Functional Anatomy and Adaptation of Male Gorillas (*Gorilla gorilla gorilla*) with Comparison to Male Orangutans (*Pongo pygmaeus*)

ADRIENNE L. ZIHLMAN,[1*] ROBIN K. McFARLAND,[2] AND CAROL E. UNDERWOOD[1]

[1]Department of Anthropology, University of California, Santa Cruz, California 95064
[2]Department of Biology, Cabrillo College, Aptos, California

ABSTRACT

Great apes diversified during the Miocene in Old World forests. Two lineages, gorillas in Africa and orangutans in Asia, have sexual dimorphisms of super-sized males, though they presumably diverged from a smaller common ancestor. We test the hypothesis that they increased in body mass independently and convergently, and that their many postcranial differences reflect locomotor differences. Whole body dissections of five adult male gorillas and four adult male orangutans allowed quantification of body mass distribution to limb segments, of body composition (muscle, bone, skin, and fat relative to total body mass), and of muscle distribution and proportions. Results demonstrate that gorilla forelimb anatomy accommodates shoulder joint mobility for vertical climbing and reaching while maintaining joint stability during quadrupedal locomotion. The heavily muscled hind limbs are equipped for propulsion and weight-bearing over relatively stable substrates on the forest floor. In contrast, orangutan forelimb length, muscle mass, and joint construction are modified for strength and mobility in climbing, bridging, and traveling over flexible supports through the forest canopy. Muscles of hip, knee, and ankle joints provide rotational and prehensile strength essential for moving on unstable and discontinuous branches. We conclude that anatomical similarities are due to common ancestry and that differences in postcranial anatomy reflect powerful selection for divergent locomotor adaptations. These data further support the evolutionary conclusion that gorillas fall with chimpanzees and humans as part of the African hominoid radiation; orangutans are a specialized outlier. Anat Rec, 294:1842–1855, 2011.   © 2011 Wiley-Liss, Inc.

Key words: gorilla; orangutan; musculo-skeleton; body composition; locomotor behavior

INTRODUCTION

Male gorillas (*Gorilla gorilla gorilla*) and male orangutans (*Pongo pygmaeus*) capture our attention because of our mutual evolutionary proximity and of giantism that led to their extreme sexual dimorphism, locomotor divergence, and geographic isolation. They originated from a common hominoid lineage about 16 million years ago and diverged about 11 million years ago into African and Asian branches (Pilbeam, 1996; Stauffer et al., 2001). Since they likely arose from a smaller common ancestor with the same body structure and locomotor skills, the development of large body size and unique sexually dimorphic anatomies is convergent (Zihlman, 1997). A

TABLE 1. (A and B). Gorilla and orangutan sample

Animal	Age	Mass (gm)	Cause of death	Cranial capacity/brain weight
(A)				
G1 MO	37	148,300	Chronic heart failure	570 ml
G2 MI	27	172,000	Cardiac arrest	568 ml
G3 BW[a]	36	172,700	Perforated ileum	642 ml
G4 KU	29	185,000	Accute lung infection	570 ml
G5 CO[a]	36	209,100	Aortic dissection	n.a.
(B)				
O1 BE[b]	15	102,060	Chronic pneumonia	434 gm
O2 TH	31	112,000	Unknown	436 gm
O3 BU	24	126,000	Peritonitis	443 gm
O4 JI	old	136,000	Canine tooth infection	400 gm

[a]Some data from these individuals were published in Zihlman and McFarland (2000).
[b]Some data from this individual was published in Morbeck and Zihlman (1988).

profile of segment proportions, body composition, and distribution of muscle is the central test for the hypothesis that their similarities are due to common descent, whereas postcranial differences are due to locomotor divergence as a result of geographical isolation in different habitats.

Historically, anatomical investigations of apes were based on a single animal, on one limb or body region, or on descriptions of body shape, internal organs, skin, and hair or muscle attachments (e.g., Owen, 1830, 1859; MacAlister, 1873; Chapman, 1878, 1880; Sonntag, 1924a, b; Sullivan and Osgood, 1927; Boyer, 1935, 1939). The Raven volume *Anatomy of the Gorilla* (Gregory, 1950) analyzes just one individual, Bushman, a male born in Cameroon residing until age 22 in Chicago's Lincoln Park Zoo. The volume reports on muscle attachments, the skeleton, the nervous and vascular systems, the skin, and thoracic viscera. However, other than weights of some organs (Steiner, 1954) the volume has no quantitative or functional information.

Other approaches to gorilla and orangutan anatomy have addressed function with quantitative information by focusing on one component, for example skeletal proportions (e.g., Schultz, 1930, 1937, 1956); biomechanics of scapula or limbs (e.g., Miller, 1932; Oxnard, 1967; Roberts, 1974; Taylor, 1997), regional muscle and limb weights and inertial properties (e.g., Preuschoft, 1961, 1963; Payne et al., 2006a, b; Isler et al., 2006; Oishi et al., 2008, 2009). On live captive gorillas and orangutans, direct measures of muscle function or joint motion derive from electromyography during specific limb movements (e.g., Tuttle and Basmajian, 1974a, b, 1978; Tuttle et al., 1975; Stern and Susman, 1981; Tuttle et al., 1983) and from cinematography of climbing modes (e.g., Isler and Thorpe, 2003; Isler, 2005).

Few comparative studies focus on joints and the associated soft tissue; both are important, but the opportunity for their combined study is rare (e.g., Wright-Fitzgerald et al., 2010; Davis, 1961; Zihlman et al., 2011). Whole animals provide multiple ways to analyze and compare, for example body segments relative to total body mass (TBM), forelimb to hind limb mass, joint configuration, and corresponding muscles. Although description of individual bones, muscles, segment weights, single limbs or joints can be a starting point, our whole body analysis also incorporates information about locomotion, energetics, and environment; this robust methodology results in an integrated approach for comparing and testing hypotheses about adaptation.

Testing the hypothesis that the different postcranial anatomies of these two large-bodied male apes are a result of selection for divergent locomotor adaptations requires a multifaceted approach. Our inquiry necessarily "must begin with the whole organism rather than its parts" (Rodman and Cant, 1984: 2). As a first step, we present, as a unique baseline, dissection data on nine adult males that quantify distribution of body mass to segments, and body composition (muscle, bone, skin, and fat). We further analyze muscle distribution, joint properties, and functional muscle groups. Medical and health records for each individual help evaluate the impact of age and wellness on body composition. Such analyses are almost nonexistent due to the rarity of whole gorillas and orangutans available for dissection. Finally, to test our hypothesis about adaptation, we compare field observations on the locomotor challenges of travel, foraging, and feeding. This contextualizes the anatomy by connecting function to structure (Davis, 1960).

Our unique sample and whole-body study add significantly to what is known about these large male apes. This approach extends the role of comparative anatomy and the contribution it must play in the interpretation of evolutionary history, that is, the inclusion of soft tissue in analyzes to evaluate divergence from a common ancestor.

MATERIALS AND METHODS
The Sample

The five silverback lowland gorillas (all *G. gorilla gorilla*) from various zoological gardens were necropsied before dissection at the Anthropology Laboratories, University of California, Santa Cruz. Body weights taken during life, just before death, or at time of necropsy are available for the sample. Information recorded during their lives helps interpret anatomical findings from this unique data set. Table 1a.

Gorilla 1 (MO), 37, wild born (Cameroon), lived from about age 2 years in captivity and is the oldest in the sample. He suffered from chronic heart failure that became acute during the last 4–6 weeks of life, leading to edema, pneumonia, multiple organ failure, and loss of body mass. At death he was the lightest.

Gorilla 2 (MI), 27, wild born (Cameroon) was housed in a large outdoor grassy enclosure with multiple structures for climbing. He is the youngest, leanest and most muscular of the sample and was in the prime of life.

TABLE 2. Functional muscle groups

Joint	Muscles
Shoulder	External trunk muscles: latissimus dorsi, pectoralis major, teres major
	Rotator cuff: supraspinatus, infraspinatus, subscapularis, teres minor Deltoid
Elbow	Flexors: biceps brachii, brachialis, brachioradialis
	Extensors: triceps brachii, dorsoepitrochlearis
Wrist	Flexors: flexor carpi radialis, flexor carpi ulnaris, palmaris longus (when present)
	Extensors: extensor carpi ulnaris, extensor carpi radialis longus, extensor carpi radialis brevis
Digits	Flexors: flexor digitorum superficialis, flexor digitorum profundus (includes flexor pollicis longus)
	Extensors: extensor digiti communis, extensor indicus, extensor digiti minimi
Hip	Abductors: gluteus maximus, gluteus medius/minimus, piriformis
	Adductors: gracilis, pectineus, adductor longus, magnus, brevis
	Rotators: obturator internus and externus, gemelli, quadratus femoris
	Flexors: sartorius, rectus femoris, iliopsoas
	Extensors: biceps femoris (long head), semitendinosus, semimembranosus
Knee	Flexors (posterior thigh): hamstrings: biceps femoris, semitendinosus, semimembranosus
	Extensors (anterior thigh): quadriceps femoris: rectus femoris, vastus lateralis, vastus medialis, vastus intermedius
Ankle	
Talo-crural	Plantarflexors: gastrocnemius, soleus, tibialis posterior
	Dorsiflexors: extensor digitorum longus, extensor hallucis longus, tibialis anterior
Subtalar	Invertors: tibialis anterior
	Evertors: peroneus longus, peroneus brevis
Digits	Flexors: flexor digitorum fibularis, flexor digitorum tibialis
	Extensors: extensor digitorum longus, extensor hallucis longus, extensor digitorum brevis

He exhibited no overt health problems, but died of sudden cardiac arrest due to undetected fibrosing cardiomyopathy.

