Chapter 2
Evolutionary Relationships Among the Gibbons: A Biogeographic Perspective

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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 Linneaus' *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
Hylobates	44	*lar* group	*H. lar*	White-handed gibbon
			H. agilis	Agile gibbon
			H. albibarbis[a]	White-bearded gibbon
			H. muelleri	Müller's gibbon
			H. moloch	Silvery gibbon
			H. pileatus	Pileated gibbon
			H. klossii	Kloss's gibbon
Hoolock	38		*H. hoolock*	Hoolock
Nomascus	52	*Concolor* group	*N. concolor*	Western black crested gibbon
		Crested gibbons	*N.* sp. cf. *nasutus*[b]	Eastern black crested gibbon
			N. gabriellae	Yellow-cheeked crested gibbon
			N. leucogenys	Northern white-cheeked crested gibbon
			N. siki[c]	Southern white-cheeked crested gibbon
			N. hainanus[d]	Hainan gibbon
Symphalangus	50		*S. syndactylus*	Siamang

[a] As recognized by Groves (2001).
[b] As recognized by Geissmann (2002) and Brandon-Jones et al. (2004).
[c] As recognized by Groves (2001).
[d] 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

Table 2.2 Geographic distributions of the Family *Hylobatidae* (after Groves 2001; Brandon-Jones et al. 2004)

Genus	Species	Distribution (for detail see: Groves 2001; Brandon-Jones et al. 2004)
Hylobates	*H. lar*	Northern Sumatra; Malaysia; Burma; Thailand; China
	H. agilis	Sumatra; Malay Peninsula
	H. albibarbis[a]	Southwestern Borneo
	H. muelleri	Borneo (except southwestern area)
	H. moloch	Java
	H. pileatus	Cambodia; Southwestern Laos; Southeastern Thailand
	H. klossii	Mentawai Islands (Indonesia)
Bunopithecus	*B. hoolock*	India; Northern Burma; China
Nomascus	*N. concolor*	China; Vietnam; Laos
	N. sp. cf. *nasutus*[b]	Northeastern Vietnam
	N. gabriellae	South Laos; South Vietnam; East Cambodia
	N. leucogenys	China; North Laos; Northwestern Vietnam
	N. siki[c]	South Laos; Central Vietnam
	N. hainanus[d]	Hainan Island (China)
Symphalangus	*S. syndactylus*	Sumatra; Malay Peninsula

[a] As recognized by Groves (2001).
[b] As recognized by Geissmann (2002) and Brandon-Jones et al. (2004).
[c] As recognized by Groves (2001).
[d] As recognized by Groves (2001).

province of China, and northerly parts of Vietnam and Laos; *N. leucogenys* in south Yunnan, north and central Vietnam and Laos; *N. gabriellae* in south Laos, south Vietnam, and western Cambodia (Fig. 2.3). The siamang is found on Sumatra and mainland Malay Peninsula (Fig. 2.1).

In most areas, species are separated by rivers or straits (Figs. 2.1, 2.2, and 2.3). These stretches of water could be barriers to gene exchange since it is well documented that gibbons will not cross large bodies of water (Marshall and Sugardjito 1986). There are several areas of contact, however, and these usually occur at the headwaters of the rivers. In such contact areas, there is evidence of hybrid zones forming and these will be discussed shortly. The other main areas of overlap occur where species are sympatric with each other.

The siamang is sympatric with other gibbons across the whole of its range: on southern Sumatra with *H. agilis*, and on northern Sumatra and mainland Malay Peninsula with *H. lar*. These instances of sympatry are presumably made possible by the significant size difference between the siamang and the other gibbons, combined with the fact that the siamang's diet is suggested to be more folivorous and less frugivorous (Chivers 1974; MacKinnon 1977). However, a recent comparison of siamang and other gibbon diets finds no difference in levels of frugivory (Elder this volume).

Geissmann (1995) reports three areas of sympatry among species in the genus *Hylobates* (numbers 1–3 on Fig. 2.2): between *H. lar* and *H. pileatus* at

