Anatomical Contributions to Hylobatid Taxonomy and Adaptation

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Abstract Compared with the great apes, the small-bodied hylobatids were treated historically as a relatively uniform group with 2 genera, *Hylobates* and the larger-bodied *Symphalangus*. Four genera are now recognized, each with a different chromosome number: *Hoolock* (hoolock) (38), *Hylobates* (44), *Nomascus* (crested gibbon) (52), and *Symphalangus* (siamang) (50). Previous morphological studies based on relative bone lengths, e.g., intermembral indices; molar tooth sizes; and body masses did not distinguish the 4 genera from each other. We applied quantitative anatomical methods to test the hypothesis that each genus can be differentiated from the others using the relative distribution of body mass to the forelimbs and hind limbs. Based on dissections of 13 hylobatids from captive facilities, our findings demonstrate that each of the 4 genera has a distinct pattern of body mass distribution. For example, the adult *Hoolock* has limb proportions of nearly equal mass, a pattern that differentiates it from species in the genus *Hylobates*, e.g., *H. lar* (lar gibbon), *H. moloch* (Javan gibbon), *H. pileatus* (pileated gibbon), *Nomascus*, and *Symphalangus*. *Hylobates* is distinct in having heavy hind limbs. Although *Symphalangus* has been treated as a scaled up version of *Hylobates*, its forelimb exceeds its hind limb mass, an unusual primate pattern otherwise found only in orangutans. This research provides new information on whole body anatomy and adds to the genetic, ecological, and behavioral evidence for clarifying the taxonomy of the hylobatids. The research also underscores the important contribution of studies on rare species in captivity.

Keywords Anatomy · Body proportions · *Hylobates* · Hylobatids · Limb mass · *Symphalangus* · Gibbon · Siamang · Taxonomy

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Introduction

Among the apes (superfamily Hominoidea), the hylobatids have the largest number of species, yet are the least known. Current taxonomies define 4 genera with 14–19 gibbon species (Mootnick 2006; Roos *et al.* 2007; Thinh *et al.* 2010). Traditionally, gibbons and siamangs (family Hylobatidae) have been referred to as the small apes when compared to the larger-bodied and more sexually dimorphic orangutans (*Pongo*), gorillas (*Gorilla*), and chimpanzees (*Pan*) (family Pongidae). A. H. Schultz (1930, 1933) recognized only 2 genera: *Hylobates* and *Symphalangus*, both with long upper limbs compared to their lower limbs, small body sizes, and little sexual dimorphism, thus distinguishing them from the pongid apes. Combining information on linear variables of the skull and skeleton and on body weights, Schultz (1933) listed 7 species of *Hylobates* (the smaller-bodied genus) and a single species of *Symphalangus* (the larger-bodied genus).

Studies on karyotypes in the 1960s and 1970s confirmed generic differences between *Symphalangus* and *Hylobates* in their chromosome numbers, 50 and 44, respectively (Bender and Chu 1963; Chiarelli 1963, 1972). *Nomascus* (crested gibbon), formerly included with *Hylobates* as *concolor* (Creel and Preuschoft 1976; Cronin *et al.* 1984; Groves 1972), has 52 chromosomes (Wurster and Benirschke 1969). The hoolock gibbon with 38 chromosomes was initially placed into its own subgenus called *Bunopithecus* based on a fossil (Prouty *et al.* 1983), and later designated as *Hoolock* when elevated to genus level (Mootnick and Groves 2005).

More recently, molecular data show that genetic differentiation among the hylobatid species exceeds the range of difference between chimpanzees and humans (Roos and Geissmann 2001; Takacs *et al.* 2005; Whittaker *et al.* 2007). For example, molecular distances based on sequences of mtDNA show that *Homo* and *Pan* differ by 9.6%; *Hylobates* and *Hoolock*, 10.3%; *Symphalangus* and *Hoolock*, 10.6%; *Nomascus* and other genera, 12.8% (Roos and Geissmann 2001). Thus, although superficially similar in body size and long forelimbs, the hylobatids apparently differ significantly.

Anatomical studies contributed only minimally to sorting the hylobatids for at least 2 reasons. Data collected before the recognition of 4 genera (Geissmann 2002) resulted in misguided taxonomy and poorly understood findings. Second, with the exception of cranial–facial morphology (Creel and Preuschoft 1976), the 3 non-*Symphalangus* genera cannot be differentiated from each other morphologically with consistent results. The message from combined karyotypic and DNA studies is that differences among the hylobatid apes are not obvious in their bones, teeth, and body masses.