Gorilla 3 (BW), 36, wild born (Cameroon), lived in captivity from about age 18 months, was housed in a social group, and sired three offspring. His last 14 years were spent in a large outdoor, grassy enclosure with trees and rocky structures. He was generally healthy during life, though he died within a week from a perforated ileum.

Gorilla 4 (KU), 29, was sired by male Gorilla 3 (BW) and lived his entire life in his natal social group where he fathered three offspring. For several years, he suffered a chronic lung infection that became acute; he died as a result of surgery to save his life.

Gorilla 5 (CO), 36, wild born from an unknown locality in western Africa, was a large, robust individual, very well muscled, although described as obese in his medical records. The immediate cause of death was a two-day illness from an aortic dissection.

The orangutan sample consists of four flanged adult males who lived most of their lives in captivity. One orangutan (BU) was dissected at University of California, Santa Cruz, another (BE) at Arizona State University. T. Grand contributed data from his two orangutan dissections. Table 1b.

Orangutan 1 (BE), 15–20 years old, died of chronic pneumonia as a result of a respiratory infection. Orangutan 2 (TH), 31, was dissected by T. Grand at the National Zoological Park, Smithsonian. Only individual muscle weights are available for this animal. Orangutan 3 (BU), 24, was Bornean, born and raised in captivity. He died of peritonitis after a brief illness.

Orangutan 4 (JI) from the Cheyenne Mountain Zoo was very obese and died as a result of a canine tooth infection that spread to his brain. T. Grand and his anatomy class at University of Colorado, Boulder dissected him. His body mass was estimated based on the combined mass of the dissected parts. Body composition is not included in the orangutan average but is included in the discussion on variation.

Methods

The bodies were received frozen, were thawed, and then dissected. We use standardized methods (Grand, 1977; Zihlman, 1984; Zihlman and McFarland, 2000). On one side of the body, referred to as the segment side, we separate the entire forelimb at the shoulder joint by cutting the skin around the joint, releasing trunk and rotator cuff muscles from the humerus, and the arm muscles from the trunk. We then partition the limb into three pieces: the (upper) arm segment is separated at the elbow joint; the hand segment is severed from the forearm segment by cutting through the tendons and ligaments at the radiocarpal joint. Immediately after detaching, we weigh the entire forelimb, and then each separated segment on an A&D FV-150K A1 industrial scale. Similarly, we separate the hind limb at the hip joint by cutting the skin around the inguinal region, below the ischium to the pubic symphysis. The hip muscles are detached from the femur and the thigh muscles from the innominate. We separate the leg from the thigh segment keeping the patella with the leg, and detach the foot segment from the leg by cutting through the tendons and ligaments at the talo-crural joint. We weigh the entire hind limb, and then each segment is weighed immediately after it is detached.

We separate and weigh the major tissue components—muscle, bone, skin, and "other"—from each segment. In the head/trunk, all muscle is separated and weighed. "Other" tissue includes trunk contents removed at necropsy (e.g., organs and viscera), the diaphragm, facial muscles, blood vessels and nerves, tongue, larynx, hyoid and associated structures, reproductive organs, connective tissue, and fat removed during dissection.

TABLE 3. Body components and limb segments, weight in grams

Animal	Age	Body Mass	Muscle	Bone	Skin[a]	Arm	Forearm	Hand	Thigh	Leg	Foot
G1 MO	37	148,300	50,971.9	18,683.7	16,947.7	5,227.2	4,090.9	1,500.0	8,138.4	3,454.5	1,959.0
G2 MI	27	172,000	79,856.0	22,487.2	23,133.9	8,613.2	5,319.3	1,650.9	10,727.2	4,045.5	1,727.3
G3 BW	36	172,700	65,523.0	23,361.8	28,738.6	6,450.0	4,900.0	1,646.1	9,450.0	4,350.0	1,909.0
G4 KU	29	185,000	71,845.0	23,223.6	23,621.0	7,781.3	4,707.3	1,727.3	10,920.4	4,054.0	2,090.9
G5 CO	36	209,100	76,273.5	22,145.4	32,700.0	Whole segments not available, skin removed					
O1 BE	15[b]	102,060	34,561.3	11,740.6	13,634.6	3,310.0	3,733.0	1,441.0	3,370.0	1,758.0	1,265.2
O2 TH	31	112,000	Not available			Whole segments not available					
O3 BU	24	126,000	45,226.2	15,173.9	21,293.0	5,644.8	5,150.0	1,727.3	6,281.8	3,050.0	1,818.2
O4 JI	Old	136,000[b]	14,444.0	13,894.6	14,947.1	3,260.3	3,288.6	1,304.0	6,804.0	2,608.2	1,417.5

[a]Skin may include fat.
[b]Estimate.

On the other side of the body, the muscle-by-muscle side, we detach each muscle with its tendon and weigh immediately to the nearest tenth of a gram on an Intell Lab Balance WPX 4500 scale. Bone, skin, and other tissues are separated and weighed as the dissection of that region proceeds.

We measure hand length from midradiocarpal joint to tip of third digit, and foot length from heel (calcaneus) to tip of third digit on intact segments; maximum lengths of long bones are taken on cleaned specimens.

In the analysis we determine the following:

Body proportions. We calculate the contribution of the forelimbs by doubling the weight of the forelimb segment to represent both limbs, then calculate its percentage relative to TBM. Similarly, we double the weight of the hind limb segment and calculate as a percent of TBM. The head/trunk mass combined with limb masses constitute 100%.

Segment proportions. We calculate the contribution of each segment of the forelimb (arm, forearm, and hand) relative to total forelimb mass. Similarly, we calculate each segment of the hind limb (thigh, leg, and foot) relative to total hind limb mass.

Body composition. We add the weights of each tissue type—muscle, bone, skin—from the limb and head/trunk segments and divide by TBM. Adipose tissue is an important component of body mass but is rarely available as a direct measure. At necropsy, thoracic and abdominal contents, which include fat, are routinely removed. Data from our dissections of one, unnecropsied, "lean" chimpanzee and one gibbon showed that thoracic and abdominal contents come to 12% of body mass. Therefore, to obtain a minimum estimate of body fat, we begin with the percent assigned to the category of "other tissue," subtract 12% to represent trunk contents, and 5%–8% that includes connective tissue, blood vessels, nerves, diaphragm, tongue, and facial muscles. To this total, we add the body fat recorded during dissection, for example, orangutan cheek pads, and intermuscular fat and any remaining fat on the walls within the trunk cavity. This method, applied consistently, provides a rough approximation of body fat for the individuals in this study.

Muscle distribution. All body muscle is added and taken as 100%. To determine its regional distribution to the forelimbs, we add all muscle from the arm, forearm, and hand segments, plus the rotator cuff and external trunk muscles (Table 2) that act on the humerus; we calculate this amount as a percent of total body muscle. Similarly, for the hind limb, we add all muscle from the thigh, leg, and foot segments, as well as hip joint muscles that attach to the femur and calculate relative to total body muscle. Muscles from the head/trunk segment combined with limb muscles equal 100%.

Muscle groups and joint function. We group muscles according to their functional relationship to joints, that is, muscles that pull in the same direction, and determine percent profiles based on individual muscle weights (Table 2). We determine relative contribution of elbow flexors and extensors to their combined mass; and do the same with wrist flexors and extensors; and digital flexors and extensors (after Grand, 1968a; Tuttle, 1969). Hip joint muscles are grouped to approximate movement potentials (after Grand, 1968b). Knee extensors (quadriceps femoris) and the posterior flexors (hamstrings) are calculated as a percent of combined mass. At the ankle, the contribution of plantar flexors to dorsiflexors is determined; invertors to evertors at the subtalar joint, and the digital flexors to extensors.

Bones. We calculate the relative contribution of segments within each limb: humerus, radius, hand relative to total forelimb length; femur, tibia, and foot relative to total hind limb segment length. After the skull is cleaned and dried, we calculate cranial capacity using mustard seed after Bolter and Zihlman (2003).

Small samples limit statistics to means and ranges; to supplement, we provide raw data on body composition, and limb segments (Table 3).

RESULTS
Body and Segment Proportions

Gorillas and orangutans show distinct patterns in distribution of body mass to the limbs and in the segments within the limbs. Although the head/trunk mass is similar (65.7% and 66.6%, respectively), gorillas have lighter forelimbs with heavier hind limbs, a pattern that is reversed in orangutans (Fig. 1). Gorillas' heavy proximal segments (arm and thigh) contrast with orangutans' equal arm and forearm mass, and heavy hand (Fig. 2).
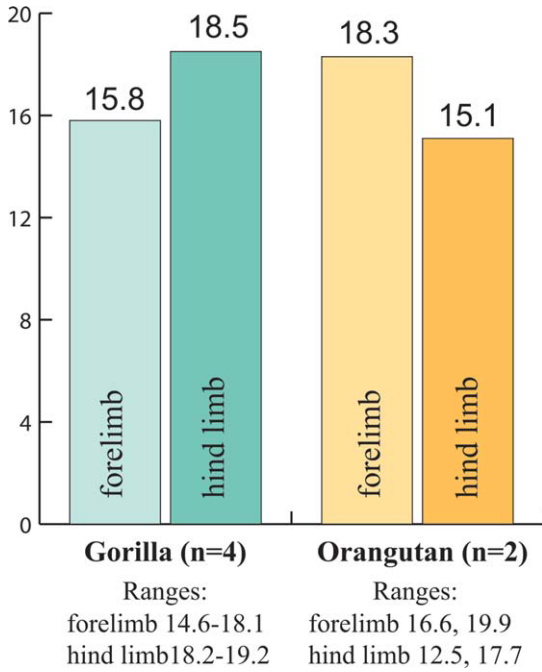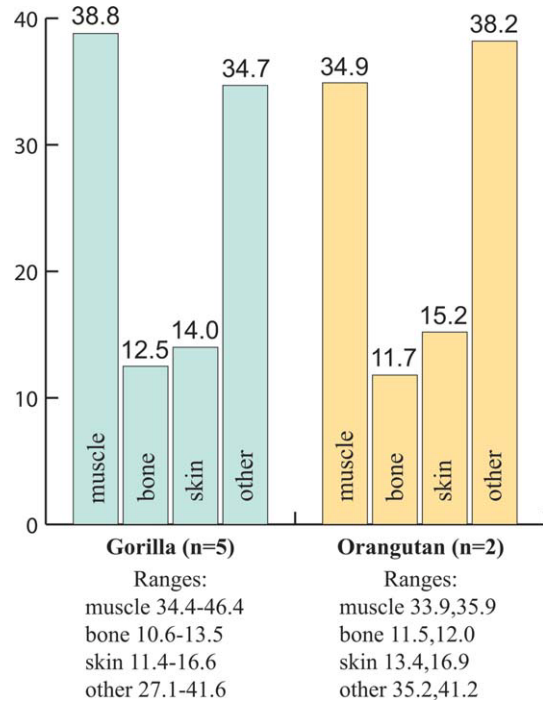
Fig. 1. Forelimbs and Hind limbs as % of TBM.

