Orang-utan Biology

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Body Composition and Limb Proportions

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The orang-utan *(Pongo pygmaeus)*, the large-bodied arboreal "loner" of the Bornean and Sumatran rain forest, is an unusual mammal and an unusual primate. It is the largest arboreal species, and the largest mammalian frugivore. Its social life is limited; only mother-young groups are stable, and associations of adults including mating pairs are temporary. However, in other features, including relative brain size and cognitive abilities, orang-utans are similar to the other great apes.

Locomotor, postural, and manipulative skills within the hominoid radiation have been built upon vertical orientation of the trunk and enhanced shoulder mobility through positioning the large, well-developed clavicle on a broad chest, humeroulnar stability, forearm rotation, wrist flexibility, and grasping hands (Schultz, 1968, 1969b; Washburn, 1968). Hominoids present a spectrum of forelimb and hindlimb adaptations, with orang-utans at one end and humans at the other. Human upper limbs are adapted for fine-tuned manipulations rather than for locomotion or body support; those of African apes for arboreal climbing and terrestrial knuckle-walking; and those of orang-utans for slow climbing among the trees—elongated forelimbs with large hands and very mobile shoulders. In hindlimb morphology, at one end of the spectrum, humans have long lower limbs and reduced mobility of hip, knee, and ankle joints; at the other, orang-utans have short lower limbs, large feet, and pronounced hip, knee, ankle, and foot mobility. Among the hominoids, humans have the shortest upper and longest lower limbs, relative to trunk length, orang-utans the longest upper and shortest lower limbs.

Locomotion and posture integrate all aspects of an animal's activity within a particular environment and require an efficient system of joints, links, and segments. The distribution of weight to these segments and the relative proportion of tissues also reflect an animal's locomotor type and way of life (Grand, 1977). The body weight of an individual animal reflects many interrelated variables of physiological function and structural design: metabolism, stage of growth, health and diet, locomotor energetics, and mechanics. Total body weight, limb proportions, and tissue composition in adults, like other morphological and physical features, are a product of the species' evolutionary history, as well as an individual's genotype, an individual's sex, and the environmental influences acting on an individual during its life history. These factors affect the time of onset, speed, and duration of stages in growth and development.

In this chapter we analyze several parameters of morphology—linear measurements, joint surface area, tissue composition, and segment weight. Through these types of data it is possible to obtain a more comprehensive picture of the relationship between anatomy and locomotor abilities, and also of the components of sexual dimorphism, than is available from simple weight and linear dimensions. Measures of joint surface area, for example, reflect dual functions of weight transfer and mobility and so provide a functional sense of locomotor dynamics. Such information provides clues to the evolutionary history of the species.

MATERIALS AND METHODS

Dissections were carried out on adult male and female orang-utans. Also skeletons of nine wild-shot Bornean orang-utans were studied: six females and three males, collected by W. L. Abbott and housed in the Smithsonian Institution. These data form part of a larger study of fossil and extant catarrhines designed to interpret and explain morphological variation as it relates to locomotion, posture, and sexual dimorphism.

Both cadaver and skeletal data on individuals of known sex and body weight are used to quantify relationships among (1) total body weight; (2) composition and distribution of weight in segments determined from dissections; (3) size and shape of postcranial joint surface areas; (4) linear values taken from latex templates and di-
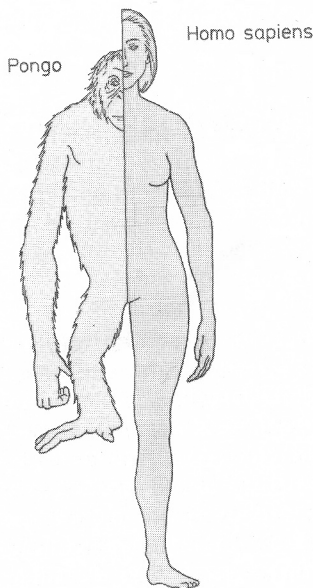
FIG. 21–1. Comparison of body build in *Pongo pygmaeus* and *Homo sapiens*. Drawn approximately to scale.

rectly from bones and teeth; and (5) weights of cleaned bones. Free-ranging adult males average 66 kg (Sumatra) and 73 kg (Borneo), whereas adult females average 37 kg (Eckhardt, 1975). These substantial differences between males and females raise questions about the kinds of differences of linear, surface area, and volume dimensions associated with weight differences.

Cadavers

Two orang-utans were dissected using body segment techniques (Grand, 1977; Zihlman, 1984) to determine body tissue composition and distribution of weight to segment. These captive individuals include (1) a 15–20-year-old adult male Bornean orang-utan and (2) a 9-year-old female orang-utan. The cadavers, frozen to preserve tissue weights, were then thawed, reweighed, and dissected following procedures outlined in Grand (1977) and modified in Zihlman (1984).

