Chapter 7
The Fossil Record of Gibbons

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Modern gibbons of the family Hylobatidae are distinguished from other living apes by a suite of shared-derived characteristics (synapomorphies) related to their unique mode of overhead suspensory locomotion and territorial defense. These characteristics include a greatly elongated and highly mobile forelimb, greatly reduced or nonexistent sexual dimorphism in body and canine tooth size, a predominantly monogamous social organization, and stereotyped vocalizations that function to establish and maintain boundaries between family groups. In recent years, there has been considerable debate as to whether gibbons so defined are an ancient lineage with roots well back into the middle Miocene or whether they are of more recent origin. Here, one immediately confronts the difficulty that identification of true gibbons in the fossil record is limited to characters of the skeleton and dentition and, thus, only assays half of the features that define the Family.

In this chapter, we first update and review what is known of the fossil record of the Hylobatidae. We include in this review a discussion of the changes in distribution of gibbons through time, which can be inferred from the fossil record. This is done with reference to the environmental history of Southeast Asia, paying special attention to the patterns of sea-level change and to the development of paleorivers that would have affected gibbon evolution. Second, we then propose a scenario of deployment for the gibbons based on the fossil record and the environmental history of Southeast Asia, which is consistent with current understanding of the phylogeny of the group. Finally, we discuss the biological and ecological factors that influenced the distribution of gibbons through time.

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The Nature of the Fossil Record of Gibbons and Gibbon-Like Primates

Until the widespread adoption of molecular genetic and auditory sonagraphic methods, knowledge of the evolutionary history of gibbons rested largely on the interpretation of controversial fossil evidence. Although Hylobatidae were once regarded as the best-documented evolutionary lineage of primates (Simons and Fleagle 1973), considerable controversy exists as to which taxa belong to or were ancestral to the Hylobatidae. The Miocene fossil record of Eurasia and East Africa is filled with small apes including members of the families Propliopithecidae (*Propliopithecus*), Pliopithecidae (*Pliopithecus*), and Proconsulidae (*Micropithecus*, *Dendropithecus*, *Limnopithecus*, *Dionysopithecus*, and *Platodontopithecus*) that have been nominated as possible gibbon ancestors because of their small size and simple molar cusp morphology (Simons and Fleagle 1973). These genera are now generally viewed as early catarrhines or early hominoids, whose primitive characteristics do not ally any of them with modern gibbons (Harrison 1987; Tyler 1993; Fleagle 1999; Harrison 2002). It is more likely that modern hylobatids are not the descendants of small Miocene apes, but are instead phyletic dwarfs descended from larger Asian hominoids of the middle Miocene (Tyler 1993). In contrast to the upsizing that occurred in many mammalian lineages when species faced increasing environmental seasonality, downsizing was common among later Miocene hominoids. In these moderately to highly encephalized mammals, smaller body sizes worked to reduce the total energy intake required to maintain health and reproductive fitness.

Of all the Miocene species that have been suggested as candidates for gibbon ancestry or sister taxon status, the Chinese fossil species *Laccopithecus robustus* from approximately 8 myr old deposits at Lufeng, Yunnan (Wu and Pan 1984, 1985, 1994), is the most persuasive contender. *Laccopithecus* is distinguished from modern hylobatids in its possession of an extreme amount of canine tooth dimorphism (Pan et al. 1989), but the rest of its cranial and dental anatomy is very similar to that of modern gibbons. The only identified postcranial element of *Laccopithecus*, a proximal fifth phalanx, is similar to the modern siamang (Meldrum and Pan 1988). This evidence sways us to support the tentative placement of *Laccopithecus* within the Hylobatidae rather than the Pliopithecidae (Tyler 1993), but other workers have disagreed and have classified it as a pliopithecid (Harrison et al. 2002). Further evidence of the highly diagnostic ear region and postcrania is required for a definitive assignment. *Laccopithecus robustus* is excluded from our compilation of fossil Hylobatidae for these reasons, but it should be noted that one of the two Pliocene localities for fossil Hylobatidae is also at Lufeng, Yunnan.

Unequivocal evidence of true Hylobatidae in the fossil record is known from deposits of latest Miocene or earliest Pliocene age onward (i.e., 6–5 Ma), with most fossils deriving from the Late Pleistocene and Holocene (Hooijer 1960; de Vos 1983; Gu 1986, 1989; Ciochon and Olsen 1991; Zong et al. 1991; Wu and

Poirier 1995; Ciochon et al. 1996; Harrison 1998; Jablonski et al. 2000; Tougard 2001; van den Bergh et al. 2001; Storm et al. 2005; Zeitoun et al. 2005; Harrison et al. 2006). From a taphonomic perspective, gibbons are rare elements of the fossil record because their preference for forested habitats, their relatively small bodies (<10 kg), and gracile bones militate against long-term preservation. The known fossil localities for the Hylobatidae are presented in Table 7.1, where they are generalized to a scale of 1 M:1. Locality data were compiled from the original reports cited above, in which the ages of fossil-producing deposits were determined mostly by faunal correlation. The geological ages of fossil localities are, thus, given only as epochs or sub-epochs. We did not inspect or compare most of the gibbon fossils discussed in this paper because they are held in widely dispersed repositories with restricted access in Asia. Most of the gibbon fossils reported in the literature are isolated molar teeth or small portions of jaws with teeth, and diagnosis of such remains to the species level is uncertain because gibbons, with the exception of *Symphalangus*, are not strongly differentiated by their dental morphology. Most of the features that distinguish the species of gibbons today are integumentary and behavioral; the skeletal and dental differentiation that exists is extremely subtle and difficult to detect in the fossil record. The species names and ages of fossils provided in Table 7.1 are those derived from the original published descriptions of the fossils. The names provided in the original reports must be treated with caution, because in many cases species assignments were given on the basis of geographical propinquity of fossil localities to sites of living populations, not on thorough comparisons of morphology. The conventions for genus designations within Hylobatidae are those followed throughout this volume. Fossils not originally assigned to species are here attributed to "Hylobatidae gen. et sp. indet."