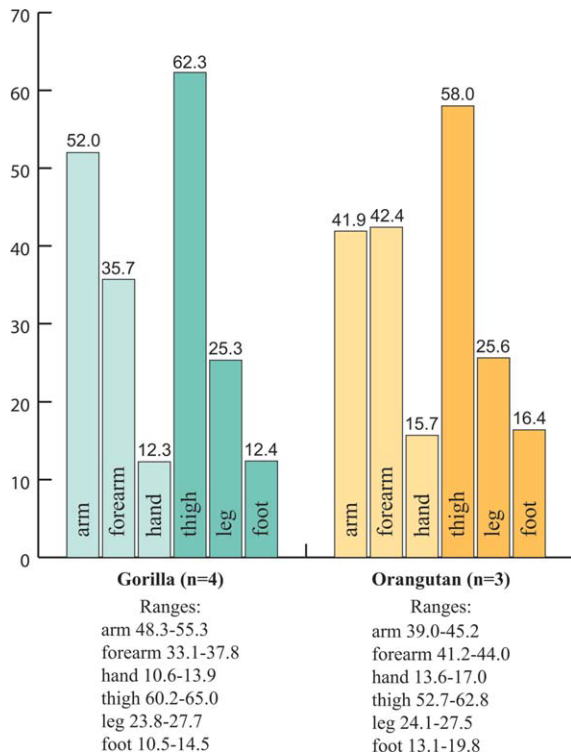Fig. 3. Body composition as % of TBM.

Fig. 2. Limb segments as % total limb mass.

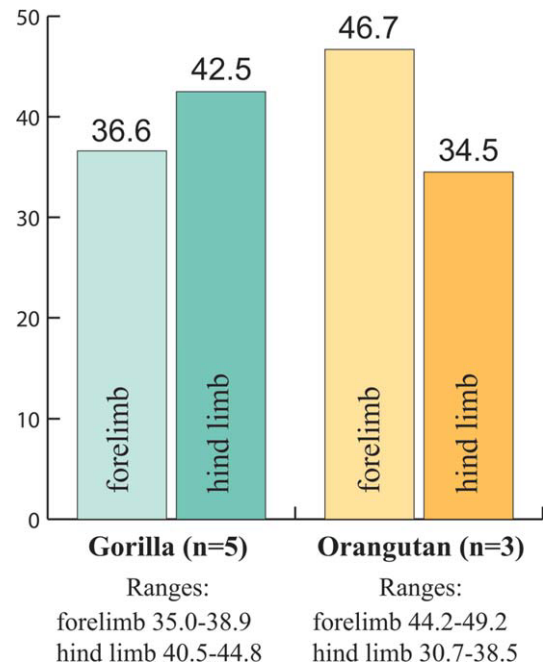Fig. 4. Muscle distribution as % of total muscle mass.

Distribution of Muscle

Gorillas have less muscle in the forelimbs than in the hind limbs; orangutan forelimb muscle is heavier, hind limb lighter, and the ranges of the two species do not overlap. The head/trunk is similar, 20.9% and 18.7%, respectively (Fig. 4).

Body Composition

Gorillas and orangutans overlap in relative mass of muscle, skin, bone, and "other", though averages differ (Fig. 3).

TABLE 4. Individual muscle weights. Forelimb and hind Limb

	Gorillas					Orangutans			
	1 (MO)	2 (MI)	3 (BW)	4 (KU)	5 (CO)	1 (BE)	2 (TH)	3 (BU)	4 (JI)
Forelimb muscles									
Trunk									
Pectoralis major	654.8	1454.5	1013.2	1314.7[a]	1586.0[a]	264.9	389.4	507.3	609.3
Latissimus dorsi	900.0	1636.4	1350.0	1550.0	1550.0	970.0	734.0	1450.0	736.6
Teres major	363.0	823.7	540.0	624.7	602.5	213.6	148.0	391.9	171.2
Rotator cuff									
Teres minor	84.2	101.8	107.8	111.8	115.4	62.1	w/infra	94.0	49.9
Subscapularis	751.0	954.5	710.8	931.4	1050.0	384.8	285.4	585.4	312.9
Infraspinatus	401.0	626.9	626.0	583.3	704.9	299.3	298.0	399.6	204.1
Supraspinatus	262.0	463.2	349.2	306.6	424.6	179.2	115.0	257.4	126.1
Arm									
Deltoid	950.0	1972.0	1409.1	1681.8	2243.8	730.0	534.3	1006.0	501.2
Biceps brachii: long	699.4	954.3	241.9	326.7	367.2	115.3	207.3	225.7	191.5
Biceps brachii: short	w/long hd	w/long hd	414.7	402.2	483.8	127.7		318.2	
Coracobrachialis	96.8	129.7	99.7	123.8	131.4	58.4	72.0	104.6	61.4
Brachialis	357.9	785.6	544.2	646.6	726.4	336.3	357.0	561.6	313.0
Triceps: long	1110.7	2050.0	398.5	1545.4	441.4	205.2	640.3	274.0	170.2
Triceps: lateral	Combined	Combined	650.0	Combined	645.4	263.2	Combined	410.5	191.9
Triceps: medial	Combined	Combined	206.4	Combined	645.6	200.5	Combined	395.0	265.2
Dorsoepitrochlearis	60.3	102.7	53.6	63.9	77.9	56.0		103.5	75.4
Forearm									
Brachioradialis	113.0	367.1	175.8	335.0	299.0	456.6	404.5	532.0	327.8
Anconeus		17.5			19.2	19.0			
Palmaris longus	n.p.[b]	n.p.[b]	n.p.[b]	n.p.[b]	n.p.[b]	53.5		62.5	65.9
Flexor carpi radialis	157.0	306.5		206.4	341.0	151.0		149.2	114.3
Flexor carpi ulnaris	167.6	327.0		246.4	208.8	100.5		157.5	126.2
Flexor dig superfic	316.3	446.4		477.7	274.8	223.6		281.8	173.0
Flexor digit profund	331.0	565.4		428.2	447.8	462.8		452.7	383.0
Flexor pollicis longus[c]	85.4	141.5		99.6	126.6				
Pronator teres	195.0	187.5	140.6	156.6	176.0	86.5	w/sup	135.0	87.0
Pronator quadratus	26.0	33.0	35.2	19.5	38.5	17.8	15.8	30.0	20.0
Supinator	140.0	138.8	137.0	198.5	129.4	91.5	84.0	133.1	94.4
Ext. carpi rad. Longus	102.4	112.0		119.5	114.0	59.5		109.9	55.5
Ext. carpi rad. brevis	118.0	171.7		164.7	160.0	93.0		119.8	88.5
Ext. carpi ulnaris	110.0	187.6		116.0	130.0	90.1		92.1	71.4
Ext. digiti minimi	8.0	55.0		30.6	36.0	39.2		26.0	w/edc
Ext. digiti communis	135.6	269.0		189.4	223.0	139.5		165.9	213.6
Extensor indicis	65.6	21.0		12.8	15.7	33.8		31.5	w/edc
Abductor poll. long	53.3	63.0	38.4	59.6	119.3	50.7		57.6	
Extensor poll. long	37.3	34.5	24.5	24.0	23.0	20.8		18.6	
Extensor poll. brevis	35.0	59.4	50.0	35.4	w/abd lg	15.4		33.5	
Hind limb									
Hip									
Adductors—(pectineus, magnus, brevis, longus)	1889.0	2252.4	1841.7	2654.0	2885.9	784.9	680.0	1416.9	720.6
Gluteus maximus	1182.0	1863.6	1450.0	2000.0	2000.0	609.5		1223.4	575.5
Tensor fascia latae									
Gluteus medius	1091.0	1818.2	1447.5	1863.6	1636.4	335.4	306.0	773.6	427.7
Piriformis	52.1	w/med	w/med	109.1	w/med	35.6	w/med	56	w/med
Gluteus minimus	180.0	266.6	258.2	276.5	201.2	90.3	w/med	134.0	w/med
Gemelli	w/obt int		12.6			28.4	5.0	19.0	14.3
Obturator externus	155.7	198.0	94.8	144.3	200.9	62.9	68.1	85.5	54.4
Obturator internus	115.4	157.9	154.0	184.3	167.1	58.4		65.0	34.0
Quadratus femoris		62.6	47.7	52.0		40.2	47.6	47.0	47.9
Thigh									
Gracilis	432.0	637.4	388.0	532.0	495.0	205.0	228.0	407.3	221.7
Semimembranosus	177.8	291.8	165.5	220.6	428.0	191.2	206.0	335.0	142.3
Semitendinosus	517.0	830.1	594.6	811.6	721.3	290.6	166.3	493.5	249.1
Biceps femoris: long	263.3	426.9	391.0	426.7	632.5	197.3	342.0	324.7	239.5
Biceps femoris: short	147.3	308.8	227.3	308.7	296.4	56.3		86.6	100.8
Sartorius	156.6	232.0	180.8	270.6	229.9	77.1	66.5	101.1	51.1
Iliopsoas+p.minor	726.7	1259.8	969.1	1409.0	1200.3	409.4	300.0	580.4	234.7
Rectus femoris	271.6	517.2	367.5	409.0		122.2	566.3	198.0	147.3
Vasti muscles (3)	1227.0	2154.0	1929.0	1954.5		444.9	w/r fem	741.8	419.4