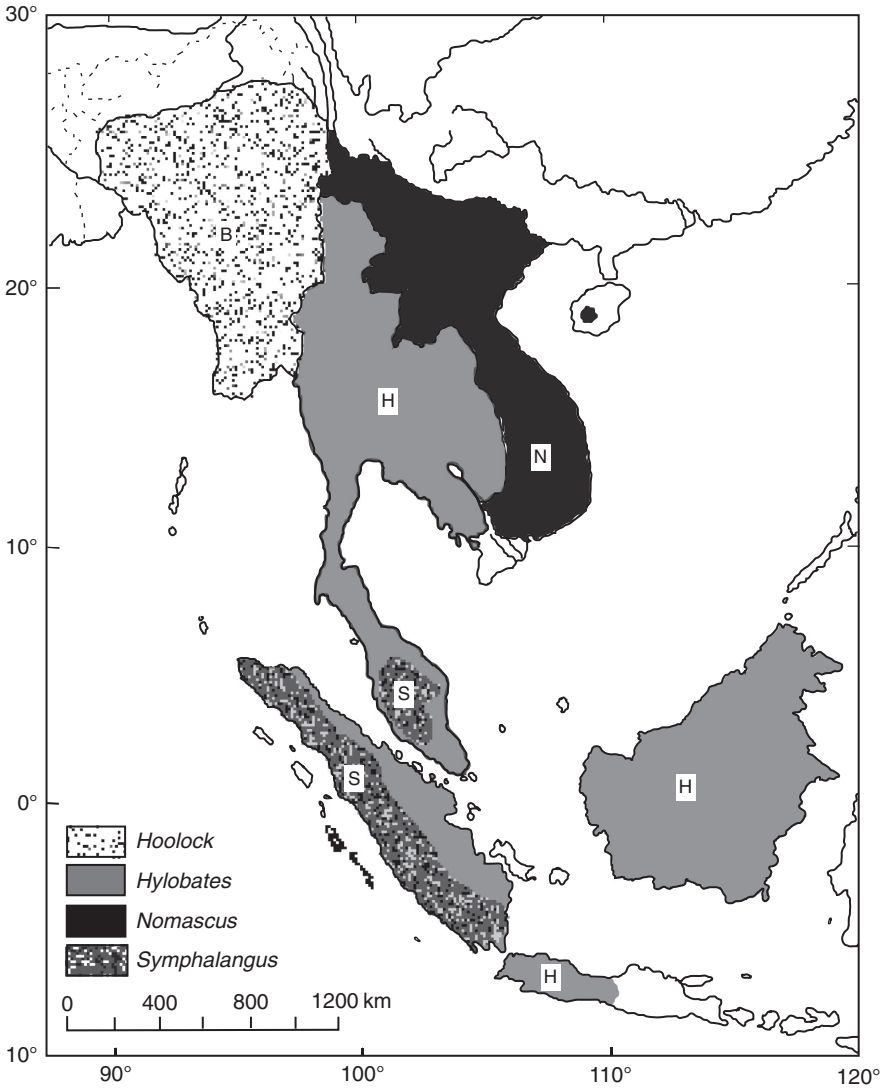


Fig. 2.1 Geographic distributions of gibbons (after Geissmann 1995)

the headwaters of the Takhon River in Khao Yai National Park, about 120 km northeast of Bangkok in Thailand [1]; between *H. lar* and *H. agilis* at the headwaters of the Muda River in the north-western part of mainland Malay Peninsula [2]; and between *H. agilis* and *H. muelleri* at the headwaters of the Barito River in Kalimantan, Borneo [3].

At each of these areas of sympatry, there have been reports of hybrid zones forming. In Khao Yai National Park, the area of overlap between *H. lar* and

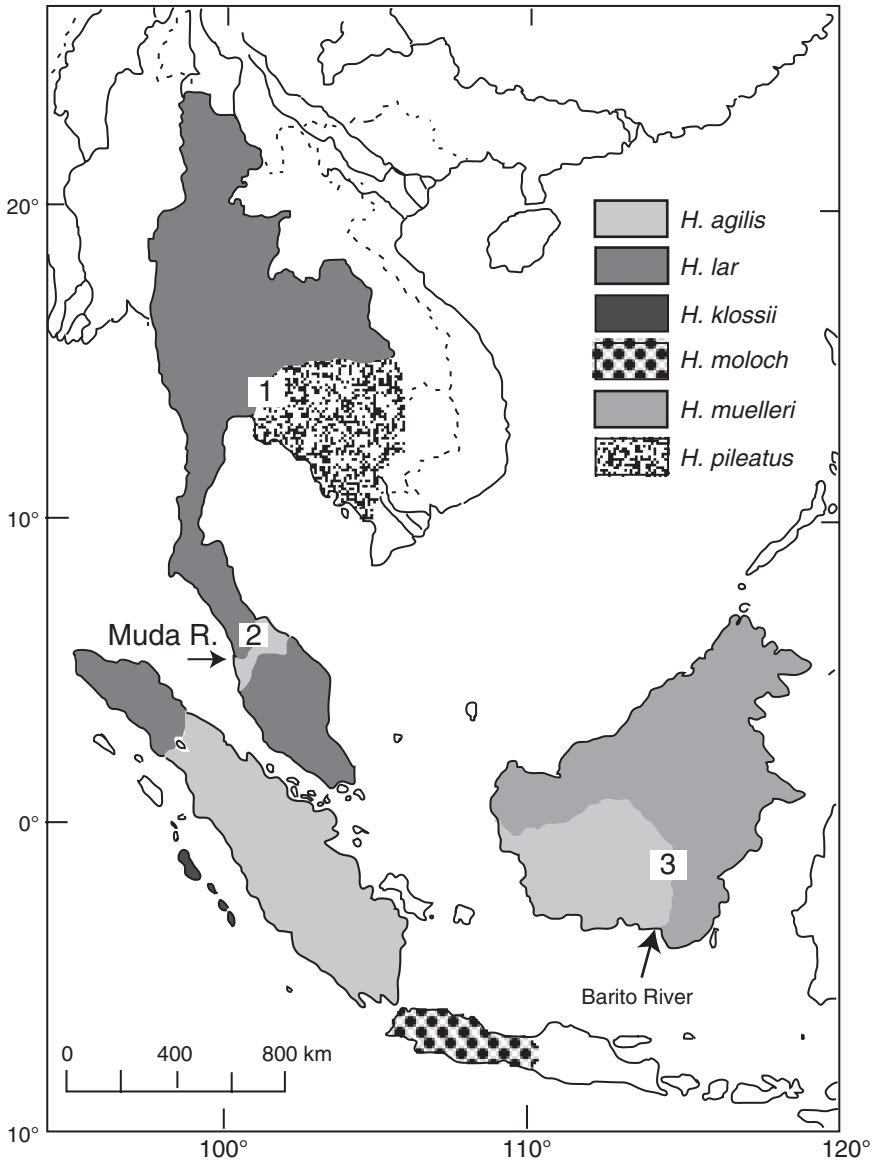


Fig. 2.2 Distribution of species in the genus *Hylobates*, after Geissmann (1995). The numbers represent areas of sympatry: (1) between *H. lar* and *H. pileatus* at the headwaters of the Takhon River in Khao Yai National Park, Thailand; (2) between *H. lar* and *H. agilis* at the headwaters of the Muda River in the north-western part of mainland Malay Peninsula; (3) between *H. agilis* and *H. muelleri* at the headwaters of the Barito River in Kalimantan, Borneo

