HANDS and FEET: COMPARATIVE ANATOMY of APES

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I. INTRODUCTION

Hands and feet interface directly with the environment through contact with ground and tree surfaces, food items, and other physical objects. This gross anatomical study focuses on both hands and feet in the same individuals and across four species and analyzes soft and hard tissue. Comparison of hand and foot proportions, composition, and muscle distribution show similarities and differences in locomotor patterns among the apes.

II. MATERIALS and METHODS

The dissection sample includes 4 ape species, *Hylobates*, *Pongo*, *Gorilla*, *Pan* (*paniscus*); all are adult individuals of known body mass. Sample sizes vary and are indicated on the figures.

Prior to dissection, hand and foot prints and length of segments are taken. Old World monkey (*Semnopithecus entellus*) hand and foot prints provide an out-group for length comparisons. Tissues in the ape hands and feet – muscle, bone, skin/fat – are separated, weighed, and proportions determined. Intrinsic muscles are then weighed individually, and distribution of functional groups is calculated. Skeletal regions and relative portions are determined after Schultz (1963).

III. RESULTS

Apes have similar hand to foot lengths, with pollex and hallux both prominent. *Semnopithecus*, in contrast, has much longer feet and reduced first digits. When considered by body mass, *Pongo* has a long hand and foot while *Gorilla* hand and foot are short **(Fig. 1)**.

Overall, Asian apes have narrow heels in contrast to pronounced ones in African apes. Relative contribution of each tissue – muscle, bone, skin/fat – show remarkably similar patterns in the hand and feet within each species. Across species, general trends emerge. Bone ranges from 25.7% (*Pongo*) to 44.0% (*Hylobates*). Skin comprises at least a third, up to slightly over half the segment mass. Muscle consistently contributes the least amount to segment mass of the hands and feet, with *Pan* having the most muscle of the apes at 28.6% (hand) and 30.0% (foot) **(Fig. 2)**.

Distribution of intrinsic muscles of the hand (pollex, palm, digit V) and foot (hallux, sole, digits) contrasts within species. Relative palm muscle mass is comparable in all apes (59 – 61%). Asian apes have relatively more muscle to the pollex (28%). The hallux is well muscled in *Hylobates* (60%) and African apes (~50%). *Pongo* is an outlier, with the least muscle mass to the hallux at 35% **(Table 1, Fig. 3)**.

In skeletal proportions Asian apes have a short carpus and tarsus and long phalanges. African apes have shorter phalanges and longer carpus and tarsus **(Fig. 4)**.

IV. DISCUSSION

Quantitative dissection methods provide analytical information to test against locomotor function, thereby signaling divergent roles of hands and feet among ape species. The hand, generally equal in size to the foot, is a distinctive ape feature; it is an integral part of the forelimb adaptation and plays a role in canopy suspension, arm-swinging, and grasping. In contrast, monkeys' short hand to long foot reflects hindlimb dominance in quadrupedal propulsion and weight bearing during running and leaping. The ape foot is functionally equipped to grasp supports and thus stabilize the body while sitting in or moving through the trees. Percentage of muscle in hands and feet is consistent across all apes (~20-30%); the well-muscled hallux, consistently heavier-muscled than the pollex, indicates the foot's important role in gripping.

(DISCUSSION CONTINUED)

Hylobates Gibbon brachiation draws on the mobility and skill of forelimb and hand, along with brief bouts of bipedal running interspersed with air borne phases. The gibbon hand, longer than the foot, has long curved phalanges that form a hook-like grip on branch contours. Pollex and hallux have the most muscle of the apes. Deep clefts in the palms and soles between digits I and II enable wide grasps. Weight of the foot is borne mainly on the metatarsal pad between digits I and II (Tuttle 1972). Gibbons move easily among small branches, and the combination of muscle strength and clefts makes larger diameter supports accessible to both hand and foot holds.

Pongo Orangutans live life in the trees, and infrequently travel on the ground. The hand is similar to other apes in distribution of intrinsic muscle to the palm. The foot departs from the other apes in its mobility, power grip and overall length. The short hallux and equal muscle distribution to the hallux, sole, and digits, provides a strong anchoring mechanism. Long powerful hands and feet with highly curved phalanges are well adapted for supporting the body in all positions and for grasping both slender lianas and larger branches as orangutans maneuver through the canopy (Tuttle 1970; Povenelli & Cant 1995; Thorpe et al. 2009).