The Distribution of Fossil Gibbons in Relation to Changing Sea Levels and Landforms

The date of the great ape-gibbon split is widely regarded as 15 Ma (Tyler 1993; Chatterjee 2006), based on molecular clock estimates. The absence of informative fossils marking the origin of the gibbon lineage led Chatterjee to undertake further molecular clock analyses to estimate the origin of the gibbon radiation at about 10.5 Ma (Chatterjee 2006, this volume). No fossils unequivocally attributed to Hylobatidae are known before the terminal Miocene, and the early fossil record of the Family is particularly sparse. This account complements the summary of the paleontological record of gibbons provided by Chatterjee (this volume), by emphasizing the distribution of gibbon fossil sites relative to the physiographic features that would have influenced gibbon distributions through time.

Since the estimated time for the beginning of the gibbon radiation, fluctuating sea levels have influenced the configuration and connectivity of land masses

Table 7.1 Occurrences of fossil Hylobatidae, collected from the literature (see body of text for citations)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Hylobatidae gen. indet.	sp.	Hudieliangzi	Yunnan	China	25° 55′ N	101° 46′ E	Pliocene
Hylobatidae gen. indet.	sp.	Lufeng	Yunnan	China	25° 3′ N	102° 4′ E	Pliocene
Nomascus	*sericus* (= *concolor*)	Wanxian	Sichuan	China	30° 25′ N	108° 10′ E	Early Pleistocene
Hylobatidae gen. indet.	sp.	Baojing	Hunan	China	28° 42′ N	109° 40′ E	Early Pleistocene
Nomascus	*concolor*	Xinshuishan Cave	Guangxi	China	22° 52′ N	107° 14′ E	Middle Pleistocene
Nomascus	*concolor*	Tham Khuyen	Lang Song	Vietnam	21° 51′ 17 N	106° 28′ 15 E	Middle Pleistocene
Hylobates	*hoolock*	Daxin	Guangxi	China	22° 52′ N	107° 13′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Ban Fa Suai	Chiang Dai	Thailand	19° 29′ 8 N	97° 59′ 35 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Hang Hum	Hoang Lien Son	Vietnam	21° 51′ N	104° 50′ 30 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Keo Leng	Lang Song	Vietnam	21° 58′ 30 N	106° 33′ 20 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Tham OM	Nghetinh	Vietnam	19° 34′ 25 N	105° 8′ 5 E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Lang Trang	Ba Thuoc	Vietnam	20° 40′ N	105° 0′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Bama	Guangxi	China	24° 10′ N	107° 15′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Daxin	Guangxi	China	23° 20′ N	110° 25′ E	Middle Pleistocene
Hylobatidae gen. indet.	sp.	Tongzi	Guizhou	China	28° 15′ N	106° 45′ E	Middle Pleistocene
Nomascus	*sericus* (= *concolor*)	Yanjingkou	Sichuan	China	30° 35′ 40 N	108° 25′ 40 E	Middle Pleistocene
Nomascus	*concolor*	Baise	Guangxi	China	23° 55′ N	106° 37′ E	Late Pleistocene
Nomascus	*concolor*	Guilin	Guangxi	China	25° 14′ N	110° 17′ E	Late Pleistocene
Nomascus	*concolor*	Lingyan Cave	Guangxi	China	24° 15′ N	109° 25′ E	Late Pleistocene
Nomascus	*concolor*	Lipu	Guangxi	China	24° 30′ N	110° 24′ E	Late Pleistocene
Nomascus	*concolor*	Shanglin	Guangxi	China	23° 27′ N	108° 34′ E	Late Pleistocene
Nomascus	*concolor*	Yangshuo	Guangxi	China	24° 43′ N	110° 29′ E	Late Pleistocene

Table 7.1 (continued)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Nomascus	*concolor*	Qiongzhong	Hainan	China	19° 5′ N	109° 50′ E	Late Pleistocene
Nomascus	*concolor*	Liujiang	Sichuan	China	24° 15′ N	109° 25′ E	Late Pleistocene
Nomascus	*concolor*	Baoshan	Yunnan	China	25° 5′ N	99° 5′ E	Late Pleistocene
Nomascus	*concolor*	Jiangcheng	Yunnan	China	22° 40′ N	101° 53′ E	Late Pleistocene
Nomascus	*concolor*	Jingdong	Yunnan	China	24° 35′ N	102° 39′ E	Late Pleistocene
Nomascus	*concolor*	Luchun	Yunnan	China	22° 55′ N	102° 23′ E	Late Pleistocene
Nomascus	*concolor*	Mengla	Yunnan	China	21° 27′ N	101° 30′ E	Late Pleistocene
Nomascus	*concolor*	Shangyong	Yunnan	China	21° 38′ N	101° 38′ E	Late Pleistocene
Nomascus	*concolor*	Shuangbai	Yunnan	China	24° 38′ N	101° 25′ E	Late Pleistocene
Nomascus	*concolor*	Xinping	Yunnan	China	24° 2′ N	101° 57′ E	Late Pleistocene
Nomascus	*concolor?*	Du′an	Guangxi	China	23° 17′ N	106° 30′ E	Late Pleistocene
Hylobates	*hoolock*	Lipu	Guangxi	China	24° 30′ N	110° 24′ E	Late Pleistocene
Hylobates	*hoolock*	Baoshan	Yunnan	China	25° 5′ N	99° 5′ E	Late Pleistocene
Hylobates	*hoolock*	Lianghe	Yunnan	China	24° 55′ N	98° 0′ E	Late Pleistocene
Hylobates	*hoolock*	Tengchong	Yunnan	China	25° 4′ N	98° 7′ E	Late Pleistocene
Hylobates	*hoolock*	Yingjiang	Yunnan	China	24° 40′ N	97° 8′ E	Late Pleistocene
Hylobates	*leuciscus* (= *moloch*)	Punung	Java	Indonesia	8° 8′ 28 S	111° 1′ 48 E	Late Pleistocene
Hylobates	*muelleri*	Niah Cave	Sarawak	Malaysia	3° 46′ N	113° 42′ 20 E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Baojiyan	Guangxi	China	25° 13′ N	109° 50′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Bose	Guangxi	China	23° 56′ N	106° 34′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Du′an	Guangxi	China	23° 57′ N	108° 6′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Liuzhou	Guangxi	China	24° 20′ N	109° 26′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Longlin	Guangxi	China	24° 45′ N	105° 20′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Shanzhongmen	Guangxi	China	24° 15′ N	109° 10′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Taipingyan	Guangxi	China	25° 22′ N	110° 24′ E	Late Pleistocene