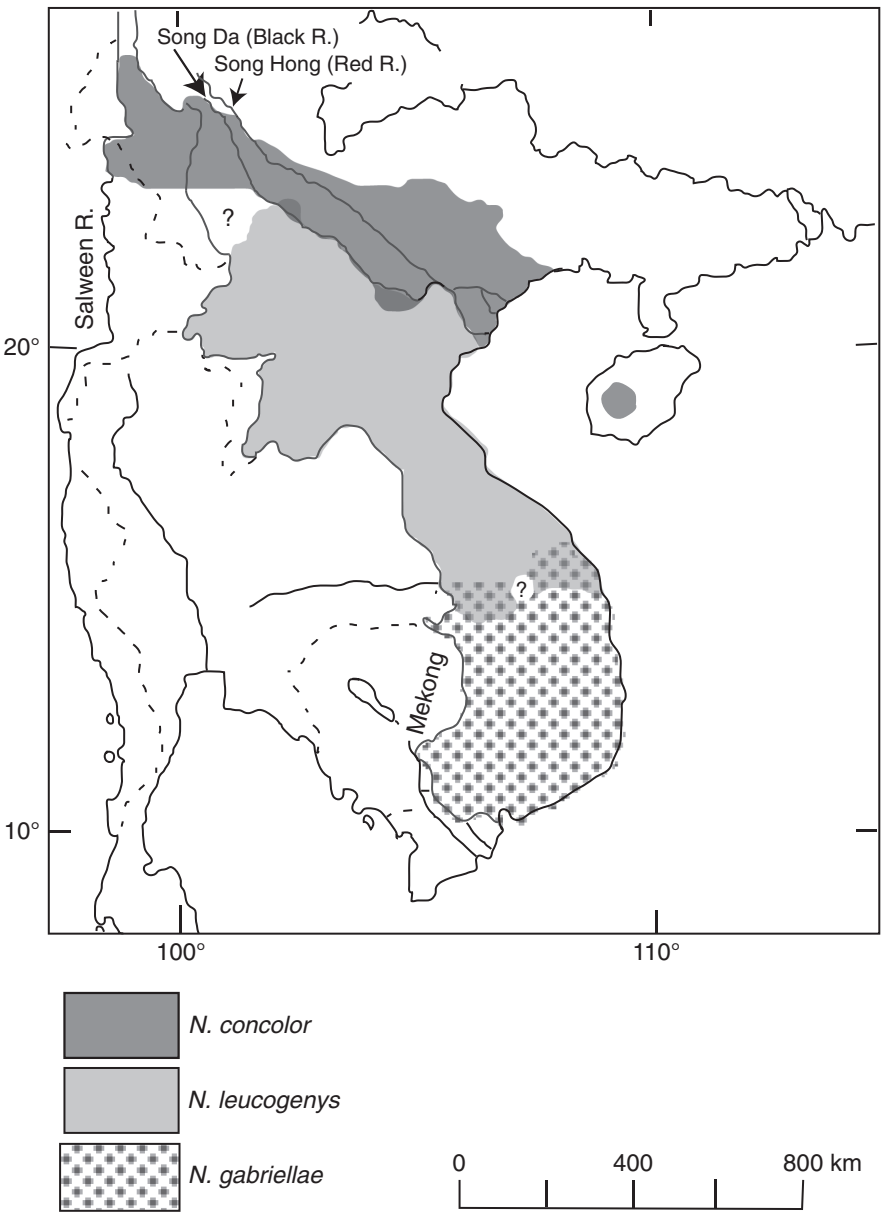


Fig. 2.3 Distribution of species in the genus *Nomascus*, after Geissmann (1995)

H. pileatus is about 100 km^2 with hybrids constituting approximately 5% of the breeding population (Brockelman and Gittins 1984; Marshall and Sugardjito 1986; Marshall and Brockelman 1986). Brockelman and Gittins (1984) and Gittins (1978) report a small number of mixed groups and hybrids of *H. lar* and *H. agilis* on the shores of an artificial lake at the headwaters of the Muda River. Chivers and Burton (1991) report an area of hybridization between *H. agilis* and *H. muelleri* on one part of the Barito River in Borneo (SE Kalimantan), and Mather (1992) reported a zone of at least 3,500 km^2 on Borneo inhabited by an apparently stable hybrid population of *H. agilis* and *H. muelleri*.

There is also some evidence for the existence of contact zones among species from the genus *Nomascus* (Geissmann 1995). Dao (1983) and Ma and Wang (1986) reported a small area of sympatry between *N. concolor* and *N. leucogenys* in southern Yunnan in China and in northern Vietnam. Furthermore, Geissmann (1995) has described a possible wild-born hybrid between *N. concolor* and *N. leucogenys*. Finally, there is some evidence of hybridization in the areas of contact between *N. gabriellae* and *N. leucogenys siki* in southern Vietnam and Laos (Groves 1972).

The implications for the species status of the breeding pairs in these hybrid zones are potentially profound. The debate regarding gibbon taxonomy largely comes down to which species concept is favored and which phenotypic characters take precedence with respect to species recognition. Most of the above studies regarding gibbon taxonomy are based on the recognition concept, since they rely on auto-recognition factors such as pelage and vocalizations to distinguish species. Regarding the species status of gibbons from hybrid zones, current information relating to the reproductive success of individuals in such hybrid zones is scarce. Until such data become available, the species status of those taxa involved cannot be fully assessed. Continuing molecular studies offer alternative views regarding phylogenetic relationships amongst these taxa and this will be the topic of the proceeding section.

Phylogenetic Inter-relationships

Phylogenetic relationships among gibbon species, and even the four genera, are controversial. Numerous studies based on molecular, morphological, and behavioral data have provided conflicting results (Groves 1972; Chivers 1977; Haimoff et al. 1982; Garza and Woodruff 1992; Hayashi et al. 1995; Purvis 1995; Hall et al. 1996; Zhang 1997; Hall et al. 1998; Zehr 1999; Chatterjee 2001; Roos and Geissmann 2001; Takacs et al. 2005; Chatterjee 2006; Whittaker et al. 2007; Creel and Preucshoft 1984; Fig. 2.4).

There is overwhelming support, from morphological and molecular studies, for the monophyletic grouping of taxa in the genera *Hylobates* and *Nomascus*. There is much less agreement regarding intergeneric relationships, particularly with respect to the earliest gibbon divergence. Many of the morphological

approaches to gibbon phylogeny proposed the siamang as the ancestral group, mainly based on its large size. More recent molecular work has been unable to resolve this question, with *Nomascus* (Hayashi et al. 1995; Zhang 1997; Chatterjee 2001; Roos and Geissmann 2001; Chatterjee 2006), *Symphalangus* (Garza and Woodruff 1992; Hall et al. 1998), and *Hoolock* (Zehr 1999; Takacs et al. 2005) being proposed as basal by one or more studies. Others studies have been unable to resolve the basal node showing a polytomy (Purvis 1995; Geissmann 2002).