TABLE 4. Individual muscle weights. Forelimb and hind Limb (*Continued*)

	Gorillas					Orangutans			
	1 (MO)	2 (MI)	3 (BW)	4 (KU)	5 (CO)	1 (BE)	2 (TH)	3 (BU)	4 (JI)
Leg									
Popliteus	92.0	92.8	78.2	104.3	108.4	51.6	32.7	49.0	33.8
Gastrocnemius	281.0	417.3	441.5	497.7	476.3	157.9	262.0	200.0	163.6
Soleus	394.3	542.0	422.5	506.7	472.6	116.8	w/gst	189.1	159.3
Plantaris									35.5
Tibialis posterior	128.1	175.0	128.0	99.1	209.9	45.1		59.1	77.5
Tibialis anterior	283.2	395.0	213.0	212.0	259.7	81.8		154.6	110.7
Peroneals	188.4	325.2	202.5	221.8	271.0	108.6	92.0	146.7	60.3
Flexor dig. fib./hal.	218.8	298.8	164.5	180.0		137.0		187.9	99.7
Flexor dig. tibialis/long	96.2	79.5	89.4	89.4		105.7		126.5	81.6
Ext. digitorum longus	109.1	187.0	132.0	116.4	191.8	69.8		99.0	108.7
Ext. hallucis longus	28.0	55.5	42.8	40.8	42.7	13.9		20.2	16.5

[a]Incomplete due to necropsy.
[b]n.p. = not present.
[c]Attached on digit II.
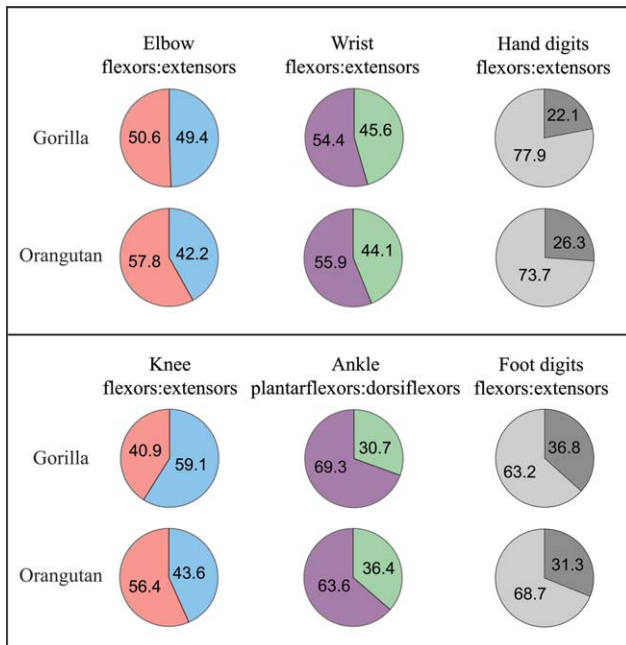
Fig. 5. Muscle proportions.

Functional Muscles Groups

Relative muscle weights serve as gross approximations of their functional importance (e.g., Grand, 1968a; Tuttle, 1972). Individual muscles of the limb, when available, are listed in Table 4 and Fig. 5.

Shoulder joint. Of total body musculature, 19.3% acts on the gorilla shoulder joint, and 22.5% on orangutans. In gorillas, latissimus dorsi comprises 44.2% (range, 41.5–46.9) of the three major trunk muscles, but 58.8% (range, 48.6–67.0) in orangutans, whereas the rotator cuff muscles do not differ in their contribution to shoulder musculature. The combination of rotator cuff muscles, associated ligaments and tendons, and bony shape maintain the integrity of the gleno-humeral joint. The gorilla humeral head is somewhat restricted, in contrast to the less confined orangutan's due to the scapu-la's less projecting acromion and coracoid processes and a shallower glenoid fossa (Fig. 6).

Elbow joint. Ratios of elbow flexors and extensors differ in the two species, and the ranges do not overlap. Gorilla flexors are 50.6% (range, 49.5–51.5), with brachioradialis contributing 15%; extensors are 49.4% (range, 48.5–51.3). In orangutans, the flexors are 57.8% (range, 54.2–60.2), extensors 42.7 (range, 38.8–45.8); the brachioradialis contributes 40% to the flexors mass and has a prominent attachment on the lateral epicondylar ridge. The bony joint architecture reflects the differences in muscle mass and function. The gorilla's humero-ulnar joint has a broad trochlea and wide trochlear waist, with greater surface area. The orangutan joint reflects a tighter fit with its crescent-shaped trochlear notch, constricted trochlear waist and coronoid process, and a rounded pronounced capitulum for rotation of the radius with the humerus (Fig. 7).

Wrist joint and hand. Of gorilla forelimb musculature, 22.4% acts on the wrist joint and fingers. Palmaris longus muscle is absent in all of the five gorillas (see also Raven, 1950; Tuttle, 1969; Gibbs et al., 2002). Of orangutan forelimb musculature, 28.6% acts on the wrist joint and fingers; and palmaris longus contributes about 19% to the wrist flexors. The digital flexors are heavier than extensors in both species. The flexor pollicis longus has no slip to the thumb in either the gorillas or orangutans (also see Sullivan and Osgood, 1927; Raven, 1950; Tuttle, 1969; Gibbs et al., 2002).

Hip joint. The expanded innominate reflects the gorilla's muscular hind limb. The abductors attach on a broad ilium and high greater trochanter; the acetabulum is deep and the femoral head has a fovea for the ligamentum teres. Orangutan rotators are prominent; the abductors attach on a low greater trochanter; the acetabulum is shallow, and the nearly perfect spherical femoral head lacks a liagmentum teres (Fig. 8).

Knee joint. Gorilla knee extensors (quadriceps femoris) are heavier than the flexors (hamstrings), and attach over a well-developed patella on to the tibial tuberosity. In orangutans the masses are completely
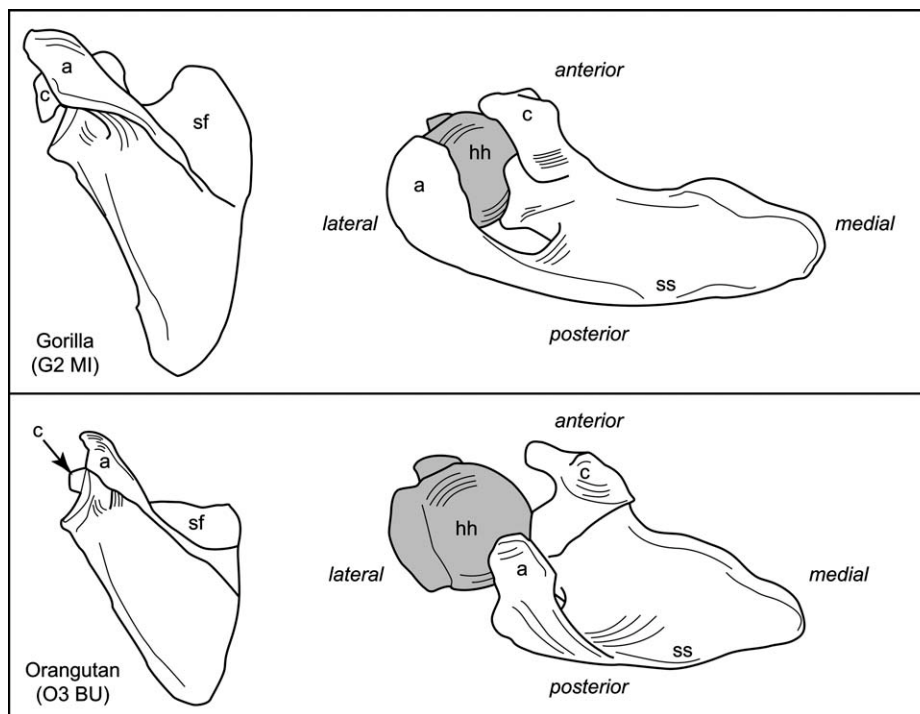
Scapula posterior view (left), superior view (right) with humeral head: (**a**) acromion; (**c**) coracoid process; (**hh**) humeral head; (**sf**) supraspinous fossa; (**ss**) scapular spine. Drawn to scale.

Fig. 6. Scapula and gleno-humeral joint.

reversed and do not overlap with gorillas: the extensors attach over a small patella, and the heavier knee flexors have an important role in knee rotation indicated by the convex surface of the tibial condyles and large sesamoid bone in the tendon of the popliteus.

Ankle joint and foot. In both species the plantar-flexors (talo-crural joint extensors) are heavier than dorsiflexors, as are the digital flexors compared to extensors. The invertors and evertors are similar in proportions (gorilla: 52.8% and 47.2%; orangutans 53.0 and 47.0), even though the orientation of the talo-crural and subtalar joints and foot proportions differ significantly in the two species.