Total body weight (TBW) is taken as body weight at time of death prior to postmortem procedures. Some tissue weights were lost as a consequence of necropsy. For example, since the adult male brain was removed but not weighed, its weight was estimated.[1]

One side of each body was dissected segmentally. Head, trunk, pelvis, upper arm, forearm, hand, thigh, leg, and foot segments were separated at the relevant joints. Muscles crossing

these joints were cut at the attachment sites. Skin, muscle, bone, fat, and "other" were dissected and weighed wet to the nearest gram. Here, "other" includes only tissue that cannot be classified in another category, unlike Grand (1977) who included trunk, neck, and masticatory muscles in the "other" category.

On the opposite side of the body, muscles and joints were dissected in detail. Muscles were weighed individually and muscle attachments noted, as were details of joint structure. Bones were weighed fresh and again after cleaning in order to be comparable to data derived from the skeletal series.

Within each segment, tissue weight is expressed as a percentage of segment weight. Combined tissue weight is expressed as a percentage of total body weight. Body segment weights also are expressed as a percentage of total body weight; forelimb and hindlimb segment weights are doubled to represent the whole body condition.

From the dissected animals it was possible to obtain information on (1) head, trunk, and upper and lower limb segments relative to total body weight; (2) relative proportions of tissues (muscle, bone, skin, fat, and other); and (3) bone weights, joint surface areas, and linear measurements.

Skeletons

Data on the nine wild-shot *Pongo pygmaeus pygmaeus* from the Smithsonian provide a sample for comparison with the dissected specimens. The requirement that individuals have known body weights and sex limited the potential sample. However, at least for long bone length and breadth measurements, we can compare data from a larger sample that includes both Bornean and Sumatran individuals ($N = 25$: 12 males, 13 females, Morbeck, unpublished data).

Bones of the cranium, mandible, vertebral column, forelimb, and hindlimb were weighed. Thirty-seven linear measurements (in millimeters) were taken directly on the skull, face, teeth, limb bones, and trunk, and 22 linear measurements were taken from latex templates of joint surfaces. Joint surface areas were measured via latex templates on cleaned, dry bones (Gomberg, 1981; Gomberg and Morbeck, 1983). Modifying the method described in Gomberg (1981), latex templates were mounted with tape on clear plastic and measured using a Zeiss MOP 3 Image Analyzer.

Joint surface area and shape reflect stability

and weight transfer, as well as the direction and range of motion. For instance, a low ratio of the area of the glenoid fossa to the humeral head area is characteristic of orang-utans and other hominoids and reflects shoulder mobility of a large humeral head. Further, the high ratio of the humeral trochlear area to capitular area, combined with the distinctive distal humeral joint shape, indicates a greater emphasis on weight transfer and stability in the medial aspect of the elbow joint complex.

Joint size and shape determined from bones alone, as with linear measurements, tell only part of the functional story. Soft tissue contributes to the functional joint surface and increases the articular area. In the orang-utan wrist joint, for example, the triangular disc of cartilage connects the radius and broad ulnar head; the shoulder and hip joints each have a labrum surrounding the proximal joint surface. Size, shape, and placement of ligaments can both facilitate and limit motion. However, the joint surface area data used here provide a better reflection of joint features than do linear measurements alone.

We recognize the problems of a small sample—two dissected animals and nine museum skeletons. However, the pattern of variation in the dissected specimens parallels the variation observed in the skeletons. Statistical analyses have been carried out where appropriate. Selected variables are compared trait by trait in an effort to delineate patterns of variation in body size, linear, and joint area size and proportions.

RESULTS

Our data confirm marked sexual dimorphism in weight and linear measures in orang-utans (Eckhardt, 1975; Schultz, 1941). The male-female differences are further expressed through segmental masses, tissue proportions and joint surface areas, which vary with body weight and secondary sexual characteristics.

Body Weight, Body Segments, and Tissue Composition

Body Weight

Ranges of male and female body weight in our Bornean sample do not overlap. The captive Bornean male (102 kg) exceeds the group range (83.9–90.7 kg) which represents the heavier males in Eckhardt's (1975) compilation using a larger sample (Bornean male range 34.0–90.7 kg, mean 72.8 kg). The captive Sumatran female (27.8 kg) falls below the group range of known body weights for free-ranging adult females (31.7–45.4 kg).[2]

Body Segments

Body proportions and features within segments differ in the adult pair (Figure 21–2; Table 21–1). The male's head is similar in relative weight to the female's but his trunk is relatively larger. The forelimbs are similar (16.7 vs. 16.3% of TBW), but the male's hindlimbs are considerably lighter (12.0 vs. 17.8% of TBW). Within the forelimb, the forearm of the male is relatively heavier, the upper arm and hand lighter. However, despite the marked difference in hindlimbs relative to TBW, within the hindlimb, the segmental proportions of the thigh, ankle, and foot are nearly identical in both individuals (Table 21–1). This unexpected finding suggests geometric similarity.

Tissue Composition

Differences in the contribution of body segments to TBW and variation in tissue composition within segments relate to overall body size and, in part, to sexual dimorphism, especially in muscle size and distribution of fat deposits. The male has a higher proportion of musculature, 35% of TBW compared to 27% in the female. Bone, skin, and fat (and other) are relatively greater in the female (Table 21–2A), even though the male has extensive laryngeal sacs with fat deposits and an additional fat deposit on its upper back.