Table 7.1 (continued)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Hylobatidae gen. indet.	sp.	Xichou	Guangxi	China	24° 22′ N	109° 25′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Yishan Cave	Guangxi	China	24° 30′ N	108° 40′ E	Late Pleistocene
Hylobatidae gen. indet.	sp.	Tongzi	Guizhou	China	28° 15′ N	106° 45′ E	Late Pleistocene
Symphalangus	*syndactylus*	Gunung Dawung	Java	Indonesia	8° 7′ 33 S	110° 59′ 15 E	Late Pleistocene
Symphalangus	*syndactylus*	Punung	Java	Indonesia	8° 8′ 28 S	111° 1′ 48 E	Late Pleistocene
Symphalangus	*syndactylus*	Lida Ayer	Sumatra	Indonesia	0° 19′ 19 S	100° 29′ 7 E	Late Pleistocene
Symphalangus	*syndactylus*	Sibrambang	Sumatra	Indonesia	0° 36′ 56 S	100° 38′ 6 E	Late Pleistocene
Hylobates	*muelleri*	Madai	Sabah	Malaysia	4° 40′ 46 N	118° 7′ E	Holocene
Hylobates	*muelleri*	Bua	Sarawak	Malaysia	1° 19′ 16 N	110° 8′ 30 E	Holocene
Hylobates	*muelleri*	Gua Sireh	Sarawak	Malaysia	1° 5′ 57 N	110° 26′ 23 E	Holocene
Hylobatidae gen. indet.	sp.	Fuzhou	Fujian	China	26° 4′ N	119° 15′ E	Holocene
Hylobatidae gen. indet.	sp.	Dian Bai	Guangdong	China	21° 27′ N	111° 0′ E	Holocene
Hylobatidae gen. indet.	sp.	Gaozhou	Guangdong	China	21° 52′ N	110° 52′ E	Holocene
Hylobatidae gen. indet.	sp.	Luoding	Guangdong	China	22° 42′ N	111° 31′ E	Holocene
Hylobatidae gen. indet.	sp.	Maoming	Guangdong	China	21° 36′ N	110° 52′ E	Holocene
Hylobatidae gen. indet.	sp.	Heng County	Guangxi	China	22° 41′ N	109° 17′ E	Holocene
Hylobatidae gen. indet.	sp.	Nanning	Guangxi	China	22° 47′ N	108° 20′ E	Holocene
Hylobatidae gen. indet.	sp.	Yulin	Guangxi	China	22° 37′ N	110° 7′ E	Holocene
Hylobatidae gen. indet.	sp.	Ding′an	Hainan	China	19° 39′ N	110° 20′ E	Holocene
Hylobatidae gen. indet.	sp.	Ling Shui	Hainan	China	18° 31′ N	110° 0′ E	Holocene
Hylobatidae gen. indet.	sp.	Qiongshan	Hainan	China	19° 58′ N	110° 20′ E	Holocene
Hylobatidae gen. indet.	sp.	Wen Chang	Hainan	China	19° 38′ N	110° 40′ E	Holocene
Hylobatidae gen. indet.	sp.	Wuzhi Shan	Hainan	China	18° 47′ N	109° 40′ E	Holocene
Hylobatidae gen. indet.	sp.	Anxiang	Henan	China	29° 24′ N	112° 8′ E	Holocene
Hylobatidae gen. indet.	sp.	Cili County	Henan	China	29° 24′ N	111° 7′ E	Holocene

Table 7.1 (continued)

Genus	Species (original and current equivalent)	Locality	Province	Country	Latitude	Longitude	Period
Hylobatidae gen. indet.	sp.	Dayong	Henan	China	29° 10′ N	110° 28′ E	Holocene
Hylobatidae gen. indet.	sp.	Li Xian	Henan	China	29° 39′ N	111° 43′ E	Holocene
Hylobatidae gen. indet.	sp.	Linli County	Henan	China	29° 27′ N	111° 37′ E	Holocene
Hylobatidae gen. indet.	sp.	Shimen	Henan	China	29° 36′ N	111° 22′ E	Holocene
Hylobatidae gen. indet.	sp.	Guangnan	Yunnan	China	24° 3′ N	105° 7′ E	Holocene
Hylobatidae gen. indet.	sp.	Longling	Yunnan	China	24° 35′ N	98° 2′ E	Holocene
Hylobatidae gen. indet.	sp.	Luxi County	Yunnan	China	24° 28′ N	103° 47′ E	Holocene
Hylobatidae gen. indet.	sp.	Pu′er	Yunnan	China	23° 3′ N	101° 4′ E	Holocene
Hylobatidae gen. indet.	sp.	Yuanjiang	Yunnan	China	23° 30′ N	102° 0′ E	Holocene
Hylobatidae gen. indet.	sp.	Anji	Zhejiang	China	30° 39′ N	119° 42′ E	Holocene
Hylobatidae gen. indet.	sp.	Tianmu Shan	Zhejiang	China	30° 20′ N	119° 30′ E	Holocene