Linear Dimensions

In relative length, gorilla segments of the forelimb and hind limb taper from longer to shorter in linear dimensions, but orangutans do not (Table 5).

DISCUSSION
Shared Anatomy and Evolutionary History

Gorillas and orangutans had a common ancestor and therefore share anatomical features associated with an orthograde trunk: long clavicle, dorsal position of the scapula on a broad rib cage, lateral orientation of the glenoid cavity, short lumbar region, reduced tail vertebrae (coccyx), and broad iliac blades. Forelimb dominance, reflected in an intermembral index over 100, is shared among all apes unlike most monkeys (e.g.,

Schultz, 1937; Washburn, 1951, 1963; Aiello and Dean, 1990). The joints of the shoulder (for circumduction), elbow (rotation), and wrist (adduction) each have a greater range of motion than in monkeys, which translates into greater range for hand placement and significant control of the body in three-dimensional space (Grand, 1964; Lewis, 1969). The relatively long forelimbs, mobile joints, and strong grasping hands thus allow male gorillas and orangutans to achieve considerable body mass while retaining the ability to climb vertically, suspend, reach in all directions, and feed at the ends of branches while moving into, through and out of the canopy (Grand, 1972).

This complex of ape features has been retained in these two large bodied apes. This study reveals additional similarities: 1) overall proportions of bone, skin, and muscle relative to TBM; 2) relative percents of bone and muscle in the head/trunk segment; 3) emphasis on flexors muscle groups of the elbow, wrist, and hand; 4) long hands that span more than 25% of forelimb length; and 5) similar proportions of muscle that act on the subtalar joint.

Divergent Anatomies and Evolutionary Histories

Whereas, evolutionary history accounts for their anatomical similarities, differences correlate with species-specific adaptations developed after gorillas and orangutans diverged into two lineages some 10 million to 12 million years ago (Pilbeam, 1996; Stauffer et al., 2001). Perhaps during the middle Miocene period in Africa,
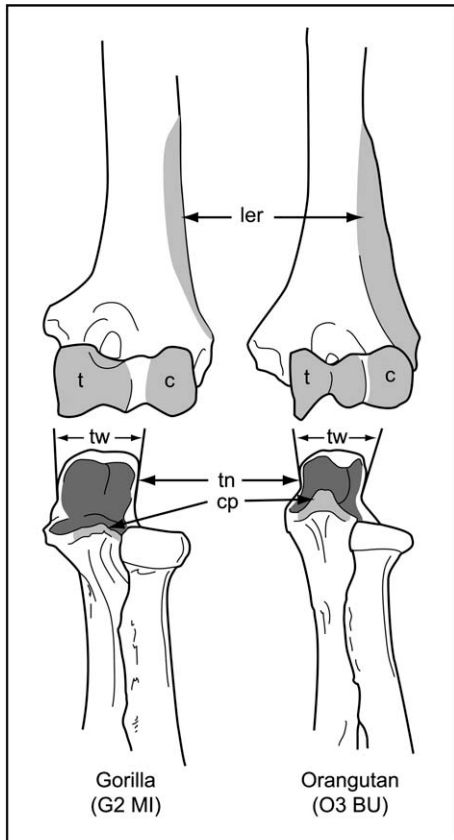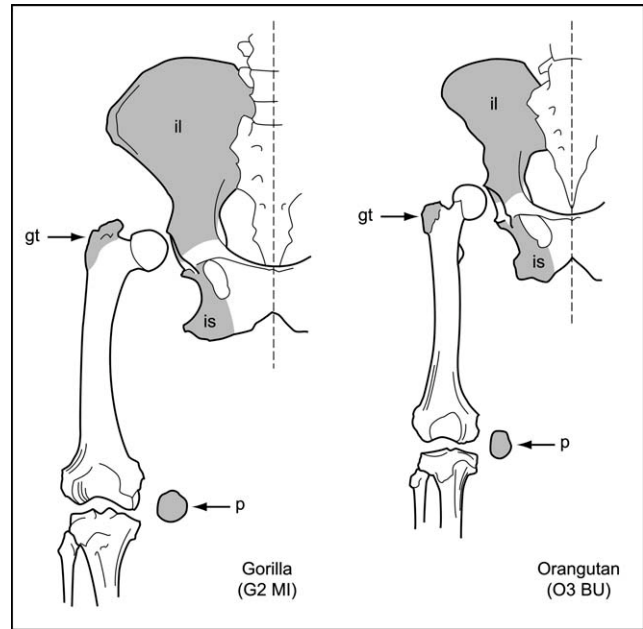
Anterior view of the distal humerus (top) and proximal ulna and radius (bottom): (**c**) capitulum; (**cp**) coronoid process; (**ler**) lateral epicondylar ridge; (**t**) trochlea; (**tn**) trochlear notch; (**tw**) trochlear waist. Drawn to scale.

Fig. 7.   Elbow joint.

Anterior view of innominate, femur, and proximal tibia: (**gt**) greater trochanter; (**il**) ilium; (**is**) ischium; (**p**) patella. Drawn to scale.

Fig. 8.   Hip and knee joints.

TABLE 5. Limb segments relative to total limb lengths compared to relative limb mass

Species	Humerus (arm)	Radius (forearm)	Hand	Femur (thigh)	Tibia (leg)	Foot
Gorilla (N = 4)						
Linear	39.9	33.2	26.9	38.2	31.4	30.4
Mass	52	35.7	12.3	62.3	25.3	12.4
Orangutan (N = 2)						
Linear	35.3	36.1	28.6	33.3	30.7	36.0
Mass	41.9	42.4	15.7	58	25.6	16.4

gorilla and chimpanzee ancestors began to forage and travel on the ground. Anatomy associated with knuckle-walking enabled gorillas to support a large body size as they moved quadrupedally over stable substrates. In contrast, maneuverability remained essential to orangutan travel through the dense and flexible supports of the forest canopy. The competing demands of support and mobility in these large animals can account for shifts in functional muscle groups and associated joint configurations. Subtle variations in musculo-skeletal anatomy underlie the ability to accommodate divergent locomotor adaptations in gorillas and orangutans.

Gorilla adaptation. The gorilla's heavy body is supported above the fore- and hind limbs that bear the compressive forces generated from quadrupedal weight-bearing and propulsion over the forest floor (Fig. 9). Muscle-bone-joint relationships reflect a lack of extreme flexibility at the shoulder, hip, knee, and ankle joints. Limb musculature is concentrated proximally to augment stability of the "deep" bony structures of the shoulder and hip joints. At the scapula, prominent acromion and coracoid processes encapsulate and restrict the humeral head (Tuttle, 1970; Roberts, 1974). At the hip, the gorilla acetabulum is deepest among the apes (Schultz, 1963a). This anatomical configuration is reflected in behavior, confirmed by observations on locomotion of captive males (Isler, 2005).

The elbow and knee are less restricted by bony joint configuration than the proximal joints. Muscles of the arm and thigh prevent rotation under compressive forces, which would destabilize a heavy quadruped during ground travel. Elbow extensors (triceps) and flexors are nearly equal in mass. Electromyography indicates the long head of triceps stabilizes the elbow during extension and against flexor rotational forces and is continuously active while the forelimb is bearing weight (Tuttle and Basmajian, 1974a, b). At the knee, the more massive quadriceps femoris relative to hamstrings (59.1% and 40.9%) correlate with propulsive power and joint stability.

At the wrist, their tightly packed carpals compared to orangutans reflect forces during quadrupedal walking (Tuttle, 1970). At the ankle, the plantar-flexors provide significant propulsive action during quadrupedal walking. The broad sole and the prominent talus and calcaneus, 40% of foot length, provide a stable platform for heel touchdown in initial weight bearing (Schultz, 1963b; Tuttle, 1970; Gebo, 1992). The relatively heavy thighs and lighter feet provide propulsive power and

Fig. 9. Schematic of functional muscle groups.

trees. With the coordination of their short but muscular hind limbs and their powerful forelimbs, they climb vertically, up to 30 m to reach fruit; long forelimbs extend their reach. They remain close to the core of the tree and distribute their weight among the larger branches (Remis, 1994, 1999). In the trees, the males also generate sway of branches, make bridges, and suspend and scramble through the branches to feed between trees or to flee from observers; they mimic ground postures and movements in the canopy while they feed or construct nests—sit, squat, suspend, stand bipedally, tripedally, and quadrupedally (Remis, 1995). Thus, they effectively use the trees, even if their motions in the canopy are ungainly, deliberate and cautious.

Orangutan adaptation. Adult male orangutans, the largest-bodied primate to inhabit the canopy, orient their heavy torso in a variety of angles above or below supports (Figure 9). Their limbs can be recruited to act in nonstereotyped positions relative to the body and to each other (Cant, 1992; Povinelli and Cant, 1995). Joint flexibility is crucial to the variety of postures and modes in feeding, nesting, and moving in trees, including vertically climbing, and suspending (Sugardjito and van Hooff, 1986; Cant, 1987; Thorpe and Crompton, 2006). Pronounced rotational capabilities in the shoulder, wrist, hip, and knee joints facilitate clambering movements (Morbeck and Zihlman, 1988; Tuttle and Cortright, 1988) and are well suited to maneuvering across arboreal pathways and crossing gaps.

The considerable mass and length of the forelimbs reflect reliance on upper body strength and an extended reach. The well-muscled shoulder joint with small acromion and coracoid processes trade stability for strength and mobility. As in the gorilla, orangutan limb muscle is concentrated proximally, but is distributed differently along the lengths of the limbs with less distal tapering. Bone at the hip joint is also less restrictive as reflected in the shallow acetabulum and reduced greater trochanter. The lack of a ligamentum teres (connecting the femoral head and acetabulum) and on average, heavy hip rotators, combine to permit hip circumduction and elevation of the hind limb far above the hip in contrast with gorillas (Isler, 2005). During dissection, we noted the gluteal muscles divide easily; the gluteus maximus has a superior portion on the posterior ilium, and a distinctly separate portion on the ischial tuberosity (ischiofemoralis), whereas, these two portions are continuous in gorillas (Sigmon, 1974; Stern and Susman, 1981). Such divisions may assist a given muscle to act with greater independence and so increase its mobility (Sigmon, 1974, 1975).