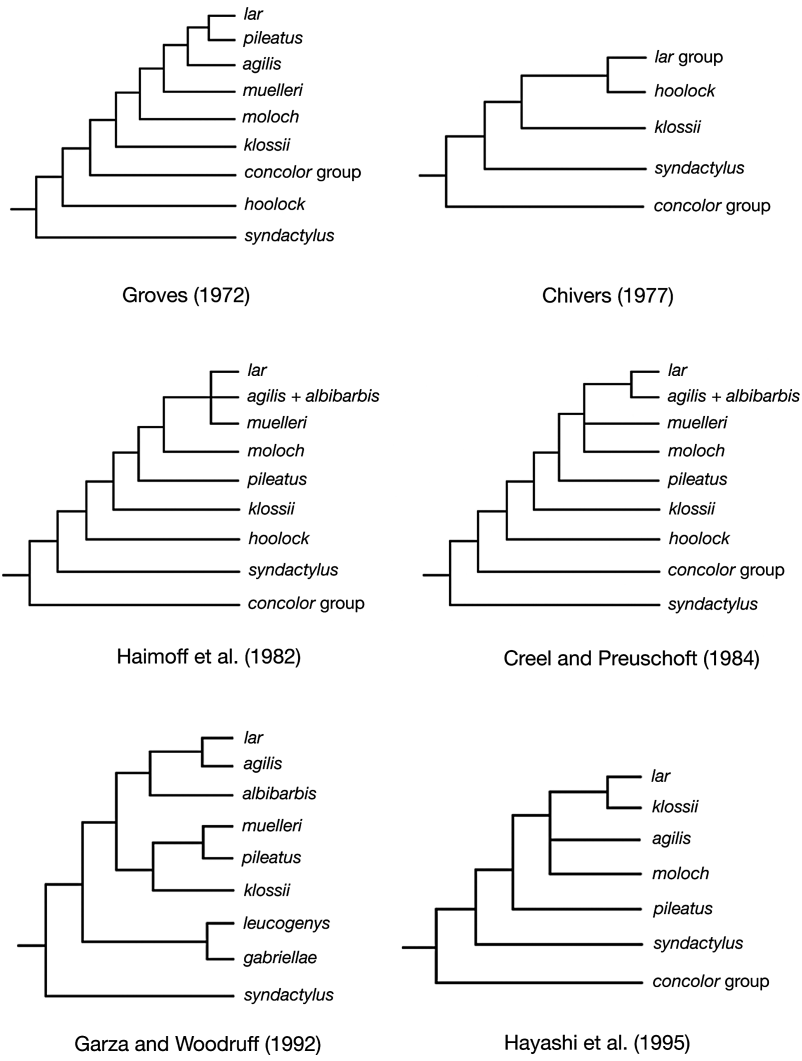


Fig. 2.4 Gibbon phylogenies based on morphological and molecular characters

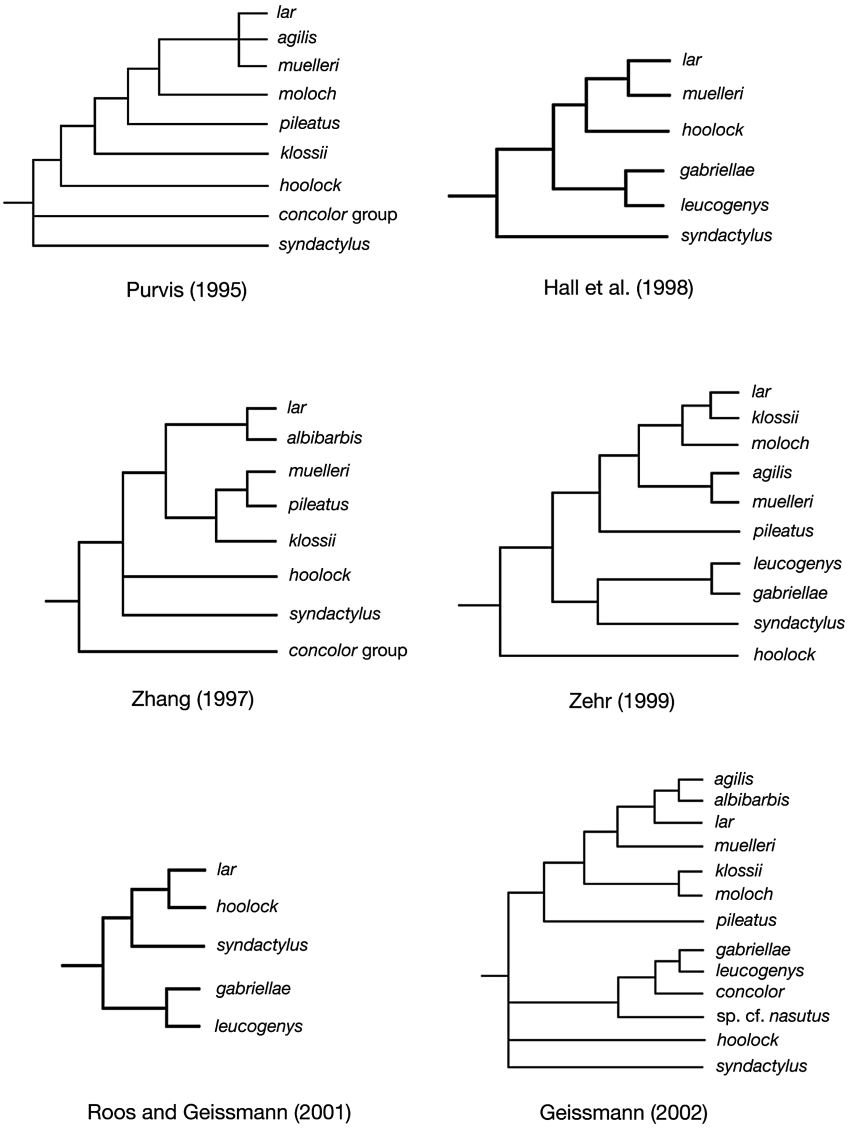


Fig. 2.4 (continued)