Brain weight in the female (341 g) represents 1.2% of body weight and about 18% of head segment weight. In the male, brain weight, based on our estimate (434 g) is 0.4% of body weight and only 6% of the head segment.

In the forelimb and hindlimb, tissue composition differs slightly (Table 21–2B). In the forelimb, the amounts of muscle and bone are similar; in the hindlimb, however, the male has a greater percentage of muscle (57 vs. 50%). The most marked differences are in trunk/hip muscle, being one and one-half times greater in males than females (64 vs. 36%).

Sexual dimorphism is evident within the head. Although the heads are similar in relative size (7 vs. 6.9%, Fig. 21–1), the muscles of mastication in the male are more than twice that of the female (15.9 vs. 6.6%): the temporalis is about four times larger and the masseter is more than twice as large (Table 21–3).
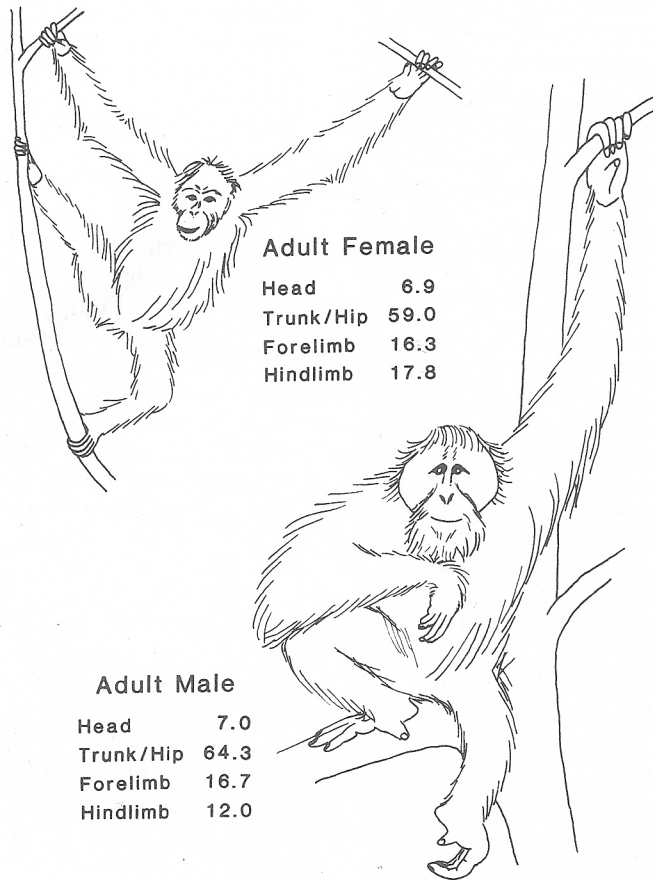
Adult Female

Head	6.9
Trunk/Hip	59.0
Forelimb	16.3
Hindlimb	17.8

Adult Male

Head	7.0
Trunk/Hip	64.3
Forelimb	16.7
Hindlimb	12.0

FIG. 21–2. Major body segments expressed as a percentage of total body weight (TBW).

Adult males have extensive connective tissue and fat deposits in the cheek flanges. Cheek pad weight in this male accounts for about 13% of head segment weight. Detailed dissection reveals that skin contributes 28% and fat with connective tissue 72% of total cheek pad weight.

The relative weight of the segments, and tissue composition within them, reflect male-female differences in secondary sexual characteristics and body size. Sex differences are easily delineated. Body size relationships will become clearer in a larger sample of several adults which vary in body weight.

Linear, Joint Surface, and Weight Measurements

In the Bornean skeletal sample, the extreme sexual dimorphism in body size is expressed in bone lengths, breadths, circumferences and

TABLE 21–1. Segments Within Forelimbs and Hindlimbs Expressed as a Percentage of Forelimb and Hindlimb Weight

	Adult Male	Adult Female
Forelimb		
Upper arm	39.3	44.9
Forearm	46.7	39.7
Hand	14.0	15.4
(Total = 100%)		
Hindlimb		
Thigh	52.1	53.1
Leg	28.9	26.8
Foot	19.0	20.1
(Total = 100%)		

TABLE 21–2A. Tissue Composition Expressed as a Percentage of Total Body Weight (TBW)

	Adult Male	Adult Female
Muscle	35.0	26.9
Bone	10.7	14.7
Skin	13.2	14.1
Other	41.1	44.3
(Total = 100%)		

TABLE 21–2B. Tissue Composition Expressed as a Percentage of Trunk/Hip, Forelimb and Hindlimb Body Segments