The forearm segment, though relatively longer, is equal in mass to the arm segment. The humero-ulnar joint is tightly constructed to provide stability for the heavy forearm and hand. The heavy wrist and digital flexors provide leverage to pull the large body forward. They also contribute stability during elbow extension and power during humero-radial rotation. The prominent brachioradialis acts during powerful flexion of the elbow, augmenting the action of other brachial flexors (Tuttle et al., 1983).

The knee joint contrasts with the elbow joint. The convex articular surface of the proximal tibia and a large sesamoid at the lateral condylar insertions of the

retraction against a stable substrate, typical of catarrhine primates that spend time on the ground or leap (Grand, 1977).

Gorillas range throughout their habitat foraging on vegetation and insects near the forest floor (Tutin et al., 1991; Cipolletta et al., 2007). However, when seeking preferred foods, they may travel distances to swampy areas for aquatic herbs or widely dispersed fruit sources on the ground (Nishihara, 1995; Yamagiwa et al., 1996; Remis, 1997b; Goldsmith, 1999; Rogers et al., 2004). When succulent fruits are seasonally available, their day ranges increase by several times such that their mean day journey lengths approach 3 km, similar to those of the more persistently frugivorous chimpanzees (Tutin and Fernandez, 1993; Yamagiwa et al., 1996; Remis, 1997a,b).

Even with their considerable bulk, silverback males maintain sufficient mobility to make occasional use of

popliteus muscle promote rotation and flexion. Knee flexors are proportionally greater than extensors; the reverse of the distribution in the gorilla. The hamstrings attach low and medially on the tibia and fibula to promote rotation, and a small patella corresponds with the reduced mass of the quadriceps femoris muscle. Hip and knee rotation function in concert to place the foot in positions that anchor and propel the body through the canopy.

The wrist joint suggests an adaptive shift toward a ball and socket mechanism specifically to facilitate expanded rotation (Lewis, 1969; Tuttle, 1970; Jenkins and Fleagle, 1975; Sarmiento, 1988). The hand's digital extensors are heavier than those of the gorilla and correlate with ease of extension and the large and open palm for effective grasping on to small supports (Tuttle, 1970).

The orangutan foot as the terminal link in the hind limb is a powerful grasping organ due to its relative mass, bone and joint structure, and muscle design. The foot comprises more than a third of total limb length (36%), an important part of the extended reach of the whole limb. Within the foot itself the tarsus is only a fourth of the foot's length; long, curved phalanges dwarf the other features (Schultz, 1963b; Rose, 1988). Orientation at the talo-crural and subtalar joints naturally inverts the sole and requires little muscle action to maintain a grasping position (Grand, 1967). This same joint configuration contributes to weight bearing predominately on the foot's lateral aspect when walking on a stable substrate. Muscle architecture designed for moving joints through large ranges enables foot and digit mobility (Payne et al., 2006b). Heavy dorsiflexors and digital flexors assist in lifting and placing the foot in a three-dimensional environment.

Orangutans are dedicated frugivores (MacKinnon, 1974; Rijksen, 1978). When fruit is abundant, they may consume it exclusively but settle for other items in the trees when it is not (Galdikas, 1988; Knott, 1998, 2005). Consequently, males remain in the canopy most of the time to feed and travel between trees to new food patches. As they move across flexible, unstable supports, their considerable mass deforms branches downward and opens gaps between adjacent trees (Grand, 1984). Orangutans solve this problem by distributing their weight over multiple supports, preferably lianas less than 10 cm in diameter (Povinelli and Cant, 1995; van Schaik, 2004; Thorpe et al., 2009). Using their bulk, they sway branches and form bridges to adjacent trees, and use their long and powerful arms and hands to pull in flexible branches to cross gaps. They recruit their prehensile feet to grasp nearby branches and propel themselves through the canopy (Chevalier-Skolnikoff et al., 1982; Sugardjito, 1982; Cant, 1987, 1992; Thorpe and Crompton, 2006). Their cognitive skills assist in assessing the biomechanics of branch flexibility and in assuming the most effective body positions to make their way through the canopy (Povinelli and Cant, 1995).

Male orangutans have limited skill in ground travel. They fist-walk with hyper-extended wrist joints; they stand with fully extended and locked hip and knee joints, using the hands on adjacent surfaces or objects to ensure stability (Tuttle, 1970; Stern and Susman, 1981; Thorpe et al., 2007). Their inverted foot is not well suited for sustaining compressive forces during quadrupedal walking over relatively stable surfaces. Hence, males compromise bipedal and quadrupedal weight-bear-ing postures to achieve extreme joint mobility, and as a result, their ground travel is laborious.

Body Composition and Individual Variation

Components of body mass—muscle, bone, skin, and fat—from this sample of male gorillas and orangutans overlap in ranges but differ in the means. For these species, as for other primates, 60%–70% of body mass is devoted to the locomotor system in the muscles, the skeletal infrastructure, and the overlying skin (Grand, 1977). Closer analysis of body composition reveals individual and species differences not apparent in a comparison of means and ranges. Records of the animals kept during life document body mass, age, cause of death and overall premortem fitness and provide a basis for interpreting observed variation.

As in humans, age influences body composition (Clarys et al., 1999). The youngest individual, Gorilla 2 (MI), healthy before a sudden death, was very well muscled (46.4%) and had little measurable body fat estimated at about 7%–8%. The high proportion of muscle and low fat parallels observations on young adult male chimpanzees (McFarland and Zihlman, 1996, 1999) and represents the "prime adult male African ape." The young male (Gorilla 2 MI) contrasts with Gorilla 1 (MO), the oldest and least fit, who has the lowest muscle (34%) and most fat, estimated at over 20%. These proportions reflect aging when fat replaces muscle coupled with chronic health problems and gradual weight loss. Gorilla 5 (CO) was very well muscled and had higher muscle and lower fat (about 17%) than Gorilla 1 (MO); his death followed a brief illness, with no weight loss. Gorilla 3 (BW) maintained a relatively constant body mass during the last 14 years of his life; nevertheless, as with human aging, the percentage of muscle and fat probably shifted. At death his muscle was 38% and the adipose store estimated at 12%–15%.

Orangutans, by contrast, average less muscle and more body fat than gorillas. Although the sample is small, the lower percent of muscle is typical of exclusively arboreal-living animals compared to their more ground-dwelling relatives (Grand, 1978). The variation among orangutans in the sample perhaps can be attributed to state of health before death and to age changes. Orangutan 1 (BE) although young, was chronically ill, had less muscle (33.9%) and more estimated fat (over 20%) than the other two. Orangutan 3 (BU), also young, died suddenly had more muscle (35.9%) and less estimated fat (15%). Orangutan 4 (JI) was extremely obese, not untypical for captive orangutans; he was old, only 10.6% muscle, and estimated body fat above 45% of total mass.

Orangutan males have a unique mechanism for storing fat in addition to considerable inter-muscular fat. Flanged males with their larger body size can carry substantial fat in their cheek pads, neck, and throat (Winkler, 1989). The cheek pads of Orangutan 4 (JI) weighed 2.6 kg comprising 33% of head weight. Orangutan 3 (BU) cheek pads weighed 2.5 kg and measured 380 mm, equal to his shoulder breadth (as measured between the two acromion processes). This measurement is comparable to the 370 mm cheek breadth reported for a 23 year-old captive male (Fooden and Izor, 1983). Cheek flanges probably serve at least two functions: fat storage in a

location that does not interfere with locomotion, and as a signal to females and other males of developmental state. The capacity to accumulate fat is part of the orangutan adaptation to help maintain a positive energy balance in the face of a highly seasonal environment. High caloric intake accompanied by increased fat stores, however, is punctuated by periods of low food quality, lower caloric diet, and fat loss (Knott, 1998; Harrison et al., 2010). Fat depots provide additional energy stores to sustain males in the quest for food and mates, and in fighting with other males during reproductive times (Knott, 1998). Enhanced capacity to accumulate fat in captivity—due to reduced activity and steady food supply—makes captive orangutans particularly prone to obesity and diabetes mellitus (Gresl et al., 2000). It appears that the great apes have the potential to put on body fat, but orangutans carry this ability to an extreme because of more frequent fluctuations in quality of food.

CONCLUSIONS

Quantitative analysis of body mass that integrates skeletal and soft tissue, lengths and masses of segments, and the relative mobility of joints provide data to evaluate the relationship between anatomy and adaptation, and to test hypotheses that postcranial differences reflect locomotor divergences. Cumulatively, the distribution of body mass, the regional and functional concentrations of musculature, and range of joint motion underlie the preferences of gorillas to move across the forest floor on relatively stable supports and the divergence of orangutans to travel over uneven, flexible ones. The reduced frequency of gorilla vertical climbing into and through the trees contrasts with orangutans which move across small and unstable support surfaces of the forest canopy. The orangutan's expanded range of joint mobility permits the animal to clamber, grasp, and bridge with all four of its limbs, giving it complete control in three-dimensional space. Its heavy upper limbs with lengthened, muscular arms, forearms, and hands and relatively short, but extremely mobile lower limbs seem to represent the great ape extreme.