The present study applies a quantitative anatomical approach to the question of hylobatid taxonomy and variation. This method analyzes body mass and differentiates mammals, including primates, at the genus level and allows comparison among individuals of the same or different body masses (Grand 1977, 1978, 1990; McFarland *et al.* 2004). Here we test the hypothesis that each genus of hylobatid will show a distinct pattern from the others in relative distribution of body mass to the forelimbs and hind limbs. The methods promote a more detailed comparison of morphological adaptation, because relative limb masses indicate functional importance and offer insights into the individual's moving and feeding in its habitat

(Grand 1978). In contrast, body mass alone as a single measure defines only smaller or larger and consequently cannot distinguish among the hylobatids.

Materials and Methods

The Sample

We obtained 13 individuals from captive facilities over a 30-year period, consisting of 7 *Hylobates* and 4 *Symphalangus*, and only single specimens of *Hoolock* and *Nomascus* because they are extremely rare in captivity. The sample has 6 females and 7 males, ranging in age from 6.5 yr to 42 yr. Ted Grand contributed data for *Nomascus*. Body masses taken at the time of death prior to necropsy include brain and organs; we record individual body weights (Table I). We include the 6.5-yr-old as adult because he has the markers of adult: third molars (M3s) erupted and proximal humerus fused (after Bolter and Zihlman 2003). To behaviorists who study hylobatids in the wild, this age may at first appear to classify it as a subadult (Reichard and Barelli 2008), but in captivity monkeys and apes grow faster and mature earlier than their wild counterparts (Bolter and Zihlman 2010; Zihlman *et al.* 2004).

Dissection Methods

We use standardized methods on specimens received frozen and thawed before dissection (Grand 1977; Zihlman and McFarland 2000). We separate the entire

Table I Sample of 4 genera of Hylobatidae: *Hylobates, Hoolock, Nomascus,* and *Symphalangus*

Species	Age	Sex	Body weight (grams) gms	Cranial capacity (cc)	Intermembral index	Humero-femoral index
Hylobates lar	10 yr	male	7570	116.3	121	107
H. lar	41 yr	female	4050	90.3	125	110
H. pileatus[a]	28 yr	female	5711	87.3	124	110
H. pileatus	6.5 yr	male	6410	n. a.	118	105
H. moloch	31 yr	male	7270	n. a.	116	105
H. moloch	17 yr	male	7120	113.3	118	104
H. moloch	28 yr	female	5600	98.3	124	113
Hoolock leuconedys	42 yr	female	4950	95.0	125	111
Nomascus leucogenys	26 yr	female	9500	n. a.	n. a.	n. a.
Symphalangus	40 yr	male	10400	129.7	138	124
Symphalangus[b]	adult	female	7480	109.2	142	125
Symphalangus	26 yr	male	7010	142.6	143	127
Symphalangus[c]	subad	male	n. a.	120.6	141	125

[a] Died giving birth; body mass without fetus or placenta.

[b] Some data were published from this individual in Zihlman (1984).

[c] Cranial capacity and linear dimensions of limb bones used.

forelimb at the shoulder joint and weigh it to the nearest tenth of a gram. We partition the limb into 3 pieces: the (upper) arm (separated at the elbow joint), the forearm (separated at the wrist joint), and the hand. Note that the arm is only a part of the forelimb, although in nonanatomical studies the 2 terms may be synonymous. We weigh each of the segments of the forelimb. Similarly, we separate the hind limb at the hip joint: the thigh (separated at the knee joint), the leg (separated at the ankle joint), and the foot. Note that the leg is only a part of the hind limb, although in nonanatomical studies the two terms may be synonymous.

Analysis

We determined the following:

1) Body proportions. We calculate the distribution of body mass to body segments, i.e., how much of the individual's total body mass lies in the forelimbs, the hind limbs, and the head/trunk. We calculate the contribution of both forelimbs relative to total body mass and the hind limbs to total body mass. The head/trunk mass, along with the limbs, constitute 100% of the individual's body mass.
2) Segment proportions. We determine the distribution of mass within the forelimb and hind limb segments. Forelimb mass represents 100%; we calculate the contribution of each of its parts (arm, forearm, hand) relative to total forelimb mass. Similarly, we calculate the thigh, leg, and foot, as a percent of the entire hind limb (=100%).
3) Indices. We clean the long bones with dermestid beetles, then measure, and determine indices: intermembral [ratio: forelimb (humerus+radius) to hind limb (femur+tibia)], humerofemoral (ratio: humerus to femur), brachial (ratio: radius to humerus), crural (ratio: tibia to femur).
4) We measure cranial capacity (after Bolter and Zihlman 2003) using mustard seed and report it in cubic centimeters (cc).