	Adult Male	Adult Female
Trunk/hip		
Muscle	63.9	36.3
Bone	13.4	24.7
Skin	16.7	19.9
Other	6.0	19.1
(Total = 100%)		
Forelimb		
Muscle	53.0	52.2
Bone	15.7	16.5
Skin	27.2	24.2
Other	4.1	7.1
(Total = 100%)		
Hindlimb		
Muscle	56.7	49.8
Bone	17.6	18.0
Skin	21.3	22.1
Other	4.4	10.1
(Total = 100%)		

weights, joint size, and in some cranial and dental measurements. Male and female ranges tend not to overlap. However, the male-female differences in linear, area, and weight measurements do not show the same pattern. For example, in this sample, male and female ranges in long bone lengths overlap in the humerus, but not in the radius, femur, or tibia. But in long bone lengths from a larger *Pongo* sample (Morbeck, unpublished data) there is overlap in the ranges between males and females of each of these bones. Long bone lengths average 118% longer in males than in females (Bornean sample) and 114% in the larger Bornean-Sumatran sample. (This difference in ranges may reflect subspecific variation or error related to a small sample.)

On the other hand, with the exception of only the acetabular area, males have relatively larger joint surface areas than observed in linear values, ranging from 125 to 225% of female size. Although there is a wide range of variation, male postcranial bone weights also are relatively greater than linear values and average 210% of female weights.

TABLE 21–3A. Muscles of Mastication Expressed as a Percentage of Head Segment and Total Body Weight (TBW)

	Adult Male	Adult Female
% Head segment	15.9	6.6
% Total body weight	1.1	0.5

TABLE 21–3B. Muscles of Mastication Expressed as a Percentage of the Head Segment[1]

	Adult Male	Adult Female
Temporalis	7.9	2.2
Masseter	5.2	2.2
Lateral Pterygoid	0.8	0.6
Medial Pterygoid	2.0	1.4

[1]Percents are based on muscle weights for the left side only. Left-side weights are doubled to express to bilateral condition. These data differ slightly from summary data in Fig. 21–2 since there is some asymmetry between right and left sides and the summary data represent added values.

In the head, male/female ratios of cranial and mandibular bone weight from the museum skeletal collection mirror the cadaver results: compared to those of females, male mandibles are 196% larger, and their crania are 171% larger. The heavier mandible of the male parallels the heavier musculature and larger anterior teeth. The skulls and jaws comprise only a slightly larger percent of total body weight in females (1.5%) than in males (1.1%).

Four linear skull measurements (cranial length, cranial base length, palatal length, and palatal breadth) show some overlap in ranges. Male/female ratios are lower than those observed in bone weight variables, (e.g., 124% male/female ratio in cranial base length and 109% in palatal breadth). In contrast, the length (L) and breadth (B) of the lower second molar (M_2) is slightly larger in females than in males (female: $M_2L = 13.9$ mm; $M_2B = 12.9$ mm; male: $M_2L = 13.6$ mm, $M_2B = 12.7$ mm). This is particularly interesting because M_2 measurements have been used to predict total body weight in fossils.

Joint surface area of limb bones shows pronounced sexual dimorphism, although the lumbar and sacroiliac joint areas are more variable. Apparently, there is an increase in the relative area of the shoulder and a decrease in hip joint with increasing body weight. Males have absolutely larger scapular glenoid fossa, humeral head, acetabulum, and femoral head surface areas. Male glenoid fossa and humeral head areas are, respectively, 168 and 174% larger than those of females; male acetabulum and femoral head areas are, respectively, 152 and 158% larger than those of females. Thus, the areas of the acetabulum and femoral head in females are relatively larger, compared in the surface areas of the glenoid fossa and humeral head, than in males.

An alternative way of demonstrating this is by comparing the area of the glenoid fossa to the

area of the acetabulum as well as humeral head to femoral head surface areas. Males exhibit a larger surface area in the upper limb joints: glenoid fossa/acetablum is 55% in males vs. 50% in females. Humeral to femoral head is 115% in males and 105% in females.

Male-female differences may be seen in comparisons of joint surface to total "limb bone joint area" (LBJA). The LBJA is the sum of each of the smaller components of limb bone joints in our data set (i.e., glenoid fossa, ulna trochlear notch, radial head, acetabulum, tibia proximal and distal facets). Glenoid fossa-to-limb bone-joint area is similar in males and females (14.4 vs. 14.2%), and humeral head-to-limb bone joint area is 57% in males vs. 54% in females. The humeral head is relatively larger in males.

The hip joint is somewhat larger in females. Acetabulum-to-limb bone joint area is 26% in males and 29% in females, whereas the femoral head is 49% in males and 52% in females. The acetabulum-to-femur head ratio also suggests that males have relatively smaller acetabula than females (53 vs. 56%, respectively). Analysis by least-squares regression suggests a strong relationship between increasing body weight and increasing humeral head surface area, but the plots of the other joint surfaces show a wide scatter, especially among the females.

The distal humerus appears to increase with larger size in males. The articular surfaces are large in males when one compares corresponding radial and ulnar joint surfaces. More skeletal and cadaver data will clarify the relationships of body weight to joint surface area.

