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Gibbon (Hylobatidae) Species Identification Recommended for Rescue or Breeding Centers

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Abstract: Gibbons, Family Hylobatidae Gray, 1870, are small, arboreal apes of the tropical and semi-deciduous forests of southeast Asia and parts of south and east Asia. Four genera and about 14 species are currently recognized; a number of them threatened with extinction. Two of the reasons for breeding gibbons in captivity are to retain species and subspecies diversity and to create a viable gene pool, with the ultimate goal of releasing animals into protected native habitat. Accurate taxonomic identification may be complicated for *some* gibbon species due to (1) variation in coat color, (2) sexual dichromatism, and (3) the occurrence of coat color changes from infancy through sexual maturity, and for *all* species because of (4) the impacts of such as malnutrition and housing on coloration (for example, their maintenance indoors only or in full sunlight), (5) the ease with which the vocalizations of the different species can be confused, (6) the difficulties in distinguishing some gibbon subspecies from each other, and (7) errors in, or the lack of, information concerning the origin of confiscated gibbons. Given these problems, it is not surprising that rescue and breeding centers encounter difficulties in identifying the gibbons they receive. I review the characteristics and identifying features of the species and subspecies of gibbons, including information from museum specimens, live gibbons housed at the Gibbon Conservation Center, Santa Clarita, California, and a number of zoos worldwide.
Key Words: Primates, gibbons, Hylobatidae, conservation breeding, taxonomy

Introduction

Gibbons, Family Hylobatidae Gray, 1870, are small, arboreal apes, inhabiting the tropical and semideciduous forests of southeast Asia, and a small section of south and east Asia. They occur in northeast India and eastern Bangladesh through south China, Laos, Vietnam, Cambodia, Thailand, the Malay Peninsula, Sumatra, to Java and Borneo. Many of the species go through pelage color changes. These may be during infancy and before adulthood, from infancy through subadulthood, or from infancy through adulthood. There are also certain color variations in some of the wider-ranging gibbon species or subspecies that can be identified by their geographic distribution. Pelage color changes in gibbons may also be attributed to environmental factors such as malnutrition, pregnancy, age, nursing, staining from urine or sweat glands in light pelage (Fig. 1) or bleaching of hair in dark pelage, and housing (for example, indoors only or in full sunlight). Inexperienced taxonomists may have difficulties distinguishing different gibbon species through their vocalizations, which are nevertheless distinct and consistent. Gibbon taxonomy at the subspecific level has been difficult and controversial to comprehend. Some taxonomists use different names to describe the same coloration or species. In some cases, English names used to describe a color might not translate into another language. Many taxonomic studies of the number and names of gibbon genera, species, and subspecies have been conducted over the years (Elliot 1913; Fooden 1969; Groves 1972, 2001; Marshall and Sugardjito 1986; Geissmann 1995; Roos and Geissmann 2001; Brandon-Jones *et al.* 2004; Mootnick and Groves 2005). Current taxonomies indicate that there may be 12–14 gibbon species (Groves 2001; Brandon-Jones *et al.* 2004), four genera (see Mootnick and Groves 2005) and 25 or more species and subspecies.

There are a number of issues and, in some cases, complications with regard to our understanding of gibbon variation and taxonomy. The formal descriptions of many of the gibbons are based on museum specimens. Some species or subspecies hybridize in their native habitat in areas where they overlap in distribution, generally at the headwaters of the riv-

ers that divide them (Groves 1967; Marshall and Brockelman 1986; Marshall and Sugardjito 1986; Geissmann *et al.* 2000). In some cases, the pelage color of museum specimens can be faded from exposure to sunlight and treatments with certain preservatives (Downing 1945). Incorrect labeling is also a factor which confuses our attempts to understand the geographic basis of their taxonomy. A few museum specimens were listed as adults, but the pelage and dentition revealed that they were subadults in a color transition. Some published taxonomic descriptions have been incomplete or ambiguous. A few manuscripts that provided the coordinates for localities where gibbons occur were in error by 1 or 2 degrees on a few localities. Confiscated live gibbons can provide a plethora of information, including an understanding of their occurrence in parts of their geographical range where they are now locally extinct. In many cases the information on their origin, however, is lacking, incomplete or incorrect.

Given these variables, it is not surprising that rescue and breeding centers may encounter difficulties in the species identification of gibbons. Besides this, genetic, vocalization, behavioral, or skeletal analysis may be beyond the capabilities for some facilities to use as a means of species identification. It is extremely important not to hybridize species or subspecies through captive breeding programs if the progeny of those gibbons will possibly be released into an area where gibbons coexist. Thus, before releasing gibbons back into a secure habitat it is important to confirm what subspecies already exists in those areas. It is of the utmost importance, therefore, to be able to determine what species or subspecies of gibbon is housed in all facilities before they are placed in any type of conservation or reintroduction program.

Methods

This study was based on observations of gibbons housed at the Gibbon Conservation Center (GCC) between 1976–2006, some gibbons in zoos or rescue centers in Asia and the USA, and skins at the following museums: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); Field Museum of Natural History, Chicago (FMNH); Institute of Ecology and Biological Resources, Hanoi (IEBR); Harvard Museum of Comparative Zoology, Cambridge (MCZ); Muséum national d'Histoire Naturelle, Paris (MNHN); Museum Zoologicum Borgoriense, Bogor (MZB); National Museum of Natural History, Washington, DC (USNM); Zoological Museum, Vietnam National University, Hanoi (ZMVNU); Zoological Reference Collection, National University of Singapore, Singapore (ZRC). Additional criteria for determining taxonomic status followed Groves (1972, 2001), Marshall and Sugardjito (1986), and Geissmann (1995). Specimens examined are listed in Appendix I. Vocalizations of live specimens were compared to Marshall *et al.* (1972, 1984), Marshall and Marshall (1978), Marshall (1981) and Marshall and Sugardjito (1986).

Genus *Symphalangus* Gloger, 1841

Symphalangus syndactylus (Raffles, 1821) Siamang

Siamangs are the largest of the gibbons. They are stocky and black, with a large inflatable throat sac (Fig. 2), long hair on their upper body, and a broad chest (Fig. 3). The female's skull is intermediate in size between male siamangs and other gibbons (Hooijer 1952). The crown hair lies flat and swirls laterally above the brow. The second and third toes are webbed (Schultz 1933) up to the second phalanx (Raffles 1821). The extent of the webbing is individually variable but typically goes as far as the proximal interphalangeal joint (Fig. 4), although in some individuals it may reach as far as the distal interphalangeal joint (Fig. 5). A few instances of webbing can be found between the proximal phalanges of the fourth and fifth toes (A. Mootnick and L. Theisen-Watt pers. obs.) (Figs. 5 and 6), and in one individual (GCC Rumi) this was observed on only one foot. Males have a very long genital tuft (Groves 1972), up to 135 mm long (Marshall and Sugardjito 1986) directed downwards. Immatures are the same color as the parents and also have a visible throat sac. As they mature they may obtain creamy hair around the chin and brow (Geissmann 2003). In one adult male siamang, the pelage had a silverish golden streak running down both sides of the abdomen and along the front of the thighs (GCC Montgomery). No distinguishing features have been reported between the two subspecies in C-banding, G-banding or silver staining of their chromosomes (vanTuinen and Ledbetter 1983). Siamangs are placed in their own genus *Symphalangus* by Groves (2005) and Mootnick and Groves (2005), which is characterized by a diploid chromosome number of 50 (Klinger 1963). The single species has two subspecies, but there are few visual features that reliably distinguish them.

Symphalangus syndactylus syndactylus (Raffles, 1821) Sumatran siamang

Mountains and swamp forests of Sumatra

Symphalangus s. syndactylus appears to have a larger cranium, tooth row, and body than the mainland subspecies (Groves 1972). A shallow medial sagittal groove reaches nearly into the tip of the nose. The nose, although of course variable, has a long tapering point over the nostrils (A. Mootnick prelim. obs.) (Figs. 7 and 8).

Symphalangus syndactylus continentis Thomas, 1908 Malayan siamang

Northwest and central Malay Peninsula

The upper portion of the nose appears slightly bulbous, with an abbreviated midsagittal groove. The rounded internarial septum is separated dorsally by a slight constriction, and with a central latero-lateral depression, with a wide connection to the area above the lip. The lower half of the nose has a gradual tapering of the outer sides above the nostrils, with an increased tapering closer to the tip, giving the nose a slightly wider appearance on the lower portion than is observed in *Symphalangus s. syndactylus* (A. Mootnick prelim. obs.) (Fig. 9).

Genus *Nomascus* Miller, 1933

Crested gibbons are characterized by shorter dense hair compared to other gibbon genera. Adult males and immatures of both sexes have blackish pelage. Adult females are buff to gold to gray-tan. Adult females have a black crown patch or streak of various sizes and may have a faint white face ring. Depending on the humidity levels, female *Nomascus* can obtain a more orangey hair color resulting from their water soluble sweat (Fig. 10). The crown hair of adult males and immatures of both sexes stands erect and longer in some species, with the hair being longer in the center of the crown. The nose is long and slender (Groves 1972) with a groove running lengthwise down the center. Females have an elongated clitoris and males have a long baculum (Groves 1984). External genitalia of the two sexes appear similar which has caused confusion in identifying the sex when females are in their immature black pelage. Infants are pale at birth (Fig. 11), but begin their gradual change to a black phase at approximately six months of age, starting at the fingers, toes, and face ring (Fig. 12). The color change to black may be completed as early as 1.5 years of age (Fig. 13). The scrotal sac is easily observed at birth, through all stages of development, and throughout adulthood. Females change back to the light color phase near the age of sexual maturity, but males remain black (Pocock 1905; Delacour 1951; Deputte and Lecierc-Cassan 1981; Liu *et al*. 1989; Couturier and Lernould 1991). With the exception of *Nomascus gabriellae* (buff-cheeked gibbon), males have a small throat sac. Pelage description of each black-crested gibbon species and subspecies was based only on the examination of a few museum specimens and photographs or video of live specimens, either in captivity or their native habitat. This genus is characterized by a diploid chromosome number of 52 (Wurster and Benirschke 1969).

In the past, 52-chromosome gibbons were referred to as *concolor* gibbons or as belonging to the *concolor* group (Groves 1972; Marshall and Sugardjito 1986; Geissmann 1995). With the elevation of some subspecies to species in *Nomascus* (Geissmann 1995; Groves 2001) and the elevation of four subgenera to full genera (Mootnick and Groves 2005), I suggest that reference to *Nomascus* as the *concolor* group is confusing, because *concolor* refers to just one species in the genus. Common names such as crested gibbons or crested gibbon group would take in both the black crested gibbons and the light-cheeked gibbons and be more appropriate.

Nomascus concolor concolor (Harlan, 1826) Tonkin black-crested gibbon
Northern Vietnam, between the Black and Red rivers, central Yunnan

Adult males, immature males and females have blackish hair. They have long body hair for *Nomascus*, and a few white hairs at the corner of the mouth (Fig. 14) (MCZ 38114–16). The hair of the adult females can range from buffish to a light tawny; they have a black-brown or black crown streak (Ma *et al*. 1988; Geissmann 1989). They have dark hair on the ventrum, that forms an inverted triangle (Geissmann 1995) (Fig. 15) and a small white patch of hair above the mouth and below the eyes. Adult females can also have black on the first digits, and chin, with a few black hairs on the genitals, pelvis, and legs, and around the ears. Individuals I have observed had a creamy-buff throat. Groves (2001, 2005) listed four subspecies of *N. concolor*. Besides the nominate subspecies and *lu* (see below), he included two forms from China, *N. c. furvogaster* (Menglai, Cangyan, Yunnan) and *N. c. jingdongensis* (Wenbu, Jingdong, central Yunnan) described by Ma and Wang (1986) but not dealt with in this review.