There is general agreement that the most recent gibbons to diverge were those in the genus *Hylobates* (the *lar* group); relationships among these taxa are, however, less well understood. Several studies have argued for close affinities between *H. lar* and *H. agilis* (Creel and Preuschoft 1984; Garza and Woodruff 1992; Geissmann 2002), while others have suggested *H. lar* and *H. klossii* are sister taxa (Hayashi et al. 1995; Zehr 1999). It is suggested by Takacs et al. (2005) that while the inclusion of *H. klossii* in the *lar* group is recommended, the

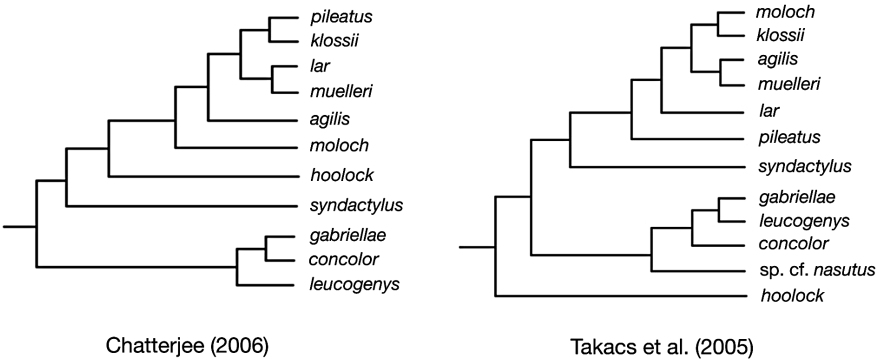


Fig. 2.4 (continued)

relationships of *H. klossii* in the context of these studies must be treated with caution since many specimens in both zoos and museums may have been subject to misidentification (Geissmann, unpublished data). Numerous permutations have been suggested regarding inter-relationships amongst *lar*-group taxa. The employment of such diverse forms of data in these analyses, including a variety of genetic loci, pelage, vocalization, and morphological characters, indicate that these taxa likely represent a rapid radiation of closely related taxa and that alternative forms of data may be required to tease out interspecific relationships. Chatterjee's (2001) attempt at using the rapidly evolving control region to address this specific question proved unfruitful. Chatterjee (2001) proposed the use of various genetic loci in a combined analysis, including nuclear genes, Y chromosome markers, and microsatellites. More recently, Whittaker et al. (2007) have shown success with D-loop genetic data, which is in line with morphological and vocal data and provides support for Takacs et al. (2005); their findings suggest *H. klossii* and *H. moloch* are sister taxa (Whittaker et al. 2007).

Relationships among the *concolor* group have been similarly debated, although most molecular studies agree that *N. concolor* forms the basal branch, followed by the sister grouping [*N. gabriellae* and *N. leucogenys*].

Relatively few studies have tackled the issue of divergence dates amongst the various gibbon clades. Numerous estimates have been put forward for the great ape-gibbon split; however, dates for this divergence are controversial, ranging from 12 Ma (million years ago) to 36 Ma, based on a variety of data (e.g. Arnason et al. 1996). Since fossil gibbons are scarce, evidence about their divergence from the other apes has mainly originated from the field of molecular biology. Combined biochemical results, based on analysis of blood groups and histocompatibility antigens, chromosome banding patterns, protein structure and antigenicity, amino acid sequences of proteins, and DNA endonuclease restriction mapping, sequencing and reassociation kinetics, indicate a great ape-gibbon split at no more than 15 Ma (see Tyler 1993 and references

therein). More recently, Raaum et al. (2005) estimate a divergence date of 15.0–18.5 Ma based on the entire mitochondrial genome.

Hayashi et al.'s (1995) molecular phylogeny of gibbons inferred from partial sequences of ND4, ND5, and tRNA genes indicated a divergence date of 6 Ma. Zehr et al. (1996) analyzed cytochrome oxidase subunit II sequence data for various species of gibbon and estimated that there was a rapid radiation of gibbons 6–8 Ma. Porter et al. (1997) analyzed sequences of the ε-globin locus from a variety of primate taxa including two species of gibbon and estimated that the gibbon radiation dates to approximately 9.9 Ma. Goodman et al. (1998) estimate a radiation dating to 8 Ma, based on a series of β-type globin genes. Based on a consensus estimate of 15 Ma for the great ape-gibbon split, Chatterjee (2006) undertook molecular clock analyses using cytochrome *b* gene data and suggests the gibbon radiation dates to approximately 10.5 Ma. According to this reconstruction, the clade comprising the genera *Symphalangus, Hoolock,* and *Hylobates* radiated between about 8 and 3 Ma. These estimates also indicate that taxa in the genus *Nomascus* represent a recent radiation between about 1.7 and 0.3 Ma (Chatterjee 2006).

Biogeography

Paleontological Record of Gibbons

The evolutionary history of gibbons has been little understood, largely due to a poor fossil record. Numerous fossil taxa have been nominated as possible gibbon ancestors on the basis of their small body size and simple molar cusp morphology, including *Pliopithecus*, *Laccopithecus*, *Micropithecus*, *Dendropithecus*, *Limnopithecus*, *Dionysopithecus,* and *Platodontopithecus*. Most of these taxa are now generally regarded as early catarrhines (Tyler 1993; Fleagle 1999). For some, however, one of these fossils remains a strong contender for the position of gibbon ancestor: *Laccopithecus robustus* (Wu and Pan 1984, 1985; Jablonski 1993; Tyler 1993). This late Miocene fossil (c. 8 Ma) is known from the Lufeng deposits in Yunnan, China. Evidence for the close phylogenetic relationship between *Laccopithecus* and extant gibbons is largely based on cranial and dental anatomy (Wu and Pan 1984, 1985). Meldrum and Pan (1988) have also presented evidence that the only identified postcranial remains of *Laccopithecus*, a proximal fifth phalanx, is similar to modern siamangs, and hence is typical of a brachiator. However, metric and morphological examination of the upper and lower dentition show a sexual dimorphism that far exceeds extant gibbons (Pan et al. 1989). According to Tyler (1993), if *Laccopithecus* is the ancestor of modern gibbons, it should be an arboreal brachiator, and have minimal sexual dimorphism. Clarification of the placement of *Laccopithecus* within the Hylobatidae warrants

further evidence from the skull, auditory region, and postcranium (Tyler 1993; Jablonski this volume).