DISCUSSION

Ever since Schultz's (1930, 1936, 1937, 1968) early systematic studies of hominoid morphology using linear dimensions of skeletons it has been clear that orang-utans are the most unusual of the large-bodied apes. We extend these observations and offer insights into the orang-utan's arboreality, sexual dimorphism, and evolutionary history.

Two aspects of posture and motion are of particular interest. First, all feeding and most movement occurs within the forest canopy. Second, orang-utans move quite differently from the other apes. Their morphological and behavioral adaptations to aboreality are well defined.

Adult females and young orang-utans live virtually independently of the forest floor (Mac-Kinnon, 1974a). Habituated males may travel long distances on the ground (Galdikas, 1979), or may become increasingly terrestrial as age and size interfere with their ability to travel through the forest canopy (MacKinnon, 1974b).

Orang-utans are slow, cautious, quadrumanous, arboreal climbers (Cant, 1987; MacKinnon, 1971, 1974b; Sugardjito, 1982). They are limited in daily travel through the forest canopy, ranging from 305 m in one study location (Rodman, 1977) to 800 m in another (Galdikas, 1979). Since the tree canopy is irregular, with branches of different sizes and angles, no single locomotor technique suffices. In transferring from tree to tree, orang-utans intentionally coordinate all four limbs and use the mechanical properties of the trees themselves in order to grab and reach adjacent branches (Chevalier-Skolnikoff et al., 1982; MacKinnon, 1974b).

Some arboreal adaptations are long upper limbs, fairly equal distribution of body weight to both fore- and hindlimbs, mobile shoulder and hip joints, and large hands and feet for gripping small lianas, branches, or large trunks. And, indeed, climbing may be THE primary locomotor adaptation of the hominoids (Fleagle et al., 1981; Washburn, 1963). For orang-utans, as for the other apes, the long forelimbs and flexible hands are used in bridging gaps, in foraging for fruits and other food items, and in nest-building. In fact, Washburn (1963:194) defines hominoid "brachiation" in its broadest sense as "climbing and eating by reaching." Thus, orang-utans have solved the problems of moving a large body through the forest canopy by an extreme version of arboreal adaptation (Tuttle, 1975), with advanced cognitive abilities (Chevalier-Skolnikoff et al., 1982) and with selective use of the forest structure (Horr, 1977; MacKinnon, 1974b).

Anatomy and Movement Capabilities

The arboreal adaptation of orang-utans is reflected in the musculoskeletal system and the flexibility of the joints, which maximize stability and movement of the trunk and forelimb (Schultz, 1930, 1937, 1956, 1968, 1969b; Washburn, 1968). All of the hominoids, with the exception of humans, have relatively long forelimbs. The weight variable gives these comparisons added significance. The living apes have relatively heavy upper limbs compared to monkeys: e.g., among monkeys, relative upper limb weight ranges from 9% in owl monkeys, to 12% in macaques and Cebus, to 14% in spider

monkeys (Grand, 1977); it is 16% in female chimpanzees and 20% in siamangs (Zihlman, 1984).

In female orang-utans, as shown here, the upper and lower limbs may be nearly equal in relative weight (16.3 and 17.8%). This pattern of muscle and mass distribution closely resembles that of other slow climbers: the lorises (forelimbs 12.4% and hindlimbs 14% of TBW) (Grand, 1967) and sloths (11 and 12.8% of TBW) (Grand, 1978). Similar to the orang-utan, the loris and sloth have mobile hip, knee, ankle, and foot joints, which allow the animals to reach in any direction.

Proportions shift throughout the postnatal period. Compared to adults, infant orang-utans have relatively longer hindlimbs (Schultz, 1941, 1956). In adults, forelimbs are emphasized. Orang-utan hindlimb bones, expressed as a percentage of total skeletal weight, are lighter and their forelimb bones are heavier than in chimpanzees and gorillas (Schultz, 1962). In fact, the orang-utan skeleton as a whole is relatively lighter than in the African apes.

The thorax is broad and shallow with a wide manubrium and long clavicle that positions the shoulder at its side and allows the scapula to ride on it posteriorly. Upper trunk and shoulder musculature emphasizes forelimb strength and mobility. Associated with the vertical orientation of the trunk, the vertebral column migrates during growth to a more central position within the thorax, as is indicated by the angulation of the dorsal aspect of the ribs.

The thoracic region of the vertebral column is long; the lumbar region is short. The iliac crests (and the position of the origin for latissimus dorsi and the gluteal muscles) rise above the lumbosacral articulation and, thus, limit lower trunk flexibility. The vertebrae reflect the distinct distribution of body weight and the weight-bearing pattern. Relative thickness of the middle lumbar vertebra is less in quadrumanous orang-utans than in bipedal humans with their smaller total body weight but compressive weight-bearing trunk (Schultz, 1953). The internal stucture of the orang-utan trabeculae also reflects their climbing, hanging, and bridging behaviors, which have little emphasis on compressive weight-bearing in the vertebral column. Lumbar vertebrae trabeculae in orang-utans show a complex "honeycomb pattern," in contrast to other large-bodied hominoids, whose trabeculae show a primarily vertical and horizontal alignment (Oxnard, 1984).

