IZN

International Zoo News

Gibbon
Systematics
and Species
Identification

Cover Illustration: Adult female Javan gibbon *(Hylobates m*oloch), Paignton Zoo, England, 22 October 1988. Notice the sharp white brow band and the distinct white goatee beard typical of this species, and the black cap which is often more prominent in females than in males. (Photo: Thomas Geissmann)

EDITORIAL

This issue ofI.Z.N. is atypical in two respects – it is dominated by a single, unusually long, feature article (which includes four pages of colour plates), and it contains, for the first time in the magazine's history, indexes to the contents of the current volume.

Thomas Geissmann's article 'Gibbon systematics and species identification' is one which I am particularly pleased and proud to be able to publish. A good all-round zoologist, perhaps, should not have favourite species; but the gibbons have had a special place in my affections ever since I first marvelled at them as a child at London Zoo. Their beauty, their agility and grace, the haunting magic of their songs, even (to anthropomorphise for a moment) their gentleness and exemplary family life, seem to give them a unique appeal. Today, of course, like every animal whose sole habitat is the South-east Asian rainforests, gibbons are under threat. More than ten years ago, only five of their taxa were reported to be 'relatively safe' in at least some part of their ranges, and the situation is unlikely to have improved since then. Ultimately, habitat protection is probably their only hope, but ex situ breeding can help in some cases. And for this, reliable species identification is a necessity, both to find suitable placements for the steady flow of confiscated, wild-caught animals, and to enable the existing zoo stock to be used to the best advantage – as Dr Geissmann points out, misidentification and consequent hybridisation are serious problems in zoos. (Surveys of European and North American zoo gibbons in the early 1980s found that over 4% were definitely hybrids, and the real total would undoubtedly be considerably higher.) So the present article – apart from its intrinsic zoological interest – is important as an aid to practical conservation. For reasons of cost it was impossible to include colour photos of infant, juvenile and subadult gibbons, whose appearance often differs considerably from that of their elders. Should funding become available, Dr Geissmann hopes to be able to publish a more comprehensive colour guide to the gibbons at some future date; he would be very glad to hear from anyone who might be able to help with this.

Coincidentally, it was a letter to me from Thomas Geissmann which triggered the changes to I.Z.N.'s presentation which I introduced at the beginning of 1995. The indexes to contributors, books reviewed and general subject-matter, which will in future be a regular feature of the last issue of each year, form a part of the same process. I hope readers will find them useful, as I myself am already starting to do. Ideally, I would like to issue similar indexes to earlier volumes; but realism compels me to admit that I am unlikely ever to do so unaided. The work is very labourintensive, and I have begun to appreciate for the first time why indexers regard their trade as one of the skilled professions! But should any readers with time on their hands fancy taking on the task of indexing one or more earlier volumes, I would be extremely grateful for their help...

Nicholas Gould

466

GIBBON SYSTEMATICS AND SPECIES IDENTIFICATION

BY THOMAS GEISSMANN

[This paper is a revised and much enlarged version of an article which was originally published in German in Zeitschrift des Kölner Zoo Vol.37, No. 2 (1994), pp. 65–78.]

Abstract

A study of wild and captive gibbons and museum specimens, and a survey of the literature suggests that gibbons (genus *Hylobates*) include at least 11, possibly 12 species, which form 4 distinct groups (subgenera *Hylobates*, *Bunopithecus*, *Nomascus*, and *Symphalangus*): These are the 44-chromosome gibbons (including the *Hylobates lar* group and *H. klossii*: 5 species); the hoolock (*H. hoolock*, 1 species); the *H. concolor* group (3, possibly 4 species); and the siamang (*H. syndactylus*, 1 species). A key for the identification of adult gibbons based on visual characteristics is presented, together with colour photographs and distribution maps of all recognised species (11). In addition, diagnostic vocal characteristics of all species are described and illustrated with sonagrams.

Introduction

The gibbons, or lesser apes (genus *Hylobates*), are a relatively small and uniform group of primates. One might assume that the systematic relationships within this group were relatively simple and easily resolved. This does not appear to be the case, however. Although several revisions of gibbon systematics have been published (e.g. Groves, 1972; Marshall and Sugardjito, 1986; Pocock, 1927) and various scenarios have been proposed to describe the radiation of this group (e.g. Chivers, 1977; Groves, 1993; Haimoff *et al*., 1982), the phylogenetic relationships even among the main divisions of the gibbons are unclear (see below).

Nevertheless, research on gibbons during recent years has considerably increased our knowledge on these apes. For instance, a number of field studies have been devoted to social structure and ecology of most gibbon species (review in Leighton, 1987). The occurrence of hybrid zones between some gibbon species are relatively recent discoveries of considerable scientific interest for gibbon systematics (e.g. Brockelman and Gittins, 1984; Mather, 1992). Marshall and Marshall (1976) systematically described, and collected tape-recordings of, the territorial songs of various gibbon species in the wild and demonstrated their importance for species identification. That publication stimulated a large number of additional studies on gibbon vocalisation whose results are of considerable value for gibbon systematics (e.g. Geissmann, 1993; Haimoff *et al*. 1982, 1984; Marshall *et al*., 1986; Mitani, 1987).

Today, gibbons may be considered one of the best studied groups of primates. Many results of the gibbon research from the last 20 years are, however, not available to the non-specialist. These findings have usually been published in hardly-accessible scientific reports and theses, and most of them seem to be very reluctant to find their way into more popular text books and teaching books. For instance, the siamang is often being referred to a distinct genus (*Symphalangus*), although other gibbon subgenera (such as *Nomascus* or *Bunopithecus*) should also be raised to genus rank if *Symphalangus* were recognised as a genus. The Kloss gibbon (*H. klossii*) – although not closely related to the siamang – is still occasionally referred to as ‚dwarf siamang' or *Symphalangus klossii*, and species such as Müller's gibbon (*H. muelleri*) and pileated gibbon (*H. pileatus*) are often ignored or listed as subspecies of the lar gibbon (*H. lar*) (e.g. Berger and Tylinek, 1984).

The *identification* of the various gibbon forms often appears to pose an even major problem, irrespective of the nomenclature adopted. A reliable identification of some gibbon species and subspecies based solely on fur coloration may not be feasible even for the specialist. In such cases, the analysis of vocal characteristics almost always resolves the uncertainty, at least when species identification is required. Unfortunately, it may be too late for a species diagnosis in the proper sense for many zoo gibbons: While visiting European and American zoos, I frequently met hybrid gibbons. In many cases, the owners did not know that their 'Javan gibbons,' 'lar gibbons' or 'hoolocks' were, in reality, mixed pairs or hybrid offspring of such pairs. Believing that they had been breeding pure taxa, some institutions had for years sent their surplus gibbon offspring as pure species to other gibbon holders, and, by doing so, had unknowingly helped spreading the species mixture in the captive population even further.

It is clear, then, that a serious lack of information exists. In the present report I would like to summarise current views on gibbon evolution and systematics and provide an identification key for all currently recognised species. Colour photographs of all species and a description of their songs are presented as an additional aid for species identification. Some other topics which would also be relevant in this context, such as the identification of subspecies and hybrid gibbons, and colour changes in young and maturing gibbons, cannot be covered here. Such a comprehensive treatment would exceed the space limitations of a journal article and must be reserved for future publications.

Gibbon Systematics

It is generally accepted that gibbons, great apes and humans together form the monophyletic group Hominoidea (Groves, 1989). It has also been widely accepted in recent years that the gibbons constitute the sister group to the great apes and humans (Fig. 1), and show the most primitive characteristics within the Hominoidea (Fleagle, 1984). This view is supported by results from comparative studies of a wide array of morphological (Biegert, 1973; Remane, 1921; Sawalischin, 1911; Schultz, 1933, 1973; Wislocki, 1929, 1932), physiological (Hellekant *et al.*, 1990), cytogenetic (Wienberg and Stanyon, 1987) and molecular data (Darga *et al.*, 1973, 1984; Dene *et al.*, 1976; Doolittle *et al.*, 1971; Felsenstein, 1987; Goldman *et al.*, 1987; Sarich and Cronin, 1976; Sibley and Ahlquist, 1984, 1987).

468
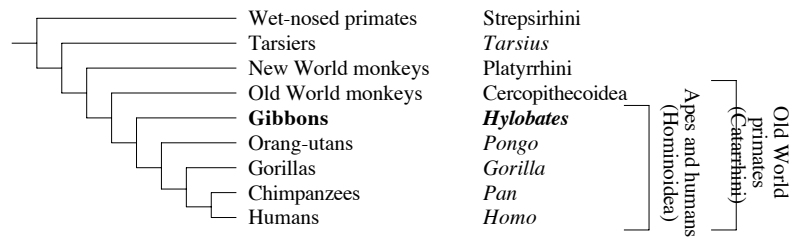
Fig. 1. Systematic position of the gibbons within the primate order.
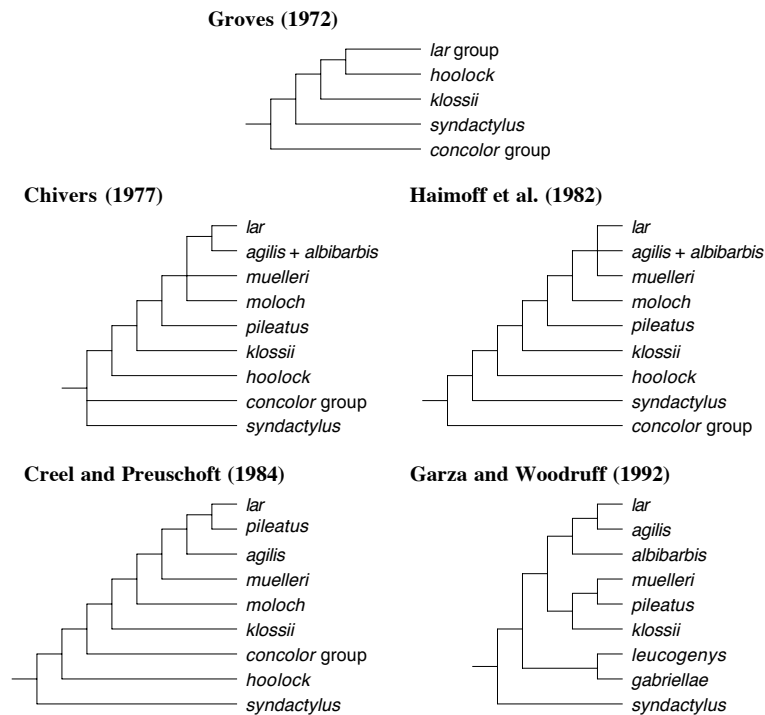
Fig. 2. A comparison of five published representations of the phylogenetic relationships among gibbon taxa.
(References: Chivers, 1977; Creel and Preuschoft, 1984; Garza and Woodruff, 1992; Groves, 1972; Haimoff *et al.*, 1982).