We were unable to obtain complete data for all individuals. Damage during necropsy to the skulls prohibited cranial capacity measures of the 6.5-yr-old *Hylobates pileatus* and 31-yr-old *H. moloch*. We did not have access to the skeleton of *Nomascus*, and only cranial capacity and limb bone data were available for subadult *Symphalangus*.

Results

Body Proportions

At the whole body level, each genus shows a distinct pattern in limb proportions relative to total body mass. *Hylobates* differ from the other 3 genera in having heavy hind limbs relative to body mass: mean 20.3%, range 19.0–21.8%. The forelimbs average 19.1% and show more variation than hind limbs (range 16.3–21.9%, Table II). *Hoolock* has nearly equal mass in the forelimbs (16.5%) and hind limbs (16.0%), a pattern distinct from that of the other genera. With the least mass in the

Table II Percent of total body mass distributed to segments: head/trunk, forelimb, and hind limb. (Total body mass=100%.)

Species	Age	Head/trunk	Forelimb	Hind limb
Hylobates lar	10 yr	59.5	19.6	20.9
H. lar	41 yr	59.2	20.1	20.7
H. pileatus	28 yr	64.0	16.3	19.7
H. pileatus	6.5 yr	57.2	21.9	20.9
H. moloch	31 yr	63.2	17.2	19.6
H. moloch	17 yr	57.9	20.3	21.8
H. moloch	28 yr	62.9	18.1	19.0
Hoolock leuconedys	42 yr	67.5	16.5	16.0
Nomascus leucogenys	26 yr	65.5	16.6	17.9
Symphalangus	40 yr	60.2	22.2	17.6
Symphalangus	adult	62.1	20.2	17.7
Symphalangus	26 yr	63.8	21.1	15.1

limbs, its head/trunk segment is the heaviest among the hylobatids. *Nomascus* has close to equal mass in the forelimbs (16.6%) and hind limbs, though with slightly heavier hind limbs (17.9%). *Symphalangus* combines heavy forelimbs (21.2%, range 20.2–22.2%) with light hind limbs (16.8%, range 15.1–17.7%, Fig. 1).

Segment Proportions

Hoolock has relatively light proximal segments (arm, thigh) with heavy distal segments (hands, feet). *Nomascus* has the heaviest arm and thigh segments with light hands and feet. One individual of *Hylobates* overlaps *Nomascus* in the arm segment, but none approach its heavy thigh segment. *Symphalangus* differs notably from the other genera in its light arm and heavy forearm segments. Its thigh is light and the foot heavy, a pattern that also sets it apart from the others (Fig. 2a, b).

Body Mass

The *Hylobates* average 6247.3 g (range 4050.0–7570.0); *Hoolock* 4950.0; *Nomascus* 9500.0; *Symphalangus* 8940.0 (7480.0–10,400.0).

Indices

The Intermembral index for *Hylobates* averages 120.9 for our 7 individuals (range 116–125); 107.7 for humerofemoral (104–113); 110.4 for brachial (108–112); and 88.3 for crural (84–93). For *Hoolock* the index is 125 for intermembral, 111 for humerofemoral, 109 for brachial, and 86 for crural. The index for *Symphalangus* averages 141 for intermembral (138–143); 125.3 for humerofemoral (124–127); 106.8 brachial (105–109); and 83.5 for crural (83–84).