The elongated scapula and associated muscu-lature promotes scapular rotation and wide-ranging glenohumeral joint movement, especially in elevated positions (Oxnard, 1984). Compared to African apes and humans, the orang-utan shoulder joint is characterized by (1) broader acromial and coracoid processes that roof the joint; (2) more cranial orientation of the glenoid fossa; (3) a large medially directed humeral head, with the articular surface rising well above the insertion sites on the tuberosities for rotator cuff muscles; (4) a narrow bicipital groove.

Orang-utans exhibit full extension of the elbow and stability of the humeroulnar joint. This ability is reflected in the short ulnar olecranon process, in the very broad trochlea on the humerus with its narrowed midportion, and in the corresponding ulnar trochlear notch which bears a prominent central ridge. Forearm mobility is reflected in the humerus in its prominent lateral trochlear edge and rounded capitulum and in the horizontally oriented, circular radial head. Distally, at the radioulnar joint, the radius rotates around a very expanded ulnar head.

The medial humeral epicondyle as well as the forearm rotators and wrist and hand flexors are large. The wrist and midcarpal joints emphasize radial and ulnar deviation, flexion, and dorsiflexion. As in chimpanzees, flexors of the orang-utan wrist and hand are twice as heavy as the extensors. Unlike the African apes, orang-utan wrist extensors and flexors are about the same size (Tuttle, 1969). The ulnar styloid process is very short and separated from a small triquetral and distally displaced pisiform, which permits increased ulnar deviation (Lewis, 1972).

Among the large hominoids, hand length is greatest in orang-utans, whose long, curved metacarpals and phalanges and reduced thumb are well adapted to suspensory grasping. Digital flexors are large and the double-locking mechanism (Napier, 1960) allows gripping of many-sized substrates.

Orang-utans are unique among the Hominoidea in their extreme mobility of hip, knee, ankle, and foot, which allows variable positioning of the limb. Weight-bearing and compression are minimal and are reflected in bone weights of the lower limb, joint size and shape, and muscle differentiation. The unusual gait of adult males in traveling on the ground strongly underscores that the hindlimb has *not* been selected for terrestrial locomotion.

The mobile hip joint has a shallow acetabulum (Schultz, 1969a), and a high, rounded femoral head lacking a ligamentum teres. Hip and

thigh musculature in orang-utans have a different arrangement compared to other apes (Sigmon, 1974). The cranial portion of gluteus maximus is thicker and covers a more extensive area of the orang-utan hip than it does in other pongids. The distal, or ischiofemoral portion is a separate muscle, whereas it is connected to the cranial part of gluteus maximus in the other pongids. Gluteus minimus is two separable muscles in orang-utans, which may allow greater independent action and, thus, more hip mobility (Sigmon, 1974).

The knee joint in orang-utans is also more mobile than in chimpanzees and gorillas. The medial tibial joint surface extends posteriorly with increased rotation contributing to marked inversion of the ankle joint. The popliteus muscle, a major knee rotator, is very large and the lateral collateral ligaments are long and lax.

The distinctive ankle and foot emphasize posterior joint mobility, lateral digital flexion and reduction, and reorientation of the hallux (Gomberg, 1981). The calcaneal tuberosity is short and narrow. Extrinsic digital flexors weigh almost as much as plantar flexors (Tuttle, 1970). Tarsal bones are smaller than in African apes and humans, but metatarsals and phalanges are long and account for the orang-utan's pronounced foot length (Schultz, 1963a,b).

The greatest potential mobility (almost "wrist-like") lies in the orang-utan talocrural, subtalar, transverse tarsal, and tarsometatarsal joints (Gomberg, 1981). The combined motion of these joints allows variable positioning of the flexed digits when gripping. The long metatarsals and phalanges increase the leverage of the large digital flexors and facilitate the double-locking mechanism (Schultz, 1963a,b; Gomberg, 1981). The hallux is small, especially in females (Tuttle and Rogers, 1966); functionally, it opposes the sole and not the other digits, as in the African apes and humans. The orang-utan's foot, therefore, emphasizes mobility but retains a powerful pincer function of the hallux.

Sexual Dimorphism

Orang-utans are one of the most sexually dimorphic species of primate. This aspect of dimorphism is most often reduced in the literature to adult body weight or canine tooth size differences, but this is misleading because (1) other anatomical features exhibiting dimorphism are neglected; (2) different traits exhibit different kinds of variability; (3) dimorphic traits may vary, at least in part, independently; and (4) the developmental mechanisms and timing in growth to produce the adult pattern are not emphasized. Sexual dimorphism is a mosaic and the overall pattern of a species may be distinct (Zihlman, 1976, 1982, 1985). Our findings show that different features may be more or less dimorphic in orang-utans. Although males may be twice the weight of females, other features do not scale similarly in length or surface area in females.