There is considerably less agreement on the phylogenetic relationships among gibbon species; some views are shown in Fig. 2. Several authors suggest that among modern gibbons, the siamang (*H. syndactylus*) was the first species to split off from the main stem (Bruce and Ayala, 1979;

Creel and Preuschoft, 1976, 1984). Others disagree and see the crested gibbons (*concolor* group) in that position (Groves, 1972; Haimoff, 1983; Haimoff *et al.*, 1982, 1984), and according to a third view the siamang and the crested gibbons share a common ancestor not shared by other gibbons (Shafer, 1986; van Tuinen and Ledbetter, 1983, 1989). Apparently, the ‚relationships of the main divisions are very even, and any dichotomy is hard to elucidate' (Groves, 1989).

There is some agreement to the extent that the genus *Hylobates* can be divided into four systematic groups which are summarised in Table 1, and it has been proposed that these should each be referred to a separate subgenus (i.e. *Symphalangus*, *Nomascus*, *Bunopithecus*, and *Hylobates*, respectively) (Marshall and Sugardjito, 1986; Prouty *et al.*, 1983). Each of the four groups is, among other characteristics, identified by a distinctive karyotype; they differ in the diploid number of chromosomes, as shown in Table 1.

Table 1. Main divisions of the genus *Hylobates*.

Subgenus	Diploid number of chromosomes	Other divisions	Species
Hylobates (=44-chromosome gibbons)	44	*Lar* group	*H. agilis*
			H. lar
			H. moloch
			H. muelleri
			H. pileatus
			H. klossii
Bunopithecus	38		*H. hoolock*
Nomascus	52	*Concolor* group	*H. concolor*
			H. gabriellae
			H. leucogenys
Symphalangus	50		*H. syndactylus*

Within the 44-chromosome gibbons (subgenus *Hylobates*), the Kloss gibbon (*H. klossii*) is frequently considered to be the first species to have differentiated from the main stock (Chivers, 1977; Creel and Preuschoft, 1976, 1984; Groves, 1989; Haimoff, 1983; Haimoff *et al.*, 1982, 1984). The remaining group of gibbons is commonly referred to as the *lar* group (Brockelman and Gittins, 1984; Groves, 1972, 1984; Haimoff *et al.*, 1984; Marshall and Sugardjito, 1986; Marshall *et al.*, 1984). According to more recent studies on gibbon vocalisations (Geissmann, 1993) and mitochondrial DNA sequences (Garza and Woodruff, 1992, Kressirer and Geissmann, in prep.), the traditional exclusion of the Kloss gibbon from the *lar* group may not be justified. On the other hand, a closer affinity

470

between the Kloss gibbon and the *concolor* group, as suggested by Berger and Tylinek (1984, p. 174), is not supported by current data.

Morphological differences within the *lar* group are slight (Groves, 1984), karyotypes are virtually identical (Stanyon *et al.*, 1987) and phylogenetic relationships highly speculative (Creel and Preuschoft, 1984); as a result, the *lar* group has been considered as a single species (i.e. *H. lar*) in at least one study (Creel and Preuschoft, 1984), in contrast to other recent studies which recognise 4 (Groves, 1984) or five species (Chivers, 1977; Chivers and Gittins, 1978; Geissmann, 1993; Haimoff, 1983; Haimoff *et al.*, 1982, 1984; Marshall and Sugardjito, 1986; Marshall *et al.*, 1984).

Adopting a Systematic Framework

In order to discuss the phylogenetic relationships within any group of animals, it is necessary at the outset to define clearly the various taxa under comparison. Therefore, the purpose of this chapter is to review briefly the current status of gibbon classification at the species level. The classification adopted here will serve as a provisional working base for the chapters to follow.

During the last 30 years, several reviews of gibbon taxonomy have been published (Chivers, 1977; Chivers and Gittins, 1978; Groves, 1972, 1984, 1993; Marshall and Sugardjito, 1986; Napier and Napier, 1967). New evidence on gibbon systematics became available in such a steady stream that each review was in need of revision only a few years after its publication – and this will without doubt happen to the present paper.

Although still frequently cited, the gibbon taxonomy used by Napier and Napier (1967) has become outdated today because of a considerable amount of new information published after the release of this important textbook. Groves' monograph (1972) not only contains a useful review of the literature on gibbon taxonomy published before 1970, but also remains to this day the most impressive compilation and review of data relating to the topic, including the most comprehensive survey of museum specimens. Chivers (1977), Chivers and Gittins (1978) and Groves (1984, 1993) presented modifications and additions to the taxonomy proposed by Groves (1972). These changes mainly resulted from the increasing knowledge gained from various field studies.

Marshall and Sugardjito (1986) combined data from their own studies on both wild gibbons and museum specimens. Their first-hand knowledge of song- and fur-characteristics of many gibbon populations, together with detailed distribution maps, colour illustrations of the subspecies within the *lar* group, and a review of the recent literature, makes this probably the single most recommendable introduction to gibbon classification at this time. With only few modifications, this paper will be used here as the standard reference for the taxonomy of the lesser apes.

The major modification concerns the crested gibbons (*concolor* group): Whereas Marshall and Sugardjito (1986) recognised only one species (namely *H. concolor*), three species are recognised here. Recognition of the light-cheeked gibbon (*H. leucogenys*) as a separate species from the black crested gibbon (*H. concolor*) was proposed mainly because of anatomical differences between the two taxa, especially in the size of the penis bone (baculum) (Dao Van Tien, 1983; Ma and Wang,

1986). In addition, evidence from museum specimens suggests that areas of sympatry between the forms exist both in China and in Vietnam (Dao Van Tien, 1983; Ma and Wang, 1986).

A suggested species-level differentiation between *H. leucogenys* and *H. gabriellae* was also based on differences in the penis bone (Groves, 1993; Groves and Wang, 1990); however, only one such bone has been studied of *H. gabriellae*. Own studies on large samples demonstrate that all three forms (*concolor*, *leucogenys* and *gabriellae*) differ markedly in their song (Geissmann, 1993, and unpublished data).

A further form, *siki*, whose distribution area is situated between those of *H. gabriellae* and *H. leucogenys*, has previously been identified as a subspecies *H. gabriellae* (Groves, 1993; Groves and Wang, 1990), based on a penis bone at the Muséum National d'Histoire Naturelle in Paris. Unfortunately, this particular bone is not suitable to determine the affinities of *siki*, because it is (1) incomplete and (2) not of *siki* but of *H. leucogenys* (Geissmann, unpublished data). On the other hand, the song of *siki*, although having distinct characteristics, resembles that of *H. leucogenys* more than that of any other form of crested gibbon, including *H. gabriellae* (Geissmann, unpublished data). Likewise, mitochondrial DNA sequences suggest that *siki* is more closely related to *leucogenys* than to *gabriellae* (Garza and Woodruff, 1992, 1994; Kressirer and Geissmann, in prep.). As a result, *siki* is recognised here as a subspecies of *H. leucogenys*. As additional evidence for a close relationship between *H. l. leucogenys* and *H. l. siki*, it should also been noted that the females of both forms are so similar in fur coloration that no distinctive features are known, at present, whereas both differ from females of *H. gabriellae* (Geissmann, unpublished data, see also below).

Ma and Wang (1986) described the subspecies *H. concolor furvogaster* from western Yunnan province (China). This subspecies is not recognised here. My own studies using all museum specimens of this form demonstrated that its distinguishing characteristics are based on the description of subadult females which have not attained their adult coloration. Adult females of '*furvogaster*' do not exhibit these characteristics but resemble females from central Yunnan which have been described as *H. c. jingdongensis*. Whether or not the latter form deserves separation from *H. c. concolor* is currently under examination by the author.

My own studies on Vietnamese museum specimens indicate that there may be one, possibly two previously unrecognised forms of black crested gibbons east of the Red River, which are tentatively referred to in this paper as *H. c.* cf. *nasutus* (sensu Geissmann, 1989) and *H. c.* ssp. nov. In addition, vocalisations of one female *H. c.* cf. *nasutus* from Vietnam as well as songs of *H. c. hainanus* from the island of Hainan differed so radically from those of all other Chinese females of *H. concolor* as to suggest the existence of a previously unrecognised taxon at the species level. These possibilities will be evaluated in a future study.

Within the *lar* group, there is some controversy about the phylogenetic affinities of the Bornean race *albibarbis* (Groves, 1984): whereas vocal characteristics of this gibbon are virtually identical to those of *H. agilis*, its fur coloration shows some similarities to *H. m. muelleri*, which also occurs in Borneo. Both forms share a common border of distribution along the Barito River in Southwest Borneo, and both hybridise at the

headwaters of the Barito River (Brockelman and Gittins, 1984; Marshall and Sugardjito, 1986; Marshall *et al*., 1984; Mather, 1992). As a result, the options for the systematic treatment of *albibarbis* include, among others, making it a subspecies of either *H. agilis* or *H. muelleri*, separating it as yet another species, or combining *H. agilis*, *H. muelleri* and *albibarbis* into one species (Groves, 1984).

In the present study, *albibarbis* is recognised as a subspecies of *H. agilis*, not only because its song is largely identical to that of *H. agilis*, but also because similarities in fur characteristics (Geissmann, 1993, and unpublished data; Marshall and Sugardjito, 1986) are more substantial than recognised in earlier studies. As a result, a comparable affinity between *albibarbis* and *H. muelleri* appears less likely than previously suggested (Groves, 1984).

