Cahiers de Paleoanthropologie, pp. 121–131. Paris: CNRS.

Susman, R. L., J. T. Stern, Jr., and W. L. Jungers
1984. Arboreality and bipedality in the hadar hominids. Folia Primatol. 43: 113–156.

Sutton, J. B.
1889. On some points in the anatomy of the chimpanzee. J. Anat. Physiol. London 18: 66–84.

Symington, J.
1889. Observations on the myology of the gorilla and the chimpanzee. Rep. Br. Assoc. Adv. Sci., pp. 629–630.

Testut, L.
1884. Les anomalies musculaires chez les homme expliques par l'anatomie comparee. Leur importance en anthropologie. Paris: G. Masson.

Traill, T. S.
1821. Observations on the anatomy of the orangoutan. Mem. Werner. Nat. Hist. Soc., Edinburgh 3: 1–49.

Turner, W.
1867. On variability in human structure, with illustrations, from the flexor muscles of the finger and toes. Tran. R. Soc. Edinburgh. 24: 175–189.

Tutin, C. E. G., and M. Fernandez
1984. Contributions to the study of alimentation of lowland gorillas in the natural state, in Rio Muni, Republic of Equatorial Guinea. Primates 18: 183–264.

Tuttle, R. H.
1967. Knuckle-walking and the evolution of the hominoid hand. Am. J. Phys. Anthrop. 26: 171–206.
1969. Quantitative and functional studies on the hands of the Anthropoidea. I. The Hominoidea. J. Morphol. 128: 309–363.
1970. Postural, propulsive and prehensile capabilities in the cheiridia of chimpanzees and other great apes. *In* G. H. Bourne (ed.), The chimpanzee. 2: 167–253. Baltimore: Univ. Park Press.
1972a. Functional and evolutionary biology of hylobatid hands and feet. *In* D. M. Rumbaugh (ed.), Gibbon and Siamang 1: 136–206. Basel: S. Karger.
1972b. Relative mass of the cheiridial muscles in catarrhine primates. *In* R. H. Tuttle (ed.), Functional and evolutionary biology of primates, pp. 262–291. Chicago: Aldine-Atherton.
1974. Darwin's apes, dental apes and the descent of man, normal science in evolutionary anthropology. Curr. Anthrop. 15: 389–426.

Tuttle, R. H., M. J. Velte, and J. V. Basmajian
1983. Electromyography of the brachial muscles of *Pan troglodytes* and *Pongo pygmaeus*. Am. J. Phys. Anthrop. 61: 75–83.

Vedder, A. L.
1984. Movement patterns of a group of free-ranging mountain gorillas *G. g. beringei* and their relationship to food availability. Amer J. Primatol. 7: 73–84.

Virchow, H.
1929. Das os centrale carpi des menschen. Morphol. Jahrb. 63: 480–530.

Vrolik, W.
1841. Recherches d'anatomie comparee sur le chimpanzee. Amsterdam: Johannes Miller.

Watts, D. P.
1983. Foraging strategy and social ecology of mountain gorillas (*Pan gorilla beringei*). Ph.D. diss., Univ. of Chicago.

Weber, B., and A. Vedder
1983. Population dynamics of the Virunga gorillas. 1959–1978. Biol. Conserv. 26: 341–366.

Weidenreich, F.
1922. Der Menschenfuss. Z. Morphol. Anthrop. 22: 51–282.

Weinert, H.
1932. Ursprung des Menschheit. Stuttgart: F. Enke.

Wells, L. H.
1935. A peroneus tertius in a chacma baboon (*Papio porcarius*). J. Anat. London 69: 508–514.

Westling, C.
1884. Beitrage sur Kenntniss des Peripheren Nervensytems. (I. *Pithecus satyrus, Ornithorhynchus paradoxus*) Bihang Till K. Svenska Vet.-Akad. Hanlingar 9: 8.

White, T. D., and G. Suwa
1987. Hominid footprints at Laetoli: facts and interpretations. Am. J. Phys. Anthrop. 72: 485–514.

Wilder, B. G.
1862. Contributions to the comparative myology of the chimpanzee. Boston J. Nat. Hist. 7: 353–384.

Wood-Jones, F. W.
1929. Man's place among the mammals. New York: Longman's.

Wyman, J.
1855. An account of the dissection of a black chimpanzee. Proc. Boston Soc. Nat. Hist. 5: 270–275.