Boundary dates for the geological epochs are as follows: Pliocene-Early Pleistocene: 1.8 Ma; Early Pleistocene- Middle Pleistocene: 0.78 Ma; Middle Pleistocene – Late Pleistocene: 0.13 Ma; Late Pleistocene – Holocene: 0.001 Ma (10 Ka). Locality data generalized to 1 million: 1.

in Southeast Asia. The study of sea level changes requires an understanding of variations in the structure and volume of oceans, the conformation of ocean basins, and changes in the vertical dimensions of coasts. Readers should appreciate that these details are beyond the scope of this report and that further information should be sought from the relevant primary geological reports (Haq et al. 1987; Fleming et al. 1998; Hall 2001, 2002). Alternating periods of exposure and inundation of portions of the Sunda Platform and Sunda Shelf dramatically affected the distribution of gibbons through time by the creation and elimination of land bridges.

The distribution and dispersal of gibbons in the past was also constrained by the courses of large rivers: the Yangzi to the north, and – at different times – the Mekong, Salween, and Irrawaddy (or Ayeyarwady) successively to the west (Geissmann 2002). These rivers are ancient waterways that share upper reaches in the eastern Himalaya and Heng Duan Mountains, where they have carried large volumes of water through erosion-resistant rocks for tens of millions of years (Chaplin 2005). The trenchant gorges scoured by the rivers have created durable geographic barriers to the dispersal of most terrestrial species and particularly to gibbons who are committed arborealists almost incapable of locomoting on the ground. Through time, gibbons came to occupy more river drainages within Southeast Asia and successively lower-altitude habitats as the animals moved distally along river courses. Changing sea levels and large rivers created opportunities for dispersal and vicariance as well as invasion, extirpation, and reinvasion.

Prior to the estimated origin of the gibbon radiation, sea levels as reconstructed by Haq (Haq et al. 1987) were considerably higher than those at present, and dispersal of mammals into Sundaland was prevented by consistently high sea-level stands. These levels ranged from a low of + 41 m at 16.4 Ma to a high of + 143 m at 15 Ma. By the estimated time of origin of the gibbon radiation, 10.5 Ma, the inundation of large areas of modern coastal Southeast Asia and the Sunda Platform had given way to a major sea-level recession of −80 m, and then another transgression to + 1 m at 9.1 Ma. A sequence of sea-level recessions and transgressions followed in the terminal Miocene and earliest Pliocene: −24 m at 7.9 Ma, + 14 m at 7.0 Ma, and + 90 m at 4.5 Ma. The widely used plate tectonic reconstructions of Southeast Asia by Hall emphasized the movement and deformation of plate blocks (Hall 1996, 1997, 2001, 2002), and all but discounted the importance of changes in sea level (Hall 2002: p. 371) that would have determined the habitability of Sundaland for terrestrial mammals. When these changes are taken into account, what emerges is the picture of a shifting patchwork of forests corridors and coastlines from the latest Miocene onward, which made increasingly southward dispersal of gibbons possible.

Most of the history of gibbons, in particular the early differentiation of the major gibbon sublineages, is not traced by the fossil record. Of the 81 known fossil localities for gibbons, two are from the latest Miocene or earliest Pliocene, two from the Early Pleistocene, 12 from the Middle Pleistocene, 37 from the Late Pleistocene, and 28 from the Holocene. The distribution of fossil gibbon localities is shown in Fig. 7.1.