Of the 11 species recognised here, *H. concolor*, *H. gabriellae* and *H. leucogenys* constitute the *concolor* group (crested gibbons, subgenus *Nomascus*) already mentioned above, whereas the *lar* group contains the species *H. agilis*, *H. lar*, *H. moloch*, *H. muelleri*, *H. pileatus*. The *lar* group and *H. klossii* together will be referred to as 44-chromosome gibbons (subgenus *Hylobates*) (see Table 1).

For most gibbon taxa, several different vernacular names are in use. There are no international guidelines for the creation of such names, but the inconsistency of their use, the inaccuracy or ambiguity of their meaning can sometimes be misleading. In this list, the most frequently used vernacular names are provided for each species. Names not recommended by this study are indicated by an asterisk.

Hylobates agilis – agile gibbon, black-handed gibbon
Hylobates concolor – concolor gibbon, black (crested) gibbon
Hylobates gabriellae – yellow-cheeked (crested) gibbon, red-cheeked (crested) gibbon
Hylobates hoolock – hoolock, white-browed gibbon
Hylobates klossii – Kloss gibbon, dwarf siamang*, dwarf gibbon*, beeloh
Hylobates lar – lar gibbon, white-handed gibbon
Hylobates leucogenys – white-cheeked (crested) gibbon
Hylobates moloch – Javan gibbon, silvery gibbon
Hylobates muelleri – Mueller's gibbon, Bornean gibbon, grey gibbon
Hylobates pileatus – pileated gibbon, capped gibbon
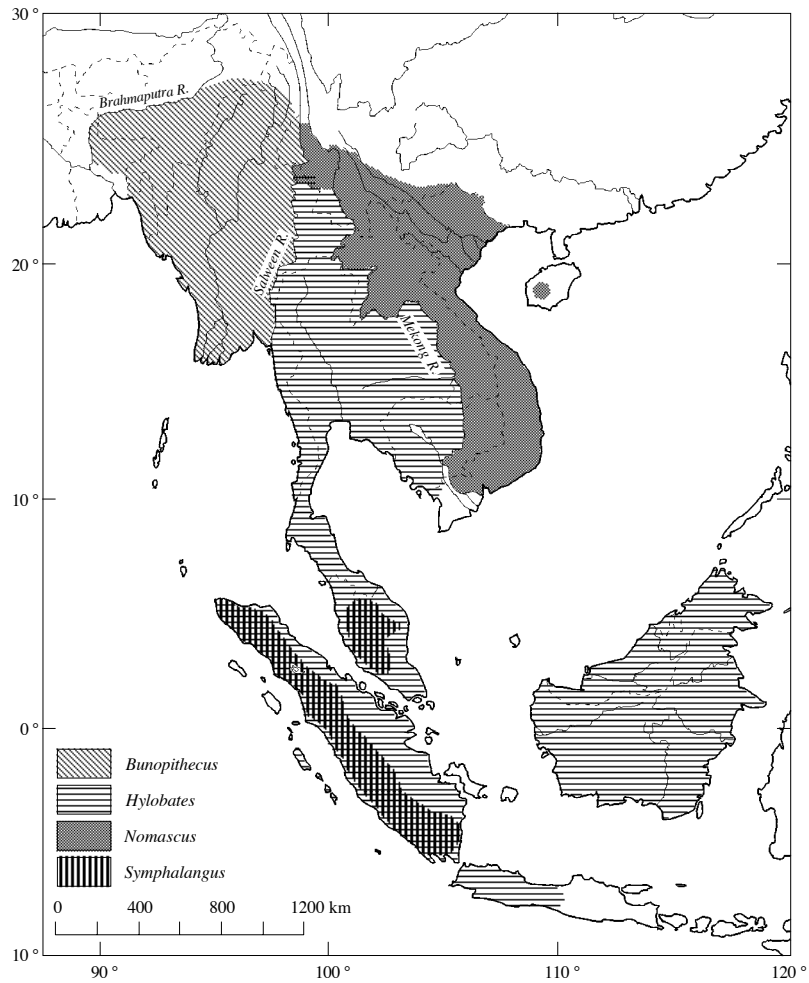*Hylobates syndactylus* – siamang

The classification of the genus *Hylobates* used in this paper is summarised in Table 2.

Gibbon Distribution

The gibbons are distributed throughout the tropical rain forests of Southeast Asia (e.g. Chivers, 1977; Groves, 1972; Marshall and Sugardjito, 1986). A distribution map of the main systematic divisions (i.e. the subgenera) of the genus *Hylobates* is shown in Figure 3; distribution maps of the species of the *concolor* group (subgenus *Nomascus*) and of the 44-chromosome gibbons (subgenus *Hylobates*) are shown in Figures 4 and 5, respectively. In order to keep these maps simple, the distribution areas are depicted like large continuous areas, which they

Table 2. Classification and distribution of the genus *Hylobates*.
(Questionable subspecies are identified with a question mark.)

Genus	Subgenus	Species	Subspecies	Distribution
Hylobates	*Bunopithecus*	*hoolock*	*hoolock*	Assam, Bangladesh, Burma west of Chindwin river
			leuconedys	Burma east of Chindwin river, west Yunnan
	Hylobates	*agilis*	*agilis*	West Sumatra
			albibarbis	Southwest Borneo between Kapuas and Barito river
			?*unko*	Malay peninsula and east Sumatra
		lar	*carpenteri*	North Thailand
			entelloides	Thailand and east Burma
			lar	Malay peninsula
			vestitus	North Sumatra
			?*yunnanensis*	Southwest Yunnan
		moloch		West Java
		muelleri	*abbotti*	West Borneo north of Kapuas river
			funereus	North Borneo
			muelleri	Southeast Borneo east of Barito river
		pileatus		East Thailand, Cambodia
		klossii		Mentawai Islands
	Nomascus	*concolor*	*concolor*	North Vietnam, central Yunnan east of Black River
			?*jingdongensis*	Central and west Yunnan, east of Salween river
			hainanus	Hainan Island
			ssp. nov.	Northeast Vietnam, east of Red River
			cf. *nasutus*	Northeast Vietnam: Hinterland of Hon Gai
			?*lu*	Northwest Laos
		leucogenys	*leucogenys*	Laos, north Vietnam, south Yunnan
			siki	Central- Laos, central Vietnam
		gabriellae		South Laos, south Vietnam, West Cambodia
	Symphalangus	*syndactylus*	?*continentis*	Malay peninsula
			syndactylus	Sumatra

474

Fig. 3. Distribution of the gibbon subgenera: *Bunopithecus* (*H. hoolock*); *Hylobates* (6 species); *Nomascus* (3 species); *Symphalangus* (*H. syndactylus*).
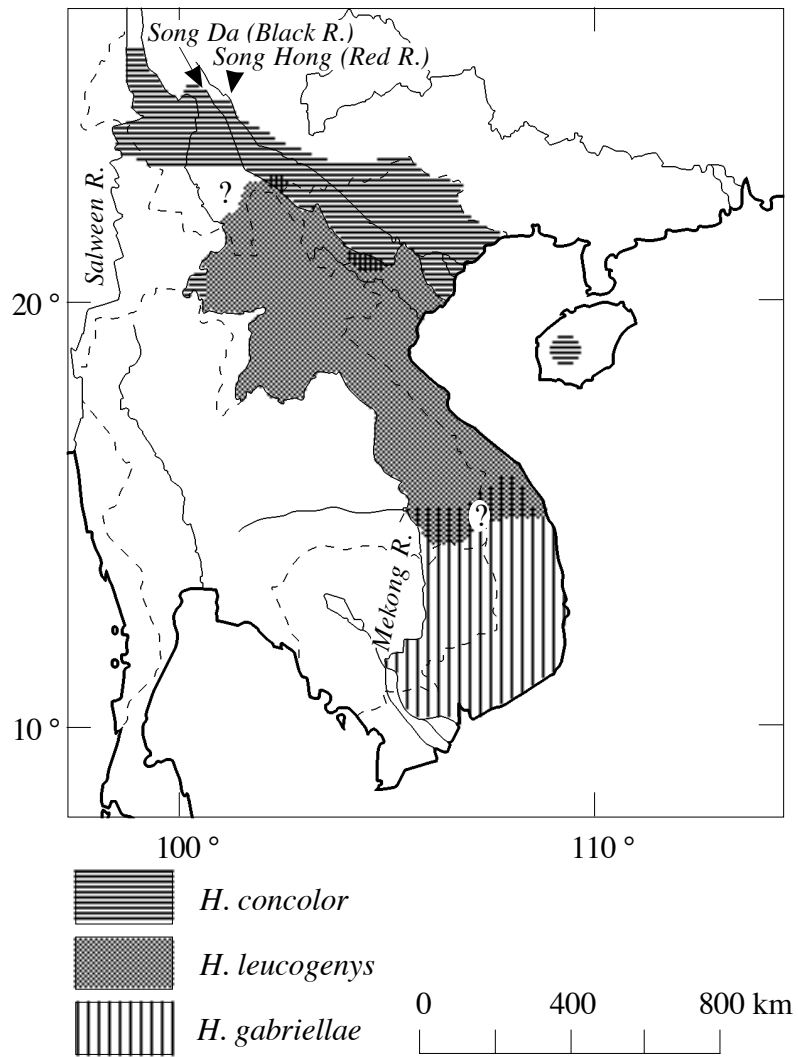
(References: Chivers, 1974; Chivers and Gittins, 1978; Fooden *et al.*, 1987; Ma and Wang, 1986; Zhang *et al.*, 1992).
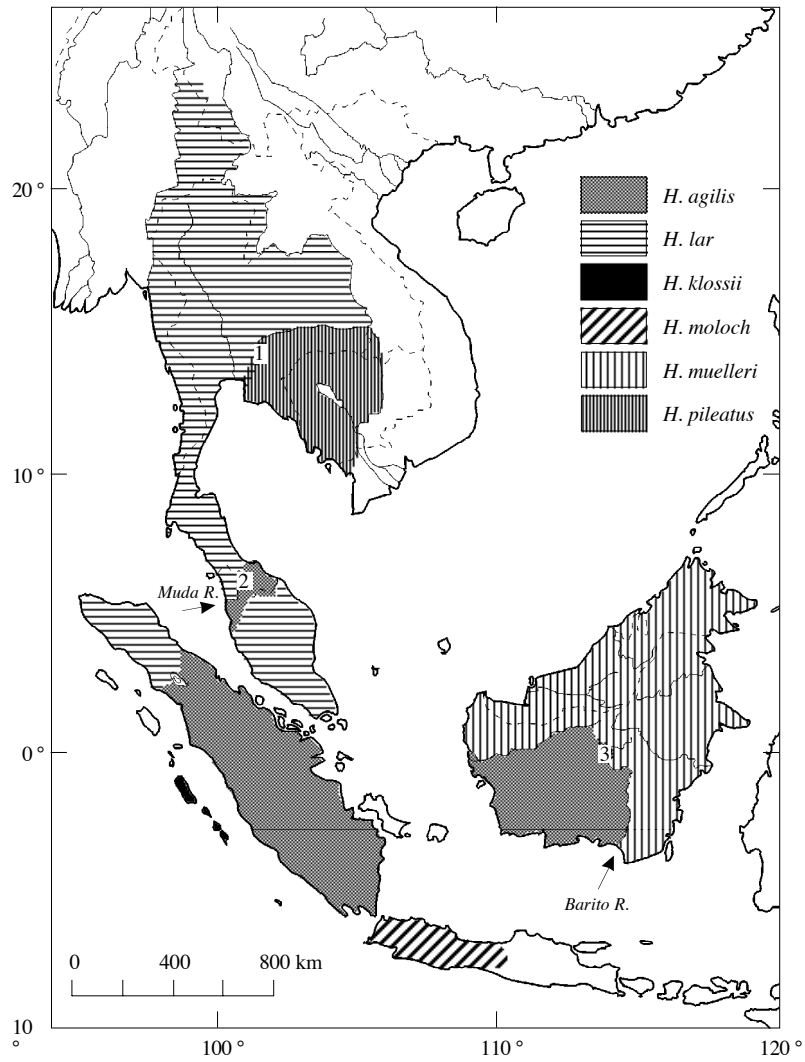
Fig. 4. Distribution of the species of the subgenus *Hylobates*.

