I. INTRODUCTION

Among the apes Gorilla and Pongo males represent giant forms with extreme sexual dimorphism. The two lineages in Africa and Asia respectively separated some 10-12 million years ago from a common ancestor (Hobolth et al., 2011). Although unknown, the common ancestor was likely of moderate body size and differed in body structure and locomotor behavior from these two modern ape genera. Once isolated, each branch independently evolved away from the common ancestor. Gorilla adapted to life on the ground in African equatorial forests, and *Pongo* to tree-living in tropical rainforests in Asia.

Even though differing markedly in locomotor anatomy (Zihlman et al., 2011), Gorilla and Pongo males converged in their large body sizes and extreme sexual dimorphisms, as they evolved over millions of years in widely different geographical locations. Large body size and associated behaviors confer advantages, and aspects of their morphologies denote "prime adult male," for Gorilla, "silverback male" and "flanged male" for *Pongo*.

II. MATERIALS and METHODS

Four adult apes were dissected using the same quantitative methods: Gorilla, adult male (age 27 years) and female (age 27 years); Pongo, adult male (age 24 years), female (age 34) (Zihlman & McFarland, 2000; Zihlman & Underwood, 2019). Data were collected and analyzed on body composition and limb mass as percent of total body mass, and on muscle distribution to body segments, that is, the percent of total body muscle acting on the forelimbs, hindlimbs, and head/trunk. Data on each male were compared to the female of the species.

On the males, cranial and facial structures were dissected and measured. A domelike structure on the male *Gorilla* head is not found on females (Schmid & Stratil, 1986). Adult male Pongo facial structures, called fat pads or flanges, are not present in females (Winkler, 1988; Zihlman & Underwood, 2019). See Figure 1. After dissections were completed and skulls cleaned, cranial capacities (ml) were determined. See Table 1.

III. RESULTS

Gorilla and Pongo males have greater body masses than the females; in these pairs females are respectively 58% and 48% of male body mass. In body composition, males have relatively more muscle than do females, most marked in gorillas. See **Table 1**. In body proportions male forelimbs comprise a higher percent of body mass than in females. In distribution of muscle to body segments, the males have a greater percent of muscle acting on the forelimbs than do the females. See Figure 2.

The heads of the males are defined by soft and hard tissue structures (Figure 1). The sexes differ in cranial-facial morphology that show up in side views. See Figure 3. A view from above shows less sex difference in the size and shape of the neurocrania, as well as in brain size measured by cranial capacity. See **Table 1** and **Figure 4**. Soft tissue structures of the head and neck are pronounced in the males and less developed in the females.

In Gorilla the dome-like structure on the head lies above the sagittal crest and consists of soft structures. See Figure 5. Welldeveloped sagittal and nuchal crests support a "cushion" of skin, fat, and connective tissue that constitute this cranial superstructure that may exceed 3 cm in thickness (at arrow), a discovery made during our gorilla dissections. The nuchal crest provides attachment for heavy neck muscles.

Mass as % al Body Ma

as M

Table 1. Sample					
	Gorilla		Pongo		
Sex	Male	Female	Male	Female	
Age (yrs)	27	27	24	34	
Body Mass (kg)	172.0	99.9	126.0	60.0	
Muscle % TBM	46.4	38.0	35.9	34.5	
Cranian Capacity (ml)	568	518	443	437	

Figure 1. Soft and Hard Tissue Structures **Defining Adult Males** Gorilla Pongo



BREUER T, et al. 2009. Physical maturation, life history classes and age estimates of free ranging western gorillas - insights from Mbe American Journal of Primatology 71:106-119. CANT JBH. 1987. Positional behavior of female Bornean orangutans (Pongo pygmaeus). American Journal of Primatology 12:71-90. ELLIS RA, MONTAGNA W. 1962 The skin of primates. VI. The skin of the gorilla (Gorilla gorilla). American Journal of Physical A FOODEN J, IZOR RJ. 1983. Growth curves, dental emergence norms, and supplementary morphological observations in known-age cap Journal of Primatology 5(4):285-301. GALDIKAS BMF. 1983. The orangutan long call and snag crashing at Tanjung Puting Reserve. Primates 24:371-384. HOBOLTH A. et al. 2011. Incomplete lineage sorting patterns among human, chimpanzee, and orangutan suggest recent oranguta selection. Genome Research 21:1-8. Cold Spring Harbor Laboratory Press. KNOTT CD, KAHLENBERG SM. 2011. Understanding forced copulations and female mating resistance. In: Primates in Perspective, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, eds. Pp. 313-326. Oxford University Press. MacKINNON J. 1974. The behaviour and ecology of wild orangutans (Pongo pygmaeus). Animal Behaviour 22:3-74. McCOWN ER. 1982. Sex differences: the female as baseline for species description. In: Sexual Dimorphism in Homo sapiens. Hall RL, ed. Pp. 37-83. Praeger, New York.