Wu and Poirier (1995) list mammalian faunas from a site called Hudieliangzi (Butterfly Hill) in Yuanmou, Yunnan, south China, which contains specimens identified as *Hylobates* sp. A more detailed taxonomic description of these specimens in not provided, but Zong et al. (1991) have dated this site to 5–6 Ma.

Undisputed gibbons do not appear in the fossil record until the Pleistocene (Hooijer 1960; Gu 1989; Tyler 1993; Jablonski this volume). Hooijer (1960) presents evidence of fossil gibbons (mainly teeth) from Sumatra (*S. syndactylus, H. agilis*), Java (*S. syndactylus*, *H. moloch*), Borneo (*H. muelleri*), and China (*H. hoolock*). Subsequently, several authors have dated the sites that contain these fossil faunas. De Vos (1983) and Van den Berg et al. (1995) have dated the so-called Punung faunal assemblage on Java and deposits on Sumatra, which contain fossils identified as *S. syndactylus*, to between 60,000 and 80,000 years old. Deposits containing the remains of *H. moloch* on Java have been dated as Recent (Van den Bergh et al. 1995). The evidence for *S. syndactylus* on Java between 60,000 and 80,000 years ago indicates this species was present on the island before *H. moloch*, Java's only present-day gibbon inhabitant.

Long et al. (1996) discuss additional evidence of fossil gibbons from the sites of Lang Trang in Vietnam dated to 80,000 years and Niah in Malaysian Borneo dated to 50,000 years, although details of taxonomic identification are not provided. Gu (1989) presents evidence of fossil gibbons from Chinese Pleistocene deposits. The fossils, mainly teeth, are identified as representing two species: *N. concolor* and *H. hoolock*.

Paleoenvironmental History of Southeast Asia

The paleoenvironmental history of Southeast Asia is complex due to a combination of orogenesis, plate tectonics, and glacial activities. These factors have affected the paleogeography of Southeast Asia, plus its climate, temperature, fauna, and flora. The Indo-Malaysian Islands are part of a complex comprising several structural divisions. At the boundaries of these plates, tectonic activity has created series of volcanoes and areas of submergence, the most dramatic of which can be seen at the margins of the Sunda Shelf (Fig. 2.5). The exposed part of the Sunda Shelf is also known as Sundaland, and comprises the Malay Peninsula, Sumatra, Java, Borneo, and other smaller island groups (Bellwood 1997).

Hall (1996, 1998) has reconstructed the paleoenvironmental history of Cenozoic SE Asia, including the distribution of land and sea. Since the fossil evidence for gibbons and gibbon ancestors dates to no earlier than the middle Miocene (approximately 15 Ma), this date will be used as a benchmark from which to briefly describe the paleoenvironmental history of Southeast Asia.

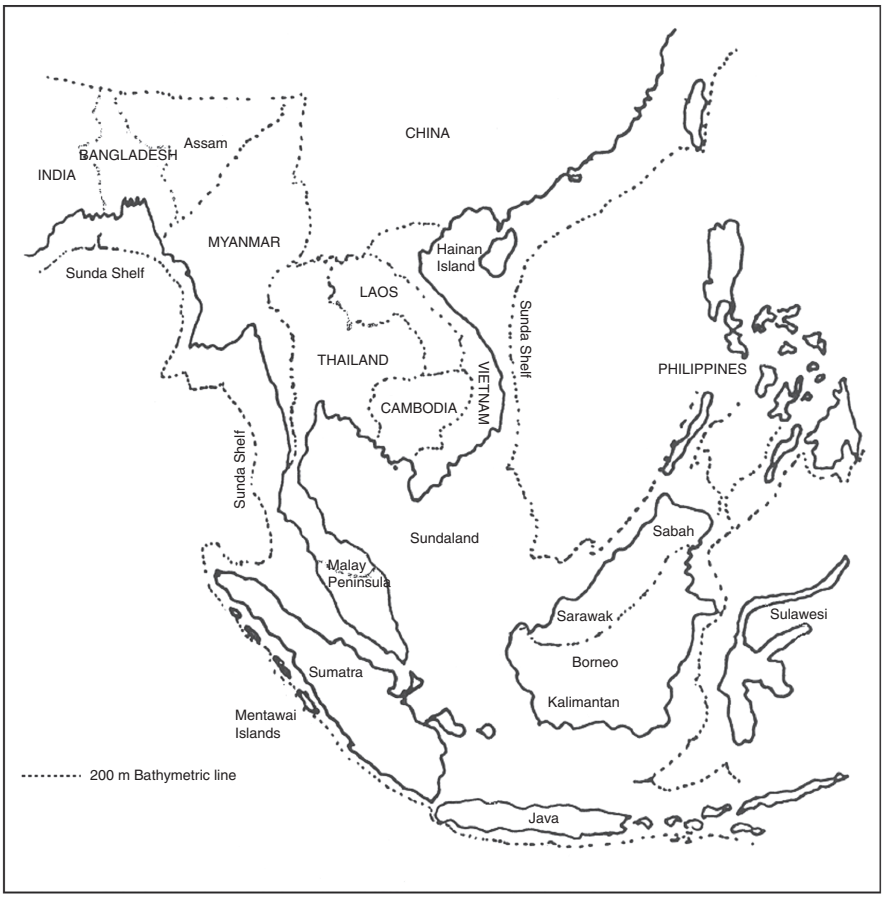


Fig. 2.5 Map of Southeast Asia showing the boundary of the Sunda Shelf, demarked by the 200 m bathymetric line (Chatterjee 2001)