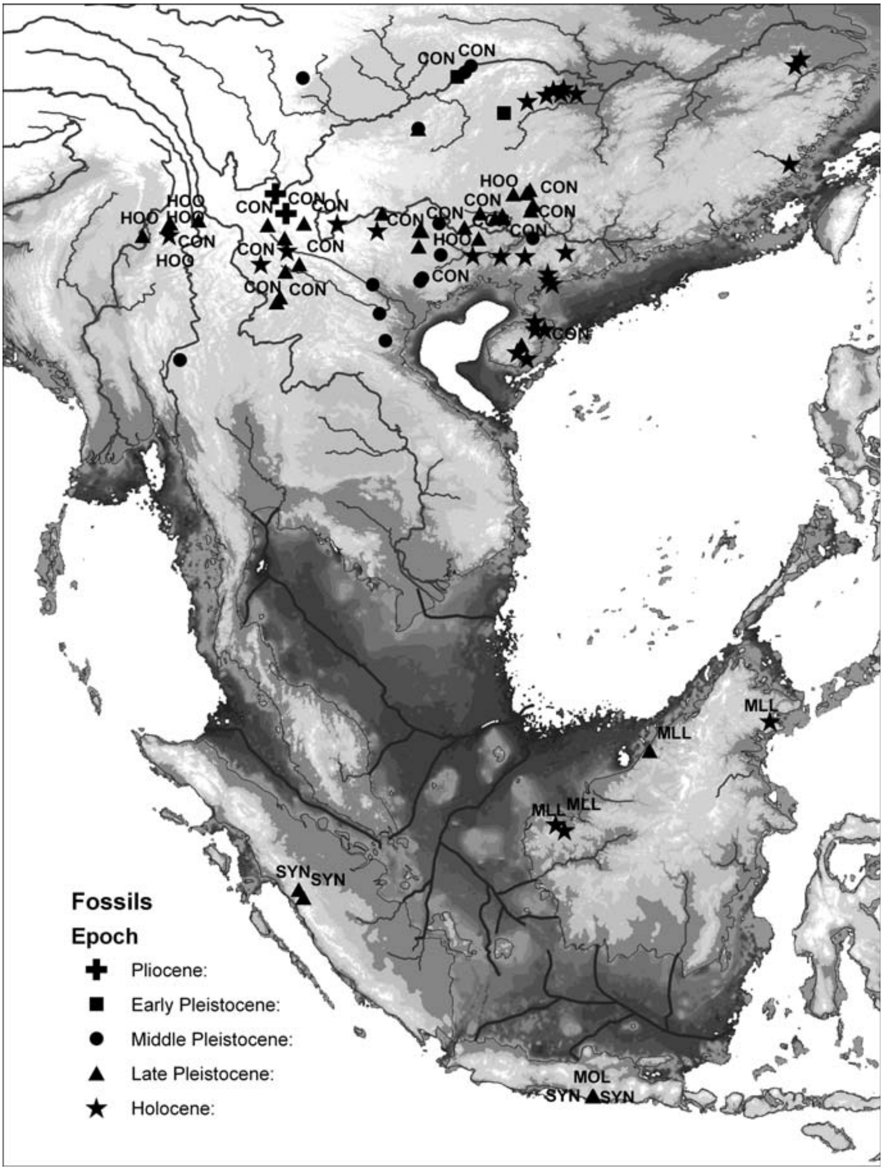

Fig. 7.1 The distribution of fossil hylobatids through time. Genus and species are indicated as follows: SYN = *S. syndactylus*, HOO = *Hoolock hoolock*, CON = *N. concolor*, MLL = *Hylobates muelleri*, MOL = *Hylobates moloch*; fossils that could not be assigned to genus and species are indicated with markers only. Sea levels were modeled at +40 m to −120 m, which are conservative estimates for the extremes of sea-level fluctuation from the later part of the Pliocene to the present

The two earliest hylobatid fossils are of latest Miocene or earliest Pliocene age and were derived from two localities south of the eastward bend of the Yangzi River, north of the Pearl and Red Rivers and east of the Mekong in Yunnan Province of China. They were not assigned to species in their original descriptions. We concur with Chatterjee (2006, this volume) that this region is probably the area of origination for the lineage. This area occupies the middle to southern part of the Yunnan Plateau. Through the later Tertiary, it was an ecologically stable area of moderate elevation (approximately 1000 m) of moist evergreen broad leaf forests that saw high amounts of endemism produced by both refugia and vicariance (Chaplin 2005). Difficult access to the region prevented encroachment from invasives, and also inhibited dispersal (Chaplin 2005). Molecular clock and phylogeographic studies suggest that differentiation of gibbons at the generic level occurred in this area at the end of the Miocene. The sequence and timing of cladogenesis in the gibbon lineage reconstructed by Chatterjee (this volume) is based on a synthesis of molecular studies (Roos and Geissmann 2001; Geissmann 2002; Chatterjee 2006) and shows that crested gibbons (genus *Nomascus*) were the first to branch off the main gibbon lineage, followed by siamangs (genus *Symphalangus*), followed by the genus *Hoolock*, and then *Hylobates*. The details of the likely vicariant events that led to this differentiation are not known, but it is important to note that early lineage-splitting events in gibbon history were not accompanied by long-distance dispersal because most of Sundaland was inundated at this time. The first expansion of the ancestral gibbon range was to the east between the Pearl and Yangzi Rivers, and possibly also between the Pearl and the Red Rivers. Early gibbons probably did not occupy low-altitude, wet evergreen forests.

The first bifurcation of the gibbon lineage was relative to the Paleo-Mekong. The proto-*Nomascus* group spread east of the Mekong and eventually radiated into the southern China and Indochina Bioprovinces, maintaining a distribution initially only east of the Mekong. The gibbons west of the Mekong were the common ancestral stock of *Symphalangus*, *Hoolock*, and *Hylobates*. A gap of over three million years separates the late Tertiary gibbon fossils from two Early Pleistocene hylobatid fossils. One of these comes from a site just south of the Yangzi River in Sichuan Province. This fossil was originally named *Bunopithecus sericus* (Matthew and Granger 1923), but was assigned to *Hylobates* (=*Nomascus*) *concolor* by Gu after a more thorough comparative study (Gu 1989). The other Early Pleistocene fossil is from nearby Hunan.

The Middle Pleistocene saw the westward expansion of gibbons across the headwaters of the Mekong and Salween Rivers into what is now referred to as the Three Rivers Region of northwestern Yunnan Province in China and northeastern Myanmar. Other Middle Pleistocene localities fall immediately south of the Yangzi River in Sichuan Province of China and along the main channel and tributaries of the Pearl River in China and the Red River in Vietnam. One Middle Pleistocene locality is known from north of the Yangzi, and marks the northernmost documented occurrence of a fossil hylobatid. Most Middle Pleistocene gibbons have not been diagnosed to the species level. The expansion of gibbon distributions at this time was made possible by a combination of factors, including environmental amelioration brought about by interglacial climate and changes in the conformation of rivers. Sudden shifts in the courses of rivers and quake dams brought about by tectonic disturbances in this highly seismically active area would have made it possible for gibbons to disperse across rivers and tributaries that previously could not have been crossed.

The gibbons that dispersed west of the Paleo-Salween were *Hoolock hoolock*. This species eventually dispersed north of the headwaters of the Irrawaddy into northern Myanmar, eastern India, and Bangladesh. No gibbon fossils have been found west of the Irrawaddy. The gibbons remaining in the narrow region were constrained by the Salween to the west and the Mekong to the east. This group included the ancestors of *Symphalangus syndactylus* and *Hylobates* spp. These animals began to disperse southward as climatic conditions deteriorated and falling sea levels exposed more of the Sunda Shelf and Sunda Platform. This is attested by a fossil locality lying just east of the Salween River in Thailand. Expansion of the range of gibbons occurred first along the western side of the Mekong in Thailand, and eventually along a forest corridor into the Malay Peninsula and Sumatra. By the end of the Middle Pleistocene and earliest Late Pleistocene, depressed sea levels made possible the colonization of Java and Borneo.