Nomascus concolor lu (Delacour, 1951) Laotian black-crested gibbon
Northwestern Laos

Delacour (1951), with the help of J. Greenway and F. Edmond-Blanc, collected six specimens of *N. concolor lu* on 7 January 1939, at Ban Nam Khueng, northwestern Laos (20°23′N, 100°15′E; coordinates from Jenkins 1990). The exact collection date of the adult male holotype BMNH ZD1952.142 and an adult female paratype BMNH ZD1952.143 is confused in that the date on the specimen labels is 17, not 7, January 1939 (P. D. Jenkins pers. comm.). I am assuming that the error is with the specimen labels, since Delacour (1951) described all of the six specimens as being collected on 7 January 1939, which included the holotype.

Delacour (1951) provided the following description of two adult females. One female (MCZ 46288) has a black crown, with the overall pelage a vivid tawny ("fauve assez vif"), but strongly mixed with black hairs on the chest and abdomen. The second female, the paratype BMNH ZD1952.143, he described as having a black crown, with the overall pelage being a vivid tawny, but mixed with black hairs, perhaps due to a color transition (Delacour 1951).

There is some controversy concerning the description of *Nomascus concolor lu*, and even whether it still exists in its native habitat. During 2004–2006, however, I received correspondence from J.-F. Reumaux stating that 11 families of *N. concolor lu* had been located in the Bokeo Nature Reserve, northwestern Laos. There were also credible reports of a further seven families there. The existence of *N. concolor lu* in this reserve was confirmed through DNA extracted from feces (C. Roos pers. comm.), as well as by tape recordings, video footage, and photographs (Figs. 16 and 17). A video of a pair and infant in the reserve (Figs. 18 and 19) showed that they were very similar to two adult specimens at the MCZ (Figs. 20 and 21) that Delacour, Greenway, and Edmond-Blanc had collected on (I presume) 7 January 1939 at Ban Nam Khueng.

From my inspection of the adult female MCZ 46288, it is tawny-buff with a small black crown (Fig. 22), similar to that of the adult female with an infant in the video that was taken at the Bokeo Nature Reserve (Fig. 23). The upper chest is buff with a few black hairs, gradually darkening, with a black grizzling on the lower chest, abdomen, and genital region (Fig. 21), again similar to the adult female of the Bokeo Nature Reserve (Fig. 19). There is a brownish orange color in the

center of the chest of MCZ 46288, possibly from her sternal gland (Fig. 21). There are a few black hairs on the fingers and toes. The chin is black (Fig. 21), with a few black hairs on the throat and above the ears. The face ring is slightly lighter than the surrounding hair. There are no long guard hairs. The female BMNH ZD1952.143 is much grayer in color than the female at the MCZ (P. D. Jenkins pers. comm.).

Delacour's adult male MCZ 46289 is entirely black, with no white hairs at the corners of the mouth. It has short black body hair, mixed with longer black guard hairs. This contrasts with *N. c. concolor* males (MCZ 3811416) which have longer hair than *N. concolor lu* (MCZ 46289). The adult male co-type MNHN CG 1952-543 that Delacour collected on 7 January 1939 is also entirely black (C. Callou pers. comm.). Delacour's descriptions differ in that MCZ 46289 and MNHN CG 1952-543 are entirely black. Delacour indicated that all the males have at least a trace of gray on the cheeks.

With only a few museum specimens to examine, Groves (1972), Dao Van Tien (1983), and Marshall and Sugardjito (1986) described *N. concolor lu* as black, with a trace of silver along the side of the head. The adult male holotype BMNH ZD1952.142 has a trace of gray (or buff) on the cheeks and a small trace of gray on either side of the crown (P. D. Jenkins pers. comm.). The skin of a juvenile female USNM 296921 was collected by R. Elbel on 26 February 1953 at Khao Tham Phra. It had numerous incisions across the face (to remove the skull), which made it difficult to interpret. Rearrangement of the facial skin, however, showed that the juvenile, in black pelage, has a moderate amount of blackish hairs mixed throughout a narrow whitish-gray cheek patch, giving it an overall grizzled appearance. The narrow cheek patch begins below the ear, but not touching the ear, and ends above the chin, but not touching the lip. There are a few grayish white hairs throughout the pelage, including a few whitish hairs under the lip, and a few buff hairs in the genital region.

A topotype, AMNH 148262 labeled male, collected on 7 January 1939 at Ban Nam Khueng, is somewhat similar to the juvenile female USNM 296921. It has, however, a slight trace of a silver streak by the temples, and less silver hair on the facial cheeks. The genital area is blackish, with slight grayish grizzling on the rump. Although labeled as a male, AMNH 148262 has a very short pubertal tuft. As an adult male, the tuft should be longer, and the scrotal sack should be visible. An X-ray of the skull of this gibbon showed that the canines and lower third molars had not yet erupted (Fig. 24), and it is similar in this respect to a 4.9 yr old female *Nomascus* (GCC Parker). The nipples of AMNH 148262 are small, which is typical of immature male and female *Nomascus* (GCC Dexter and Parker). Geissmann (1989) also concluded that AMNH 148262 was a subadult female in the early stages of her color transition.

Delacour (1951) wrote that the *N. concolor lu* holotype (BMNH ZD1952.142) male was overall black with a gray stripe over the eye to the ear. Delacour (1951) described three other males (MCZ 46289, MNHN CG 1952-543, and AMNH 148262) as having a slightly different appearance. Two of the

Delacour's (1951, p.121) description of *Hylobates concolor lu.*

"3. Hylobates concolor lu subsp.nov.
Mâle noir, avec une bande allant de l'oeil à l' oreille, et un peu au delà, d'un noir mélangé de gris argenté; fourrure longue, épaisse et grossière.

Type mâle adulte au British Museum of Natural History, collecté à Ban Nam-Khueng, Province du Haut Mékong, Laos, le 7 Janvier 1939, par J. Delacour, J. Greenway et F. Edmond-Blanc. Longueur totale: 520 mm.; oreille: 35 mm.; pied: 152 mm. Trois autres mâles et deux femelles adultes ont été obtenus au même endroit et à la même date.

Nommé d'après la tribu des *Lu* qui habite la région de Nam-Khueng. Les trois autres mâles diffèrent quelque peu; deux sont presque entièrement noirs, avec seulement des traces de gris aux joues et aux reins; le troisième a du gris à la face, comme le type, et aussi aux joues, au menton, aux épaules, aux cuisses et au bas du dos. Les deux femelles sont d'un fauve assez vif, avec la couronne noire; l' une a le fauve de la poitrine et du ventre fortement mélangé de noir; l'autre a tout le pelage mélangé de noir, ce qui n'est peut-être qu'une livrée de transition.

Distribution: L'extrême ouest du Laos, le long du Mékong, près des frontières du Siam et des Etats Shans. Il est curieux qu'une forme de *H. concolor* sans joues blanches, et extrêmement voisine de *H. c. nasutus*, ait été trouvée aussi loin de cette dernière, dont elle est séparée par le domaine très étendu de la sous-espèce à joues blanches, *H. c. leucogenys*."

English translation of Delacour (1951), page 121.

3. Hylobates concolor lu new subspecies
Male black, with a stripe going from the eye to the ear, and a little beyond it, of a black mixed with silver gray; long, thick and robust hair.

Type adult male in the British Museum of Natural History, collected in Ban Nam-Khueng, Province of Haut Mekong, Laos, on 7 January 1939, by J. Delacour, J. Greenway and F. Edmond-Blanc. Total length: 520 mm.; ear: 35 mm.; foot: 152 mm. Three other males and two adult females were obtained in the same area and on the same date.

Named after the Lu tribe that inhabits the region of Nam-Khueng. The three other males are a little different; two of them are almost entirely black with only some traces of gray at the cheeks and in the [area of] the kidneys; the third one has gray on his face, like the type, and also at the cheeks, the chin, the shoulders, the thigh and at the base of his back. The two females are a fairly vivid tawny color, with a black crown; one has the tawny color on the chest and the belly strongly mixed with black; the entire pelage of the the other is completely mixed with black, which may only be a transition coat.

Distribution: The extreme west of Laos, along the Mekong, close to the frontier with Siam and the Shans States. It is curious that such a form of *H. concolor* without white cheeks, and extremely similar to *H. c. nasutus*, can be found far away from the latter, from which it is separated by the large range of the subspecies with white cheeks, *H. c. leucogenys*.

three male *N. concolor lu* that he collected were in a black color phase, had a trace of gray on the cheeks, and a trace of gray on the loins. The third male (AMNH 148262 which appears to be a female) had a similar pattern of gray on the face as the holotype, but also a trace of gray on the cheeks, chin, and shoulders, upper thigh, and lumbar area (Delacour 1951). A somewhat similar description was given by Hill (1970) of an imported black juvenile gibbon (SDZ 024368) housed at the San Diego Zoo. It had large, white cheek-patches and white eye-patches. By 1971, the white eye-patches had faded into black (M. Jones pers. comm.). This, in some cases, is the final stage of the first color transition in *Nomascus* (Fig. 25). Hill's (1970) description was that of *N. l. leucogenys* (northern white-cheeked gibbon). Since *N. l. leucogenys* and *N. concolor lu* are found in bordering areas in northern Laos, some of the *N. concolor lu* museum specimens could be hybrids. Specimens may also be immatures undergoing color transitions, and even misidentified in their sex. DNA analysis is necessary to confirm their identity.

Nomascus nasutus nasutus (Kunkel d'Herculais, 1884) Cao Vit black-crested gibbon

Northestern Vietnam, east of the Red River

Adult males, immature males and females have blackish hair with slightly brownish hair on the chest, extending sometimes from the throat to the abdomen (Figs. 26 and 27). It is difficult to interpret from the numerous photographs in Fischer (1965; see Fig. 26), whether "Patzi" had lighter-colored chest hair when in black pelage, or if her chest hair was sparse on pale skin. Adult females are buffish to buffish gray in color, which can be mixed with few longer blackish hairs. They have a long, wide, black crown streak that can extend past the nape, to the brow, tapering to a thin face ring, and becoming thicker at the chin (Fig. 28). The rectal hair is brownish. There are some black hairs above the ear. The vocalizations of an adult female (Patzi) in the Tierpark Berlin were similar to those of *N. n. nasutus*, but her pelage differed in that she had a very long, broad, black crown streak that went past the nape, and extended to the brow, tapering to a thin face ring and becoming thicker at the chin (Geissmann *et al*. 2000; Mootnick *et al.* 2006). This female had a narrow, blackish-brown chest plate slightly wider than the face, beginning at the throat and tapering at the top of the abdomen (Fig. 29).

Nomascus nasutus hainanus (Thomas, 1892) Hainan black-crested gibbon

Hainan Island, China

Adult males have short black hair, and the crown hair is not as obvious as in other species of *Nomascus* (Fig. 30) (Pocock 1905; Groves 1972; Ma *et al*. 1988; Geissmann *et al*. 2000). Adult females have a black crown patch, brownish buff body hair, no black hairs on the limbs (Ma *et al*. 1988), and a small white patch of hair above the mouth and below the eyes (Fig. 31). Adult females have a thin, white face ring that is thicker above the mouth and below the orbital ridge (Mootnick *et al*. 2006). Comparison of the DNA of *N. nasutus hainanus* and *N. n. nasutus* may result in these two subspecies being elevated to species. Groves (2005) lists *hainanus* as a distinct species, and *nasutus* as a subspecies of *N. concolor*.

Nomascus leucogenys leucogenys (Ogilby, 1840) Northern white-cheeked gibbon

Southern Yunnan, northern Laos, and northwestern Vietnam

The cheek patches of the adult male and immature connect under a black chin and can extend up to the top of the ear (Fig. 32). Adult females range in color from dark to light buff to creamy orange often diffused with tan, gray, or black hairs. They have a white face ring, and a small to medium-length black crown patch (Figs. 11, 12, and 32). Adult females can have reddish brown to brown-black hair in the genital region; black hairs on the tips of the fingers and toes; and white hairs below the eye and above the mouth. A trace of the crown patch can extend between the scapulae. The female has few black hairs around the ears**.** Females are sometimes larger than males.

Nomascus leucogenys siki (Delacour, 1951) Southern white-cheeked gibbon

Central Vietnam and southern Laos

Nomascus l. leucogenys and *N. leucogenys siki* differ by a reciprocal translocation between chromosomes 1 and 22 not present in the former (Couturier and Lernould 1991). Groves (2001) pointed out that there is some difference of opinion as to whether the form *siki* was a subspecies of *N. leucogenys* or *N. gabriellae*. Two mtDNA studies placed it in a clade with *leucogenys* (Garza and Woodruff 1992; Zhang 1997), although it also evidently interbreeds with *N. gabriellae* in central Vietnam (see below). Following the suggestion of Zhang (1997), Groves (2001, 2005) considered it to be a distinct species. It is my opinion, however, that this conclusion is premature, since the evidence was based on only a few specimens: Until additional evidence is reported, *Nomascus l. siki* should be considered a subspecies. Adult males have small, white cheek-patches that extend as far up as the corners of the eyes, and thin, white hair partially encircles the upper lip and totally encircles the lower lip, connecting on the upper portion of the throat, and terminating at a black chin which can have a few white hairs (Fig. 33). Adult females have few black hairs above the ear, and appear to be more similar in appearance to adult female *N. l. leucogenys* than to *N. gabriellae* females (Geissmann 1995), with a thin white face-ring that is wider above the mouth and below the eye, which gives them an older appearance (Fig. 25).

Nomascus gabriellae × *Nomascus leucogenys siki* Light-cheeked gibbon hybrid

Central Vietnam

These two forms have a natural hybrid zone in central Vietnam. Adult and immature males and immature female hybrids look more like *N. gabriellae* than *N. leucogenys siki* (Fig. 34), and adult female hybrids have features similar to both *N. gabriellae* and *N. leucogenys siki* (Fig. 35). The

hybrids can easily be identified by karyotyping (P. vanTuinen pers. comm.).

Nomascus gabriellae Thomas, 1909 Buff-cheeked gibbon
Southern Vietnam, southern Laos, and eastern Cambodia

Nomascus gabriellae has been referred to as the buff-cheeked gibbon (Osgood 1932), red-cheeked gibbon (Groves 1972, 2001, 2005), yellow-cheeked gibbon (Geissmann 1995), and golden-cheeked gibbon (Varsik 2000). Adult males are mainly blackish but generally have dark brown to buffish brown on the upper chest, and can be lighter in color around the nipples. They have small, light buffish white cheek patches that extend to the bottom of the orbital ridge and can be slightly separated at the throat, with black hair under the eyes (Fig. 36). Adult females can be smaller than adult males and *Nomascus l. leucogenys* females. Adult females are generally buff to strawberry-buff and can have a very slight grizzling of darker hairs on the chest, on the edges and tips of the fingers and toes, and on the outer forearm. Their blackish crown patch can taper down the nape of the neck and sometimes has a few black hairs extending to the center of the scapulae. There is black hair under the eyes, and a black fringe around the ears. Adult females may have slightly red-brown to black genital hairs, with a few slightly red-brown to black hairs surrounding the anus, and usually there is a trace of a white fringe encircling the face.

Genus *Hoolock* Mootnick and Groves, 2005 Hoolock or white-browed gibbon

Mootnick and Groves (2005) suggested that the two known hoolock gibbons, western and eastern, be considered as separate species. Although there is compelling evidence for this, I do not consider it conclusive. In a comparative study of the two, there was a 2.5–3% difference in the mitochondrial cytochrome b gene, a separation nearly comparable with those seen between *Nomascus gabriellae* and *N. leucogenys* (C. Roos pers. comm.). There is a greater difference in the pelage of the two forms than that observed between *N. gabriellae* and *N. leucogenys*. However, a comparative study of *Hoolock* vocalizations would also be of great interest in determining the degree of difference between them, and further karyological and molecular genetic studies, using a larger sample size, are needed.

Adult males have blackish hair with a thick white brow, and a thin tuft of hair at the chin. Adult female pelage is varying shades of buff, tan to copper-tan with different shades of brown hair on the sides of the face, throat, chest, and inner thighs. As observed in *Nomascus*, adult female *Hoolock* also have a slight color variation in the same individual resulting from their sweat that can give them a copper-tan appearance. Shorter hairs on the sides of the neck give this gibbon's face a triangular appearance. The tooth row is wider compared to *Hylobates* and *Nomascus*, and the chest region is narrow. Ischial callosities are heavily furred. The coats of young infants are gray-white with a yellow tinge (McCann 1933) (Fig. 37) and contrast more strongly in color to the pelage of the mother than is observed in most other gibbon species. They go through a fast color change to mainly black with a white brow and a trace of a face ring. They lose most of the grizzling throughout the coat at approximately 1.5 years old. At puberty, the female's entire pelage is mostly light in color, while males remain black throughout adult life. Adult and immature hoolock gibbons are the only gibbon species to produce a guttural growl during their vocalization (Mootnick and Groves 2005). Captive *Hylobates agilis* (agile gibbon) and *Hylobates muelleri* (Müller's gibbon) have occasionally been misidentified as hoolock gibbons, and this is probably the case of Chu and Bender (1961). The genus is characterized by a diploid chromosome number of 38 (Prouty *et al*. 1983a, 1983b).

Hoolock hoolock (Harlan, 1834) Western hoolock gibbon
Myanmar west of the Chindwin River, northeastern India, and northeastern and southeastern Bangladesh

Juvenile through adult males, and juvenile through the beginning stages of subadulthood females are black with a thick, white brow of varying heights that grows upwards, that flicks up at the ends and generally not separated in the middle (Figs. 38 and 39). They have a black chin tuft. The black genital tuft of the adult males grows dorsally to about 52 mm in length, and parts in the middle lengthwise. Some males have slightly longer black hair under and toward the center of the brow, giving the appearance of a separated brow. The infant's white brow is large, with a trace of white along the sides of the head by the end of the first color transition and afterwards, and the chin tuft is pale (Fig. 40). The thick, white brow of the adult female turns upwards at the ends, is narrower as it travels down the orbital ridge and the muzzle, and then connects with the white chin tuft. White hair encircles the bridge of the nose and extends around the muzzle to connect with the chin tuft creating a face ring like a figure of eight. The throat and chest of the adult female is generally darker than the adult female *Hoolock leuconedys* (eastern hoolock gibbon) (Fig. 41). The hair on the hands and feet of the adult female is generally the same color as the body hair, but there is a black fringe on the fingers, the edge of the hands, and toes (Groves 1972; Mootnick *et al*. 1987) that encircles the foot, and there is some blackish brown in the genital region (Mootnick and Groves 2005) (Fig. 42) and around the anus.

Hoolock leuconedys (Groves, 1967) Eastern hoolock gibbon
Myanmar east of the Chindwin River, south western Yunnan, and Lohit District, Arunachal Pradesh, northeast India

Recent surveys confirmed that *H. leuconedys* also occurs between the Lohit River and the mountains in the Dafa Bum, Arunachal Pradesh, in northeast India in a continuous range into Myanmar (Das *et al.* 2006). The adult males are black, with a long silvery testicle tuft that parts in the middle lengthwise and is approximately 75 mm long, directed dorsally. The chest of the adult male is grizzled with silverish hair (Fig. 43) that can be seen first when approximately nine years old

(GCC HHL304). By the time the adult male has a grizzled, silver chest and the female is completing her final color change, there are two parallel white lines of hair connecting to the medial aspect of the thick, white brow where it is separated in the middle, which descend then diverge to encircle the muzzle and connect with the chin tuft (Figs. 44 and 45). Starting at the outer aspect of the thick, white brow of the adult female, there is white hair encircling the orbital ridge that runs just above the diverging white line of hair above the bridge of the nose that then connects at the medial aspect of the brow. This gives the female the appearance of a double figure of eight face ring (Fig. 45). The hands and feet of the adult female are slightly paler than the limbs, and may have a trace of white (Groves 1972) (Fig. 44). The adult female sometimes has a lighter coloration running through the center of the light brown chest hair (Fig. 43); the digits may have a trace of black on them; and the crown hair is lighter and grows slightly upwards and toward the nape of the neck and is slightly directed toward the sides of the head (Fig. 46) (Mootnick *et al*. 1987). The adult female's genital region is generally lighter in color compared to the surrounding area, whereas the hair surrounding the anus is brown. Some females from Yunnan and the east of the Chindwin River have been observed to have brown hair on the genital region. At subadulthood, the male begins to acquire a brownish color to the hair on the chest, and the testicle tuft is beginning to lengthen with silverish hair. Before the chest turns brown, the thin, face-ring slowly decreases on the sides of the face, and white hairs begin to encircle the bridge of the nose, and eventually connect with the white hairs under the chin. At this time the white brow is beginning to thicken above the orbital ridge. Immatures in the black color phase have white chin hairs and a large, white brow separated in the middle, with white hair along the lateral aspect of the orbital ridge, giving the appearance of a face ring (Fig. 45).

Genus *Hylobates* Illiger, 1811

The remaining gibbon species are classified in the genus *Hylobates*. This genus is characterized by a diploid chromosome number of 44 (Chu and Bender 1961; Chiarelli 1962). Referring to *Hylobates* as the *lar* group is now misleading, and a new name should be given to the 44-chromosome gibbons—the *Hylobates* group or the 44-chromosome gibbon group.

Female genital swelling is very prominent in this genus, and most obvious in *Hylobates moloch* (Javan gibbon), *H. muelleri*, *H. agilis*, *H. albibarbis* (Bornean white-bearded gibbon), and *H. lar* (lar gibbon). The genital swelling is not as pronounced in *H. pileatus* (pileated gibbon) (A. Mootnick pers. obs.). I reserve judgment on *H. klossii* in this respect as my observations are limited to just two adult females.

Hylobates klossii (Miller, 1903) Kloss' gibbon
Mentawai Islands, Indonesia

Both sexes have short, black hair, and are known to remain this color at all life stages. *Hylobates klossii* has a broad chest and long legs, thumbs, and big toes (Groves 1972) (Fig. 47). The hair forming the genital tuft is short. There is inter-digital webbing on the feet (Groves 1972), but it only extends approximately one-third of the way along the proximal phalange between the second and third digits (Fig. 48). Adults have the most compact skull, smallest jaw, and teeth in comparison to other gibbons (Marshall and Sugardjito 1986). The hair on top of the head is flat. Immature crown hair stands erect (Fig. 49). The spectacular great call of the adult female *H. klossii* is more similar to those of female *H. pileatus* and *H. muelleri* than it is to female *H. lar*, *H. albibarbis* and *H. agilis*. No subspecies have been described, but there are some variations in hair length, the direction of hair grown on the outer side of the forearm, and in body size on different islands (Groves 1972, 1984). Of the four captive females observed, two were in transition from juvenile to adulthood (A. Mootnick pers. obs.). When one of the females became a young adult she had a slight tawny-colored grizzling on the chest (Fig. 50).

Hylobates pileatus Gray, 1861 Pileated or capped gibbon
Western Cambodia, southeastern Thailand, and southwestern Laos

Hylobates pileatus is the most sexually dichromatic of the gibbons in the *Hylobates* group. Adult males have short, black hair with a thick, white brow band that becomes thinner as it encircles the face. The fingers and toes of the adult males are white, with a slight fringe running halfway up the sides of the hands and feet (Fig. 51). There is a white prepubertal patch. The crown cap is encircled by a grizzled, light, sliverish streak on the sides of the head that becomes faint on the back of the head, with a few white hairs on the nape, shoulder and upper back. Adult males may have a faint, gray grizzling on the lower back and lower legs. Subadult and adult females are silver-buff with a black, heavily furred throat, and an inverted triangle on the ventrum that branches off to the underarm area but stops short of the genital region (Figs. 1 and 52). This black coloration extends upwards to the bottom of the ears and narrows in front of the ear to connect with the cap. The cap of the female is large and black, with long, silver-buff hair curved over the temples. Subadult and adult females have a white brow (which becomes thinner depending on age, physical condition or pregnancy) (Figs. 52, 53, 54 and 55) that sometimes extends laterally around the orbital ridge; there can be a trace of a white facial ring (Fig. 52). Since infants do not have bi-colored hair (darker hair at the base), they are lighter buff than subadults and adult females (Figs. 1, 53 and 55). Infants, as in all hylobatids, initially have some light creamy-pink skin (Fig. 54) that turns various darker colors depending on the species and parts of the body. During infancy the palms, soles and face turn to a tawny gray (Fig. 1) and, depending on age and amount of sunlight exposure, they end up having a charcoal-gray pigmentation.

Hylobates pileatus is the only species in the genus in which males undergo a complete color change from infancy to adulthood (buff to black). Both males and females begin

their color change at about 10–12 months old. The change starts at either the center of the chest or the crown (Figs. 53 and 56). At 9.5 months old, black hair was noticeable on the crown of one female (GCC Jitka) but not on the chest. The first signs of black on the center of the throat closest to the chest plate were observed for a male at 37 months old, and the white brow and a partial face ring became evident (GCC Truman). The females can complete their color change at 4 years of age (Fig. 52), whereas the process is still ongoing in males when 4.5 years old (Fig. 57). Both sexes have a lateral tuft along the sides of the crown. By seven years of age, the female's crown hair has lengthened to the point that it hangs over the temples (Figs. 53 and 54), which Marshall and Sugardjito (1986) referred to as Dagwood tufts. In some females the tuft curls upwards (Fig. 55). Males complete their color change by 6.5 years of age (GCC Kokopelli, Mateus Binti); the lower back and lower limbs are the last areas where the color change is noticeable (Fig. 58).

Hylobates moloch (Audebert, 1797) Javan, silvery, or moloch gibbon
Western and central Java

Both sexes are silvery gray, and generally have long, dense hair at the neck, sides of the head, upper arms, and on the shoulders. The hair length between the shoulders ranges from 50 mm to 70 mm (Groves 1968). The outer hair coloration can turn a mouse gray in harsh sunlight. Either sex may have a distinct light-to-blackish gray cap depending on whether they are from central or western Java, and the same dark coloration as the cap is occasionally seen under the whitish brow. There is charcoal-gray hair in the genital region and surrounding the anus. The female's chest is sometimes charcoal-gray colored (Fig. 59) (Geissmann 1995). The transition from a gray chest to a dark chest plate can begin as early as 5 years old at the center of the chest, and can eventually resemble a wide, inverted triangle that tapers towards the abdomen and becomes a line as it gets closer to the groin (GCC Chloe) or observed only on the upper chest (GCC Khusus). An adult male from central Java (MZB 3320) has a thin charcoal-gray colored vertical streak running down the center of the chest. Immature chest coloration darkens from a light, silverish gray to silver gray, or gray by the time they are mature. Both sexes have white to white-gray hair on the brow and surrounding the chin; this hair usually connects to slightly darker hair on the side of the face to form a face ring (Fig. 60). Hair under the chin grows upward, giving the appearance of a "goatee". Infants are lighter in color than adults and change to silvery gray shortly after birth (Figs. 59 and 61) (Groves 1972) and their cap darkens as they mature (Figs. 61 and 62). *Hylobates moloch* is sometimes confused with *H. muelleri* because of similarities in coat color. However, the great call of the female *H. moloch* is more similar to those of female *H. agilis*, *H. albibarbis*, and *H. lar* than it is to *H. muelleri*.

Following the suggestion of Andayani *et al.* (2001; see also Supriatna *et al.* 1999; Supriatna 2006), Brandon-Jones *et al*. (2004) listed two subspecies of *H. moloch*: *H. m. moloch*, the west Javan silvery gibbon, and *H. m. pongoalsoni* Sody, 1949, the central Javan silvery gibbon. I do not consider them here, and they are not recognized by Groves (2001, 2005) or Geissmann *et al*. (2002). *Hylobates m. pongoalsoni* has a lighter cap than the gibbons of western Java. Research on their vocalizations, and additional molecular genetic and chromosome studies may shed further light on this (Geissmann *et al*. 2002).

Hylobates muelleri Martin, 1841 Müller's, Bornean, or gray gibbon
Borneo, except for the southwest

Adult male and female *Hylobates muelleri* are similar in their coat color, which varies from gray to gray-brown, or blackish. The hair of the adult male's genital tuft is 25 mm long (Marshall and Sugardjito 1986) and is typically darker than the body hair. Infant coat color is lighter than the parents (Fig. 63). This species lacks a uniform appearance in areas of geographic overlap with other Müller's gibbon subspecies. The great call of the female is somewhat similar to that of female *H. pileatus*.

Marshall and Sugardjito (1986) recognized three subspecies (see Groves 2001, 2005), which we list here. Some people have difficulties distinguishing two of them, *H. m. muelleri* (Eastern Müller's gibbon), and *H. m. abbotti* (Abbott's gray gibbon) from *H. moloch* because of similarities in coat color. *Hylobates m. funereus* (northern Müller's gibbon) is occasionally misidentified as *H. albibarbis* for the same reason.

Hylobates muelleri muelleri Martin, 1841 Eastern Müller's gibbon
Southeastern Borneo

Hylobates m. muelleri is pale gray or gray-brown, with a thick, white brow that is wider at the center. The cap is blackish, and can grow slightly down the nape with black grizzling through the gray hair as it approaches the center of the back. The ventrum, abdomen, genitals, hands or just the fingers, and toes are blackish (Fig. 63). The outer portion of the legs and arms are gray to gray-brown, and the inner aspects of the limbs are darker in color (Figs. 63 and 64), and vary between individuals.

Hylobates muelleri funereus I. Geoffroy St. Hilaire, 1850 Northern Müller's gibbon
Northern Borneo

Hylobates m. funereus is dark gray or gray-brown with a blackish to blackish-brown cap, ventrum, throat, inner aspects of the limbs (which can vary between individuals), anus, and genitals (Fig. 65). The outer area of the lower limbs, elbow, and tips of the fingers, toes, and in some individuals the back, can be paler in color. They have a large, white brow that is wider at the center. Toes and fingers are black on specimens from southern regions where the subspecies overlaps geographically with *H. m. muelleri*. There is a report of a very large *Hylobates m. funereus* and a blackish color phase in the Kinabatangan Wildlife Sanctuary (Ancrenaz 2001).

Hylobates muelleri abbotti Kloss, 1929 Abbott's gray gibbon
Western Borneo

Hylobates m. abbotti has short, mouse-gray body hair, and can have dark hair in the genital region (Fig. 66), while the lumbar region can be slightly lighter than the upper back. The brow is slightly paler than the head hair and it can have blackish hair below the brow and above the eyes. Populations closer to the bordering area of *H. m. funereus* sometimes have blackish hair on the throat, fingers, and toes, and a slightly darker cap (Fig. 67), and upper chest and inner aspects of the limbs, reflecting a possible subspecific hybridization in areas of overlap. The *H. muelleri* that were found in Sarawak 4th Division, Ulu Selio at an elevation of 3,500 feet (FMNH 88551-60) somewhat resembles both *H. m. abbotti* and *H. m. funereus.*

Hylobates agilis F. Cuvier, 1821 Agile or dark-handed gibbon
Sumatra, south from Lake Toba, and Malay Peninsula between the Perak and Mudah rivers

Marshall and Sugardjito (1986) and Brandon-Jones *et al.* (2004) list three subspecies of *H. agilis*: *H. a. agilis* (the mountain agile gibbon); *H. a. unko* (lowland agile gibbon); and *H. a. albibarbis*. Groves (2001, 2005) lists *albibarbis* as a full species on the basis of morphological and pelage differences. Hirai *et al.* (2003, 2005) reinforce this view and I follow Groves' (2001) recommendation in this case. Based on similarities in the vocalization and some aspects of the pelage, J. T. Marshall maintains the view that the form *albibarbis* is a subspecies of *H. agilis*; an arrangement suggested earlier in Marshall and Marshall (1976) (J. T. Marshall pers. comm. 2005-06). Groves (2001, 2005) listed *unko* as a junior synonym of *H. agilis*.

With a captive weight of as little as 5.8 kg (GCC Mumma), some adult *Hylobates agilis* can be considered the smallest of the gibbons.. Males and females have very prominent orbital ridges (Griffith 1827), can be either buffish, buffish with darker underparts, brownish, reddish, blackish, or with a lighter colored lumbar region (Fig. 68). Immature through adult males and immature females have whitish brows and cheek patches, which resemble a beard (Fig. 69). The hair of the adult male's genital tuft is 50 mm long, and is generally the same color as, or slightly paler than, the body hair (Marshall and Sugardjito 1986). Starting at the chin, females begin to lose their cheek patches at approximately 6 years old, and finish their color change between 7 and 14 years old (Fig. 70). Adult females who have been housed in low light conditions, who are pregnant or lactating, or who have nutritional deficiencies, may lack the white brow and if in black pelage they could resemble *H. klossii*. The lumbar region and rump of young infants are mixed with slightly lighter coloration. *H. agilis* can have webbing between the second and third toe on the proximal phalanges (Elliot 1913) (Fig. 71). The female's great call is similar to female *H. albibarbis* and somewhat similar to the female *H. lar*.

Marshall and Sugardjito (1986) concurred with Wilson and Wilson (1977) that there is a high percentage of *Hylobates agilis* in black pelage east of the Barisan Mountains, in the swamp forests and eastern lowlands of Sumatra, and in west Malaysia, and that there is a high percentage of light-colored phase *Hylobates agilis* in the mountainous range of the Barisan Mountains, which is the native habitat of the robust black *Symphalangus syndactylus*. For this reason Marshall and Sugardjito (1986) confirmed that *Hylobates agilis unko* is located east of Barisan Mountains and west Malaysia, and *H. a. agilis* occurred in the mountainous range of west Sumatra. It is possible that sympatry with *S. syndactylus* in west Sumatra, is the reason for the occurrence of the lighter form, *H. a. agilis*.

I have also found a small but observable difference between the facial pelage of *H. agilis* in the mountains and lowlands of Sumatra and Malay Peninsula (Mootnick *et al.* 1996, A. Mootnick, in prep.). Distinct differences exist in the color and amount of white surrounding the face or on the brow in museum specimens from Sumatra and Malay Peninsula, when compared with live specimens. My preliminary notes on museum specimens indicate that elevation plays a role in the amount of white on the brow and/or cheek patches, or shade of white on the cheek patches, an aspect which has led to me to give the common names for the *Hylobates a. agilis* (mountain agile gibbon) and *H. agilis unko* (lowland agile gibbon) (Mootnick *et al.* 1996). *H. agilis* is easily determined through G-banding when compared with the chromosomes of other *Hylobates* gibbons (vanTuinen *et al.* 1999) and in C-banding analysis (Hirai *et al.* 2003).

Hylobates agilis agilis F. Cuvier, 1821 Mountain agile gibbon
Highlands of northern Malay Peninsula and western Sumatra south of Lake Toba

The pelage of *H. a. agilis* is buff, reddish-orange, reddish-brown, brown or blackish. My observations indicate that the adult males and immature males and females have white cheek patches that generally connect under the chin and brow (Fig. 72). The adult female's brow is wide and white, tapering towards the ends, and not divided in the middle (Fig. 73).

Hylobates agilis unko Lesson, 1829 Lowland agile gibbon
Lowlands of northern Malay Peninsula and eastern Sumatra south of Lake Toba

Hylobates agilis unko possesses few characteristics that reliably distinguish it from *H. a. agilis*. Based on a preliminary study, the cheek patches are creamy-white to a grizzled white, sparser than *Hylobates a. agilis*, and do not connect under the chin or brow (Fig. 74). The adult female's brow marking is thin and short and can be separated in the middle. The lumbar region is paler than the rest of the body in some *Hylobates a. unko*.

Hylobates albibarbis Lyon, 1911 Bornean white-bearded gibbon
Southwestern Borneo

First described as a subspecies of *H. muelleri* (Lyon 1911), Marshall and Sugardjito (1986) and Brandon-Jones *et al.* (2004) listed this gibbon as a subspecies of *H. agilis* (see

above). Overall, *H. albibarbis* varies in shades of light brown with a large, dark brown cap and darker brown under parts, with the lower back being buffish in color (Lyons 1911). The description that follows was compiled from museum specimens. The hands and feet vary from brown to blackish brown with darker fingers and toes. The brow is whitish and can be separated. Immature and adult males have white to creamy-white cheek patches. The chest and abdomen are dark-brown. The lower back is buff (Fig. 75). The shoulders, upper back, and from the nape to the back of the ear, vary in shades of tawny. The front portion of the sides of the face up to the front of the ear is brown. The throat varies from light to dark brown. The rump and hips vary from brown to tawny. The outer portion of the legs are tawny, and are generally darker on the inner portion. The outer portion of the arm varies from tawny to brown, and the inside of the arm is generally darker. The hair surrounding the anus is brown. The hair surrounding the female's genitals is dark brown, whereas the male's genital tuft is tawny. Because there is so much color variation in this species and since, historically, it has been misidentified with *Hylobates muelleri funereus* it would be important to confirm the species identification through its vocalizations, karyotype or DNA. The female's song has longer and slower notes when compared with the *H. a. agilis* and *H. a. unko*. Karyotyping wild-born, or captive-born individuals whose parents have been confirmed to be *H. albibarbis*, can easily distinguish this form from *H. a. agilis* and *H. a. unko* (vanTuinen *et al.* 1999; Hirai *et al.* 2003, 2005).

Hylobates lar (Linnaeus, 1771) Lar or white-handed gibbon

Marshall and Sugardjito (1986) recognized four subspecies of *Hylobates lar*: *H. lar lar* (Malayan lar gibbon); *H. lar carpenteri* (Carpenter's lar gibbon); *H. lar entelloides* (mainland lar gibbon); and *H. lar vestitus* (Sumatran lar gibbon). Ma and Wang (1986) described a fifth subspecies, *H. lar yunnanensis* (Yunnan lar gibbon). This arrangement follows Groves (2001, 2005). Adults of both sexes have white hands and feet and a complete face ring. Males and females can be dark or light in color, ranging from creamy-buff to brown to blackish. Depending on the subspecies, the hair on the head lies flat or points upward, and hair texture ranges from straight to frizzy. The great call of the female *H. lar* is somewhat similar to those of female *H. agilis* or *H. albibarbis*. The pelage of the lumbar region, rump, and outer thigh of infants are mixed with light coloration, and lighter than that of young infant *H. agilis* (Fig. 76). Some infants have been observed with a pale abdomen and chest (Fig. 77).

Hylobates lar lar (Linnaeus, 1771) Malayan lar gibbon

Central and southern Malay Peninsula and southern Thailand

Both sexes are generally dark chocolate brown in color, but approximately one-third of the population is creamy-buff (Fig. 78) (Marshall and Sugardjito 1986). The darker hair base ranges from 50–66% of the length of the hair (Groves 1972). The hair length between the shoulders ranges from 36 mm to 55 mm (Groves 1972). The genital region is darker than the body hair. The white hair on the hands and feet extends slightly past the wrist and ankle. The face ring is thin above and on the outer sides of the eyes. It widens at the bottom of the ears, and remains wider as far as the chin. A partial face ring has been observed in some specimens (Blyth 1847; Gulik 1967; Groves 1972), but without genetic testing it is difficult to determine if they are descendents of *H. agilis* or if this is a phenomenon of this subspecies.

Hylobates lar carpenteri Groves, 1968 Carpenter's lar gibbon

Northern Thailand

This subspecies has long hair, and can have more facial hair than the mainland lar gibbon (*H. l. entelloides*). Silvery base hairs give it a brownish charcoal or white-buff appearance depending on the color phase. These base hairs are deeper in color in the darker color phase, and base hairs are up to 50% of the hair length (Groves 1972). *Hylobates l. carpenteri* has a white face ring. The pubic region is similar in color to the rest of the body, with few white hairs. The white on the hands and feet can extend up to the wrists and ankles (Groves 1968). Hair length between the shoulders varies from 79 mm to103 mm (Groves 1968).

Hylobates lar entelloides I. Geoffroy St. Hilaire, 1842 Mainland lar gibbon

Central and southern Thailand, and southeastern Myanmar

Hylobates l. entelloides can be blackish, tawny, or blackish brown with a brownish chest and a trace of white hairs on the nape, with brownish buff with slight grizzling of black hairs on body, or overall buff in coloration (Fig. 79). The hair base extends to about one-third up the hair shaft (Groves 1972). Hair length between the shoulders varies from 29 mm to 56 mm (Groves 1968). The white face ring can vary in width depending on the geographical location, and is wider on the sides of the face and chin. The hands and feet are whitish and can be grizzled with the color of the body hair. A trace of the body hair color on the back of the wrist can also taper (almost forming a triangle) towards the knuckles. The black color phase of this subspecies is darker than the dark phase of *H. l. lar* or *H. lar carpenteri*. Some black color phase males have grizzled white hair in the genital tuft.

Hylobates lar vestitus Miller, 1942 Sumatran lar gibbon

Northern Sumatra, north of Lake Toba

Unlike the other lar gibbons, *H. l. vestitus* lacks a dark color phase. The Sumatran lar gibbon varies in color from red-buff, to red-brown, to light-brown, with a slightly darker crown, scapular, genital region, forearm, calf, and throat, and a paler lumbar region (Fig. 80) (Marshall and Sugardjito 1986), or white grizzling through the body. The hair length between the shoulders range from 44 mm to 60 mm (Groves 1972). The white on hands and feet has a slight grizzling of the body hair, and was observed to have the white not extending up to the wrist or the ankle, or extending past the wrist. The face ring is white and medium in size.

Hylobates lar yunnanensis Ma and Wang, 1986 Yunnan lar gibbon
South western Yunnan

Hylobates l. yunnanensis differs from the other subspecies in having the lighter base hairs extend only to 10–20% of the hair length (Ma and Wang 1986). The pelage of the pale phase is creamy in color and can have a darker tone ranging from buff to tawny buff to brownish buff on the cap, chest, legs, and outer aspects of the arms. There is a trace of brown to reddish brown hair in the genital region. The hair is longer on the scapular and shoulders. Hands and feet are white. Hair length on the upper back is 120–150 mm (Ma and Wang 1986). Brandon-Jones *et al.* (2004) point out that *H. l. yunnanensis* may be a synonym of *H. l. carpenteri.* This, one would hope, can be resolved by a comparative morphological and DNA study.

Discussion

Museum specimens provide ample material for a comparative study on species identification. Pelage coloration is genetically determined and can vary according to age, sex, or color phase. My findings indicate four genera and 14 species of gibbon. The highest diversity can be found in Yunnan, China, where there are three genera and five species. Further studies may well argue for the elevation of some subspecies to species, and there remains the possibility that new subspecies will be discovered. *Hylobates lar entelloides*, for example, has a wide distribution, from Thailand to southeastern Myanmar, and, with so much pelage variation, future studies on genetics, morphology, and vocalization may identify additional subspecies.

The *Hoolock leuconedys* and *Hylobates lar* that were observed in more northern localities had longer hair on the upper body, which could serve to protect them in the colder environment. *Nomascus c. concolor* and *N. l. leucogenys* did have slightly longer hair than has been observed in other *Nomascus* species or subspecies, but still the hair length in the upper body (especially the upper arms) is very short in comparison to the other three genera of hylobatids. Since the distribution of *Nomascus* is from southern China to southern Vietnam, one would expect to see more variation in hair length within the species in *Nomascus*. The short dense hair could be more advantageous in the higher altitudes where it could snow or in the southern region where it is hot, and at the same time protect them from mosquitoes.

Delacour (1951) described the adult male holotype of *Nomascus concolor lu* as mainly black with a gray stripe over the eye to the ear, and that the other three males that he collected were similar but also had at least a trace of gray on the cheeks. After the inspection of these four black specimens that Delacour (1951) collected, it was revealed that two of the adult males were entirely black, and one of the males was actually a subadult female going through a color transition. The photos and video of the *N. concolor lu* that I observed from the Bokeo Nature Reserve in black pelage were black without any gray on the face. In addition, since there is a hybrid zone of *N. concolor lu* and *N. l. leucogenys*, I would then suggest that the description of the adult male *N. concolor lu* needs to be revised to entirely black.

A color chart is necessary when describing the pelage of gibbons. I attempted to use color guidebooks (Smithe 1974, 1975; Munsell 1994) whenever possible, but shades varied so much even these were inadequate. If feasible, it would seem expedient to create a universal color guide specifically for the hylobatids to facilitate future comparisons.

Depending on the species, the status in the wild ranges from Critically Endangered to Least Concern, although some taxa remain Data Deficient (Eudey 1987; IUCN 2006). Some of the species and subspecies rank among the most threatened primates in the world (see Mootnick *et al*. 2006). International captive breeding and rehabilitation programs have been established to preserve the gene pool of some gibbon species (for example, for *H. moloch*: Supriatna and Manullang 1999; Supriatna 2006); unfortunately, some have proved difficult to maintain in captivity. Factors contributing to the decline of some captive gibbons include hybridization, a monogamous mating system, few population founders from the rarer species, stress (Mootnick *et al.* 2006), and behavioral abnormalities attendant with human-rearing (Mootnick and Nadler 1997).

Gibbon systematics traditionally has been controversial and confusing. One of the many purposes of rescue and breeding centers is to provide for the reproduction of gibbons, whether in captivity or once released, so that species and subspecies diversity is retained. If mentally and physically healthy gibbons are to be released into their native habitat, it is very important that they are released in the proper location with the same subspecies, and not in the range of other gibbon taxa.

Accurate visual identification of an individual gibbon may be complicated by the existence of different colors for the two sexes in some gibbon species, and the different colors within some gibbon species according to age and color phase. If our intentions are to save species from becoming extinct, it is of the utmost importance to make sure hybridization at the subspecific level does not occur in conservation programs. It is hoped that this description of gibbon coat colors will properly assist in the identification of captive and wild species and subspecies to prevent hybridization and maintain their diversity.

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Appendix I. Specimens Examined

The gibbons that were examined are listed consecutively under the localities alphabetically, and identification numbers or house name. Museum specimens are listed first.

AMNH = American Museum of Natural History, New York, USA
BMNH. ZD = Zoology Department, British Museum (Natural History), London, UK
FMNH = Field Museum of Natural History, Chicago, Illinois, USA
GCC = Gibbon Conservation Center, Santa Clarita, California, USA
IEBR = Institute of Ecology and Biological Resources, Hanoi, Vietnam
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge Massachusetts, USA
MZB = Museum Zoologicum Bogoriense, Bogor, Java, Indonesia
USNM = National Museum of Natural History, Washington, DC, USA
ZMVNU = Zoological Museum, Vietnam National University, Hanoi, Vietnam
ZRC = Zoological Reference Collection, Department of Zoology, University of Singapore, Singapore. (Formerly National Museum and formerly Raffles Museum)

Symphalangus s. syndactylus, Sumatra: Alur Purba: MZB 3107; Bukit Dulu: AMNH 102187–88, 102190; Bukit Sanggul: MZB 6455, AMNH 106582–83; Gunung Dempo: MZB 6454, 6467, AMNH 106581; Lubuk Linggau: MZB 6465, AMNH 102186, 102193–97; Muara Beliti: AMNH 10292; Muara Dua AMNH 102720–21, 102725–27 102729; Teluk Aru: USNM 143577–81; Teluk Tapanuli: ZRC 4-711. GCC: Karenina, Olive-Oyl, Rumi, Saphire.

Symphalangus s. continentis, Malay Peninsula: Kledang Hill: 4-701-2; Kuala Tahan: ZRC 4-704; Selangor Pass: USNM 171981; Wray's Camp: ZRC 4-703. GCC: Ella, Fatima, Kino.

Symphalangus syndactylus, Range unknown: FMNH 60340, 60555, 95842, 99366; GCC: Amos, Holly, Marlow, Montgomery, Raub.

Nomascus concolor concolor, Vietnam: Chapa, Tonkin FMNH 39149-50, MCZ 38114–16.

Nomascus concolor lu, Laos: Ban Nam Kaueng: AMNH 148262, MCZ 46288–89; Khao Tham Phra: USNM 296921.

Nomascus n. nasutus, Vietnam: Tam Dao District: ZMVNU 3.101.5; Thai Nguyen Province ZMVNU 3.55.0, 3.56.0; Trung Khanh District: IEBR 48, 50, 51.

Nomascus l. leucogenys, Laos: Lao Fou Tahai: FMNH 31760; Muong Yo: FMNH 31769–70; Phong Saly: USNM 240490–92. Vietnam: Bai Thuong Thanh Hoa: ZMVNU 3.53.2; Chi Ne District: ZMVNU 3.100.4; Dung Tan Ky Nghi: IEBR 563; Ho- Xuan: USNM 39151; Lai Chau: FMNH 31761, 31768, IEBR D2, K53; Muong Moun: USNM 31771; Tenky District: IEBR 528, 564, 736; Vuon Ma Trang: ZMVNU 3.102.0. GCC: Asia, Dexter, Jane, Parker, Ricky, Sasha, St. Paddy, Vok. Moorpark College: Samantha.

Nomascus leucogenys siki, Laos: Nakai: AMNH 87251; Vietnam: Quy Chau District: IEBR 503, 695-96.

Nomascus gabriellae × *Nomascus leucogenys siki*, natural hybrid: GCC: Kim Khi.

Nomascus gabriellae, Laos: Plateau Bolovens: AMNH 87252. Vietnam: Ban Methuot: FMNH 46495, 46497, 46499–501, 46503, 46505–06, 46508; Dalat: USNM 320789; Gialai Kontum: ZMVNU 733–35. GCC: Lulu, Alfalfa. Los Angeles Zoo: Andrea, China, Enik, Robin, Tina, Victor, Yang.

Hoolock hoolock, India: Bara Hapjan: USNM 257987; Changchang: AMNH 83419, 83425–26; Khasi Hills: AMNH 171169; Lushai Hills: FMNH 75881. Myanmar: Chenga Hka: AMNH 112690; Dagung Hka: AMNH 112954; Haibum: AMNH 112385–86, 112694, 112698–99, 112701, 112707; Hkamti: AMNH 112704; Linhpa West: AMNH 112709; Mt. Victoria: AMNH 163633. Bangladesh: Natural History Museum Dhaka Zoological Gardens: Mounted specimen; one adult male and female. GCC: Alfa, Beta

Hoolock leuconedys, Myanmar: Dalu: AMNH 112983; Gokteik: USNM 257988; Gora: AMNH 112982; Limpa east bank: 112708; Mansun: AMNH 112678; AMNH 25 miles west of Myithyina 279146; N'bunghku: AMNH 112680–81; Phawzaw, east bank: AMNH 112713; Tawman: AMNH 112673; Yunnan: Homushu Pass: AMNH 43065, 43068. Range unknown: GCC: Arthur, Betty, Chester, Drew, Fia, Gelson, U Maung Manug.

Hylobates klossii, Mentawei Islands: north Pagai 121675–77; south Pagai: USNM 121689, 121679, FMNH 43333; Siberut: USNM 252308–11; Sipora: USNM 252307. Gibbon Foundation, Indonesia: Nanam. Taman Safari, Indonesia: Ani; Pusat Primata Schmutzer: December 2003. One adult female and two immatures.

Hylobates pileatus, Thailand: Khlong Yai: ZRC 4-665, USNM 257686; Laem Ngop: USNM 201555; Nongkhor: ZRC 4-661, 4-662, USNM 241018–19; Cambodia: Kiri Rom Plateau: USNM: 321549. Distribution unknown: FMNH 53750; GCC: Anasazi, Birute, Cambio, Chewy, Geebone, Harry, Ila, Jitka, Josh, JR, Kanako, Kokopelli, Louis, Lula, Maggie, Mateus-Binti. Truman, Tuk, Valentina.

Hylobates moloch, Java: Gunung Salak: MZB 3349, 6416–17; Karang Gardang: MZB 2453; Purwakarta: MZB 6418; Slamet: MZB 3320–22; Sumedang: AMNH 101807. MZB Location unknown: 6419–20, 6429, 11140, 11145. GCC: Chilibi, Chloe, Isaac, Isabella, Ivan, Khusus, Leon, Ling, Lionel, Medena, Reg, Shelby, Ushko.

Hylobates muelleri muelleri, Borneo: Klumpang Bay: FMNH 41514; GCC: Bob.

Hylobates muelleri funereus, Borneo: Bukit Selidang (Sarawak 3rd Division 4000'): FMNH 88567; Kalabakan, Sungai Tibas Camp: FMNH 85925; Kinabalu: FMNH 8370; Pa Barang: FMNH 88263, 88266; Sandakan, 8 miles west: 33542–44; Sandakan, 5 miles north: FMNH 68681; Sungai Kretam Kecil: FMNH 68674–80; Ulu Selio (Sarawak 4th Division 3500'): FMNH 88552–54, 88556–57, 88559–60; Usun Apau Padang: FMNH 88566. Distribution unknown: GCC: Abbey.

Hylobates muelleri abbotti, Borneo: Perbuah: MZB 6570–71, AMNH 106766, 106779, 107102; Poch Mountain: FMNH 8369; Sarawak: FMNH 1171;

Hylobates a. agilis, (elevation 455–1,500 m) Malay Peninsula: Batu Tugoh: BMNH ZD.1955.1484, ZRC 4-554–56. Maxwell's Hill: BMNH ZD.1955.1487. Tea Garden, Larut Hills: BMNH ZD.1955.1485. Sumatra: Bukit Sanggul: AMNH 106570–76, 106578–80, 106672, 106675–79, 18836. Distribution unknown: GCC: Mumma, Sonny, Shorty.

Hylobates agilis, Since the seconds were not given for the coordinates, the elevations could vary from 21–568 m for some of the below listed gibbons. These locations were next to river basins and mountainous areas, or mountainous areas near a bay. Sumatra: Lampung: MZB 6438 (facial pelage coloration resembles *H. agilis unko)*; Muara Dua: AMNH 102470–74, 102771–79 (facial pelage coloration varies considerably within this location; AMNH catalog lists Muara Dua at 100 m. Muara Dua has a river basin next to a mountainous area); Tapanuli Bay: USNM 114499–501 (facial pelage coloration resembles *H. agilis unko)*; Teluk Betong: FMNH 14804 (brow was difficult to detect, next to the buff pelage).

Hylobates agilis unko, (7–200 m) Malay Peninsula: Tandjong Autu: BMNH ZD.1955.1486; Ulu Ijok: BMNH ZD.1934.7.18.9, 1934.7.18.11; Ulu Selama: ZRC 4-557. Sumatra: Babat: MZB 6435, 6437, 6441; Kluang: MZB 6434, 6436; Kota Pinang: ZRC 4-558–60; Kayutanam, Palembang: MZB 6440; Muara Beliti: AMNH 102161–62, 102199; USNM 102161–62, 102199; Muara Enim: ZRC 191 (facial pelage coloration resembles *H. a. agilis)*; Muara Lakitan: AMNH 102198; Pan Ji, Teluk: ZRC 4-562191 (facial pelage coloration resembles *H. a. agilis)*; Sekayu: MZB 6439; Selat Rupat: USNM 143572–76; Siak Kecil (6 miles up): USNM 144089, 144091–92; Siak Kecil (30 miles up): USNM 144090; Sungei Inderagiri: USNM 113176–80; Sungei Kateman: USNM 123151–55; Teluk Tarisan: USNM 141157–59. Distribution unknown: GCC: Kingfisher, Homer, Lulu, Elaine.

Hylobates albibarbis, Borneo: Batu Jurong: USNM 153797–99, Matan River: USNM 145328–29, Parit, Sungei Cempaga: AMNH 103441–46, 103449–56. Riam: AMNH 106053,106130, Sukadana: USNM 145326; Sungei Kendawangan: USNM 153800–01. GCC: Jackie.

Hylobates lar lar, West Malaysia, Jambu Luang: USNM 112710–11; Johore, Jambu Luang: USNM 112711; Pahang State including Labatuah, Rurpin River: USNM 115501–02; Selangor: USNM 171982.

Hylobates lar carpenteri, Thailand, Chiang Mai: Ban Mae Lamao: 99754–56; Ban Na Muang: USNM 307751; Dansai: USNM 307754; Mae Sariang: FMNH 99763–64;

Hylobates lar entelloides, Myanmar: Tenassarim, Balik River: USNM 111988; Bankachon: FMNH 828821–22; Toak Plateau: AMNH 54663, 54671. Thailand, Kampaengphet: Ban Nam Lai Tai:

FMNH 99759; Ban Kerng Chada: FMNH 99743; Katataek: FMNH 99746–49; Khlong Suan Mak: FMNH 99760–62; Khlong Tawai: FMNH 99750–51; Ko Kaew: 99752–53; Sisawat District (Baw Ngam): FMNH 99736, 99739–41; Wang Phato: FMNH 99744–45. GCC: Chan Chan, Judy.