Fig. 1 Means of head/trunk, forelimb, and hind limb mass distribution as percent of total body mass.
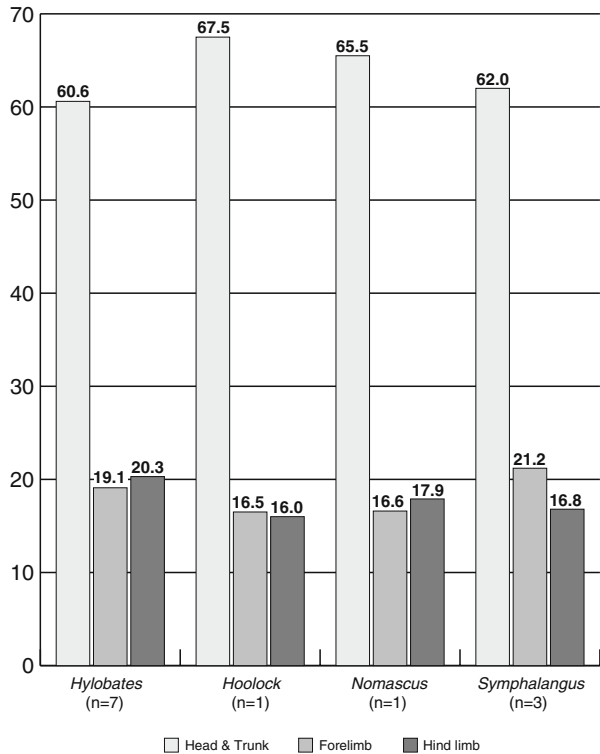

Cranial Capacities

Hylobates average 101.1 (87.3–116.3); *Hoolock*, 95; and *Symphalangus*, 125.5 (109.2–142.6).

Discussion

Discriminating among the 3 non-*Symphalangus* genera is particularly challenging, given the paucity of data on *Hoolock* and *Nomascus*. By taking the whole body as the focus of analysis, we here distinguish *Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus* from each other in relative body mass distribution to the limbs. This finding adds a useful anatomical dimension to taxonomy, suggests functional differences, and acts as a guide for future studies.

Within our sample of *Hylobates*, individuals vary in age, sex, reproductive state, and body mass; however, close examination shows that *Hylobates* conform to a pattern that is distinct from that of the other 3 genera. For example, in relative forelimb mass the 28-yr-old pregnant *Hylobates pileatus* and the 6.5-yr-old male *H. pileatus* represent the 2 ends of the range, whereas their heavy hind limbs fall with the other *Hylobates*. Even with very different ages and body masses, the 10-yr-old male *Hylobates lar* and 41-yr-old female *Hylobates lar* have relative limb masses that are nearly identical. This 41-yr-old female *Hylobates* is similar in age and body

Fig. 2 (**a**) Means and ranges of arm, forearm, and hand segments as percent of total forelimb mass. (**b**) Means and ranges of thigh, leg, and foot segments as percent of total hind limb mass.
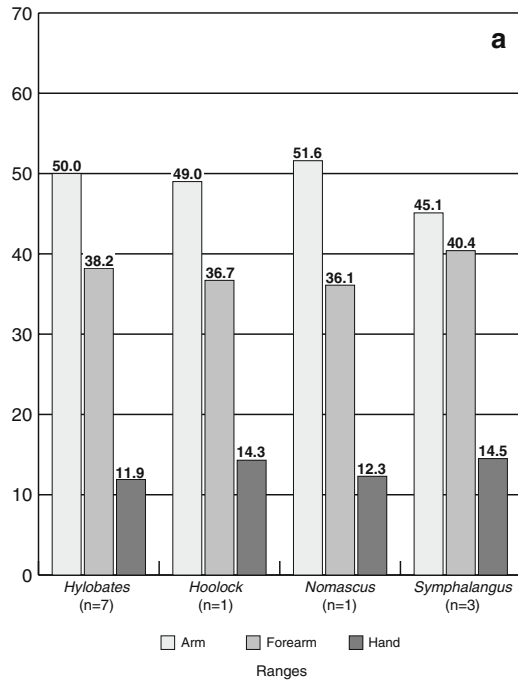
Hylobates: Arm (46.6-55.6); Forearm (32.9-40.6); Hand (9.4-13.4)
Symphalangus: Arm (43.4-47.4); Forearm (38.4-42.3); Hand (14.2-15.0)
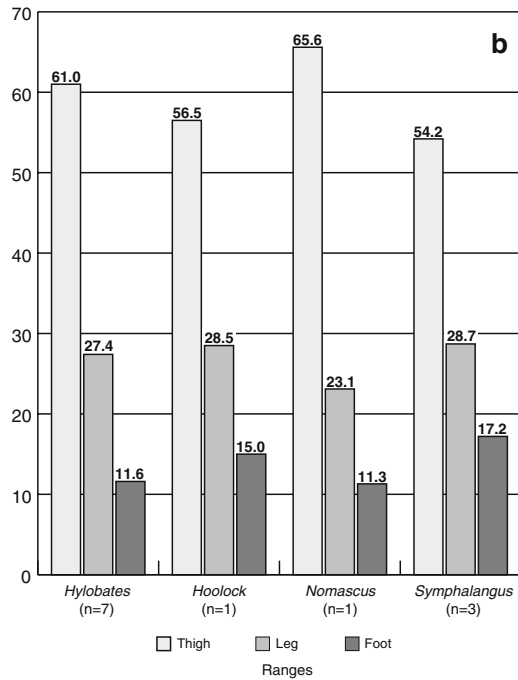
Hylobates: Thigh (55.0-64.5); Leg (24.8-30.9); Foot (9.9-14.1)
Symphalangus: Thigh (53.8-54.4); Leg (25.8-30.7); Foot (15.0-20.4)