The relative importance of ground travel and propulsive force explains the gorilla's body composition, limb proportions and muscular lower limbs that most resembles chimpanzees and prefigures fully committed hominin bipedality (McFarland and Zihlman, 1999; Zihlman, 2004, 2005). Orangutans do not resemble the African apes; they show correspondences with the siamang in having heavier forelimbs than hindlimbs, but curiously, not the gibbons (*Hylobates*) (Schultz, 1933; Zihlman et al., 2011). Overall, the orangutan hind limb is unique among catarrhine primates in its extreme flexibility and in the mass and length of the foot that extends its reach. In any case, the proposal that 'orangutan bipedalism' constitutes a serious model for human bipedalism (e.g., Thorpe et al., 2007) is anatomically untenable given their total body configuration of mobile hip and knee joints, light knee extensors, and inverted foot orientation. The gorilla's lower limb is similar to chimpanzees and humans, for example, in the deeper hip joint, the heavy knee extensors, and a broad flat foot, which underscores their common evolutionary history.

The fossil record does not and cannot preserve soft tissues, so that our approach actually 'brackets' the fossil evidence we do have. For example, addition of segment mass for comparison to linear dimensions of ape fossils can take the evidence beyond an exclusive dependence on osteology and expand potential interpretations. Furthermore, application of soft tissue data can serve as another line of evidence along with molecular, dental–cranial, and skeletal to contribute to phylogeny (Pilbeam, 2000; Gibbs et al., 2000, 2002; Zihlman et al., 2011).

LITERATURE CITED

Aiello L, Dean C. 1990. Human evolutionary anatomy. New York: Academic Press. p 608.

Boyer EL. 1935. The musculature of the inferior extremity of the orang-utan *Simia satyrus*. Am J Anat 56:193–256.

Boyer EL. 1939. The cranio-mandibular musculature of the orang-utan, *Simia satyrus*. Am J Phys Anthropol 24:417–427.

Bolter D, Zihlman AL. 2003. Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns across Old World monkeys, apes, and humans. J Zool Lond 260:99–110.

Cant JH. 1987. Effects of sexual dimorphism in body size on feeding postural behavior of Sumatran orangutans (*Pongo pygmaeus*). Am J Phys Anthropol 74:143–148.

Cant JH. 1992. Positional behavior and body size of arboreal primates: a theoretical framework for field studies and an illustration of its application. Am J Phys Anthropol 88:273–283.

Chapman HC. 1878. On the structure of the gorilla. Proc Zool Soc Lond 30:385–394.

Chapman HC. 1880. On the structure of the orang outang. Proc Zool Soc Lond 32:160–174.

Chevalier-Skolnikoff S, Galdikas BMF, Skolnikoff AZ. 1982. The adaptive significance of higher intelligence in wild orangutans: a preliminary report. J Hum Evol 11:639–652.

Cipolletta C, Spagnoletti N, Todd A, Robbins MM, Cohen H, Pacyna S. 2007. Termite feeding by *Gorilla gorilla gorilla* at Bai Hokou, Central African Republic. Int J Primatol 28:457–476.

Clarys JP, Martin AD, Marfell-Jones MJ, Janssens V, Caboor D, Drinkwater DT. 1999. Human body composition: a review of adult dissection data. Amer J Hum Anat 11:167–174.

Davis DD. 1960. The proper goal of comparative anatomy. In: Purchon RD, editor. Proceedings of the Centenary and Bicentenary Congress of biology Singapore. Singapore: University of Malaya Press. p 44–50.

Davis DD. 1961. Origin of the mammalian feeding mechanism. Am Zool 1:229–234.

Galdikas B. 1988. Orangutan diet, range, and activity at Tanjung Putting, Central Borneo. Int J Primatol 9:1–35.

Gebo DL. 1992. Plantigrady and foot adaptation in African apes: implications for hominid evolution. Am J Phys Anthropol 89:29–58.

Gibbs S, Collard M, Wood B. 2000. Soft tissue characteristics in higher primate phylogenetics. Proc Natl Acad Sci USA 97:11130–11132.

Gibbs S, Collard M, Wood B. 2002. Soft tissue anatomy of the extant hominoids: a review and phylogenetic analysis. J Anat 200:3–49.

Goldsmith ML. 1999. Ecological constraints on the foraging effort of western gorillas (Gorilla gorilla gorilla) at Bai Hokou, Central African Republic. Int J Primatol 20:1–23.

Grand TI. 1964. The functional anatomy of the shoulder of the chimpanzee. PhD Thesis, University of California, Berkeley.

Grand TI. 1967. The functional anatomy of the ankle and foot of the slow loris (Nycticebus coucang). Am J Phys Anthropol 26:207–218.

Grand TI. 1968a. Functional anatomy of the upper limb. In: Biology of the howler monkey (Alouatta caraya). Basel, New York: Karger, Bibl Primat. p 104–125.

Grand TI. 1968b. The functional anatomy of the lower limb of the howler monkey (Alouatta caraya). Am J Phys Anthropol 28:163–181.

Grand TI. 1972. A mechanical interpretation of terminal branch feeding. J Mammal 53:198–201.

Grand TI. 1977. Body weight: its relation to tissue composition, segment distribution, and motor function. I. Interspecific comparisons. Am J Phys Anthropol 47:211–239.

Grand TI. 1978. Adaptations of tissue and limb segments to facilitate moving and feeding in arboreal folivores. In: Montgomery GG, editor. The Ecology of arboreal folivores. Washington DC: Smithsonian Institution Press. p 231–241.

Grand TI. 1984. Motion economy within the canopy: four strategies for mobility. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates. New York: Columbia University Press. p 54–72.

Grand TI. 1997. How muscle mass is part of the fabric of behavioral ecology in East African bovids (Madoqua, Gazella, Damaliscus, Hippotragus). Anat Embryol 195:375–386.

Gregory WK. 1950. The Henry Cushier Raven memorial volume. The anatomy of the gorilla. New York: Columbia University Press. p 259.

Gresl TA, Baum ST, Kenmitz JW. 2000. Glucose regulation in captive Pongo pygmaeus abeli, P.p. pygmaeus, and P.p. abeli x P.p.pygmaeus. Zoo Biol 19:193–208.

Harrison ME, Morrogh-Bernard HC, Chivers DJ. 2010. Orang-utan energetics and the influence of fruit availability in the nonmasting peat-swamp forest of Sabangau, Indonesia, Borneo. Int J Primatol 31:585–607.

Isler K. 2005. 3D-Kinematics of vertical climbing in hominoids. Am J Phys Anthropol 126:66–81.

Isler K, Payne RC, Gunther MM, Thorpe SKS, Li Y, Savage R, Crompton RH. 2006. Inertial properties of hominoid limb segments. J Anat 209:201–218.

Isler K, Thorpe SKS. 2003. Gait parameters in vertical climbing of captive rehabilitant and wild Sumatran orang-utans (Pongo pygmaeus abelii). J Exp Biol 206:4081–4096.

Jenkins FA, Fleagle JG. 1975. Knuckle-walking and the functional anatomy of wrists in living apes. In: Tuttle RH, editor. Functional morphology and evolution. The Hague: Mouton. p 213–227.

Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. Int J Primatol 19:1061–1079.

Knott CD. 2005. Energetic responses to food availability in the great apes: implications for hominin evolution. In: Brockman DK, van Schaik CP, editors. Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge: Cambridge University Press. p 351–378.

Lewis OJ. 1969. The hominoid wrist joint. Am J Phys Anthropol 30:251–268.

MacAlister A. 1873. The muscular anatomy of the gorilla. Proc Royal Irish Acad 11:501–506.

MacKinnon J. 1974. The behaviour and ecology of wild orangutans (Pongo pygmaeus). Anim Behav 22:2–74.

McFarland RK, Zihlman AL. 1996. Body composition in male chimpanzees (P. paniscus and P. troglodytes): a preliminary report. Am J Phys Anthropol Suppl 22:251.

McFarland RK, Zihlman AL. 1999. Analysis of body weight in chimpanzees and gorillas: a functional interpretation. Am J Primatol 499:79–80.

Miller RA. 1932. Evolution of the pectoral girdle and forelimb in primates. Am J Phys Anthropol 17:1–56.

Morbeck ME, Zihlman AL. 1988. Body composition and limb proportions. In: Schwartz J, editor. Orangutan biology. New York: Oxford University Press. p 285–297.

Nishihara T. 1995. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park. Primates 36:151–168.

Oishi M, Ogihara N, Endo H, Asari M. 2008. Muscle architecture of the upper limb in the orangutan. Primates 49:204–209.

Oishi M, Ogihara N, Endo H, Ichihara N, Asari M. 2009. Dimensions of forelimb muscles in orangutans and chimpanzees. J Anat 215:373–382.

Owen R. 1843. Notes of the dissection of a female orang-utan (Simia satyrus, Linn.). Proc Zool Soc Lond 11:123–124.

Owen R. 1859. On the gorilla (Troglodytes gorilla, Sav.). Proc Zool Soc Lond 27:1–23.

Oxnard CE. 1967. The functional morphology of the primate shoulder as revealed by comparative anatomical, osteometric, and discriminant function techniques. Am J Phys Anthropol 26:219–240.

Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunther MM, Thorpe SKS, D'Aout K. 2006a. Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. J Anat 208:709–724.

Payne RC, Crompton RH, Isler K, Savage R, Vereecke EE, Gunther MM, Thorpe SKS, D'Aout K. 2006b. Morphological analysis of the hindlimb in apes and humans. II. Moment arms. J Anat 208:725–742.

Pilbeam D. 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. Mol Phylogen Evol 5:155–168.

Pilbeam D. 2000. Hominoid systematics: the soft evidence. Proc Natl Acad Sci USA 97:10684–10686.

Povinelli DJ, Cant JGH. 1995. Arboreal clambering and the evolution of self-conception. Quart Rev Biol 70:393–421.