For example, head weights are similar, but the masticatory muscles are more than twice as heavy in males. Within the dentition, the degree of dimorphism varies. The maxillary canine male-to-female ratio is 133% in length and 132% in breadth; similarly, the mandibular canine male-to-female ratio is 127% in length and 142% in breadth, based on data compiled by Oxnard et al. (1985). In our skeletal sample of lower second molars, molars of females are slightly larger than those of males. In the much larger sample of Oxnard et al., molars of males are 10% larger. This pattern is reported in other species. In gorillas, canines of males are 60% larger than those of females, whereas molars of males are only 6% larger than those of females (McCown, 1982). And among rhesus monkeys, adult females have much larger molar teeth for their body weight than do males (Cochard, 1985).

McCown (1982) has argued that the female expresses the basic anatomy of the species. Thus, male morphology is viewed as the "anatomy of aggression," which is added on to the female baseline. Male-female differences are presented as part of a total morphological pattern, rather than as a sum of single, unrelated characters. This approach, however, does not take into account the constraints of female anatomy for reproduction.

Most secondary sexual characteristics do not appear until puberty. Female orang-utans are on a "fast track" and reach reproductive maturity at 8 years (in the wild) compared to 14–15 years for males (MacKinnon, 1974b). In addition to differences in the onset of reproductive potential, rates of growth and duration of growth differ between the sexes (Schultz, 1941). Secondary sexual characters of males—for example, canine teeth and specifically cheek flanges, laryngeal apparatus, and large skull (Short, 1981)—are not fully expressed until adulthood.

What maintains large body size in males? Is it sexual selection and mating pattern, or niche utilization, some combination, or other factors? Rather than ask why males are so large, we might ask why females are smaller. Reproductive demands provide some clues. Lactation, especially, may be the primary factor in determin-

ing body size in females (Lancaster, 1984). That females eat as much as males is suggested by both anatomy and behavior. Females spend more time feeding than males (61 vs. 59%) in spite of the much larger male body size (Galdikas and Teleki, 1981). The proportions of food may also differ. Rodman (1977) reports that a male orang-utan consumed less fruit than females (58.6 vs. 67%) but four times as much bark (16.5 vs. 4.9%) and half as many insects (0.8% vs. 1.9%). Female requirements differ from the male due to the energetics of long pregnancy and lactation as well as carrying the young for several years. Perhaps female orang-utans cannot afford to increase too much in size and still meet reproductive demands.

Anatomically and behaviorally, adult males are set apart from other age/sex classes by their large body size, inflatable throat pouches, enlarged fatty cheek pouches, and fatty neck region. Adult males eat a greater proportion of less nutritious foods, which is reflected in their larger masticatory muscles. They also use the lower levels of the canopy more frequently, sometimes travel on the forest floor, have larger home ranges and greater mean and maximum day ranges, give long calls, and are the least social of all age/sex categories (Galdikas, 1979, 1985; Rodman, 1977, 1979). The adult male long calls may keep adult males apart and may attract receptive females (Galdikas, 1983; Mitani, 1985). These calls, combined with the visual signals of the face and large body, may be part of the "anatomy of aggression" that minimizes fighting.

EVOLUTIONARY HISTORY

The details of orang-utan evolution, as for the other large-bodied hominoids, are unknown. Several scenarios and suggestions about lineages have been proposed: the large body size of orang-utans indicates descent from some terrestrial ancestor (Smith and Pilbeam, 1980); or orang-utans are direct descendants of *Sivapithecus* (Andrews and Cronin, 1981). Whatever picture emerges, morphology, behavior, and ecology of living orang-utans, as well as the molecular, fossil, and paleoecological data, must all be evaluated.

The fossils (i.e., morphological data) provide the critical test for hypotheses about when, where, and under what circumstances each hominoid evolved. Molecular data place orang-utans within branching patterns and approximate times of divergence. Studies on DNA and proteins (Cronin, 1983; Cronin et al., 1984; Hasegawa and Yano, 1984; Hasegawa et al., 1985; Sibley and Ahlquist, 1984) show that orang-utans separated from other hominoids after the gibbon group and prior to the African hominoid group. Using the molecular clock estimates from nucleic acid, sequence, immunological, and electrophoretic data, the orang-utan lineage may have diverged about 10–11 million years before present, after the gibbons (13–15 my B.P.), and prior to African hominoids (5–6 my B.P.) (Cronin et al., 1984).

As discussed here, the postcranial morphology of orang-utans distinguishes them from other hominoids and emphasizes their arboreal adaptations. Specializations of the craniofacial and dental complexes are also distinctive. The skull, face, and jaws of *Pongo* differ from African apes and humans in their extreme airorhynchous condition. Many of the distinctive features of the orbits, midface, and jaws may relate to the particular positioning of the face relative to the cranium (Shea, 1985). Molar enamel structure is also distinctive with its "intermediate/thick enamel" (Martin, 1985) and occlusal surface wrinkling.

Fossils with these defining traits would provide direct information about the evolution of modern orang-utans. Pleistocene and recent deposits in China, North Vietnam, and islands of southeast Asia have yielded more than 5,000 subfossil and fossil *Pongo* teeth (von Koenigswald, 1982). These teeth are larger and perhaps had a greater degree of sexual dimorphism than in modern *Pongo* (Hooijer, 1948). However, as discussed above, larger teeth may or may not indicate larger body weight.