mass to the 42-yr-old female *Hoolock*, yet devotes more body mass to the limbs, and the 2 genera contrast in their proportions. In addition, differences in state of health do not alter proportions. For example, in *Symphalangus*—adult female, old male, and young male that was ill and lost weight—their heavy forelimbs and lighter hind limbs conform closely to a species-specific pattern and contrast with *Nomascus*, which is similar in body mass to the old male.

The analysis within the limb segments also shows distinctions, though less than those for whole body proportions. *Nomascus* has a heavy thigh and light leg, unlike the other genera, and *Hoolock* is distinct from *Hylobates* in its relatively heavy hands and feet. Across the genera, *Symphalangus* has similar mass in its arm and forearm segments, and in its light thigh and heavy foot. The combination of proportions of the whole body and proportions within the limbs gives each genus an anatomical fingerprint that is a useful taxonomic marker.

Body mass, cranial capacity, dentition, and long bone indices vary and overlap in the hylobatids and do not show consistent findings useful for taxonomic purposes. The compiled data highlight the problems (Table III). Body mass is not reliable as a taxonomic feature because it is so variable; it fluctuates throughout an individual's life, particularly in adult females during reproduction. It is not surprising then that body mass in this sample of 13 overlaps considerably among the genera. For example, *Hoolock* fits within the range of *Hylobates*, the female *Nomascus* is in the range of *Symphalangus*, and the female *Symphalangus* is in the range of *Hylobates*. In measurements of cranial capacity, some individuals of *Symphalangus* are in the range of *Hylobates*. No information is available on cranial capacity for *Nomascus.*

Similarly, dental dimensions do not distinguish among the genera (Frisch 1973). For example, averages of mesiodistal diameters of permanent molars overlap in *Hylobates lar*, *Hoolock*, and *Symphalangus* (1973, p. 76). This finding led Frisch to conclude that "there is a continuum in the size of the dentition between the smallest and the largest-toothed living species of the hylobatid families... This observation makes it clear that for taxonomic purposes, no exclusive reliance should be set on measurements independent of a consideration of the morphology" (1973, p. 77). In addition to cranial capacity and dentition, intermembral indices overlap among the genera and therefore are unreliable for taxonomy. The intermembral index of *Hylobates* (116–125) in our sample encompasses *Hoolock* (125). Likewise, *Nomascus* intermembral indices from the literature (141.1, 140.3) fall comfortably into our range for *Symphalangus* (138–143).

Body Proportions and Locomotor Function

The distinct pattern of limb masses described for each of the 4 genera suggests functional correlates and corresponding differences in locomotor patterns. Where there is information from the wild, descriptions of locomotor behavior of *Hylobates* and *Symphalangus* show differences that correspond to their anatomical divergences (Caldecott 1980; Chivers 1972; Ellefson 1967, 1974; Fleagle 1976; Gittins 1983). The well developed forelimbs and particularly the heavy hind limbs promote flexibility in posture and locomotion of *Hylobates* moving through the forest canopy, described and illustrated by Grand (1972, 1984) based on John Ellefson's films on wild *Hylobates lar*. Movements are whole body actions: suspension under branches,

Table III Data from this study are combined with those from previously published work to show the overlap between genera in body mass, cranial capacity, and indices