Between 20 and 10 Ma, changes in the orientation of several tectonic plate boundaries throughout Southeast Asia resulted in the tectonic pattern recognizable today (Hall 1998). These changes, described in detail in Hall (1998), had dramatic effects on the paleogeography of the area. Between 15 and 5 Ma, large parts of Sundaland were exposed. According to Hall's reconstruction during the middle Miocene at 15 Ma, emergent land persisted from China, Vietnam, Laos, Cambodia, Thailand, and the Malay Peninsula, connecting these areas with large parts of Borneo. During this time, only the southern parts of Borneo were covered by shallow seas. A ridge of volcanoes running east to west across central Borneo (on the Sarawak-Kalimantan border) created areas of highland. This situation persisted through the late Miocene, approximately 10 Ma. Subduction of the Indian plate under the Sunda Shelf also created a ridge of volcanoes across Sumatra and Java, with patches of emergent land appearing

at 15 Ma. By 10 Ma, these isolated patches of land joined to form a long, thin strip of land linking Sumatra, Java, and Sundaland. Between 15 and 10 Ma, Hainan Island was also joined to Mainland China, but by 5 Ma this corridor was covered by shallow seas. At 5 Ma, the area of emergent land was reduced. However, even at this time the Malay Peninsula, Borneo, Sumatra, and Java were linked via emergent land on the Sunda Shelf. Also at this time, patches of emergent land became evident at the position of the present day Mentawai Islands, although these patches were not connected to Sumatra. Throughout this time, deep basins east of Borneo may have represented barriers to dispersal to islands such as the Philippines, Sulawesi, and New Guinea.

Thus, there is evidence indicating that emergent land probably extended from Indochina to Borneo in the Miocene, and according to Morley and Flenley (1987) both seasonal and everwet rain forests were present. Other evidence indicates that tropical rain forest extended as far north as southern China, southern Japan, and westward to northern India during the late Miocene (Heaney 1991; Jablonski 1993). According to Heaney (1991), by approximately 5 Ma the insular and tropical nature of Southeast Asia was well established.

Batchelor (1979) suggests that up until the end of the Pliocene the extent of exposed Sundaland covered some 2,000 km east to west, and incorporated much of the Malay Peninsula, Sumatra, and Borneo. However, at this time major changes in sea level began as a result of glacial activity on a global scale. The major worldwide effects of glaciation were to alter sea levels, temperature, and the extent of vegetation zones. Evidence from deepsea cores and deeply stratified terrestrial gastropod- and pollen-bearing cores indicates that since about 2.5 Ma there have been a number (approximately 20) of glacial and interglacial cycles. During glaciations the vast quantities of water trapped in ice sheets across the globe immobilized large amounts of ^{16}O and the cold seas were as a result relatively rich in ^{18}O. During interglacials the ratio was reversed. Fluctuations in these ratios have been plotted from deepsea cores, and indicate the timing and extent of glacial waxing and waning (Shackleton and Opdyke 1973; Lowe and Walker 1997).

In Southeast Asia, as in many parts of the world, the periodicity of glaciations had the effect of altering sea level and hence the extent of exposed land, as well as affecting climate and vegetation. During periods of low sea level, large parts of Sundaland were exposed to between 120 and 160 m below present sea level (Morley and Flenley 1987; Heaney 1991; Bellwood 1997). This had the effect of linking the islands of Sumatra, Borneo, and Java to the mainland, creating a geography similar to that seen during the Miocene. Several authors present evidence of the environmental effects of Quaternary glaciations in Southeast Asia (e.g. de Vos 1983; Morley and Flenley 1987; Heaney 1991; Jablonski 1993; Van den Bergh et al. 1995; Brandon-Jones 1996). These studies provide evidence of the paleoecological implications of environmental change, plus fossil locality and dating information for numerous sites across Southeast Asia. However, the exact nature and timing of these variations are still actively debated (Jablonski 1993, 1997).

In summary, it is apparent that the prehistory of gibbons remains unclear due to a lack of crucial fossil evidence from the late Miocene and Pliocene. However, according to reconstructions by Hall (1996, 1998) and others (e.g. Heaney 1991; Jablonski 1993), much of the area uniting Sumatra, Borneo, and Java to mainland Malaysia was exposed for long periods during the late Miocene, Pliocene, and periodically throughout the Pleistocene. Furthermore, several studies have shown that tropical rain forests were present in these areas, and that these habitats supported a diverse primate fauna (Morley and Flenley 1987; Heaney 1991; Jablonski 1993). Despite evidence that climatic deterioration from the late Miocene onward affected some primate fauna, this does not appear to be the case with respect to the gibbons (Jablonski 1993). Jablonski (1993, 1998) presents evidence from the paleontological and paleoenvironmental record of China, which indicates that in spite of increased seasonality and habitat fragmentation, gibbons were among the most successful primates. Further, Jablonski (1998) suggests that this success was facilitated by a small body size and efficient life history parameters, such as an advanced age for the onset of reproduction and long inter-birth intervals.

The Radiation of Gibbons in Southeast Asia

Few scenarios have been proposed to describe the pattern of radiation of gibbons in Southeast Asia (Groves 1972; Chivers 1977). Groves (1972) proposed a scenario for the radiation of the *lar* group of gibbons; eustatic lowering of sea level in the Pleistocene was used to explain the dispersal of these gibbons. Chivers (1977) assimilated data on the sequence of geological, climatic, floral, and faunal events during the past few million years. This study provided a chronological history of the paleoenvironment of Southeast Asia, including possible migration routes for different gibbon taxa. Chivers' (1977) and Groves' (1972) schematic illustrations of the radiation of gibbons are useful for visualizing the possible migration routes of different taxa, but they are not congruent with recent advances in molecular estimates of the possible timing of the gibbon radiation.