“Sundaland” or the Sunda Shelf is depicted in various configurations on maps of the Pleistocene topography of Asia. At its brief maximum extent, it comprised the area between Borneo, Sumatra, Java, and the south of Indochina (Voris 2000) and covered various geological provinces. The Sunda Platform geologic province extends from north of Natuna Island across to Singapore and the east coast of southern Sumatra to just south of Bangka Island; it then crosses back eastwards to Belitung Island and into southern Borneo, incorporating most of that island’s western and central districts (Bishop 2000a, b; Doust and Noble 2008). The Sunda Platform geologic province is more stable than adjacent areas. Between the Sunda Platform and Java are the North Java Basin and East Java Basin. North of the Sunda Platform are the West Natuna, Panjang, Cardomomes, Mekong, Cuulong, Vung Tau, Malay, and Thai Basins. Unlike the Sunda Platform, these basins have been subjected to extreme deformation. They are being compressed by the Indian and Australian tectonic plates at a rate of about 60 mm per year. The cumulative effect of this movement over the last 10–15 Ma has been hundreds of kilometers of crustal deformation and compression.

Sundaland, as exposed during most of the Late Pleistocene, was a region of low relief, covered with poorly drained forests and swamps and dissected by large rivers (Voris 2000). The course of the major paleo-rivers and land areas of Sundaland is reconstructed in Fig. 7.2. The rivers of Sundaland were large and access across them was limited. Part of northern Sundaland was drained by the Paleo-Siam-Chao Phyra river and encompassed some one million km^2, or approximately half of the area of the Yangzi or Mekong river drainage basins.

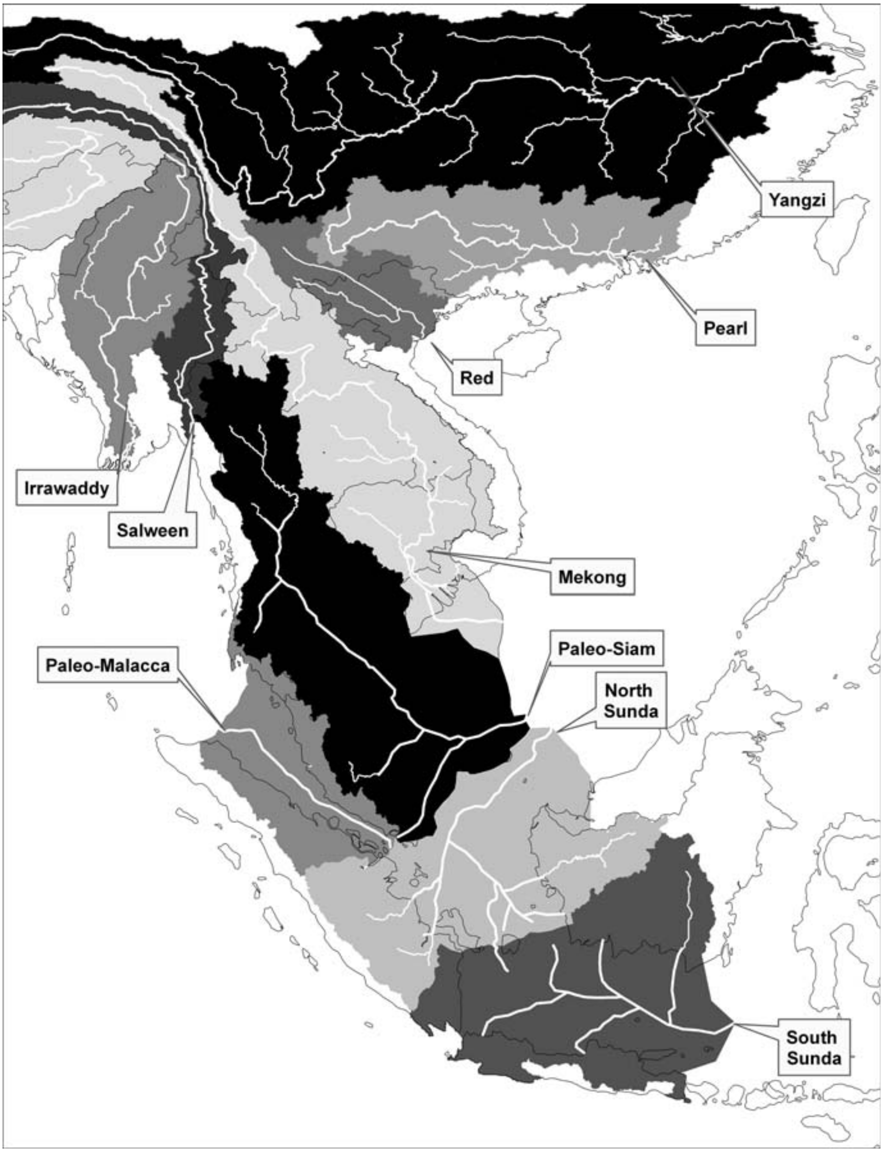

Fig. 7.2 The courses and drainages of the paleo-river of Sundaland, following the methodology and naming conventions of Voris (2000). River courses were drawn with respect to basin geometry and current bathymetry as derived from USGS ETOPO 2 data, and information derived from seismic investigations conducted in connection with oil exploration (Bishop 2000a, b; Nguyen and Hung 2004; Doust and Noble 2008). Continental river courses and catchment areas were derived from USGS HYDRO1K data

The Paleo-North Sunda river drained the remaining roughly 750,000 km^2 of the northern part of the Sunda Platform. The Paleo-South Sunda river drained the southern part of the Sunda Platform and the basin of the Java Sea, an area that encompassed 800,000 km^2. Sumatra was separated from the future Malay Peninsula by the Paleo-Malacca river, which drained an area of 350,000 km^2. Being located in areas of equatorial rainfall, these paleo-rivers carried prodigious volumes of water and would have posed formidable barriers to gibbon dispersal, even during the driest intervals of the Late Pleistocene.

By the Late Pleistocene, a large number of hylobatid fossils mostly assigned to *Nomascus concolor* are recognized within the Pearl River drainage, and thus south of the Yangzi and east of the Mekong in southeastern China. A smaller number assigned mostly to *Hoolock hoolock* were distributed between the Irrawaddy and Salween Rivers in far western Yunnan Province of China and eastern Myanmar. A few were found in the distal extremities of Southeast Asia, with the southern-most fossils attributed to *Symphalangus syndactylus* on the Indonesian islands of Java and Sumatra, *Hylobates moloch* (=*leuciscus*) on Java, and *Hylobates muelleri* on Borneo (Sarawak and Sabah, Malaysia). The pattern and timing of hylobatid dispersal into Sundaland bears similarities to those of freshwater fishes, which were equally constrained by rivers (Yap 2002).

The Holocene witnessed a re-radiation of gibbons into the northern areas along the Yangzi and an expansion of the range of gibbons into nearly all of previously occupied areas. Known Holocene occurrences of hylobatids include clusters of sites in mostly low-lying regions south of the Yangzi River – in Hunan, Guangdong, and Hainan Provinces of China – that have yielded fossils of indeterminate species. Three localities for *H. muelleri* on Borneo are also known. The *lar* group of gibbons probably originated in southern Sundaland and dispersed northward toward the Heng Duan Range, with populations constrained by the tributaries of the Mekong, Salween, and Irrawaddy Rivers. Some *lar* group gibbons eventually became sympatric with *Symphalangus syndactylus*.

Life History, Diet, and the Evolution of Gibbons

The Late Miocene witnessed dramatic changes in the diversity and primacy of catarrhine lineages in Africa and Eurasia, with a marked decline in diversity and distribution of hominoids and a gradual increase in diversity and distribution of cercopithecoids (Jablonski and Kelley 1997; Jablonski et al. 2000; Barry et al. 2002; Jablonski 2005). The radiation of gibbons was a conspicuous and important exception to this trend, but the relative success of the group relative to other hominoids demands an explanation.

Hylobatids and other hominoids are characterized by an advanced age for the onset of reproduction, long gestation periods, long weaning periods, and long interbirth intervals (Table 7.2) (Jablonski et al. 2000). Mammals with such

Table 7.2 Life history parameters of gibbons from China and Southeast Asia compared to *Macaca mulatta* and *Pongo pygmaeus*

Species	Adult mass, male (g)	Adult mass, female (g)	Neonatal mass (g)	Age at first birth	Gestation (d)	Weaning age (yr)	Interbirth interval (yr)
Hylobates lar	5940	5303	389	10	199–215	1.5–2.0	2.0–4.0
Symphalangus syndactylus	10913	10600	537	–	230–235	1.0–2.0	2.0–3.0
Pongo pygmaeus	74483	37143	1750	12.0–15.0	244	3.0–4.0	7.0–8.0
Macaca mulatta	7883	4743	475	4.0	167	0.5–1.0	1.0

Data were collected from the literature on adult body mass (Leigh 1994), neonatal body mass (Hayssen et al. 1993; Geissmann and Orgeldinger 1995), age at first birth (Hayssen et al. 1993), gestation periods (Galdikas and Wood 1990; Hayssen et al. 1993; Markham 1994), weaning age (Chivers and Raemaekers 1980; Treesucon 1984; Hayssen et al. 1993; Lappan 2005), and interbirth intervals (Galdikas and Wood 1990; Hayssen et al. 1993).

slow life histories are characterized by high parental investment in low numbers of offspring per lifetime, and a low intrinsic rate of increase of population. This pattern originally evolved under the more stable environmental conditions of the early and middle Miocene in Eurasia (Kelley 1997), characterized by low to moderate levels of seasonality and more highly predictable regimes of forest productivity (Janis 1993; Morley 2000; Morley 2002). Hominoid life history parameters were established early in the Miocene, when extensive belts of low-seasonality forests were widespread. The highest levels of diversity and the maximum total distribution area of hominoid species were attained when Miocene forests reached their areal maxima, approximately 17–12 Ma (Kelley and Pilbeam 1986; Andrews 1992). Apart from species in the human lineage, no hominoid ever significantly utilized nonforest habitats.

The subtropical and, especially, the tropical forests of the Miocene forests produced juicy fruits and leaf flush on a regular basis and this characteristic undoubtedly sustained hominoid populations living there. Anatomical evidence suggests that at least three groups of Miocene apes, in addition to the hylobatids and orang-utan ancestors, utilized suspensory postures and locomotion, primarily as an adaptation to harvest widely separated, high-quality food items (Andrews et al. 1997). The Hylobatidae took this adaptation to anatomical and behavioral extremes.

Of all the apes, hylobatids have exhibited the most flexibility in terms of abilities to survive periods of environmental change and withstand increases in seasonality. Gibbons maintained distributions in subtropical environments throughout the Pleistocene whereas the orangutan (*Pongo*) and *Gigantopithecus* did not (Jablonski et al. 2000). Large hominoids paid the metabolic penalty of a combination of larger body size and encephalization by not being able to survive in forests in which seasonality had become extreme. When tree fruiting events became so irregular and widely spaced that animals could not maintain their body weight and first female reproduction was greatly delayed, the chances of survival were greatly reduced. Marked increases in seasonality would have had a particularly adverse effect on pregnant or lactating females, who could not forage as widely for preferred foods. Gibbons largely avoided this problem with their smaller body mass and, thus, lower absolute energy requirements. Also in their favor were levels of encephalization comparable to cercopithecoids and a highly energy-efficient mode of locomotion that allowed them to travel swiftly through the forest canopy to reach available high-quality foods. Today, young leaves are a significant component of the diet of most gibbons but, as is the case with larger hominoids, ripe fruits with juicy pulps are undoubtedly their preferred food items (Chivers 1984; Elder this volume). Populations of *Nomascus concolor* inhabiting evergreen broadleaf forests in southwestern Yunnan prefer fruits when they are available, but become nearly exclusively folivorous when they are not (Lan 1993). The ability of gibbons to undertake some food-switching permits them to inhabit the higher altitudes of evergreen broadleaf forests (at approximately 1000–2000 m), but not the higher coniferous forests, which – if they are inhabited by primates at all – are the homes of colobine monkeys like the snub-nosed langurs of China. Of all the hominoids, only gibbons succeeded in subtropical forest environments where others failed, but in habitats of moderate altitude (>1500 m) their populations are stressed and their densities are low. Among the *Hylobates lar* of Khao Yai, Thailand, populations at higher altitudes exhibit lower densities, delayed onset of reproduction, and longer interbirth intervals than those at lower altitudes (Warren Brockelman, pers. comm.). Gibbon food preferences limit them to certain kinds of forest with particular types of food supply (Chivers 1984).

Despite their greater ecological flexibility relative to larger hominoids, hylobatids experienced southern compression of their range because of the episodic and severe climatic changes of the Pleistocene, and the marked fluctuations in environmental seasonality they created. Shifts in gibbon distribution tracked the southward shifts of the tropical and subtropical zones as climates deteriorated, sea levels fell, and Sundaland expanded. Natural populations of animals like gibbons respond to climatic change by latitudinal shifts in abundance or geographic range boundaries or both (Graham et al. 1996; Roy et al. 1996). Environmental changes during the Pleistocene in eastern and southeastern Asia were more marked than in other parts of the Northern Hemisphere, because the local climatic effects of the Himalayas and Qinghai-Xizang (Tibetan) Plateau magnified the orbitally induced climatic fluctuations associated with glacials and interglacials worldwide (Jablonski et al. 2000) and because of immense increases in southerly land mass resulting from exposure of the Sunda Shelf and Sunda Platform. Heightened environmental seasonality at all latitudes, increasing environmental heterogeneity and fragmentation, an increasing potential for physical isolation of populations as a result of habitat fragmentation, and changes in the configuration of biogeographic corridors were the most important consequences of these changes for mammalian populations (Ferguson 1993; Jablonski 1993).

The relatively great antiquity of the gibbon radiation begs the question as to why gibbon species exhibit so little morphological, ecological, or behavioral variation. Warren Brockelman (this volume) has proposed that the relative lack of behavioral diversity within the family Hylobatidae was due to ecological and associated morphological constraints. The fundamental constraints to gibbon diversification were those of food preference and obligate arboreality, which were heritage characteristics handed down from their Miocene ape ancestors (Jablonski and Brockelman 2003). High-quality foods such as ripe fruits and young leaves are not only preferred but also essential for normal reproduction in ape species with slow life history parameters. As for obligate arboreality, the locomotor anatomy – specifically the relatively long forelimbs and short hindlimbs – that is well suited to bridging postures and suspensory locomotion in the high forest canopy also precludes extensive terrestriality. Gibbons are truly prisoners of the forest canopy.

The most morphologically distinct member of the Hylobatidae, the siamang, is the only hylobatid that lives in sympatry with any others – with *H. lar* in peninsular Malaysia and northern Sumatra and with *H. agilis* in southern Sumatra. The distribution of other hylobatid species overlaps little because the animals' shared preference for often widely distributed juicy fruits leads to enforced allopatry. Siamangs, with their diet composed of somewhat more leaves and less fruit than smaller gibbons, have evolved the most monkey-like dental and gut adaptations of the hominoids. Their larger body evolved *pari passu*, being related to lower food quality and the need for longer gut retention times. This may have been related to their use of higher-altitude forests.

The gibbon niche is defined by small body size, energetically efficient arboreal locomotion, small group size, and territorial behavior (Jablonski and Brockelman 2003). Further, the food resource requirements and territorial behavior of gibbons have prevented sympatry between the species (excepting the siamang), and hence largely restricted adaptive radiation within the family.

Summary and Conclusions

The fossil record of the Hylobatidae is not rich, but it is informative. Although fossils representing putative Miocene Hylobatidae do not exist (with the possible exception of *Laccopithecus robustus*), gibbon fossils from the latest Miocene and earliest Pliocene indicate that gibbons probably originated on the Yunnan Plateau, in a region of moderate altitude (about 1000 m) bounded by the Yangzi River to the north, the Pearl and Red Rivers in the south, and the Mekong to the west. Differentiation of the ancestral hylobatid stock into generic lineages probably occurred in the late Miocene and early Pliocene, as suggested by molecular clock analyses, but these cladogenetic events probably were not accompanied by a marked or permanent southward dispersal of gibbons because Sundaland was inundated periodically during the late Miocene and markedly (with a +90 m sea level transgression) at 4.5 Ma. Through time, dispersal of gibbons has been restricted most strongly by rivers, with the courses of the Yangzi, Mekong, Salween, and Irrawaddy rivers confining gibbon dispersal, especially westward. The southward dispersal of gibbons into the southern parts of Sundaland probably occurred only in the Pleistocene and was confined by rivers, mirroring that of freshwater fishes.

The environmental deterioration of the Pleistocene did not affect gibbons as seriously as it did other hominoids. Hylobatids were driven into lower-altitude habitats during the Middle and Late Pleistocene, but they survived probably because of their smaller body size (and absolutely lower food requirements), relatively smaller brains, highly vagile habitus, and food-switching abilities. The gibbon niche may be a highly specialized one, but it has survived the test of time.

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