	Sample	Body Mass	Cranial capacity	Intermembral	Humero-femoral	Brachial	Crural
Hylobates							
Our Data	(n=7)	6247.3 (4050-7570)	101.1[a] (87.3-116.3)	120.9 (116-125)	107.7 (104-113)	110.4 (108-112)	88.3 (84-93)
Geissmann (1993)	(n=228)	(3860-8390)					
Schultz (1930, 1933, 1944)	(n=238)		(78-125)	(120.5-136.9)	na	(104.8-123)	(85-93.5)
Jungers (1984)	(n=78)			(126.1-131)	(110.3-116.9)	(110.8-115.5)	(86.2-89.5)
Hoolock							
Our Data	(n=1)	4950	95	125	111	109	86
Geissmann (1993)	(n=18)	(5300-8500)					
Schultz (1933)	(n=3)		(93-100)	(125-133)	na	(107.8-111.2)	(86.1-87.7)
Jungers (1984)	(n=9)			129.8	113.5	114.5	87.9
Nomascus							
Our Data	(n=1)	9500	na	na	na	na	na
Geissmann (1993)	(n=32)	(5500-10000)					
Groves (1972)	(n=9)			141.1		114.3	
Jungers (1984)	(n=12)			140.3	122.2	115.5	87.5
Symphalangus							
Our Data	(n=4)	8940[b] (7480-10400)	125.5 (109.2-142.6)	141 (138-143)	125.3 (124-127)	106.8 (105-109)	83.5 (83-84)
Geissmann (1993)	(n=17)	(8400-15120)					
Schultz (1937, 1973)	(n=19)		(106-143)	(145-155)	na	(106-114)	(84-90)
Jungers (1984)	(n=17)			147	128.5	110	84.8

[a] Cranial capacity (n=5).

[b] Body mass (n=2)

fast ricochetal swinging across the upper canopy, propulsive action of the hind limbs that contributes to speed and the ricochet effect, climbing and descending trees, leaping across large gaps in the canopy, and moving bipedally across tree limbs. *Hylobates* prefer open canopy and are uniquely able to navigate the discontinuous forests with their agile, strong hind limb leaps (Caldecott 1980; Gittins 1983).

Field data for *Hylobates* serve as comparison with *Symphalangus*, whose heavy forelimbs and less massive hind limbs are adapted to forelimb-dominated climbing. In contrast to *Hylobates*, *Symphalangus* do not engage in fast brachiation and thrust little with the hind limbs in propulsion and leaping (Fleagle 1976). Further, they are unable to cross horizontal gaps much more than 10 m and more often use a 3-limbed support stance 72% of the time, vs. gibbons at 40% (Fleagle 1976). Siamangs leap and cross discontinuities in the forest less often; they make use of a more closed canopy and persist in these denser vegetations that support fewer large-branch pathways but offer multiple, smaller supports for moving and resting (Caldecott 1980; Fleagle 1976).

Summary and Conclusions

The anatomical data on body proportions and limb masses presented here distinguish the genera *Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus* from each other and therefore contribute information useful for taxonomy. However, additional whole-body anatomical data on a larger sample of individuals, especially *Hoolock* and *Nomascus*, will further clarify or elaborate the extent to which the genera differ.

The majority of hylobatid species are endangered, with some critically endangered. *Hoolock* and *Nomascus* are limited in their distribution in the wild, with some species numbering 20 and 110 (Chan *et al.* 2005; Long and Nadler 2009; Mootnick *et al.* 2007). Of the 10 gibbon species housed in North America, there are <20 individuals in 6 of those species.

The value of studies on captive rare primates is emphasized by the attention given to these individuals during their lives. Our specimens come from captive facilities that practice exceptional care in animal husbandry and offer seminaturalistic habitats that allow the individuals free range of locomotor expression (Doolittle and Grand 1995; Fernandez and Timberlake 2008). Even after death, these individuals, infrequently available for anatomical studies, can reveal additional insights about variation and adaptation and lay the foundation for hypotheses that can be tested in the field. The yet unexplored behavior, ecology, and anatomy of so many populations of hylobatids highlight the importance of conservation and continued study of these less known apes.

Future Research

Though studies on locomotor behavior have been few, available field data on *Hylobates* and *Symphalangus* show correspondences between limb proportions and locomotor function. Given the new anatomical data, we hypothesize that future field studies will uncover locomotor profiles that will show additional differences. Few field observations mention locomotor behavior of *Hoolock*, though its divergent

anatomical configuration suggests that its posture and locomotion may also show subtle distinctions from other genera. The locomotor behavior of *Nomascus* is also relatively unknown; their body and limb proportions, particularly the heavy arm and thigh segments, indicate power in shoulder, hip, and knee motions that can be assessed in the field. Future field studies that direct attention to posture and locomotion will likely find distinctions among the genera by making connections between locomotor anatomy and activity budget, foraging behavior, daily range size, forest level, and substrate size. Such research may clarify the specific adaptation of each genus and further our understanding of how so many species of hylobatids evolved and adapted to a wide range of habitats in Southeast, east, and south Asia.

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