Gorilla Gorillas, in spite of their large body size, are effective tree climbers (Remis 1995). Travel is on the ground rather than through trees. Hands and feet are structured for effective ground travel on stable supports and for tree climbing on round ones. The terminal appendages of gorillas are the least muscled (22%) and less flexible compared to other apes. Half of the muscle mass in the foot acts on a long hallux and gives power to the foot in grasping tree branches and lianas when climbing and sitting in trees. Body weight during travel is supported on the dorsal surfaces of middle phalanges II-IV of the hand, i.e. knuckle-walking (Tuttle 1970). The relatively long and rigid tarsus, short and stout toes, and broad heel support the body as the heel first contacts the ground when walking (Gebo 1992).

Pan paniscus Hands and feet are structured for proficiency in negotiating the canopy as well as for travelling distances on the ground (Doran 1993). Like gorillas, *paniscus* chimpanzee hands bear weight in knuckle-walking. The carpus and tarsus are long, and the digits retain length for grasping. Among the apes, their hands and feet have the most muscle. Half of the foot muscle goes to the hallux for a strong grip; in the hand, 61.0% goes to the palm, commensurate with the relatively long metacarpals. The muscular hands enable postures and functions during foraging and object manipulation (Boesch & Boesch 1993; Marzke et al. 2015; Lesnik et al. 2015).

V. SUMMARY and CONCLUSIONS

- ***Similar sized hands and feet is a distinctive ape character and part of the forelimb adaptation for suspension***
- ***Hand and foot proportions and musculature reflect divergent locomotor functions***
- ***Two distinct patterns emerge: Asian and African apes***
- ***Feet show more differences between ape species even though hands have a broader array of functions***

Figure 1. Hand and Foot Prints

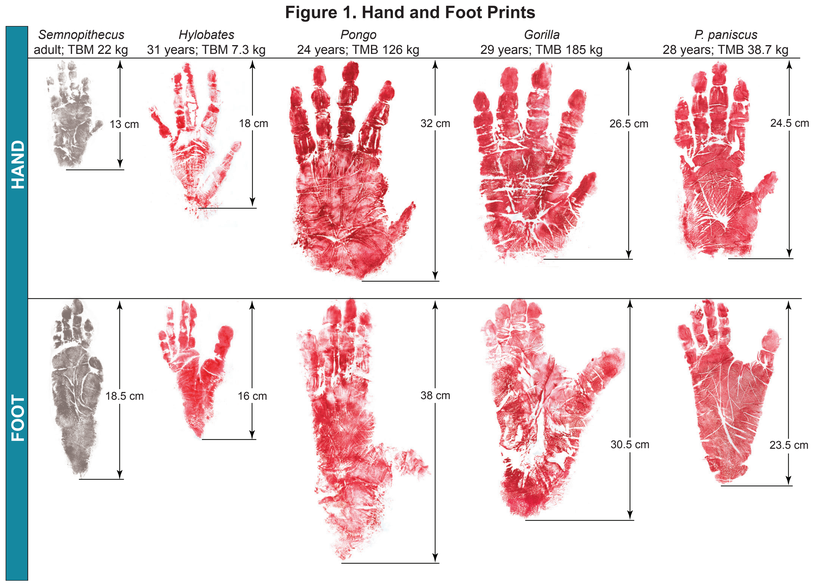


Figure 2. Percent Tissue Composition of the Hand and Foot

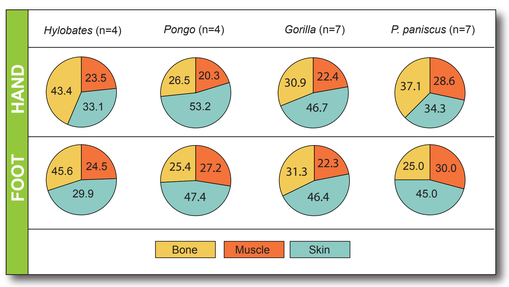


Table 1. Percent Intrinsic Muscle Distribution to the Hand and Foot

	HAND			FOOT		
Species	Pollex	Palm	Digit V	Hallux	Sole	Digits II-V
Hylobates (n=7)	28	59	13	57	21	22
Orangutan (n=4)	28	59	13	35	31	35
Gorilla (n=8)	22	57	21	49	19	32
P. paniscus (n=8)	24	61	15	50	25	25

Figure 3. Intrinsic Muscles of the Hand and Foot

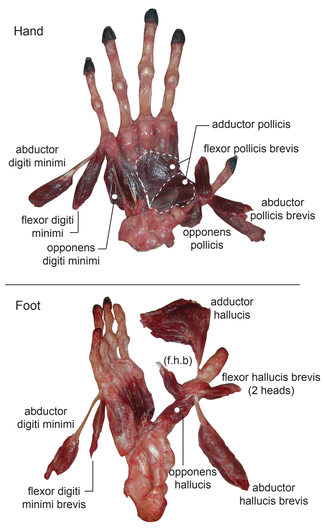
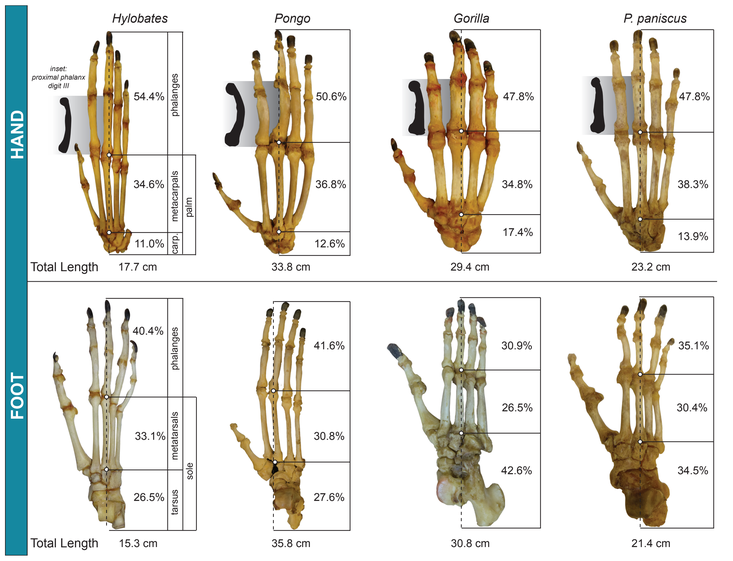


Figure 4. Skeletal Proportions of the Hand and Foot



VI. ACKNOWLEDGMENTS & BIBLIOGRAPHY

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Boesch C, Boesch H. 1993. Different hand postures for pounding nuts with natural hammers by wild chimpanzees. In: Preuschoft H, Chivers DJ, ed. Hands of Primates. Springer, New York pp 31-43.

Doran D. 1993. The comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. *American Journal of Physical Anthropology* 91: 83-98.

Gebo DL. 1992. Plantigrady and foot adaptation in African apes: implications for hominid origins. *American Journal of Physical Anthropology* 89: 29-58.

Lesnik JJ, Sanz, Morgan DB. 2015. The interdigital brace and other grips for termite nest performance by chimpanzees of the Goualougo Triangle, Republic of Congo. *American Journal Physical Anthropology* 157: 252-259.

Marzke MW, Marchant LF, McGrew WC, Reece SP. 2015. Grips and hand movements of chimpanzees during feeding in Mahale Mountain National Park, Tanzania. *American Journal Physical Anthropology* 156: 317-326.

Povenelli DJ, Cant JGH. 1995. Arboreal clambering and the evolution of self-conception. *Quarterly Review of Biology* 70: 393-421.

Remis MJ. 1995. The effects of body size and social context on the arboreal activities of Western lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology* 97: 413-433.

Schultz AH. 1963. Relations between the lengths of the main parts of the foot skeleton in primates. *Folia Primatologica* 1: 150-171.

Thorpe SKS, Holder R, Crompton RH. 2009. Orangutans employ unique strategies to control branch flexibility. *Proc. Nat. Academy of Sciences* 106(31): 12646-12651.

Tuttle RH. 1969. The way apes walk. *Science Journal* 5A (5): 66-72. University of Chicago.

Tuttle RH. 1970. Postural, propulsive, and prehensile capabilities in the cheiridia of chimpanzees and other great apes. The Chimpanzee, vol 2: 167-253. Karger, Basel, GH Bourne, editor.

Tuttle, RH. 1972. Functional and evolutionary biology of Hylobatid hands and feet. Gibbon and Siamang vol. 1: 136-206. Karger Basel.