ANATOMICAL CONVERGENCES IN ADULT GORILLA AND PONGO MALES

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	V. BIBLIOGRAPHY
eli Bai, Republic of Congo.	MITANI JC. 1985. Sexual selection and adult orang-utan long calls. Animal Behavior 33:272-283.
	REMIS MJ. 1999. Tree structure and sex differences in arboreality among western lowland gorillas (C Republic. <i>Primates</i> 40:383-396.
Anthropology 20:79-94. Otive orangutans. American	SCHMID P, STRATIL Z. 1986. Growth changes, variations, and sexual dimorphism in the gorilla skull. In: University Press, UK.
	SUGARDJITO J. 1982. Locomotor behaviour of the Sumatran orang-utan (<i>Pongo pygmaeus abelii</i>) at Ke Journal 35:57-64.
an species and widespread 2nd Edition. Campbell CJ,	WINKLER L. 1989. Morphology and relationships of the orangutan fatty cheek pads. American Journal
	ZIHLMAN AL. 1998. Natural history of apes: life history features in females and males. In: <u>The Evol</u> Galloway A, Zihlman AL, eds. Pp. 86-103. Princeton University Press, Princeton, NJ.
	ZIHLMAN AL, McFARLAND RK. 2000. Body mass in lowland gorillas. A quantitative analysis. America
	ZIHLMAN AL, McFARLAND RK, UNDERWOOD CE. 2011. Functional anatomy and adaptation of ma male orangutans (<i>Pongo pygmaeus</i>). <i>Anatomical Record</i> 294:1842-1855.

ZIHLMAN AL, UNDERWOOD CU. 2019. Ape Anatomy and Evolution, forthcoming.

(RESULTS CONTINUED)

In Pongo the broad facial extensions in males, called flanges or fat pads, widen the face and consist of fat and connective tissue with facial muscles interdigitating into them. In our dissection, the pads weighed 2.5 kg. The breadth of the flanges across the face was equal to the male's shoulder breadth at 380 mm, as measured between the two acromion processes (Zihlman et al., 2011). This measurement is comparable to the 370 mm cheek breadth reported for a 23 year old captive male (Fooden & Izor, 1983).

IV. DISCUSSION

The large body masses of *Gorilla* and *Pongo* males confer similar advantages. Formidable body size reduces vulnerability from terrestrial predators or conspecific males and holds large guts for digesting high fiber foods and "space" to store body fat. Massive and well-muscled forelimbs give these males considerable strength to climb and bridge as they feed and nest in the trees. On the down side, heavier body masses require greater caution for large males to move through the trees, avoiding the smaller more peripheral branches (*Gorilla*) and utilizing the lower levels of the canopy more frequently than females (*Pongo*) (e.g. Remis, 1999; MacKinnon, 1974; Sugardjito, 1982; Cant, 1987).

Silverback male gorillas as high-ranking males are so-called due to having white hair on the thoracic and lumbar regions, a distinguishing feature from younger and lower-ranking 'black-backed' males (Breuer et al., 2009). Silverback males have a pungent odor from prominent "axillary organs" of concentrated apocrine sweat glands in the armpits (Ellis & Montagna, 1962). The combination of massive shoulders and neck, broad chest and arm girth, and pronounced dome-shaped head give a silverback its distinct body and head profile enhanced by a majestic quadrupedal stance and shape.

There are two male orangutan morphotypes, flanged and unflanged (Knott & Kahlenberg, 2011). A flanged male stands out in the forest, having a heavy body, thick neck, long hair, strong odor and distinct fatty cheek pads that constitute visual markers of a prime adult male. A prominent inflatable throat sac enables the production of loud distinct vocalizations that advertise a male's location to conspecifics (Galdikas, 1983; Mitani, 1985). Flanged males are more attractive to females and aggressive to other males. 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 female *Gorilla* and *Pongo* are similar to each other in having smaller canine teeth and larger brain sizes relative to body mass compared to the males, apparent from the neurocranium as well as brain volume, a characteristic that reaches adult size early in life. Timing to maturity differs between females and males in different body systems, such as dentition, brain, and body mass. Because females mature in these systems before males do, they best express the basic anatomy of the species; male characteristics "add on" to the species base through extended growth (McCown, 1982; Zihlman & Underwood, 2019).

These African and Asian male apes share large, sexually dimorphic body size and distinct anatomical markers in body hair and pattern and in cranio-facial morphology. These male characteristics, superimposed upon divergent locomotor adaptations, presumably reflect shared selective pressures that produced extreme male body size, heavier upper bodies and cranial/facial superstructures that identify high rank or mark "prime males." Females apparently prefer to mate with these high-ranking males. Convergences in body size and anatomies of these two ape genera have evolved over more than 10 million years of independent evolution on each branch.

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Gorilla gorilla gorilla) at Bai Hokou, Central African

: Primate Evolution. Else J. ed. Pp. 239-247. Cambridge

etambe, Gunung Leuser National Park. Malayan Nature

of Physical Anthropology 17:305-319.

ving Female. A life history perspective. Morbeck ME,

ican Journal of Physical Anthropology 113:61-78. ale gorillas (Gorilla gorilla gorilla) with comparison to



Ape Anatomy and Evolution (2019) presents for the first time a comparative anatomy of all four lineages of apes - gibbons and siamangs, orangutans, gorillas, and chimpanzees. Following the tradition of blending art and anatomy Zihlman and Underwood emphasize a whole animal perspective and formfunction relationships. They detail methods of data collection, analytical procedures, and quantitative comparative results. Each ape is individually profiled in behavioral ecology, evolutionary and life history, locomotion and the musculoskeleton. Attentive to sexual variation, they compare the four apes along these same dimensions. Applying lessons from this comparative anatomy and bipedalism, they present new ideas on human origins as one of three lineages emerging from an African ape parental population and propose the components for the evolutionary success of this new lineage.

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