(References: Chivers and Gittins, 1978; Geissmann, 1991; Ma and Wang, 1986; Marshall and Sugardjito, 1986).

Nos. 1-3 refer to areas of sympatry and hybridisation which are described in the text.

Fig. 5. Distribution of the species of the subgenus *Nomascus*.

(References: Fooden *et al.*, 1987; Geissmann, 1989 and unpublished data; Groves, 1993; Groves and Wang, 1990; Ma and Wang, 1986).

probably were in the origin. Mainly as a result of habitat destruction, present distributions are considerably more fragmented than indicated in these figures, often consisting of isolated – and sometimes very small – patches of more or less virginal forest. Maps of the remaining areas of the tropical forests in Asia are shown in Collins *et al.* (1991).

Gibbon species are almost everywhere separated by rivers and straits. The only extensive degree of sympatry is between the siamang and the *lar* group and was probably made possible by the strong size difference between them: Over the whole range of its distribution, the siamang occurs in sympatry with either *H. agilis* or *H. lar*. A small area of sympatry apparently exists (or existed) between the *concolor* group (*H. concolor*) and the *lar* group (*H. lar*) in southwestern Yunnan (see Fig. 3) (Ma and Wang, 1986; Zhang *et al.*, 1992).

Within the *lar* group, three areas of sympatry with some hybridisation are known. They are numbered in Figure 4 as follows:
1) *H. lar* and *H. pileatus* at the headwaters of the Takhon River in Khao Yai National Park, about 120 km NE of Bangkok (Thailand). As late as 1925, sympatry between these two species apparently also extended to about 80 km SE of Bangkok (Geissmann, 1991), but gibbon habitat now appears to have been destroyed in most parts of this zone. The area of overlap in the Khao Yai National Park is about 100 km^2, where hybrids constitute about 5% of the breeding population (Brockelman and Gittins, 1984; Marshall and Sugardjito, 1986; Marshall and Brockelman, 1986).
(2) *H. agilis* and *H. lar* at the headwaters of the Muda River in the north-western part of Peninsular Malaysia. A small number of mixed groups and hybrids have been found there on the shores of a artificial lake (Brockelman and Gittins, 1984; Gittins, 1978).
(3) *H. agilis* and *H. muelleri* at the headwaters of the Barito River in Kalimantan (Brockelman and Gittins, 1984; Marshall and Sugardjito, 1986). This area is particularly interesting: a zone of at least 3,500 km^2 is inhabited by an apparently stable hybrid population (Mather, 1992). No pure-species individuals have been found in the area, suggesting that gene flow from the adjacent pure populations into the area must be very limited.

Contact zones between species of the *concolor* group are less well known. Small areas of sympatry have been reported to occur between *H. concolor* and *H. leucogenys* in southern Yunnan (China) and northern Vietnam (Dao Van Tien, 1983; Ma and Wang, 1986). A possible wild-born hybrid between these two species has been described by Geissmann (1995). A contact zone of unknown extent, possibly with some hybridi-sation, may occur between the respective distribution areas of *H. gabriellae* and *H. leucogenys siki* in southern Vietnam and Laos (see Fig. 5), but not much data on that zone is available. Groves (1972) regards museum specimens from Saravane (Laos) as intergrades between *gabriellae* and *siki*. Gibbon songs from Xe Piane (southern Laos) appear to be intermediates between *gabriellae* and *siki*. Gibbon songs from the Bolovens Plateau (southern Laos, NE of Xe Piane) and from Bach Ma (central Vietnam) sound like *siki*, but Museum specimens from the same localities (American Museum of Natural History, New York, and Natur-historiska Riksmuseet, Stockholm, respectively) clearly look like *gabriellae*.

While Chinese gibbons today are restricted to southern Yunnan and Hainan (Fooden *et al.*, 1987; Geissmann, 1989; Groves and Wang, 1990;

478

Ma and Wang, 1986), their distribution range extended as far north as the Yellow River in historical times (Gao *et al.*, 1981; van Gulik, 1967; Zhang *et al.*, 1992). The identity of these gibbons is unclear. Although the more southern populations were, in all probability, members of the *concolor* group, Pleistocene fossils (mainly confined to individual teeth) from the more northern part of this now gibbon-less area have been referred to both *H. concolor* and *H. hoolock* (Groves, 1972; Gu, 1989; Marshall and Sugardjito, 1986). Several old Chinese paintings of gibbons are reproduced in Van Gulik (1967). At least the most naturalistic of these paintings strikingly resembles *H. hoolock*. It was painted by Yi Yuanji (I Yüan-chi) (*ca* A.D. 1000–1064), who had reportedly wandered all over south Hubei and north Hunan Provinces in order to observe wild gibbons.

Identification Key

The following identification key includes all currently recognised gibbon species, but applies to adult individuals only. The body weights refer to adult wild animals (Geissmann, 1993); body weights of adult zoo gibbons may be slightly higher. Colour plates of all species and some subspecies and additional notes on the identification of selected subspecies are provided in Figures 9–36.

1a – Completely black, without light pattern: **2**
1b – Not black or not completely black: **4**
2a – Body weight 8–15 kg;
  – large, inflatable throat sac;
  – males with long genital tuft (*ca* 13.5 cm): *H. syndactylus* (Fig.36)
2b – Body weight lower than 11 kg;
  – throat sac very small or absent;
  – genital tuft in males short and inconspicuous (less than 6 cm): .**3**
3a – Body weight 5–7 kg;
  – no throat sac;
  – crown fur without crest: ....*H. klossii* (Fig. 25)
3b – Body weight 6–10 kg;
  – throat sac very small and visible only when inflated during certain vocalisations;
  – crown fur stands straight up, with prolonged hairs forming a crest: ....*H. concolor*, male (Fig. 28)
4a – Almost completely black, but with light (whitish or yellowish) elements (facial pattern, genital tuft, hands and feet): **5**
4b – Not dominantly black: **10**
5a – Crown fur stands straight up, with prolonged hairs forming a crest;
  – body weight 6–10 kg;
  – light cheek beard: **6**
5b – Crown without crest;
  – body weight 4–9 kg;
  – light cheek beard present or absent: **7**
6a – Cheek beard pale yellow or orange, standing out on sides as if 'brushed' outwards, with the hairs spreading out from the corners of the mouth like a fan;
  – fur on chest rusty brown, not black: *H. gabriellae*, male (Fig. 30)
6b – Cheek beard white, rarely pale yellow, not 'brushed' outwards;
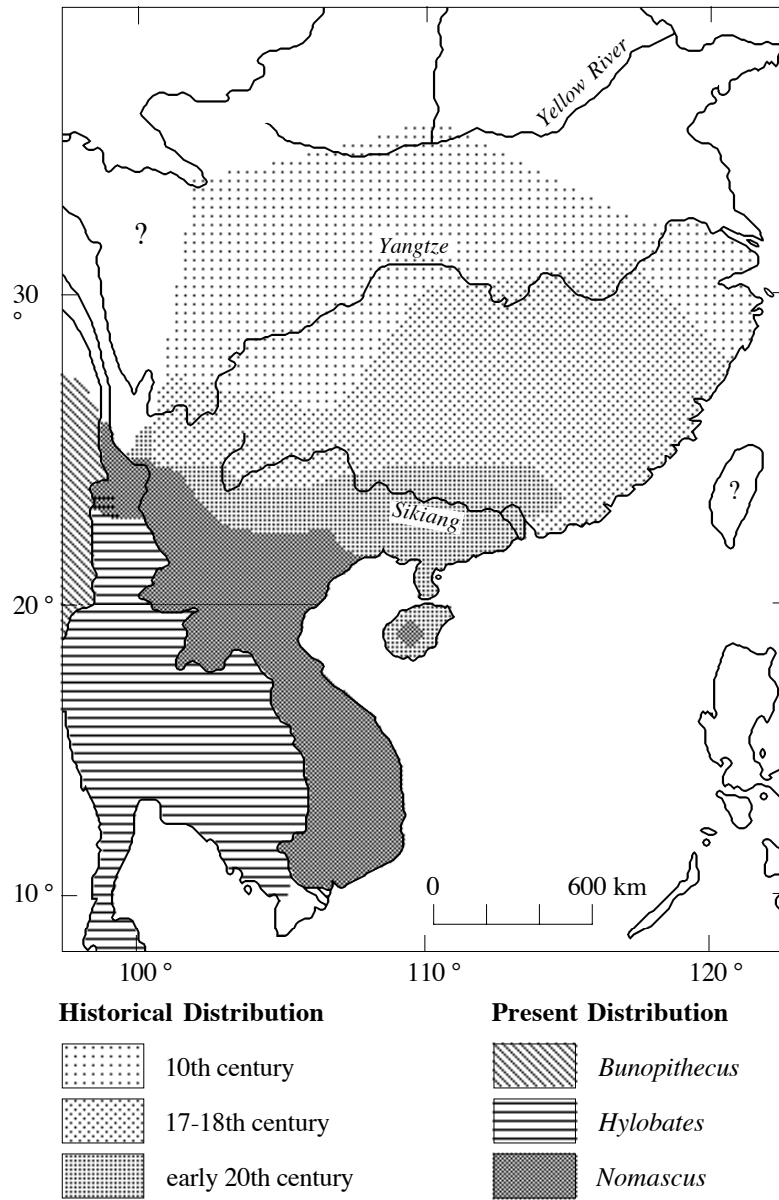
Fig. 6. Historical and present distribution of gibbons in China and adjacent regions.

(References: Gao *et al.* 1981; van Gulik, 1967; Zhang *et al.*, 1992).

-   – fur on chest black: ....*H. leucogenys*, male (Figs. 32, 35)
7a – Fur on hands and feet white: **8**
7b – Fur on hands and feet not white: **9**
8a – White face ring relatively broad and usually complete;
    – no light corona around crown of head;
    – hands and feet white up to wrist and ankle, respectively;
    – genital tuft not white: ....*H. lar* (Fig. 15)
8b – White face ring relatively thin, broad only above eyes;
    – light corona around crown of head;
    – hands and feet white only distally of wrist and ankle, respectively;
    – white genital tuft: .... *H. pileatus*, male (Fig. 23)
9a – White brow band;
    – body weight 6–9 kg;
    – no light cheeks;
    – distinct goatee beard;
    – long genital tuft (*ca* 7.5 cm): ....*H. hoolock*, male (Fig. 26)
9b – White or grey brow band (often reduced in older females);
    – body weight 4.5–7 kg;
    – males often with light cheeks (grey or whitish), females often without these;
    – no distinct goatee beard;
    – males with distinct, but relatively small genital tuft (*ca* 5 cm): *H. agilis* (Fig. 10)
10a – Back and limbs pale yellow, yellow, orange or beige brown, not grey or dark brown;
    – black cap usually set off sharply from surrounding lighter fur, with crown fur (including cap) standing straight up;
    – body weight 6–10 kg: **11**
10b – Back and limbs pale yellow, yellow, orange or beige brown, but also grey or dark brown;
    – black cap, if present, with crown hairs lying flat
    – body weight 4–9 kg: **13**
11a – Fur on chest (and sometimes belly) black or dark brown, contrasting with light back: *H. concolor*, female (Fig. 29), but excluding *H. c. hainanus* or *H. c.* ssp. nov.
11b – Fur on chest and belly light, as back: **12**
12a – Face ring usually yellowish (rarely white), often not contrastingly lighter than neck or incomplete;
    – cheek fur usually standing out on sides, as if 'brushed' outwards, with the hairs spreading out from the corners of the mouth like a fan: ....*H. gabriellae*, female (Fig. 31)
12b – Face ring usually white and distinctly lighter than neck, often thin, but usually complete;
    – cheek fur not standing out on sides: *H. leucogenys*, female (Figs. 33, 34) or *H. c. hainanus* or *H. c.* ssp. nov., female
13a – Crown fur lying flat and being light beige, contrastingly lighter than dark brown cheeks;
    – body weight 6–9 kg;
    – a thin stripe of white hair starts from cheeks and crossing the face below the eyes goes upwards across the nasal ridge;
    – distinct light goatee beard: ....*H. hoolock*, female (Fig. 27)

13b – Crown fur variably lying flat or standing up, not contrastingly lighter than cheeks;
  – body weight 4–8 kg;
  – no stripe of white hair below eyes and across nasal ridge;
  – with or without distinct light goatee beard: **14**

14a – Cap and ventral area black, both sharply set off from surrounding light grey fur; ventral shield three-cornered, with lower tip reaching genital area;
  – back and limbs light grey or cream;
  – no light face ring; thin white brow band may be present but is usually lacking;
  – long, white temple fringes hanging over black cheek region and ears: ....*H. pileatus*, female (Fig. 24)

14b – Cap and ventral area may or may not be darker than surrounding fur; if these areas are black, they are rarely set off sharply and the ventral area has no distinctly three-cornered pattern;
  – back and limbs light or dark, of variable coloration;
  – with or without light face ring; light brow band usually present;
  – no long, white temple fringes hanging over black cheek region and ears: **15**

15a – White hands and feet;
  – fur coloration variable: pale yellow, yellow, beige brown, hazel, dark brown (or black, see also **8a**), but not grey;
  – usually no dark cap and no dark ventral area (if present, these areas are brown or dark brown, not blackish);
  – face ring white and usually complete: ....*H. lar* (Figs. 14, 16)

15b – Hands and feet not white;
  – fur coloration variable like **15a**, but may also be grey;
  – with or without dark (dark brown or blackish) cap and dark ventral area;
  – face ring only partly white, usually incomplete, often reduced to brow band: **16**

16a – Silvery grey fur coloration; only cap and ventral area may be contrastingly darker (dark-gray or black) in some animals;
  – brow band broad and whitish, usually distinct and sharply set off, pointed laterally of the eyes;
  – distinct, forward projecting, whitish goatee beard: *H.   moloch* (Figs. 17, 18)

16b – Fur coloration variable; grey individuals are mouse grey rather than silvery grey; cap, underparts and limbs may be contrastingly darker (dark grey, blackish brown or black) than back; hands and toes contrastingly black in some animals;
  – brow band variable in both coloration (whitish, light grey, light buff) and extent (broad, thin, absent);
  – no distinct, forward projecting, whitish goatee beard: **17**

17a – Fur coloration variable: mouse grey, grey brown, hazel, or dark brown, but not yellow;
  – feet may be distinctly paler than legs in some animals (but not white as in *H. lar*);
  – light brow band very variable in its extent, more or less distinct, but rarely missing;

- usually no distinctly light cheek patches;
- genital tuft of male very small (*ca* 2.5 cm) and usually blackish: ....*H. muelleri* (Figs. 19–22)

17b – Fur coloration variable: pale yellow, yellow, beige brown, grey brown, nut-brown, dark brown (or almost black, see also **9b**);
- feet not distinctly paler than legs;
- brow band usually white, but may be completely absent in older blackish females;
- males often with grey, whitish or pale brownish cheek patches (often joined under the chin), females often without these;
- males with distinct, but relatively small genital tuft (*ca* 5 cm) which may be of contrastingly light colour in some brown animals (intermediate phase), but not contrasting with ventral fur in others: ....*H. agilis* (Figs. 9–13)

It should be noticed that even with this key, species identification of some adult gibbon individuals may remain problematic if based solely on characteristics of fur coloration. Some *H. muelleri abbotti*, for instance, show a considerable resemblance to *H. moloch* (especially to males), many *H. agilis albibarbis* resemble *H. muelleri muelleri*, and some dark *H. muelleri funereus* are very similar to the dark phase of *H. agilis* from Sumatra and the Malay Peninsula. These problems can usually be resolved easily if vocal characteristics of the animals in question are also used for the identification process. These characteristics are described in the following section.

Subspecies identification is, in many cases, even more difficult. This may, to some degree, be related to questionable subspecies descriptions, in the first place, as indicated in Table II (see also legends to Figs. 11 and 14). Of other subspecies, we simply do not know enough diagnostic criteria, often making it impossible to identify individual animals of unknown provenience. For instance, the number of adult females of *H. leucogenys siki* available in zoos and museum collections is not sufficient to determine which fur characteristics, if any, reliably distinguish it from female *H. l. leucogenys*. No individuals of *H. concolor hainanus* and *H. c.* ssp. nov. are currently known to exist in captivity. Females of these taxa lack the dark ventral fur of other subspecies of *H. concolor* and, thus, show a striking similarity to females of *H. leucogenys*, although they differ from the latter in their song (Geissmann, in prep.).

Future studies may reveal more reliable characteristics for subspecies identification. A particular potential in this respect may be expected from molecular studies using hair roots (e.g. Garza and Woodruff, 1992, 1994; Kressirer and Geissmann, in prep.), but the method is still expensive.

Song Vocalisations

All species of gibbons are known to produce elaborate, species-specific and sex-specific patterns of vocalisation, often referred to as 'songs' (Haimoff, 1984; Marshall and Marshall, 1976). Songs are loud and complex and are mainly uttered at specifically established times of day. In most species, mated pairs may characteristically combine their songs in a relatively rigid pattern to produce coordinated duet songs. Several functions have been attributed to gibbon songs, most of which

emphasise a role in territorial advertisement, mate attraction and maintenance of pair and family bonds (Haimoff, 1984; Leighton, 1987).

Gibbon song vocalisations are typically of pure tone, with the energy concentrated in the fundamental frequency. Depending on species, the fundamental frequency of song vocalisations ranges between 0.2 and 5 kHz.

In recent years, vocal characteristics have been used to assess systematic relationships among hylobatids and to reconstruct their phylogeny (Creel and Preuschoft, 1984; Geissmann, 1993; Haimoff, 1983; Haimoff *et al.*, 1982, 1984; Marshall *et al.*, 1984).

Female Song Contributions

The most prominent song contribution of female gibbons consists of a loud, stereotyped phrase, the great call. Depending on species, great calls typically comprise between 6-100 notes, have a duration of 6–30 seconds. The shape of individual great call notes and the intervals between the notes follow a species-specific pattern (Geissmann, 1993; Haimoff, 1983, 1984; Marler and Tenaza, 1977; Marshall and Marshall, 1976; Marshall and Sugardjito, 1986).

Whereas mated females of *H. klossii* and *H moloch* have been reported to produce solo song bouts, mated females of other species usually confine their singing behaviour to duet song bouts only. A female song bout is usually introduced by a variable but simple series of notes termed the introductory sequence; it is produced only once in a song bout. Thereafter, great calls are produced with an interval of about two minutes. In the intervals, females usually produce so-called interlude sequences consisting of shorter, more variable phrases which in many species bear some resemblance to male phrases described below. These phrases are termed 'female short phrases' here. The typical female song bout hence follows the sequential course *ABCBCBCBC...*, where *A* stands for the introductory sequence, while *BCBCBC...* represent the alternating interlude sequences and great call sequences (Haimoff, 1983, 1984; Raemaekers *et al.*, 1984). An exception to this rule are the crested gibbons (*concolor* group), where female song contributions include great calls or aborted great calls only, and where no equivalents of introductory sequence and interlude sequences are known (Haimoff, 1983, 1984). Female song bouts usually have a duration of less than 30 minutes.

Male Song Contributions

As a rule, adult males do not produce great calls, but 'male short phrases' only. Whereas female great calls remain essentially unchanged throughout a song bout, males gradually build up their phrases, beginning with single, simple notes. As less simple notes are introduced, these notes are combined to increasingly complex phrases, reaching the fully developed form only after several minutes of singing (Mitani, 1988; Raemaekers *et al.*, 1984; Tenaza, 1976). Although fully developed male phrases in most species are more variable than female great calls, they, too, show species-specific characteristics in note shape and spacing (Haimoff, 1983, 1984; Marler and Tenaza, 1977; Marshall and Marshall, 1976; Marshall and Sugardjito, 1986).

Whereas mated males of most gibbons species may produce solo song

bouts, mated males of *H. hoolock*, *H. syndactylus* and all crested gibbons (*concolor* group) usually sing in duet with their females only. Duet songs are described below. Males may engage in uninterrupted song bouts of considerable length, sometimes up to more than two hours.

Duet Songs

During duet songs, mated males and females combine their song contributions to produce complex, but relatively stereotyped vocal interactions (Haimoff, 1983, 1984; Marler and Tenaza, 1977; Marshall and Marshall, 1976; Marshall and Sugardjito, 1986). The sequential pattern of duet song bouts is largely similar to that of female song bouts described above (i.e. *ABCBCBCBC…*). Both pair partners contribute to an introductory sequence at the beginning of the song bout (*A*). Thereafter, interlude sequences (*B*) and great call sequences (*C*) are produced in successive alternation. During interlude sequences, males usually progressively develop their phrases from short and simple to longer, more complex series of notes, similar to the development of their phrases in male solo songs described above. In most species, females participate in interlude sequences with short phrases, as described for their solo songs.

During great call sequences – announced by females of the *lar* group by rhythmical hoots – the male becomes silent and does not resume calling until near or shortly after the end of the female's great call, when he will produce a coda which concludes the great call sequence. The coda resembles other male short phrases, but is more stereotyped. It usually interrupts the progressive building-up of the male short phrases described above by being more advanced in development than those uttered during the interlude sequences. *Hylobates pileatus*, *H. hoolock* and *H. syndactylus* are unusual among gibbons in that males vocalise not only at the end of the female's great call, but also during the great call. *H. moloch* and *H. klossii* are unusual in that males of these species are not known to produce codas. There is some controversy about whether these two species produce duet song bouts at all (as discussed in Geissmann, 1993). Duet song bouts, like female song bouts, usually have a duration of less than 30 minutes.

At the climax of a great call, the female typically exhibits a locomotor display, usually accompanied by her mate in the duetting species. The short and acrobatic bout of vigorous brachiation frequently includes branch shaking and (presumably intentional) breaking off of dead branches (e.g. Carpenter, 1940; Chivers, 1974; Ellefson, 1968; Kappeler, 1984).

Species Descriptions

In the present section, the vocal characteristics of each species and the type of call bout produced by mated animals are briefly described.

Figure 7 provides sonagrams of great call sequences of all gibbon species. These vocalisations have been recorded from captive specimens by the present author, with the exception of the female *H. klossii*, which was not kept in any western zoo during the period of this study. The latter sonagram was prepared from a tape-recording made in South Pagai by Dr R.R. Tenaza. Great calls recorded in the wild (Marshall and Marshall, 1976; Marshall and Sugardjito, 1986) are virtually identical to those recorded from captive gibbons during the present study.
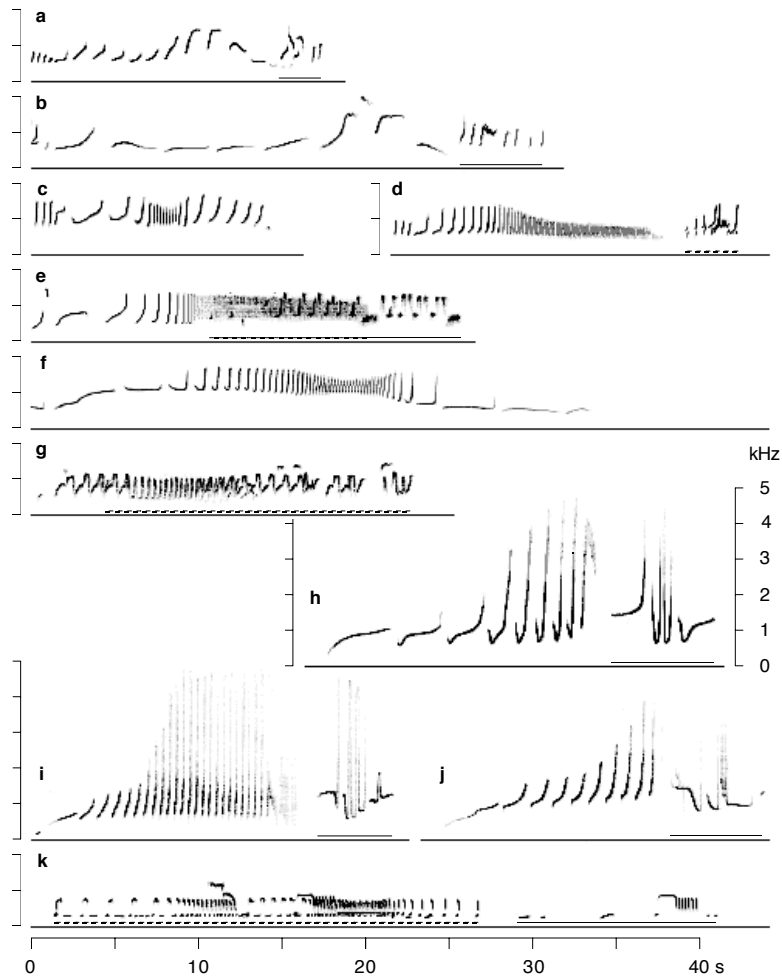
Fig. 7. Sonagrams of great call sequences of all gibbon species.

Sonagrams c and f are excerpts from female solo song bouts; all other sonagrams show duets. Male solo contributions to duets are underlined with a solid line, synchronous male and female vocalisations are underlined with a dashed line. (a) *H. agilis* (Asson Zoo, 31 May 1988); (b) *H. lar* (Paignton Zoo, 20 Oct. 1988); (c) *H. moloch* (Munich Zoo, 16 July 1987), (d) *H. muelleri* (Paignton Zoo, 22 Oct. 1988); (e) *H. pileatus* (Zürich Zoo, 5 May 1988); f. *H. klossii* (South Pagai, 27 Nov. 1987, rec. by R. R. Tenaza); (g) *H. hoolock* (Kunming Zoo, 27 July 1990); (h) *H. concolor* (Xujiaba, Ailao Mountains, 1 Aug. 1990); (i) *H. leucogenys* (Paris, Ménagerie du Jardin des Plantes, 17 May 1988); (j) *H. gabriellae* (Mulhouse Zoo, 13 Sept. 1988); (k) *H. syndactylus* (Metro Zoo, Miami, 31 July 1988).

The great call sequences in Figure 7 are excerpts from duet song bouts of all gibbon species where such duets are known to occur (i.e. all except *H. moloch* and *H. klossii*). Male contributions uttered at the same time as female vocalisations are underlined with a dashed line, while those uttered solo are underlined with a solid line.

Figure 8 provides sonagrams of fully developed male phrases of all gibbon species, all recorded from captive specimens by the present author, excepting the solo song of a male *H. concolor* (recorded in the Ailao Mountain Reserve in China by the present author) and that of a solitary *H. hoolock* (recorded at the Kunming Institute of Zoology by Mr. Lan Daoying). Again, the male phrases recorded from captive gibbons are virtually identical to those recorded in the wild (Marshall and Marshall, 1976; Marshall and Sugardjito, 1986).

H. agilis: Short phrases consisting of simple hoots, more complex hoots ('whoo-aa') and bi-phasic hoots are uttered by males and females (see Fig. 8a). Bi-phasic hoots consist of notes alternatingly produced during exhalation and inhalation ('whoo-aa'). Some males were heard to produce relatively soft, squealing sounds between their short phrases, similar to males of *H. muelleri*. Female great call consisting of long notes of modulated frequency. A first, often very weak climax in frequency is reached at the beginning of the great call; a second, more pronounced climax of higher frequency notes occurs near the end of the great call. Male produces coda (Fig. 7a). Male solo song bouts and duet song bouts.

H. lar: Short phrases consisting of simple hoots, various more complex hoots, and specific quaver notes produced by tremulous opening and semi-closing of the mouth during long hoots (Fig. 8b). Short phrases produced by males and females, but quaver notes are typically produced by males only. Female great call very similar to that of *H. agilis*, but usually longer, with longer notes, and with more pronounced first climax, and fewer notes dedicated to second climax than in *H. agilis*. Male produces coda (Fig. 7b). Male solo song bouts and duet song bouts.

H. moloch: Short phrases consisting of simple hoots and more complex hoots, among which longer hoots with one or two frequency inflections ('wa-oo', 'wa-oo-wa') are particularly prominent for this species (Fig. 8c). Short phrases uttered by males and females. Only one of the males regularly produced bi-phasic hoots (softer than those of *H. agilis*) and short trills. Female great call consisting of a series of accelerated notes; climax not marked by particular frequency modulation of notes, but by moderately accelerated rhythm of notes becoming slower again at the end of the great call. Male does not produce coda (Fig. 7c). Male solo song bouts and female solo song bouts. Duet songs uncommon or absent (see Geissmann, 1993).

H. muelleri: Short phrases consisting of simple hoots and more complex hoots, short trills, and occasional short quavering notes in males. Quavering notes are much less pronounced and shorter than in *H. lar*. Particularly prominent in this species are short phrases beginning with two or three ,wa'-notes, each slightly lower in frequency than the preceding one (Fig. 8d). Short phrases of females almost exclusively with simple hoots. Some males were heard to produce relatively soft, squealing sounds between their short phrases, similar to males of *H. agilis*.
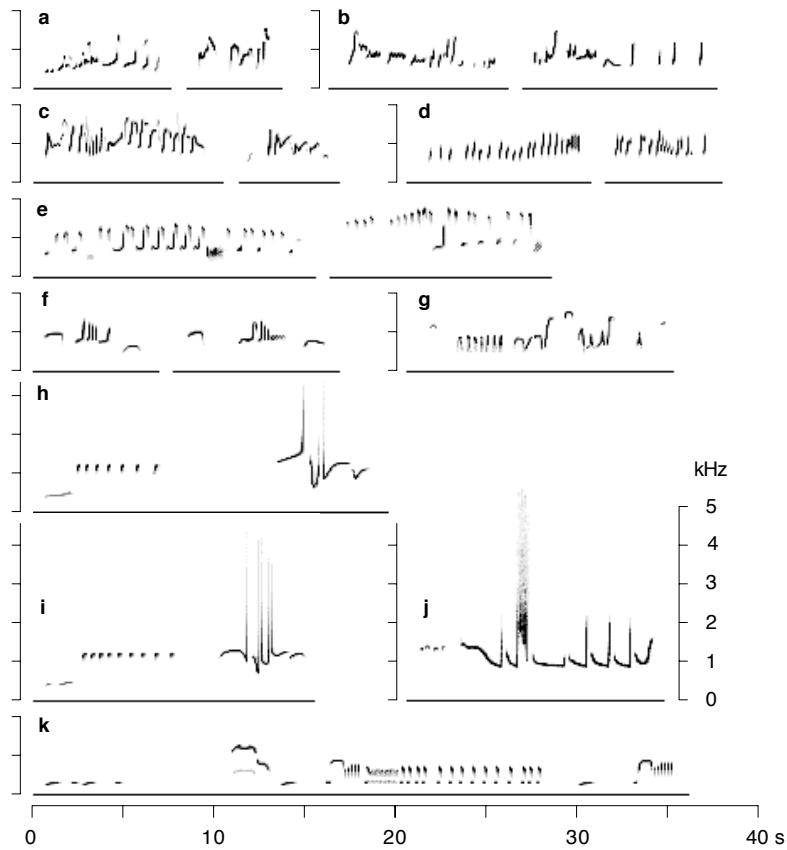
Fig. 8. Sonagrams of fully developed male phrases of all gibbon species.

In order to show variability, sonagrams of two different phrases are provided for species a–f. In *H. klossii* (f), these stem from the same male; in all other cases, two different individuals are shown. (a) *H. agilis* (Twycross Zoo, 2 Oct. 1988; and Guangzhou Zoo, 7 Sept. 1990); (b) *H. lar* (Rheine Zoo, 5 July 1987; and Twycross Zoo, 3 Oct. 1988); (c) *H. moloch* (Munich Zoo, 16 July 1987; and Howletts Zoo, 17 Oct. 1988), (d) *H. muelleri* (Doué-la-Fontaine Zoo, 25 May 1988; and Banham Zoo, 14 Oct. 1988); (e) *H. pileatus* (Zürich Zoo, 5 May 1988; and Berlin Zoo, 29 June 1988); (f) *H. klossii* (Twycross Zoo, 2 Oct. 1988); (g) *H. hoolock* (Kunming Inst. Zool., Oct. 1988, rec. by Lan Daoying); (h) *H. concolor* (Gejiu Zoo, 2 Aug. 1990); (i) *H. leucogenys* (Paris, Ménagerie du Jardin des Plantes, 17 May 1988); (j) *H. gabriellae* (La Flèche Zoo, 29 May 1988); (k) *H. syndactylus* (Howletts Zoo, 16 Oct. 1988).

488

Female great call with an acceleration-type climax, like *H. moloch*, but with much faster, bubbling note production (the single notes of the trill are not perceived as such by human ear), and without becoming slower at the end of the great call. Male optionally produces coda, sometimes accompanied by female (Fig. 7d). Male solo song bouts.

H. pileatus: Short phrases of bi-phasic hoots ('oo-wa') of hiccup-like quality, simple hoots and short trills. Bi-phasic hoots consist of notes alternatingly produced during exhalation and inhalation, as in *H. agilis*. Short series of inhalation hoots only or exhalation hoots only also occur (Fig. 8e). Short phrases are produced by either sex, but more frequently and usually louder by males. Female great call with an acceleration-type climax, like *H. muelleri*, with similar, fast bubbling note production, and without becoming slower at the end of the great call. Great call usually longer than in *H. muelleri*, and first great call notes usually more drawn out (the *muelleri* great call shown in Fig. 7 is unusually long). Male produces coda, beginning halfway through the great call (Fig. 7e). Male solo song bouts and duet song bouts.

H. klossii: Short phrases of simple hoots, more complex hoots ('ow-oo') and short trills in males (Fig. 8f). Short phrases in females consisting of simple hoots and more complex hoots ('oo-wa'), but no trills. Female great call with an acceleration-type climax, like *H. muelleri*, with similar, fast bubbling note production, but becoming slower at the end of the great call. Great call very long, usually longer than in all other gibbon species. Male does not produce coda (Fig. 7f). Male solo song bouts and female solo song bouts. Duet songs uncommon or absent (see Geissmann. 1993).

H. hoolock: Short phrases of bi-phasic hoots ('ow-wa'), simple hoots, high pitched eeks, and low pitched growls. Bi-phasic hoots consist of notes alternatingly produced during exhalation and inhalation, as in *H. agilis* (contra Haimoff, 1984) (Fig. 8g). Short phrases are produced by either sex. Apparently no sex-specific notes in song repertoire of this species. Female great call with an acceleration-type climax, like *H. moloch*, of moderate speed, usually becoming slower near end. Great call notes mainly bi-phasic. Male usually begins vocalising halfway through the great call (Fig. 7g). Duet song bouts.

H. concolor: Fully developed male vocalisations consist of three different types of notes typically uttered in the following succession: one boom produced during inflation of throat sac, a series of short simple staccato notes ('aa'), and a series of highly frequency modulated notes (termed multi-modulated figure by Haimoff, 1984). The first note of the multi-modulated figure is of ascending frequency only; rapid changes of frequency modulation occur on second and sometimes on third note (Fig. 8h). Females produce great calls only. Great call with an acceleration-type climax, like *H. moloch*, of moderate speed, not becoming slower near end. Great call consisting of 10 or less notes, notes beginning with descending frequency. Twitter-like vocalisation at the end of great call. Male produces multi-modulated phrase as coda (Fig. 7h). Duet song bouts.

H. leucogenys: Fully developed male vocalisations consist of same three different types of notes, uttered in the same succession as in *H. concolor*. The first note of the multi-modulated figure has a long section of stable frequency at the beginning; rapid changes of frequency modulation occur on second and sometimes on third note (Fig. 8i). Fe

males produce great calls only. Great call similar to *H. concolor*, but usually faster and with more notes; usually 8-18 in *H. l. siki*, about 15–30 (up to 39) in *H. l. leucogenys*. Notes begin with ascending frequency. Male produces multi-modulated phrase as coda (Fig. 7i). Duet song bouts.

H. gabriellae: Fully developed male vocalisations similar to *H. concolor*, but booms usually missing, and series of short staccato notes ('aa') uttered very softly. The first note of the multi-modulated figure beginning with a long section of descending frequency; extremely rapid changes of frequency modulation (trill) occur on second note only (Fig. 8j). Females produce great calls only. Great call similar to *H. concolor*, usually about 5–13 notes, but each beginning with ascending frequency. Notes begin at higher frequency than both *H. concolor* and *H. l. leucogenys*. Male produces multi-modulated phrase as coda (Fig. 7j). Duet song bouts.

H. syndactylus: Short phrases of booms (during inflation of throat sac), simple barks (each preceded by short boom), and ululating screams (Fig. 8k). Short phrases are produced by either sex, but ululating screams are optional in females. Female great call with *two* acceleration-type climaxes, of moderate speed; second acceleration of shorter duration. Great call beginning with longer barks than those of short phrases, each bark preceded by short boom. Male produces booms during initial stages of great call, and a different scream at each climax: a special bitonal scream at the first climax, and a ululating scream at the second climax. After second climax, male and female utter a series of rapid barks and booms (locomotion call). After a few seconds of silence and a few booms, male produces a ululating scream as final coda (Fig. 7k). Duet song bouts.

Acknowledgements

References

Berger, G. and Tylinek, E. (1984): *Das große Affenbuch*. Landbuch-Verlag GmbH, Hannover.

Biegert, J. (1973): Dermatoglyphics in gibbons and siamangs. In: Rumbaugh, D.M. (ed.), *Gibbon and Siamang, vol. 2*, pp. 163-184. Karger, Basel.

Brockelman, W.Y. and Gittins, S. P. (1984): Natural hybridization in the *Hylobates lar* species group: Implications for speciation in gibbons. In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 498-532. Edinburgh University Press, Edinburgh.

Bruce, E.J. and Ayala, F.J. (1979): Phylogenetic relationships between man and the apes: Electrophoretic evidence. *Evolution* 33: 1040-1056.

Carpenter, C.R. (1940): A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comparative Pschology Monographs* 16(5): 1-212.

Chivers, D.J. (1974): *The Siamang in Malaya – a Field Study of a Primate in Tropical Rain Forest* (Contributions to Primatology Vol. 4). Karger, Basel and New York.

Chivers, D.J. (1977): The lesser apes. In: Prince Rainier III of Monaco and Bourne, G.H. (eds.), *Primate conservation*, pp. 539-598. Academic Press, Yew York.

Chivers, D.J. and Gittins, S.P. (1978): Diagnostic features of gibbon species. *International Zoo Yearbook* 18: 157-164.

Collins, N.M.; Sayer, J.A. and Whitmore, T.C.; eds. (1991): *The Conservation Atlas of Tropical Forests. Asia and the Pacific*. Macmillan, London.

Creel, N. and Preuschoft, H. (1976): Cranial morphology of the lesser apes. A multivariate study. In: Rumbaugh, D.M. (ed.), *Gibbon and Siamang, Vol. 4*, pp. 219-303. Karger, Basel.

Creel, N. and Preuschoft, H. (1984): Systematics of the lesser apes: A quantitative taxonomic analysis of craniomatric and other variables. In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 562-613. Edinburgh University Press, Edinburgh.

Dao Van Tien (1983): On the North Indochinese gibbons (*Hylobates concolor*) (Primates: Hylobatidae) in North Vietnam. *Journal of Human Evolution* 12: 367-372.

Darga, L.L.; Baba, M. L.; Weiss, M.L. and Goodman, M. (1984): Molecular perspectives on the evolution of the lesser apes. In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 448-466. Edinburgh University Press, Edinburgh.

Darga, L.L.; Goodman, M. and Weiss, M.L. (1973): Molecular evidence on the cladistic relationships of the Hylobatidae. In: Rumbaugh, D. M. (ed.), *Gibbon and Siamang, Vol. 2*, pp. 149-162. Karger, Basel.

Dene, H.T.; Goodman, M. and Prychodko, W. (1976): Immunodiffusion evidence on the phylogeny of the primates. In: Goodman, M.; Tashian, R.E. and Tashian, J.H. (eds.), *Molecular Anthropology. Genes and Proteins in the Evolutionary Ascent of the Primates*, pp. 171-195. Plenum Press, New York.

Doolittle, R.F.; Wooding, G.L.; Lin, Y. and Riley, M. (1971): Hominoid evolution as judged by fibrinopeptid structures. *Journal of Molecular Evolution* 1: 74-83.

Ellefson, J.O. (1968): Territorial behavior in the common white-handed gibbon, *Hylobates lar* Linn. In Jay, P.C. (Ed.), *Primates: Studies in Adaptation and Variability*, pp. 180-199. Holt, Rinehart and Winston, New York.

Felsenstein, J. (1987): Estimation of hominoid phylogeny from a DNA hybridization data set. *Journal of Molecular Evolution* 26: 123-131.

Fleagle, J.G. (1984): Are there any fossil gibbons? In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 431-447. Edinburgh University Press, Edinburgh.

Fooden, J.; Quan, G. and Luo, Y. (1987): Gibbon distribution in China. *Acta Theriologica Sinica* 7: 161-167.

Gao, Y.; Wen, H. and He, Y. (1981): [The change of historical distribution of Chinese gibbons (*Hylobates*)]. *Zoological Research* 2:1-8 (Chinese text, English summary).

Garza, J.C. and Woodruff, D.S. (1992): A phylogenetic study of the gibbons (*Hylobates*) using DNA obtained non-invasively from hair. *Molecular Phylogeny and Evolution* 1: 202-210.

Garza, J.C. and Woodruff, D.S. (1994): Crested gibbon (*Hylobates* [*Nomascus*]) identification using noninvasively obtained DNA. *Zoo Biology* 13: 383-387.

Geissmann, T. (1989): A female black gibbon, *Hylobates concolor* subspecies, from northeastern Vietnam. *International Journal of Primatology* 10: 455-476.

Geissmann, T. (1991): Sympatry between white-handed gibbons (*Hylobates lar*) and pileated gibbons (*H. pileatus*) in southeastern Thailand. *Primates* 32: 357-363.

Geissmann, T. (1993): *Evolution of Communication in Gibbons (Hylobatidae)*. Ph.D. dissertation, Anthropological Institute, Phil. Fac. II, Zürich University.

Geissmann, T. (1995): Captive management and conservation of gibbons in China and Vietnam, with special reference to crested gibbons (*Hylobates concolor* group). *Primate Report* 42: 29-41.

Geissmann, T. (in press): Changes in features of crested gibbons (*Hylobates concolor* group). In: Lernould, J.-M. (ed.), *International Studbook: Hylobates concolor (Harlan, 1826) 1995, 2nd edition.* Parc Zoologique et Botanique, Mulhouse.

Gittins, S.P. (1978): The species range of the gibbon *Hylobates agilis*. In: Chivers, D.J. and Joysey, K.A. (eds.), *Recent advances in primatology, vol. 3: Evolution*, pp. 319-321) Academic Press, London and New York.

Goldman, D.; Giri, P.R. and O'Brien, S.J. (1987): A molecular phylogeny of the hominoid primates as indicated by two-dimensional protein electrophoresis. *Proceedings of the National Academy of Sciences, USA* 84: 3307-3311.

Groves, C.P. (1972): Systematics and phylogeny of gibbons. In: Rumbaugh, D.M. (ed.), *Gibbon and Siamang, Vol. 1*, pp. 1-89. Karger, Basel.

Groves, C.P. (1984): A new look at the taxonomy and phylogeny of the gibbons. In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 542-561. Edinburgh University Press, Edinburgh.

Groves, C.P. (1989): *A Theory of Human and Primate Evolution*. Clarendon Press, Oxford.

Groves, C.P. (1993): Speciation in living hominoid primates. In: Kimbel, W.H. and Martin, L.B. (eds.), *Species, Species Concepts, and Primate Evolution*, pp. 109-121. New York and London, Plenum Press.

Groves, C.P. and Wang, Y. (1990): The gibbons of the subgenus *Nomascus* (Primates, Mammalia). *Zoological Research* 11: 147-154.

Gu, Y. (1989): Preliminary research on the fossil gibbons of the Chinese Pleistocene and recent. *Human Evolution* 4:509-514.

Haimoff, E.H. (1983): *Gibbon Songs: An Acoustical, Organizational, and Behavioural Analysis*. PhD. dissertation, University of Cambridge.

Haimoff, E.H. (1984): Acoustic and organizational features of gibbon songs. In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 333-353. Edinburgh University Press, Edinburgh.

Haimoff, E.H.; Chivers, D.J.; Gittins, S.P. and Whitten, A.J. (1982): A phylogeny of gibbons based on morphological and behavioural characters. *Folia Primatologica* 39: 213-237.

Haimoff, E.H.; Gittins, S.P.; Whitten, A.J. and Chivers, D.J. (1984): A phylogeny and classification of gibbons based on morphology and ethology. In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 614-632. Edinburgh University Press, Edinburgh.

Hellekant, G.; Dubois, G.; Geissmann, T.; Glaser, D. and Van Der Weel, H. (1990): Taste responses of chorda tympani proper nerve in the white-handed gibbon (*Hylobates lar*). In: Døving, K. B. (ed.), *ISOT X. Proceedings of the Tenth International Symposium on Olfaction and Taste held at the University of Oslo, Norway, July 16-20, 1989*, pp. 115-131. GCS A.S., Oslo.

Kappeler, M. (1984): Vocal bouts and territorial maintenance in the moloch gibbon. In Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (Eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 376-389. Edinburgh University Press, Edinburgh.

Kressirer, P. and Geissmann, T. (in prep.): A molecular phylogeny of the gibbons (Hylobatidae).

Leighton, D.R. (1987): Gibbons: Territoriality and monogamy. In: Smuts, B.B.; Cheney, D.L.; Seyfarth, R.M.; Wrangham, R.W. and Struhsaker, T.T. (eds.), *Primate Societies*, pp. 135-145. University of Chicago Press, Chicago and London.

Ma, S. and Wang, Y. (1986): [The taxonomy and distribution of the gibbons in southern China and its adjacent region - with description of three new subspecies]. *Zoological Research* 7: 393-410 (Chinese text, English summary).

Marler, P. and Tenaza, R. (1977): Signaling behavior of apes with special reference to vocalization. In Sebeok, T.A. (Ed.), *How Animals Communicate*, pp. 965-1033. Indiana University Press, Bloomington and London.

Marshall, J.T. and Brockelman, W. Y. (1986): Pelage of hybrid gibbons (*Hylobates lar* x *H. pileatus*) observed in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society* 34: 145-157.

Marshall, J.T. and Marshall, E.R. (1976): Gibbons and their territorial songs. *Science* 193: 235-237.

Marshall, J.T. and Sugardjito, J. (1986): Gibbon systematics. In: Swindler, D.R. and Erwin, J. (eds.), *Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy*, pp. 137-185. Alan R. Liss, New York.

Marshall, J.T.; Sugardjito, J. and Markaya, M. (1984): Gibbons of the lar group: Relationships based on voice. In: Preuschoft, H.; Chivers, D.J.; Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes. Evolutionary and Behavioural Biology*, pp. 533-541. Edinburgh University Press, Edinburgh.

Mather, R. (1992): *A Field Study of Hybrid Gibbons in Central Kalimantan, Indonesia*. Ph.D. thesis, Cambridge University.

Mitani, J.C. (1987): Species discrimination of male song in gibbons. *American Journal of Primatology* 13: 413-423.

Mitani, J.C. (1988): Male gibbon (*Hylobates agilis*) singing behavior: Natural history, song variations and function. *Ethology* 79: 177-194.

Napier, J.R. and Napier, P.H. (1967): *A Handbook of Living Primates*. Academic Press, London and New York.

Pocock, R.I. (1927): The gibbons of the genus *Hylobates*. *Proceedings of the Zoological Society, London* 1927(2): 719-741.

Prouty, L.A.; