

# THE GIBBONS

## **DEVELOPMENTS IN PRIMATOLOGY: PROGRESS AND PROSPECTS**

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# THE GIBBONS

New Perspectives on Small Ape Socioecology  
and Population Biology

Edited by

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# Foreword

It is a great honor to be asked to introduce this exciting new volume, having been heavily involved in the first comprehensive synthesis in the early 1980s. Gibbons are the most enthralling of primates. On the one hand, they are the most appealing animals, with their upright posture and body shape, facial markings, dramatic arm-swinging locomotion and suspensory postures, and devastating duets; on the other hand, the small apes are the most diverse, hence biologically valuable and informative, of our closest relatives.

It is hard for me to believe that it is 40 years to the month since I first set foot on the Malay Peninsula to start my doctoral study of the siamang. I am very proud to have followed in the footsteps of the great pioneer of primate field study, Clarence Ray Carpenter (CR or Ray, who I was fortunate to meet twice, in Pennsylvania and in Zurich), first in Central America (in 1967) and then in Southeast Asia. It is 75 years since he studied howler monkeys on Barro Colorado Island in the Panama Canal Zone. It is 70 years since he studied the white-handed gibbon in Thailand.

Ray was a remarkable man for initiating this kind of study and for doing it so well, so perceptively. Perhaps because the howler population had increased markedly over 30 years, I was able to make an original contribution to the understanding of the role of dawn calls in the spacing of groups, showing they avoided their neighbors in any month and lived in overlapping home ranges, that they were not territorial in the classic sense. By contrast, almost every time I thought I had discovered something new about gibbon behavior, I found that if Ray had not seen it, he suggested that it might happen!

The only other student of gibbon behavior was John Ellefson, who studied the white-handed gibbon in coastal forest of east Johore, West Malaysia, in the early 1960s. He produced some excellent results, but few of his data are presented in a manner that allowed full comparison with other studies. I was fortunate to encounter him in the redwoods of California before heading for Malaysia, where I met Naoki Koyama, from the Primate Research Institute, Kyoto, who was tackling the impossible task of studying siamang in the rugged terrain of Fraser's Hill. Thus, I inherited a framework of gibbon socioecology based on monogamy, territoriality, frugivory, suspensory behavior, and

duetting (loud melodic group calls/songs), on which we have built over the years.

Susan Lappan and Danielle J. Whittaker are to be congratulated on their very real achievement of bringing together such a breadth and wealth of new information on gibbon biology, spread over two IPS Congresses. There is an impressive blend of biogeography and phylogeny, diets and community ecology, ecology and social organization, mating systems and reproductive biology, and conservation biology. The lack of material on anatomy was a deliberate decision, because it has been dealt with previously, especially in the 1984 synthesis. Readers are reminded of this first conference and book on gibbon biology. Schloss Reisenburg, the castle on the Danube near Ulm, was an amazing and stimulating venue for our very productive conference in 1980, away from the IPS Congress in Florence (which thankfully rejected our symposium proposal, even as a satellite event!). The more formal sessions in the castle lecture room were augmented by genuine round-table discussions, in the turrets close to fridges full of German beer and wine! These sessions, going on late into the night, were very productive in reaching consensus.

The editors' introductory chapter on small ape diversity and the importance of population-level studies sets out clearly the scope and contents of the book. Quantifying the role of gibbons in seed dispersal is a major advance. Gibbons may live in small territories, but they are more effective in dispersal than those traveling greater distances, often depositing seeds onto unsuitable ground. I am reassured that this intensive 'farming' of the forest is most effective, especially in the light of numerous tree-falls and such opportunities for natural forest regeneration.

Perhaps the most exciting new development is the collection of DNA by noninvasive methods to determine genetic relationships within and between gibbon families, particularly to identify paternity. This is an essential aid to understanding the more complex social systems now being described. We will have to await the publication of such results. Systematics and taxonomy is another area with a current flurry of activity, which should soon see the light of day elsewhere.

I am reminded of the conflict generated by the novel use of molecular evidence 30 years ago in defining hominoid relationships and evolution. While paleontologists and anatomists claimed that the ape-human separation was about 14–12 Mya, the molecular biologists suggested 5 Mya, but they had not allowed for increased generation time. The compromise between the two disciplines was resolved at 7–9 Mya, corresponding with the major gap in the fossil record. The DNA story, of closest affinity between African apes and humans, has reawakened the major reservation in those who have shown that ancestral Asian apes share derived morphological features, incompatible with the molecular evidence. I think we may be missing something with the current obsession with the genotype, rather than the phenotype. I live in hope that it will be shown eventually that we are descended from the lovely Asian apes, rather than those unattractive and promiscuous African apes with swollen bottoms!

I also want to caution against ‘swinging’ too far away from the monogamy and territoriality as originally assigned to gibbons. I am very happy to acknowledge the flexibility that it is entirely appropriate to assign to apes and their social systems, and the importance of long-term studies. The fact of the matter is that, in the humid tropics at least (the Sundaic region of the Oriental realm), monogamous families in territories are the norm, at least for the lifetime of the individuals concerned. I have seen this over 20 years in both Peninsular Malaysia and Indonesian Borneo, and heard of it elsewhere. The exceptions now being encountered more frequently and described more forcefully seem to me to be related clearly to isolated, disturbed, or fragmented habitats, and the various problems of overcrowding or imbalanced sex ratios associated with that. Extra-pair copulations, polygyny, and polyandry are fascinating reflections of the abilities and social flexibility of gibbons, and they need to be documented fully and interpreted carefully, without rejecting the key, basic, socioecological adaptations, which separated gibbons from orangutans, langurs, and macaques.

Still more species and subspecies of gibbons are being described, some very endangered, especially in southern China (including Hainan), northern Vietnam, western Java, Bangladesh/Assam, and, probably, Myanmar. All are threatened, some critically. Continuing to publicize and promote action to resolve such crises is urgently needed. The classification of the gibbons of Borneo, in relation to those of Sumatra and Malaya, needs to be resolved. What are the true identities of the species and subspecies? Are agile and Mueller’s gibbons one species or several?

Thus, I commend you to this feast of new information and discussion on so many aspects of gibbon biology, so well assimilated by Susan and Danielle. I hope that it will inspire continued research and the quest for understanding these, the most important of all, primates!

Cambridge, UK

David J. Chivers

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**Part I**  
**Introduction**



# Chapter 1

## The Diversity of Small Apes and the Importance of Population-Level Studies

Danielle J. Whittaker and Susan Lappan

Most primatologists, biologists, and laypeople agree that gibbons, with their incredible acrobatic displays and haunting duets, are absolutely marvelous animals. For all of their beauty and grace, however, they have received relatively little attention from the scientific community and the public alike. This volume is an attempt to begin addressing this problem by summarizing the progress of gibbon studies to date, identifying the key areas for future research, and cautioning against the belief that we already know everything worth knowing about gibbons.

Over two decades have passed since the publication of the seminal volume *The Lesser Apes: Evolutionary and Behavioural Biology* (Preuschoft et al. 1984). That book was based on a conference, the first of its kind focusing on gibbons, held in 1980 in Ulm, Germany. *The Lesser Apes* comprises a thorough summary of progress in gibbon studies up to that time, focusing on conservation, functional morphology, ecology, social behavior, and evolutionary biology. The contributors identified several areas that required additional study, including calls and songs; the basic behavioral biology of little understood species (*Hoolock* spp., *Nomascus* spp.); molecular phylogenetic studies, particularly of *Hoolock* and *Hylobates klossii*; and the fossil record. In the decades since the publication of *The Lesser Apes*, progress toward many of these goals has been made.

Twenty years later, gibbonologists gathered again, at two International Primatological Society symposia: “Gibbon Diversity and Conservation” in Beijing in 2002 and “Wild Gibbons as Members of Populations” in Torino in 2004. This book is the product of those two symposia and has been assembled in recognition of the fact that a great deal of progress has been made in the field since 1984, allowing new perspectives on gibbon socioecology.

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## Gibbon Diversity

A number of changes in gibbon taxonomy have been proposed in recent years. The four subgenera have been raised to genus level (*Hylobates*, *Nomascus*, *Symphalangus*, and *Hoolock* [formerly *Bunopithecus*]). Additional species have been identified within *Nomascus*. Also, within *Hylobates*, some evidence (e.g., Hirai et al. this volume) suggests that the Bornean taxon generally classified as *H. agilis albibarbis* may in fact be sufficiently distinctive from *H. agilis* and *H. muelleri* to be classified as a full species. Though not all researchers agree on this classification, and further study is clearly warranted, we have used the name *H. albibarbis* throughout this volume for the sake of consistency; its use by individual authors is at the editors' request and does not necessarily imply acceptance of this taxonomy. Helen Chatterjee (Chapter 2) reviews the progress to date in understanding gibbon evolution and biogeography, while Nina Jablonski (Chapter 7) discusses the role of environmental change in the evolution of gibbons. Robert Dallmann and Thomas Geissmann (Chapter 6), Hirohisa Hirai et al. (Chapter 3), Sally Keith et al. (Chapter 4), and Danielle Whittaker (Chapter 5) examine genetic and vocal evidence for and against divergence within species.

In the past two decades, our knowledge of the behavior, ecology, and evolution of gibbons has been greatly increased by additional studies on previously un- or under-studied taxa, with an emphasis on field studies. In particular, researchers have given more attention to the crested gibbons (*Nomascus* spp.: e.g., Jiang et al. 1999; Fan et al. 2006; Konrad and Geissmann 2006), hoolock gibbons (*Hoolock* spp.: e.g., Choudhury 1991; Islam and Feeroz 1992; Ahsan 1995), the Kloss's gibbon (*Hylobates klossii*: Whittaker 2005a, b), and the Javan or silvery gibbon (*H. moloch*: Andayani et al. 2001; Geissmann and Nijman 2006). Work has also continued on previously studied species (e.g., *H. lar*, *H. agilis*, *Symphalangus syndactylus*), with particular attention to understanding variation in group compositions and social and mating behavior (e.g., Brockelman et al. 1998; Reichard 2003; Lappan 2007), as well as the ecological role of gibbons in tropical forests (McConkey et al. 2002; McConkey et al. 2003). A number of long-term studies have been conducted at field sites across the gibbon distribution range, including but not limited to Khao Yai National Park in Thailand, 1979–present; Ketambe, Sumatra, Indonesia, 1980–1999; Way Canguk Research Station, Sumatra, Indonesia, 1997–present; Barito Ulu, Kalimantan, Indonesia, 1988–present; Legok Heulang Research Station, Java, Indonesia, 1994–present; and Borajan Reserve, Assam, India 1995–present. This emphasis on long-term study has revealed a great deal of previously unanticipated complexity in the social lives of gibbons. Such perspectives were impossible in shorter projects, which only gave us a “snapshot” of the lifestyles of these long-lived primates.

## **Gibbon Socioecology: Flexibility**

The first generation of intrepid researchers to study gibbons in the field described small, nuclear families, with both adults behaving as “paragons of fidelity” (Fuentes 1999, 2000): the very poster children for monogamy in the primate world. Ongoing field research, however, has on one hand, confirmed that unimale unifemale grouping is the most common pattern in all gibbon species studied to date, yet, on the other hand, it has also made clear that much more lies under the surface of gibbon social and mating systems. Far from the previously imagined enduring and faithful male–female pairs plus offspring in the style of 1950s-era American television shows, gibbon groups can include multiple adult males, multiple adult females, retained adult offspring, swapped mates, and more. Gibbon group compositions over 17 years at Khao Yai are described in Chapter 17 by Ulrich Reichard, clearly demonstrating that gibbon social and mating behavior is far from static. This flexibility in mating behavior is far more typical of other “monogamous” species, and gibbons are placed into the broader context of mammalian monogamy by Luca Morino (Chapter 14). Warren Brockelman (Chapter 11) argues for the importance of considering gibbon ecological adaptations in interpreting gibbon social monogamy. Ecological hypotheses have been suggested previously to be insufficient to explain monogamy in gibbons (van Schaik and Dunbar 1990); Thad Bartlett (Chapter 13) revisits the issue and finds evidence to the contrary. Nicholas Malone and Agustin Fuentes (Chapter 12) warn against the assumptions generated by the use of terms like “monogamous” and call for a more rigorous description of gibbon social and mating behavior. It is perhaps worth noting that primatologists appear to struggle to define monogamy and to understand any exceptions from the one-male, one-female pairing and mating rule in generally monogamous systems, whereas other biologists, who have long known that many monogamous bird species engage in extrapair mating and may change social mates every breeding season, have been much more accepting of a more flexible notion of monogamy. It may be that our closer genetic relationship to gibbons makes us susceptible to burdening the term with cultural assumptions, and we therefore feel forced to confront, uncomfortably, our own “deviations” from our ideal.

We still do not understand the social or genetic relationships among neighboring gibbon groups, but recent research has highlighted the fact that the gibbon group cannot be fully understood without reference to its neighborhood and ecological community. Based on the relatively short dispersal distances that have been observed thus far and relatively low levels of aggression among neighbors reported from several sites, it is likely that in many cases neighbors are relatives and form communities interconnected by rich networks of genetic and social ties.

In recent years, genetic methods have become powerful tools for elucidating relationships among individuals in many species and understanding the effects

of behavioral and ecological variables on individual reproductive success. Unfortunately, these methods have yet to be implemented fully in gibbon studies due to the difficulty of obtaining samples yielding reliable nuclear DNA from wild individuals. Capturing wild gibbons to draw blood samples is undesirable due to the extreme difficulty and the high potential of injuring or even killing the individual, but non-invasively collected samples (e.g., feces, urine, hair), though they often yield usable mtDNA, have proven problematic for many researchers attempting to amplify nuclear markers for paternity and relatedness analyses (Chambers et al. 2004). Nevertheless, through long-term behavioral observation and mtDNA analyses, much progress has been made in understanding such relationships. Male parental care in siamangs is examined by Susan Lappan (Chapter 16), with a special focus on polyandrous groups; mtDNA data shed some light on the relationship of extra males to the breeding female in these groups. Claudia Barelli and Michael Heistermann (Chapter 15) describe a method of non-invasively monitoring female reproductive status, which may improve researchers' ability to interpret social interactions. We hope that in the future, additional hormonal studies on wild individuals will elucidate the relationships among social variables, physiological variables, and individual behavioral decisions, and that population genetic analyses using nuclear markers will allow us to better understand genetic relationships within and among gibbon groups, neighborhoods, and populations, and the consequences of individual behavioral strategies.

In addition to the unexpected variation that gibbons display in their social and sexual behavior, Alice Elder (Chapter 8) and Nicholas Malone and Agustin Fuentes (Chapter 12) emphasize the extent to which gibbon flexibility extends into the ecological realm. While previous research suggested a dichotomy between large-bodied, folivorous siamangs and other hylobatids (previously lumped as a group into the category of small-bodied frugivores), Malone and Fuentes describe substantial dietary variation within and between gibbon genera, and Elder's analysis of gibbon diets reveals that the diets of siamangs are not significantly more folivorous than those of other gibbons, that the family as a whole is predominantly frugivorous, and that in fact the most folivorous gibbons studied to date belong to the genus *Nomascus*. While the status of most or all gibbon populations as frugivorous is fairly well established, it is clear that the original view of gibbon diets as relatively invariant across populations should be re-examined.

It is important to take a long-term, population-level perspective. Several of the chapters in this book illustrate clearly that a sample of gibbon behavior or population status from a single point in time should not be mistaken for a representation of an equilibrium condition – group compositions, behavior, and population sizes can change in a relatively short period of time, which should inject a cautionary note into conclusions or management plans based on short-term studies.

## The Limits of Flexibility

While gibbons display unexpected flexibility in their social behavior, it is becoming clear that they have some fairly rigid limits ecologically. Gibbons are selective feeders, primarily consuming ripe fruits with a specific set of features. Andrew Marshall et al. (Chapter 9) and Kim McConkey (Chapter 10) describe two of the first studies to date on the roles of gibbons in their ecological communities, highlighting different aspects of gibbon community ecology. Marshall et al. evaluate the fruit component of gibbon diets and those of their primary diurnal vertebrate competitors, and conclude that gibbon diets display pronounced overlap with those of not only other primate species but also of many other frugivorous vertebrates, while McConkey considers plant–animal interactions and the role of gibbons as seed dispersers. Both studies make it clear that gibbons are important components of functioning ecological communities in the forests of South and Southeast Asia.

Gibbons have fairly specific habitat requirements, including continuous canopy cover, and respond poorly to habitat conversion and fragmentation. Accordingly, human disturbance is a major threat to gibbon populations. Gibbons live in three of the four most populous nations on Earth (China, India, and Indonesia), as well as four of the ten nations with the highest population growth rates (India, China, Indonesia, and Bangladesh: US Census Bureau 2002). Rapid population growth and economic development in these and other habitat countries have led to an unprecedented rate of habitat destruction across the gibbon distribution range.

Gibbons reproduce relatively slowly, and it is suggested in studies of Kloss's gibbon diversity by Danielle Whittaker (Chapter 5) and Sally Keith et al. (Chapter 4) that evolutionary change in gibbons may lag behind environmental change: a vicariance event that resulted in evolutionary divergence in sympatric primate species has not yet caused genetic or vocal divergence in the gibbons. Such a long latency to change has negative implications for gibbons' ability to adapt genetically to anthropogenic change. Ben Rawson and colleagues (Chapter 18), Jayanta Das and colleagues (Chapter 19), Warren Brockelman (Chapter 20), and Achmad Yanuar (Chapter 21) review the status and distribution of several threatened gibbon species.

The picture is not all bleak, however. Large populations of gibbons remain in some areas (e.g., O'Brien et al. 2004; Cheyne et al. 2007; Rawson et al. this volume; Brockelman et al. this volume), and Rawson et al. demonstrate that effective conservation management can result in sustainable, and even growing, gibbon populations in protected areas. Even in areas that have already been fragmented or depopulated by hunting, appropriate management strategies may result in the preservation of viable gibbon populations. Das et al. (Chapter 22) describe an innovative method to provide connectivity to the discontinuous canopy in badly fragmented habitat, and Susan Cheyne (Chapter 23) discusses the potential of gibbon

reintroduction programs. Such solutions are costly in time, money, or both, however, and can meet with only limited success compared with the protection of natural habitats and populations. We believe that the dire conservation status of many gibbon populations and taxa should not be used as an excuse to justify the further neglect of any population, but rather emphasizes the importance of immediate action to protect those that remain.

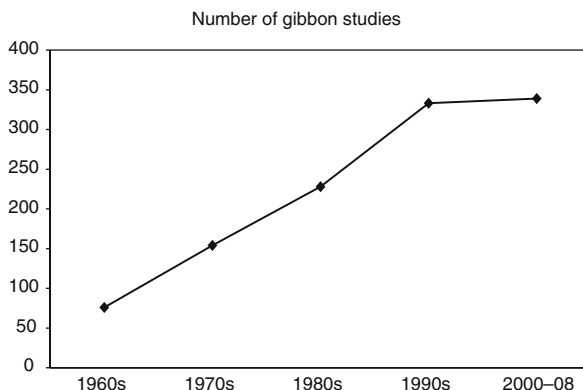
## The True Neglected Apes?

It is well established that public support is necessary for wildlife conservation to succeed. Unfortunately, despite being extremely charismatic, the small apes have received disproportionately little attention from the press, particularly in relation to their cousins, the great apes. Although the orangutan has been referred to as “The Neglected Ape” (Galdikas et al. 1995), orangutans receive far more attention than gibbons. There are up to 16 recognized species of gibbons, and half of them are critically endangered while all are experiencing some level of threat. Arguably, the most endangered extant primate is the Hainan black-crested gibbon (*Nomascus hainanus*) of which only about 17 remain, followed closely by the eastern black-crested gibbon (*Nomascus nasutus*), with ~50 individuals. While all of the living apes are threatened with extinction, no great ape species approaches such a dire situation.

A search on the Discovery Channel website (<http://dsc.discovery.com>) in April 2008 revealed only three references to gibbons, while chimpanzees, gorillas, and orangutans had 43, 22, and 7 references, respectively, and baboons (11) and macaques (19) also had more coverage. Similarly, a search for articles on the National Geographic Society Publications Index (NGSPI, <http://publicationsindex.nationalgeographic.com>) online resulted in 89 articles referring to gorillas, 54 references to chimpanzees, 39 references to orangutans, and only 5 references to gibbons. While gibbons are arguably more difficult to study and film than their more conspicuous and less arboreal cousins, this imbalance is unlikely to result simply from an absence of data or the difficulty involved in creating high-quality film footage. After all, another charismatic and endangered (and difficult to observe) animal, the tiger, was referenced 149 times.

One of the problems may be simply a matter of language. Gibbons have historically been referred to as “the lesser apes”, following the traditional English terminology used to distinguish smaller animals from their larger or “greater” relatives. However, this may have had the unfortunate consequence of suggesting to the public that the gibbons are somehow less important, interesting, or valuable than other (arguably overgrown) apes. A solution to this problem was suggested at the 2000 conference “The Apes: Challenges for the 21st Century” in Chicago, when David Chivers (2001) proposed referring to gibbons as the “small apes” rather than the “lesser apes.” We have adopted this wording in this volume, and encourage others to do the same.

**Fig. 1.1** Number of gibbon studies indexed on the search engine Primate Lit (<http://primatelit.library.wisc.edu>) per decade (accessed on April 10, 2008.)



Despite the lack of attention from the press, the number of scientific studies on gibbons has steadily increased over the years. Figure 1.1 shows the results from Primate Lit searches (<http://primatelit.library.wisc.edu/>) for each decade, using keywords “gibbon OR Hoolock OR Bunopithecus OR Hylobates OR Nomascus OR Symphalangus.” Furthermore, at least 51 honor’s, master’s, and doctoral theses focusing on gibbons were completed between 1999 and 2006 (<http://www.gibbons.de>). Our knowledge about gibbons increases steadily, even as their public image stagnates, and their population numbers decline. Researchers themselves may be neglecting opportunities to promote their work (and their study animals) to the general public. Thus, it is incumbent upon gibbon researchers to promote efforts to raise public awareness about the gibbons and their plight whenever and wherever possible. Otherwise, we are risking a future without gibbons, in a world that would be, in the words of H.J. Coolidge in his foreword to *The Lesser Apes*, much impoverished.

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**Part II**  
**Biogeography**

# Chapter 2

## Evolutionary Relationships Among the Gibbons: A Biogeographic Perspective

Helen J. Chatterjee

### Introduction

The debate regarding gibbon taxonomy and phylogeny has flourished for well over one hundred years. The first gibbon, *Homo lar*, was described by Linnaeus (1771); the siamang as *Simia syndactyla* by Raffles (1821); the first concolor gibbon as *Simia concolor* by Harlan (1826); and the hoolock as *Simia hoolock* by Harlan (1834) (Groves 1972, 2001). Throughout the 19th century, gibbon nomenclature diversified until, by the end of the century, most of the taxonomic names and divisions recognized today had been established. Phylogenetic relationships amongst these taxa have continued to cause discussion and debate, with the advent of molecular methods only serving to accelerate the discourse. In contrast, there has been startlingly little research into the biogeographic history of gibbons, largely due to their incredibly sparse fossil record. This chapter will outline current views regarding gibbon taxonomy, phylogeny, and biogeography, providing an overview of the main areas of consensus and continuing debate.

### Taxonomy

The history of gibbon systematics has seen numerous nomenclatural changes. The first gibbon to be published was given the name *Homo lar* in Linnaeus' *Systema Naturae* (1771). Over the next two centuries, as new taxa were described, several other names appear in the literature representing different gibbons. The name *Hylobates*, meaning "dweller in the trees," first appeared in the early 19th century (Groves 1972; Nowak 1991). Schultz (1933), Groves (1972, 2001), and Brandon-Jones et al. (2004) provide useful reviews of the classification systems published by other authors.

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No examination of gibbon systematics is complete without reference to some of the landmark texts that have been published. The work of Adolph Schultz in the first part of the last century contributed greatly to the understanding of interspecific variability among gibbons. This was the first large-scale study of internal and external morphological differences among gibbons. Schultz (1933) measured linear variables on the skull, plus postcranial variables including sternal, pelvic, and limb lengths and breadths, counted numbers of vertebrae, and made several observations concerning external morphology, such as hair density and interdigital webbing. On the basis of this study, Schultz postulated that nine taxa should be split into two genera: *Hylobates* and *Symphalangus*. Subsequent classification systems published during the first part of the last century, although differing slightly in their structure and composition, had the same basic form as Schultz's. It was not until the 1970s that major revisions to this taxonomy appeared.

Groves' (1972) monograph remains one of the most comprehensive studies of gibbon systematics, incorporating cranial and postcranial measurements, observations regarding pelage, hair pattern, body proportions, external features, and reproductive anatomy, serology (blood), karyology (chromosomes), distribution patterns, evidence for hybridization and sympatry, behavioral characteristics, plus data from other published sources. On the basis of these data and observations, Groves recognized six species, all confined to the genus *Hylobates*. This was further subdivided into three main subgenera; *Hylobates*, *Nomascus*, and *Symphalangus*. The subgeneric divisions were based on the diploid number of chromosomes that showed clear-cut differences between different groups of gibbons.

Over the next 20 years or so, several modifications were made to the taxonomy by Groves (1972) as a result of increased understanding of various fields (Creel and Preuschoft 1976; Chivers 1977; Chivers and Gittins 1978; Haimoff et al. 1982; Groves 1984, 1989, 1993). The most significant change to Groves' original classification was the identification of several new species in the subgenus *Hylobates*. These were formed as a result of raising several *lar* subspecies to species level. Marshall and Marshall (1976), Chivers (1977), and Marshall and Sugardjito (1986) agreed on the species status of *agilis*, *moloch*, and *muelleri* on the basis of differences in color patterns of fur on the head and around the face and differences in territorial songs. Marshall and Marshall (1976) and Marshall and Sugardjito (1986) amassed data about pelage and vocalization differences from museum pelts and wild gibbons, respectively. This work remains one of the most comprehensive studies of fur and vocal differences among gibbons. Marshall and Sugardjito (1986) presented a new taxonomy that included Prouty et al.'s (1983a, b) identification of a new subgenus, *Bunopithecus*, for the hoolock gibbon on the basis that the diploid number (*Bunopithecus* = 38) differed from the other three subgenera.

The most significant changes to Marshall and Sugardjito's (1986) classification related to the number of species in the subgenus *Nomascus*. These changes are the result of raising *H.c. leucogenys* and *H.c. gabriellae* to species level, to

create *H. leucogenys* (Dao 1983; Ma and Wang 1986; Geissmann 1993) and *H. gabriellae* (Geissmann 1995). These authors provided evidence based on differences in the anatomy of the penis bone, vocalizations, and areas of sympatry in support of species status for these taxa. The resultant taxonomy, incorporating these new species and maintaining Marshall and Sugardjito's (1986) basic structure, was published by Geissmann (1995) and forms the basis for today's widely accepted taxonomic divisions.

In recent years, gibbon taxonomists have begun to reach a general consensus regarding the main gibbon divisions and nomenclature. Groves' *Primate Taxonomy* (2001) and Brandon-Jones et al.'s *Asian Primate Classification* (2004) provide excellent sources of reference and form the basis for the overview provided here. The most recent major advance with respect to gibbon systematics has been the general acceptance that the four gibbon subgenera (*Hylobates*, *Bunopithecus*, *Nomascus*, and *Symphalangus*) should be raised to genus level (Roos and Geissmann 2001; Geissmann 2002; Brandon-Jones et al. 2004). These subgeneric names have been generally accepted as generic names, except for *Bunopithecus*. Mootnick and Groves (2005) propose that the generic nomen *Bunopithecus* is not applicable to hoolock gibbons on the basis of its historical incorporation into gibbon nomenclature. First described by Matthew and Granger (1923), the name *Bunopithecus sericus* was used to document a mandibular fragment from Sichuan, China, apparently similar in size to the hoolock gibbon. Later, *Bunopithecus* was proposed by Prouty et al. (1983b) as the subgeneric division for hoolock gibbons based on its karyological distinction from the other gibbons. The subgeneric name has pervaded the literature for some time; however, Groves (in press) found that the type of *Bunopithecus sericus* is outside the range of modern *Hylobatidae* in its dental characters. With the identity of the type in question it seems sensible to adopt Mootnick and Groves' (2005) recommendation of employing *Hoolock* as the generic description for hoolock gibbons and their scheme will be adopted here.

The family *Hylobatidae* comprises at least 12 distinct species distributed across mainland and archipelagic Southeast Asia. These are subdivided into four morphologically and karyologically distinct genera (see Table 2.1): *Hylobates*, often referred to as the *lar* group (diploid number = 44); *Hoolock* (diploid number = 38); *Nomascus*, often referred to as the *concolor* or crested group (diploid number = 52); and *Symphalangus* (diploid number = 50) (Brandon-Jones et al. 2004).

The constituent members of the genus *Hylobates* are: *H. lar*, *H. muelleri*, *H. moloch*, *H. agilis*, *H. albibarbis*, *H. pileatus*, and *H. klossii*. There is some debate as to the validity of *H. albibarbis* as a species; Groves (1972) considered *albibarbis* a geographic variant of *H. muelleri*, with no greater difference in pelage than other Bornean gibbons. Marshall and Marshall (1976) found the vocalization range of *albibarbis* to fall within that of *H. agilis*. This has caused somewhat of a puzzle regarding whether pelage or vocalizations have priority in species recognition of gibbons. Hirai et al., in this volume, provide cytogenetic and molecular genetic support for the differentiation of agile gibbon taxa

**Table 2.1** Main divisions and geographic distributions of the Family *Hylobatidae* (after Groves 2001; Geissmann 2002; Brandon-Jones et al. 2004)

Genus	Diploid number of chromosomes	Other division names	Species	Common name
<i>Hylobates</i>	44	<i>lar</i> group	<i>H. lar</i>	White-handed gibbon
			<i>H. agilis</i>	Agile gibbon
			<i>H. albibarbis</i> <sup>a</sup>	White-bearded gibbon
			<i>H. muelleri</i>	Müller's gibbon
			<i>H. moloch</i>	Silvery gibbon
			<i>H. pileatus</i>	Pileated gibbon
			<i>H. klossii</i>	Kloss's gibbon
<i>Hoolock</i>	38		<i>H. hoolock</i>	Hoolock
<i>Nomascus</i>	52	<i>Concolor</i> group	<i>N. concolor</i>	Western black crested gibbon
			<i>N. sp. cf. nasutus</i> <sup>b</sup>	Eastern black crested gibbon
		Crested gibbons	<i>N. gabriellae</i>	Yellow-cheeked crested gibbon
			<i>N. leucogenys</i>	Northern white-cheeked crested gibbon
			<i>N. siki</i> <sup>c</sup>	Southern white-cheeked crested gibbon
			<i>N. hainanus</i> <sup>d</sup>	Hainan gibbon
<i>Symphalangus</i>	50		<i>S. syndactylus</i>	Siamang

<sup>a</sup> As recognized by Groves (2001).

<sup>b</sup> As recognized by Geissmann (2002) and Brandon-Jones et al. (2004).

<sup>c</sup> As recognized by Groves (2001).

<sup>d</sup> As recognized by Groves (2001).

between Sumatra and Kalimantan. Regarding subspecies, Groves (2001) and Brandon-Jones et al. (2004) recognize five *lar* subspecies: *H. lar lar*, *H. lar carpenteri*, *H. lar entelloides*, *H. lar vestitus*, and *H. lar yunannensis*. There are three *muelleri* subspecies: *H. muelleri muelleri*, *H. muelleri abbotti*, and *H. muelleri funereus*. One or two *moloch* subspecies are discussed: *H. moloch moloch* and *H. moloch pongoalsoni*; the latter is suggested by Andayani et al. (2001) on the basis of genetic variation of purported distinct geographic lineages, but is yet to be confirmed by other genetic data. Analysis of vocalizations (Dallmann and Geissmann this volume) also reveals two distinct groups, though the proposed dividing line is different from that suggested by Andayani et al. (2001). The subspecies of *H. agilis* are, as discussed above, still a matter of debate. Brandon-Jones et al. (2004) recognize three subspecies: *H. agilis agilis*, *H. agilis albibarbis*, and *H. agilis unko*, while Groves (2001) proposes that *albibarbis* be considered at species level since it differs diagnostically from

both *H. agilis* and *H. muelleri*. Genetic data support this distinction of *H. albibarbis* (Hirai et al. this volume). No subspecies variants are proposed for *H. pileatus* or *H. klossii* (Keith et al. this volume; Whittaker this volume).

There is little discussion about the sole species members of *Hoolock* (*H. hoolock hoolock* and *H. hoolock leuconedys*) and *Symphalangus* (*S. syndactylus*), respectively, except that Brandon-Jones et al. (2004) recognize the Malayan siamang as a distinct subspecies: *S. syndactylus continentis*.

Most remaining debates about gibbon taxonomy usually focus around the crested gibbons, genus *Nomascus*. Widely accepted members of the genus include: *N. concolor*, *N. gabriellae*, and *N. leucogenys*. Brandon-Jones et al. (2004) offers an attempt to provide a consensus view of the species status of the following populations: *nasutus*, *siki*, and *hainanus*. *N. sp. cf. nasutus nasutus* is suggested to be sufficiently distinct from the *concolor* species as to be considered a separate taxon. Likewise, the Hainan Island population may also be distinct from *N. concolor* with respect to vocalizations and is proposed as a subspecies of *nasutus*: *N. sp. cf. nasutus hainanus*. The species status of *siki* is also controversial with molecular evidence, leading Zhang (1997) to consider it a distinct species while the consensus view (Brandon-Jones et al. 2004) proposes a more conservative approach, with *siki* included as a subspecies of *N. leucogenys*. Agreed subspecies include four taxa for the concolor group: *N. concolor concolor*, *N. concolor furvogaster*, *N. concolor jingdongensis*, and *N. concolor lu*. Two white-cheeked groups are proposed: *N. leucogenys leucogenys* and *N. leucogenys siki*. Finally, the red-cheeked gibbon (also referred to as yellow-cheeked), *N. gabriellae*, has no proposed subspecies (Brandon-Jones et al. 2004).

## Geographic Distributions

The geographic distributions of gibbons are shown in Table 2.2 and Figs. 2.1, 2.2, and 2.3. Excellent detailed distributions of species and subspecies are provided in Geissmann (1995), Groves (2001), and Brandon-Jones et al. (2004) and will not be belabored here, except to provide an overview.

The species of the genus *Hylobates* are broadly distributed in Southeast Asia; *H. lar* over east Burma, Thailand, mainland Malay Peninsula, and southwest Yunnan in China; *agilis* in west and east Sumatra, southwest Borneo (*H. albibarbis*, Groves 2001), and island Malay Peninsula; *H. muelleri* over the rest of Borneo from the northwest to southeast; *H. moloch* on western and central Java; *H. pileatus* in southeast Thailand, west Cambodia, southwest Laos; and *H. klossii* on the Mentawai Islands (Fig. 2.2).

The hoolock gibbon is distributed to the west in India, Burma, and Bangladesh (Fig. 2.1). Gibbons from the genus *Nomascus* have a more easterly distribution over South China, Vietnam, Laos, and Cambodia. The species are distributed in a north-south continuum: *N. concolor* to the north in the Yunnan