Recently, with the recovery of new specimens and reinterpretation of previously known pre-Pleistocene fossils from Eurasia and Africa, the evolution of the *Pongo* lineage and its relation to other hominoids, including humans, has provoked much discussion. Fossil taxa that may be close to the divergence of modern lineages are, of course, likely to have a mosaic of features. Currently, in part because of a lack of associated postcranial material, Miocene and Pliocene hominoids are not clearly linked to particular modern lineages, and controversy about descendant relationships continues.

Sivapithecus, in particular, has been promoted as a possible orang-utan ancestor and hominid relative (Andrews and Cronin, 1982; Pilbeam, 1982; Schwartz, 1984). This group, defined in different ways by different researchers, includes fragmentary skulls, faces, jaws, teeth, and unassociated limb bones from Eurasia and Africa.

The fragments range from more than 17 (at Buluk in Kenya [Leakey and Walker, 1985]) to 5½ my B.P. (in the Siwaliks [Sankhyan, 1985]). *Sivapithecus* facial and dental remains display some traits found in *Pongo* (Andrews and Cronin, 1982; Pilbeam, 1982; Shea, 1985). Associated postcranial remains are not yet known for any of the proposed taxa. And, although some forelimb fossils exhibit characteristic hominoid features (Morbeck, 1983), no specialized orang-utan features are present in any of the fossil postcranial remains.

The paleoecology of the middle and late Miocene must also be considered in orang-utan evolutionary scenarios. The shift from a closed forest habitat in the early Miocene of Africa to one of the open forest–woodland in the middle Miocene was fundamental to the argument that *Ramapithecus–Sivapithecus* hominoids were more ground-dwelling (Andrews, 1981; Kennedy, 1978). However, the middle to late Miocene environment in Indo-Pakistan was one of increasing seasonality with a cooler and drier climate (Laporte and Zihlman, 1983), and such conditions do not seem to be conducive for evolving the highly arboreal habits of modern orang-utans.

At the present time, there is no proposed scenario of orang-utan evolution that we find convincing. The large tooth size of extinct Pleistocene orang-utans is insufficient to argue in favor of a terrestrial stage of evolution. *Sivapithecus* without associated limb bones cannot be confirmed as an orang-utan ancestor. The decrease in forests further complicates hypotheses about orang-utan life style and lineage. Unequivocal data, in the form of associated postcranial fossils, will contribute to solutions (Temerin, 1980), and for any evolutionary proposal, all these lines of evidence must be included.

CONCLUSIONS

In this chapter, data and interpretations based on new methods and approaches provide a framework for explaining orang-utan adaptations and evolution. Body segment, tissue composition, and joint surface area data broaden the base for functional interpretations of locomotion and sexual dimorphism more than when only linear measurements are used.

Overall, orang-utan morphology emphasizes mobility rather than compressive weight-bearing. It is associated with slow, cautious arboreal climbing, bridging, and hanging. Specializations allow females and much larger males to be both highly arboreal and large-bodied.

Sexual dimorphism is viewed as a mosaic of morphological features with varying degrees of difference as measured by segments, tissue composition, and surface areas, as well as the usual measures of body weight and canine size. Male and female morphologies reflect their respective adaptations to feeding, social behavior, and reproduction. Reproductive demands on the female, combined with the "anatomy of aggression" of the male, provide a functional way of interpreting male-female differences.

The arboreality and extreme sexual dimorphism in extant orang-utans must be taken into account when reconstructing the selective forces that produced *Pongo pygmaeus*. The fragmentary fossil record, with only bits of the phenotype, comprises only part of the data required for interpreting the way of life of and the ancestral-descendant relationships in orang-utan evolution. Morphological, behavioral, and environmental information must be integrated at all levels in any discussion of orang-utan biology and evolution.

ACKNOWLEDGMENTS

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NOTES

1. The adult male, "Ben," was acquired by M. W. Marzke from the Phoenix Zoo. He died of natural causes while in residence at the Los Angeles Zoo. Ben weighed 102.06 kg at death. He was dissected by L. Brunker, M.

W. Marzke, M. E. Morbeck, and A. L. Zihlman at Arizona State University. The brain was removed prior to dissection and no weight was provided. An estimate of 434 g was taken to represent average male orang-utan cranial capacity (Tobias, 1975). Little difference in percentage of TBW was found using estimates of 415 and 455 g.

2. The captive-born female, "Bunga," was obtained by T. I. Grand from Yerkes Regional Primate Research Center and dissected primarily by L. Brunker at the Oregon Regional Primate Research Center. She weighed 27.8 kg at death. Zihlman (1984) reported that this female lies within the adult female range published by Schultz (1941). Smithsonian Institution individual number 153822 listed at 27.22 kg in Schultz's data, however, apparently was gutted before being weighed (Smithsonian Institution records). Therefore, Bunga lies below the known range for free-ranging adult females.