Preuschoft H. 1961. Muskeln und gelenke der hinterextremitat des gorillas (Gorilla gorilla Savege et Wymann, 1847). Gegenbaurs Morphol Jahrb 101:432–540.

Preuschoft H. 1963. Muskelgewichte bei Gorilla, Orang-Utan, und Mensch. Anthrop Anz 26:308–317.

Raven HC. 1950. Part two. Regional anatomy of the gorilla. In: Gregory WK, editor. The Henry Cushier Raven memorial volume. The anatomy of the gorilla. New York: Columbia University Press. p 15–188.

Remis MJ. 1994. Feeding ecology and positional behavior of western lowland gorillas (Gorilla gorilla gorilla) in the Central African Republic. PhD Dissertation, Yale University, New Haven, CT.

Remis MJ. 1995. The effects of body size and social context on the arboreal activities of western lowland gorillas in the Central African Republic. Am J Phys Primatol 97:413–433.

Remis MJ. 1997a. Western lowland gorillas (Gorilla gorilla gorilla) as seasonal frugivores: use of variable resources. Am J Primatol 43:87–109.

Remis MJ. 1997b. Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. Am J Primatol 43:111–133.

Remis MJ. 1999. Tree structure and sex differences in arboreality among western lowland gorillas (Gorilla gorilla gorilla) at Bai Hokou, Central African Republic. Primates 40:383–396.

Rijksen HD. 1978. A field study on Sumatran orangutans (*Pongo pygmaeus abellii*, Lesson 1827): ecology, behaviour, and conservation. Wageningen: H Veenman and BV Zonen. p 421.

Roberts D. 1974. Structure and function of the primate scapula. In: Jenkins F, editor. Primate locomotion. New York: Academic Press. p 171–200.

Rodman PS, Cant JGH. 1984. Introduction: from comparative morphology and socioecology to an organismal biology of primates. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates. New York: Columbia University Press. p 1–20.

Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CEG. 2004. Western gorilla diet: a synthesis from six sites. Am J Primatol 64:173–192.

Rose MD. 1988. Functional anatomy of the cheiridia. In: Schwartz J, editor. Orangutan biology. New York: Oxford University Press. p 299–310.

Sarmiento EE. 1988. Anatomy of the hominoid wrist joint. Its evolutionary and functional implications. Int J Primatol 9:281–345.

Schultz AH. 1930. The skeleton of the trunk and limbs of higher primates. Hum Biol 2:303–438.

Schultz AH. 1933. Observations on the growth, classification, and evolutionary specializations of gibbons and siamangs. Hum Biol 5:212–255.

Schultz AH. 1937. Proportions, variability, and asymmetries of the long bones of the limbs and the clavicles in man and apes. Hum Biol 9:281–328.

Schultz AH. 1956. Postembryonic age changes. Primatologia 1:887–964.

Schultz AH. 1963a. Observations on the acetabulum of primates. Folia Primatol (Basel) 11:181–199.

Schultz AH. 1963b. Relations between the lengths of the main parts of the foot skeleton in primates. Folia Primatol (Basel) 1:150–171.

Sigmon BA. 1974. A functional analysis of pongid hip and thigh musculature. J Hum Evol 3:161–185.

Sigmon BA. 1975. Functions and evolution of hominid hip and thigh musculatures. In: Tuttle RH, editor. Primate functional morphology and evolution. The Hague: Mouton. p 235–252.

Sonntag CF. 1924a. On the anatomy, physiology, and pathology of the orang-utan. Proc Zool Soc Lond 24:349–451.

Sonntag CF. 1924b. The morphology and evolution of the apes and man. London 11: John Bole Sons and Danielsson, Ltd. p 364.

Stauffer RI, Walker A, Ryder OA, Lyons-Weller M, Blair Hedges S. 2001. Human and ape molecular clocks and constraints on paleontological hypotheses. J Hered 92:469–474.

Steiner P. 1954. Anatomical observations in a *Gorilla gorilla*. Am J Phys Anthropol 12:145–179.

Stern JT, Susman RL. 1981. Electomyography of the gluteal muscles in *Hylobates*, *Pongo*, and *Pan*: implications for the evolution of hominid bipedality. Am J Phys Anthropol 55:153–166.

Sugardjito J. 1982. Locomotor behaviour of the Sumatran orangutan (*Pongo pygmaeus abelii*) at Ketambe, Gunung Leuser National Park. Malay Nat J 35:57–64.

Sugardjito J, van Hooff JARAM. 1986. Age-sex class differences in the positional behaviour of the Sumatran orang-utan (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park, Indonesia. Folia Primatol (Basel) 47:14–25.

Sullivan WE, Osgood CW. 1927. The musculature of the superior extremity of the orangutan, *Simia satyrus*. Anat Rec 35:193–239.

Taylor AB. 1997. Scapula form and biomechanics in gorillas. J Hum Evol 33:529–553.

Thorpe SKS, Crompton RH. 2006. Orangutan positional behavior and the nature of arboreal locomotion in the Hominoidea. Am J Phys Anthropol 131:384–401.

Thorpe SKS, Holder RL, Crompton RH. 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. Science 316:1328–1331.

Thorpe SKS, Holder RL, Crompton RH. 2009. Orangutans employ unique strategies to control branch flexibility. Proc Natl Acad Sci USA 106:12646–12651.

Tutin CEG, Fernandez M. 1993. Composition of the diet of chimpanzees and comparison with that of sympatric lowland gorillas in the Lope Reserve, Gabon. Am J Primatol 30:195–211.

Tutin CEG, Fernandez M, Rogers ME, Williamson EA, McGrew WC. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. Philos. Trans R Soc Lond B Biol Sci 334:179–186.

Tuttle RH. 1969. Quantitative and functional studies on the hands of the Anthropoidea. I. The Hominoidea. J Morphol 128:309–364.

Tuttle RH. 1970. Postural, propulsive, and prehensile capabilities in the cheiridia of chimpanzees and other great apes. In: Bourne GH, editor. The chimpanzee. Basel: Karger. Vol 2: p 167–253.

Tuttle RH. 1972. Relative mass of cheiridial muscles in catarrhine primates. In: Tuttle RH, editor. The functional and evolutionary biology of primates. Chicago, New York: Aldine Atherton. p 262–291.

Tuttle RH, Basmajian JV. 1974a. Electromyography of brachial muscles in Pan gorilla and hominoid evolution. Am J Phys Anthropol 41:71–90.

Tuttle RH, Basmajian JV. 1974b. Electromyography of forelimb musculature in Gorilla and problems related to knuckle-walking. In: Jenkins FA, editor. Primate locomotion. New York: Academic Press. p 293–348.

Tuttle RH, Basmajian JV. 1978. Electromyography of pongid shoulder muscles. II. Deltoid, rhomboids, and "rotator cuff." Am J Phys Anthropol 49:47–56.

Tuttle RH, Basmajian JV, Ishida H. 1975. Electromyography of the gluteus maximus muscle in gorilla and the evolution of hominid bipedalism. In: Tuttle RH, editor. Primate functional morphology and evolution. The Hague: Mouton. p 253–269.

Tuttle RH, Cortright GW. 1988. Positional behavior, adaptive complexes, and evolution. In: Schwartz J, editor. Orangutan biology. New York: Oxford University Press. p 311–330.

Tuttle RH, Velte J, Basmajian JV. 1983. Electromyography of brachial muscles in *Pan troglodytes* and *Pongo pygmaeus*. Am J Phys Anthropol 61:75–83.

Van Schaik C. 2004. Among orangutans. Red apes and the rise of human culture. Cambridge: Harvard University Press. p 244.

Washburn SL. 1951. Analysis of primate evolution with particular reference to the origin of man. Cold Spring Harbor Symposia on Quantitative Biology 15, 67–78. (Reprinted 1999) In: Strum SC, Lindburg D, Hamburg D, editors. The new physical anthropology. Upper Saddle River, New Jersey: Prentice-Hall. p 7–17.

Washburn SL. 1963. Behavior and human evolution. In: Washburn SL, editor. Classification and human evolution. Viking Fund Pub. 37, Current Anthropology, New York: Wenner-Gren Foundation. p 190–203.

Winkler L. 1989. Morphology and relationships of the orangutan fatty cheek pads. Am J Primatol 17:305–319.

Wright-Fitzgerald AS, Balceniuk MD, Burrows AM. 2010. Shouldering the burdens of locomotion and posture: glenohumeral joint structure in prosimians. Anat Rec 293:680–691.

Yamagiwa J, Maruhashi T, Yumoto T, Mwanza N. 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In: McGrew WC, Marchant L, Nishida T, editors. Great ape societies: Cambridge: Cambridge University Press. p 82–98.

Zihlman AL. 1984. Body build and tissue composition in *Pan paniscus* and *Pan troglodytes*, with comparisons to other hominoids. In: Susman RL, editor. The pygmy chimpanzee. New York: Plenum Publishing. p 179–200.

Zihlman AL. 1997. The natural history of apes. In: Morbeck ME, Galloway A, Zihlman AZ, editors. The evolving female: life history features in males and females. Princeton, N.J.: Princeton University Press. p 86–103.

Zihlman AL. 2004. Locomotor adaptations in great ape anatomy with implications for hominid origins. Folia primatol (Basel) 75(Suppl. 1):353.

Zihlman AL. 2005. Quantitative anatomy and locomotor adaptations in great apes. Presentation at Understanding great apes in the genomic era. University of California, San Diego, August.

Zihlman AL, McFarland RK. 2000. Body mass in lowland gorillas: a quantitative analysis. Am J Phys Anthropol 113:61–78.

Zihlman AL, Mootnick AR, Underwood C. 2011. Anatomical contributions to hylobatid taxonomy and adaptation. Int J Primat. DOI 10.1007/s10764-011-9506-y.