Hylobates lar vestitus, Sumatra: Alur Purba: MZB 3106; Kungke: USNM 271047; Pulau Munteh-Pendeng: MZB 6448; Teluk Aru: USNM 143569–70.

Hylobates lar yunnanensis, Yunnan: Nam Ting River: FMNH 39382; AMNH 43063–64.

Hylobates lar, Distribution unknown: FMNH: 44740; GCC: Ayellette, Blonde, Dagwood, Hazel Nut, Mandalay, Number 2, Spanky.

Figure 1. *Hylobates pileatus* (pileated gibbon) adult female "JR" and 6.5 week old female "Jitka", GCC. Photo by Erin Bell.

Figure 3. *Symphalangus syndactylus continentis* (Malaysian siamang) adult male "Kino", GCC. Photo by Clare Cunningham.

Figure 2. *Symphalangus syndactylus continentis* (Malaysian siamang) adult male "Kino", Gibbon Conservation Center (GCC), California. Photo by Alan Mootnick.

Figure 4. *Symphalangus syndactylus continentis* (Malaysian siamang) adult male "Kino", GCC. Syndactyly of the second and third toes. Photo by John Williams.

Figure 5. *Symphalangus syndactylus continentis* (Malaysian siamang) immature male "Valentino", Cleveland Amory's Black Beauty Ranch. Syndactyly of the second and third toes extending up to the distal interphalangeal joint. Photo by Lee Theisen-Watt.

Figure 6. *Symphalangus s. syndactylus* (Sumatran siamang) adult female "Rumi", GCC. Webbing between fourth and fifth toes. Photo by John Williams.

Figure 7. *Symphalangus s. syndactylus* (Sumatran siamang) adult female "Ebony", Twycross Zoo, England. Photo by Rod Williams.

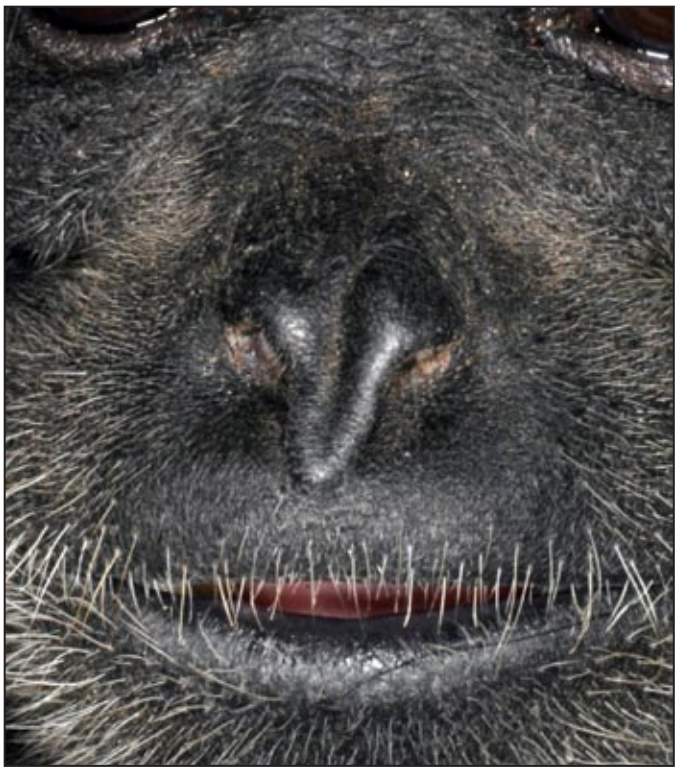

Figure 8. *Symphalangus s. syndactylus* (Sumatran siamang) adult female "Karenina", GCC. Tapering of nose and medial sagittal groove. Photo by John Williams.

Figure 9. *Symphalangus syndactylus continentis* (Malaysian siamang) adult male "Kino", Close-up of the nose. Compare with Fig. 8. GCC. Photo by John Williams.

Figure 10. *Nomascus l. leucogenys* (northern white-cheeked gibbon) adult female "Ricky", GCC. Photo by Alan Mootnick.

Figure 11. *Nomascus l. leucogenys* (northern white-cheeked gibbon) adult female "Ricky", 3 week old female "Parker", GCC. Photo by Alan Mootnick.

Figure 12. *Nomascus l. leucogenys* (northern white-cheeked gibbon) adult female "Ricky", 7 month old male "Dexter", GCC. Photo by Jim Zuckerman.

Figure 13. *Nomascus l. leucogenys* (northern white-cheeked gibbon) adult female "Ricky", 18 month old male "Dexter", GCC. Photo by Alan Mootnick.

Figure 15. *Nomascus c. concolor* (Tonkin black-crested gibbon) adult female "Hong-Hong", Gejiu Zoo, China. 3 September 1990. Photo by Thomas Geissmann.

Figure 14. *Nomascus c. concolor* (Tonkin black-crested gibbon) adult male "Zombie", Twycross Zoo, England. Photo by Elliott Haimoff.

Figure 16. *Nomascus concolor lu* (Laotian black-crested gibbon) adult female, Bokeo Nature Reserve. Photo permission: Jean-Francois Reumaux.

Figure 17. *Nomascus concolor lu* (Laotian black-crested gibbon) immature, Bokeo Nature Reserve. Photo permission: Jean-Francois Reumaux.

Figure 18. *Nomascus concolor lu* (Laotian black-crested gibbon) adult male, photo was reproduced from a video taken in the Bokeo Nature Reserve. Photo permission: Jean-Francois Reumaux.

Figure 19. *Nomascus concolor lu* (Laotian black-crested gibbon) adult female and infant, photo was reproduced from a video taken in the Bokeo Nature Reserve. Photo permission: Jean-Francois Reumaux.

Figure 20. *Nomascus concolor lu* (Laotian black-crested gibbon) adult male, MCZ 46289. Photo by Annie Lussier and Peter Weinberg, Museum of Comparative Zoology and Harvard University.

Figure 21. *Nomascus concolor lu* (Laotian black-crested gibbon) adult female, MCZ 46288. Photo by Annie Lussier and Peter Weinberg, Museum of Comparative Zoology and Harvard University.

Figure 22. *Nomascus concolor lu* (Laotian black-crested gibbon) adult female, MCZ 46288. Photo by Annie Lussier and Peter Weinberg, Museum of Comparative Zoology and Harvard University.

Figure 23. *Nomascus concolor lu* (Laotian black-crested gibbon) adult female and infant, photo was reproduced from a video taken in the Bokeo Nature Reserve. Photo permission: Jean-Francois Reumaux.

Figure 24. *Nomascus concolor lu* (Laotian black-crested gibbon) subadult, AMNH 148262. Photo permission: Jean Spence, American Museum of Natural History.

Figure 25. *Nomascus leucogenys siki* (southern white-cheeked gibbon) adult female "Fany", 1 year 10 month old male "Tai Chi", Zoo Mulhouse. June 2004. Photo by David Gomis.

Figure 26. *Nomascus n. nasutus* (Cao Vit black-crested gibbon) juvenile female "Patzi" and juvenile male *Nomascus leucogenys siki* "Mohle", Berlin Tierpark, Germany. 1963. Photo from archive of Tierpark Berlin.

Figure 27. *Nomascus n. nasutus* (Cao Vit black-crested gibbon) infant female "Patzi", Berlin Tierpark. 1962. Photo from archive of Tierpark Berlin.

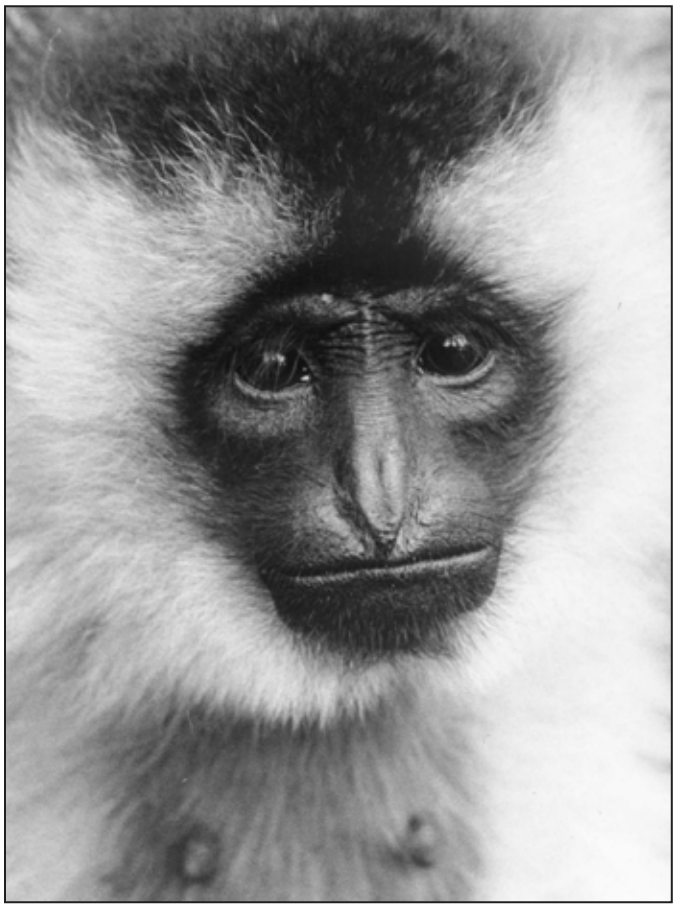

Figure 28. *Nomascus n. nasutus* (Cao Vit black-crested gibbon) adult female "Patzi", Berlin Tierpark. August 1970. Photo from archive of Tierpark Berlin.

Figure 29. *Nomascus n. nasutus* (Cao Vit black-crested gibbon) adult female "Patzi", Berlin Tierpark. 1972. Photo from archive of Tierpark Berlin.

Figure 31. *Nomascus nasutus hainanus* (Hainan black-crested gibbon) adult female and infant. Hainan. Photo by Bawangling National Nature Reserve staff.

Figure 30. *Nomascus nasutus hainanus* (Hainan black-crested gibbon) adult male, Hainan, China. Photo by Bawangling National Nature Reserve staff.

Figure 32. *Nomascus l. leucogenys* (northern white-cheeked gibbon) female left "Ricky", male right "Vok", GCC. Photo by Jim Zuckerman.

Figure 33. *Nomascus leucogenys siki* (southern white-cheeked gibbon) subadult male "Pimkie", Zoo Mulhouse, France. Photo by Aline Drouin.

Figure 35. *Nomascus leucogenys siki* × *Nomascus gabriellae* (natural hybrid) adult female "Demi", Zoo Mulhouse. Photo by Aline Drouin.

Figure 34. *Nomascus leucogenys siki* × *Nomascus gabriellae* (wild-born hybrid) juvenile female "Kim Khi", GCC. Photo by Alan Mootnick.

Figure 36. *Nomascus gabriellae* (buff-cheeked gibbon) adult female left "Bahmetoo", adult male right "Koo", Los Angeles Zoo, California. Photo by Alan Mootnick.

Figure 37. *Hoolock hoolock* (western hoolock) neonate. Borajan Reserve Forest, Assam. Photo by Kashmira Kakati.