Chatterjee (2006) employs her estimate of gibbon phylogeny within a cladistic biogeographic framework to provide a new scenario for the radiation of gibbons across Southeast Asia (Fig. 2.6). Published cytochrome *b* gene data were reanalyzed under the assumption of a molecular clock, and the resultant phylogeny employed in a dispersal-vicariance analysis (DIVA) (Ronquist 1996, 1997) to reconstruct the biogeographic history of gibbons. As with other cladistic biogeography methods, DIVA first requires the construction of a taxon-area cladogram showing geographic distributions and relationships. Geissmann's (1995) breakdown of the geographic distribution of gibbon species was used as the basis for determining area characters. Chatterjee's analysis provides a mix of informative and less informative biogeographic data, but in combination with current evidence relating to the environmental evolution of

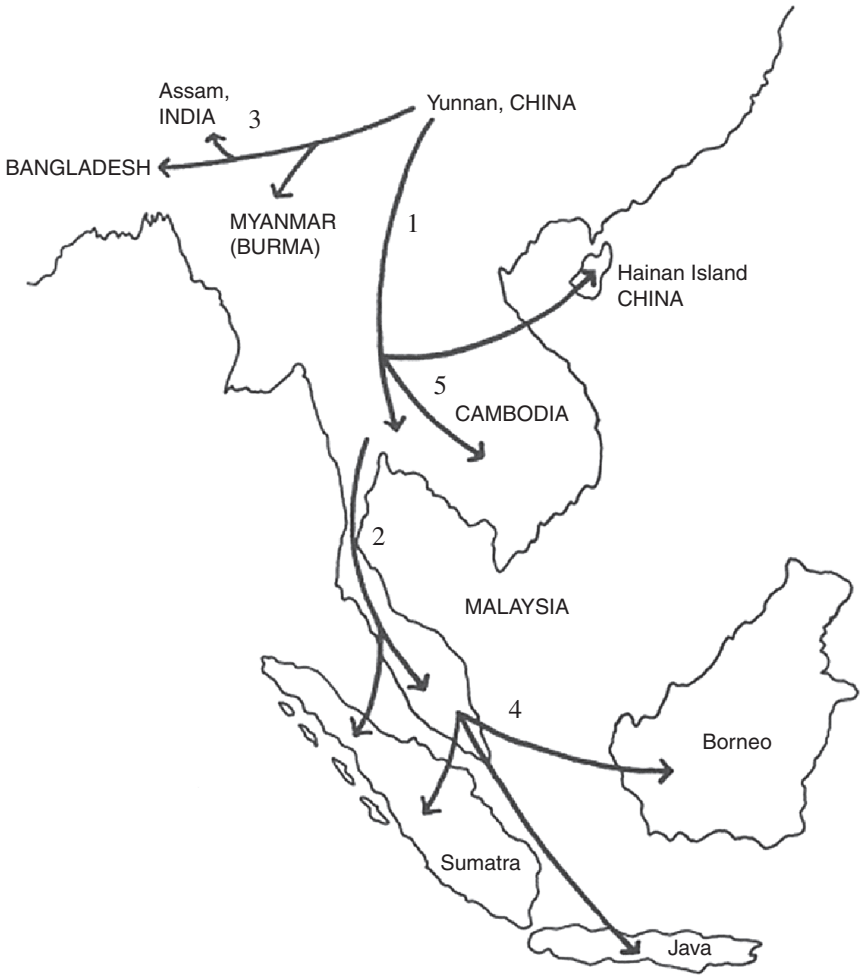


Fig. 2.6 Pattern and timing of the gibbon radiation (Chatterjee 2006)
(1) The gibbon radiation initiated approximately **10.5 Ma** in Eastern Indochina; (2) Between about **10.5 and 8.6 Ma** gibbons radiated southward to the Malay Peninsula and Sumatra, subsequently, they differentiated into two types of gibbon on Sumatra, representing the two genera *Symphalangus* and *Hylobates*; (3) Approximately **7–8 Ma** *Bunopithecus* spread into Burma, Assam, and Bangladesh; (4) At around **3–5 Ma** there was a second radiation of genus *Hylobates*, involving dispersal into the islands of Borneo, Mentawai and Java; (5) Between **0.3 and 1.8 Ma** taxa in the subgenus *Nomascus* differentiated into Cambodia and Hainan Island.

Southeast Asia and the timing of gibbon radiations derived from molecular clock analyses, a scenario for the pattern of evolution of gibbons is viable at generic level (Fig. 2.6). Results suggest that the gibbon radiation initiated approximately 10.5 Ma in Eastern Indochina. Between about 10.5 and 8.6 Ma

gibbons radiated southwards to the Malay Peninsula and Sumatra. Subsequently, they differentiated into two types of gibbon on Sumatra, representing *Symphalangus* and *Hylobates*. Approximately 7–8 Ma *Hoolock* spread into Burma, Assam, and Bangladesh. At around 3–5 Ma, there was a second radiation of taxa in genus *Hylobates*, involving dispersal onto the islands of Borneo, Mentawai, and Java. Between 0.3 and 1.8 Ma taxa in the genus *Nomascus* differentiated into Cambodia and Hainan Island.

Until such time as more gibbon fossils are recovered, our understanding of the pattern and timing of the gibbon radiation will be limited to those reconstructions combining molecular and environmental data. The advancing field of cladistic biogeography offers exciting potential in the developments of such models, but these will only ever be a proxy for the true biogeographic history of gibbons.

Conclusions

The diversity of gibbons with respect to pelage, vocalizations, geographic distributions, and evolutionary and biogeographic history renders these enigmatic apes some of the most intriguing mammals in the world. The past 20 years has seen huge advances with respect to our understanding of gibbon systematics, molecular phylogenetics, and speciation patterns. With continuing methodological developments in these fields, modern techniques offer an exciting opportunity to resolve many aspects of gibbon taxonomy, phylogeny, and biogeography. Our primary concern remains the conservation status of many gibbon taxa. With several species facing extinction, opportunities for studying gibbons are fast running out.

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