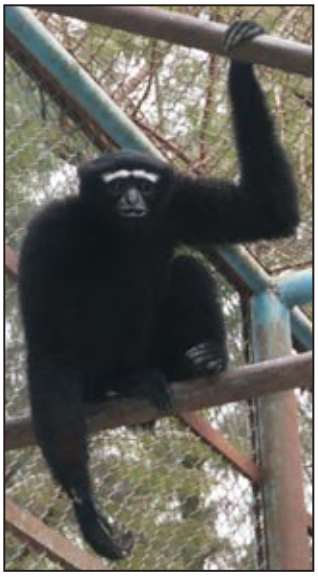

Figure 39. *Hoolock hoolock* (western hoolock) adult male "Turja" Dhaka Zoo. Bangladesh. Photo by Alan Mootnick.

Figure 38. *Hoolock hoolock* (western hoolock) subadult Alipore Zoo. India. Photo by Mike Dee.

Figure 40. *Hoolock hoolock* (western hoolock) adult female "Lucky" and 14 month old male "Sugrib" Dhaka Zoo. Bangladesh. Photo by Alan Mootnick.

Figure 41. *Hoolock hoolock* (western hoolock) adult female "Alfa",GCC. Photo by Alan Mootnick.

Figure 42. *Hoolock hoolock* (western hoolock) adult female "Alfa", GCC. Photo by Alan Mootnick.

Figure 43. *Hoolock leuconedys* (eastern hoolock) adult male "Arthur" and adult female "Betty", GCC. Photo by Erin Bell.

Figure 44. *Hoolock leuconedys* (eastern hoolock) adult male "Arthur" and adult female "Betty", GCC. Photo by Erin Bell.

Figure 45. *Hoolock leuconedys* (eastern hoolock) adult female "Drew", GCC. Photo by Erin Bell.

Figure 46. *Hoolock leuconedys* (eastern hoolock) juvenile female left "Drew", juvenile male right "Chester", GCC. Photo by Alan Mootnick.

Figure 47. *Hylobates klossii* (Kloss' gibbon) adult female, Lion County Safari, California. Photo by staff photographer.

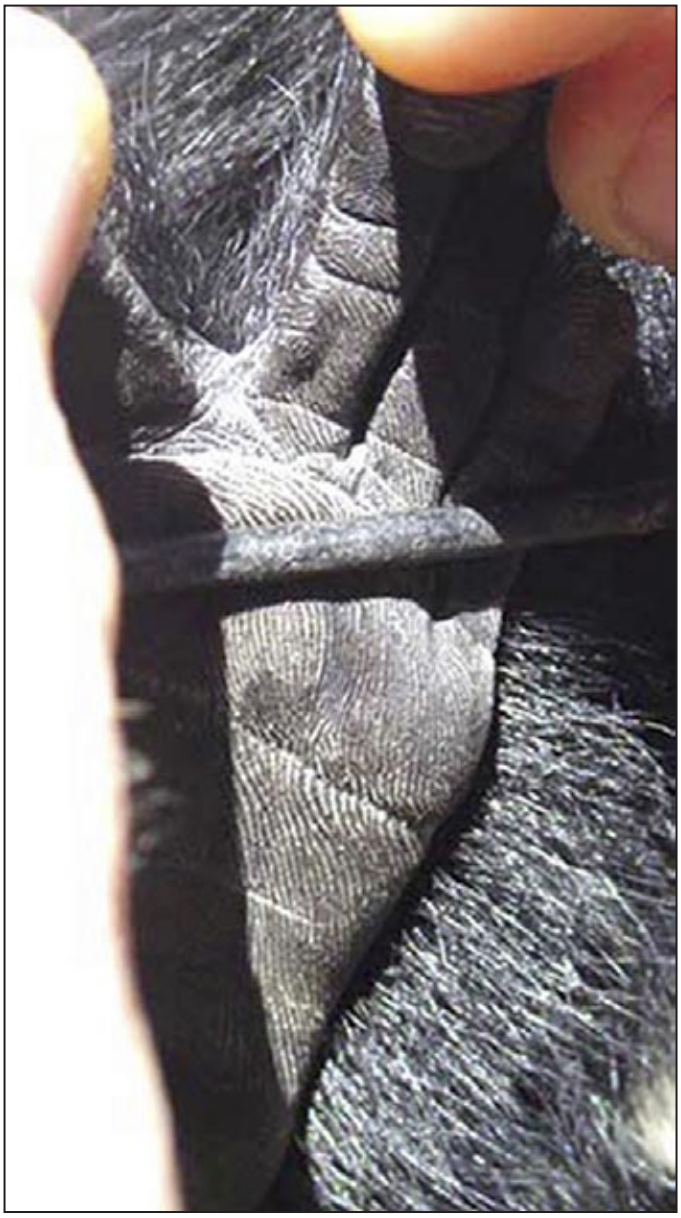

Figure 48. *Hylobates klossii* (Kloss' gibbon) female "Nanam", Gibbon Foundation, Indonesia. Slight interdigital webbing between the second and third digits. Photo by David Broadhurst.

Figure 49. *Hylobates klossii* (Kloss' gibbon) infant, South Pagai. Photo by Richard Tenaza.

Figure 50. *Hylobates klossii* (Kloss' gibbon) 8 yr old female "Nanam", Gibbon Foundation, Indonesia. Photo by Micca Rogers.

Figure 51. *Hylobates pileatus* (pileated gibbon) adult male "Birute", GCC. Photo by Alan Mootnick.

Figure 52. *Hylobates pileatus* (pileated gibbon) 52 month old female "Kanako", GCC. Photo by Erin Bell.

Figure 53. *Hylobates pileatus* (pileated gibbon) adult female "JR" in first trimester, 23 month old male "Truman", GCC. Photo by Erin Bell.

Figure 55. *Hylobates pileatus* (pileated gibbon) adult female "Tuk", GCC. Photo by Erin Bell.

Figure 54. *Hylobates pileatus* (pileated gibbon) adult female "JR", 1 day old female "Jitka", GCC. Photo by Erin Bell.

Figure 56. *Hylobates pileatus* (pileated gibbon) adult female "JR", 32 month old male "Truman", GCC. Photo by Erin Bell.

Figure 57. *Hylobates pileatus* (pileated gibbon) 4 yr 6 mo male "Kokopelli", GCC. Photo by Alan Mootnick.

Figure 58. *Hylobates pileatus* (pileated gibbon) 5 year 7 month old male "Mateas Binti", GCC. Photo by Erin Bell.

Figure 59. *Hylobates moloch* (Javan gibbon) adult female "Chloe", 1 day old male "Lionel", GCC. Photo by Alan Mootnick.

Figure 60. *Hylobates moloch* (Javan gibbon) adult male "Chilibi", GCC. Photo by Suzanne Kokel.

Figure 61. *Hylobates moloch* (Javan gibbon) adult female "Chloe", 6 month old male "Reg", GCC. Photo by Alan Mootnick.

Figure 62. *Hylobates moloch* (Javan gibbon) 3 yr old male "Lionel", 6 year 10 month old male "Isaac", GCC. Photo by Clare Cunningham.

Figure 63. *Hylobates m. muelleri* (eastern Müller's gibbon) adult female "Dongkey", 1.5 month old infant, Kalaweit. Photo by Wandy.

Figure 64. *Hylobates m. muelleri* (eastern Müller's gibbon) subadult male, Taman Safari, Indonesia. Photo by Alan Mootnick.

Figure 65. *Hylobates muelleri funereus* (northern Müller's gibbon) adult female "Abbey", GCC. Photo by Alan Mootnick.

Figure 66. *Hylobates muelleri abbotti* (Abbott's Müller's gibbon) adult female and infant, Singapore Zoo. Photo by Roland Wirth.

Figure 67. *Hylobates muelleri abbotti* (Abbott's Müller's gibbon) adult male "Hylo", Edinburgh Zoo, Great Britain. Photo by Elliott Haimoff.

Figure 68. *Hylobates agilis* (agile gibbon) adult female and infant, Singapore Zoo. Photo by staff photographer.

Figure 69. *Hylobates a. agilis* (mountain agile gibbon) juvenile female "Ruby Baby", GCC. Photo by Alan Mootnick.

Figure 70. *Hylobates a. agilis* (mountain agile gibbon) 12 year 4 month old female "Ruby Baby" and 6 day old male "Milton", GCC. Photo by Donald Johanson.

Figure 71. *Hylobates a. agilis* (mountain agile gibbon) adult male "Bebopen Baby", GCC. Photo by John Williams.

Figure 72. *Hylobates a. agilis* (mountain agile gibbon) adult male "Sonny", GCC. Photo by Suzanne Kokel.

Figure 73. *Hylobates a. agilis* (mountain agile gibbon) adult female "Mumma" and infant male "Albert", GCC. Photo by Shawn Tanaka.

Figure 74. *Hylobates agilis unko* (lowland agile gibbon) adult male "Homer", GCC. Photo by Alan Mootnick.

Figure 75. *Hylobates albibarbis* (white-bearded gibbon) adult female "Jackie", Valley Zoo, Canada. Photo by staff photographer.

Figure 76. *Hylobates lar* (lar gibbon) (brown color phase) 15 month old female "Princess", Cleveland Amory's Black Beauty Ranch, Texas. Photo by Lee Theisen-Watt.

Figure 77. *Hylobates lar* (lar gibbon) (brown color phase) 15 month old female "Princess", Cleveland Amory's Black Beauty Ranch. Photo by Lee Theisen-Watt.

Figure 78. *Hylobates l. lar* (Malaysian lar gibbon) subadult male, Zoo Negara, Malaysia. Photo by staff photographer.

Figure 79. *Hylobates lar entelloides* (Thai lar gibbon) (born in northeast Thailand) adult female "Judy", GCC. Photo by Alan Mootnick.

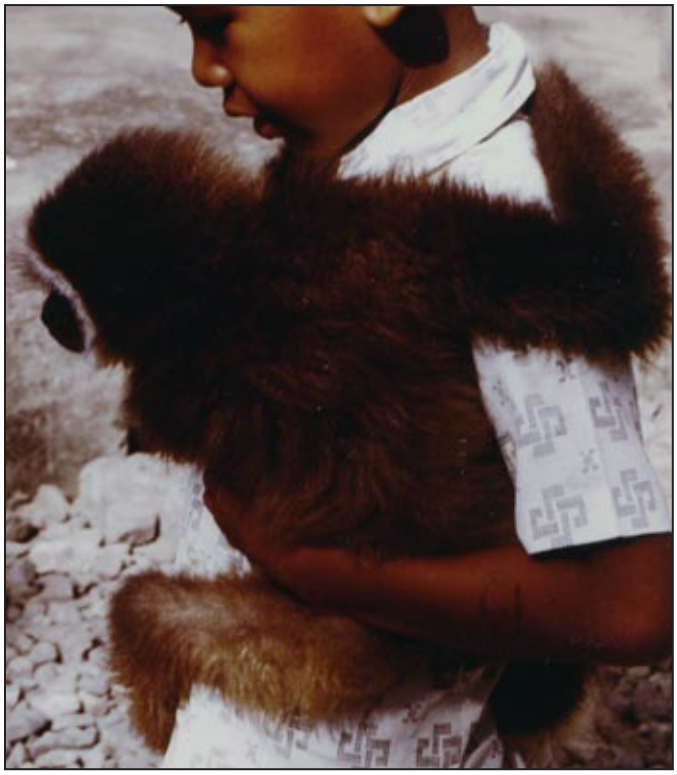

Figure 80. *Hylobates lar vestitus* (Sumatran lar gibbon) juvenile, Tapaktuan, Indonesia. Photo by Elsie Marshall.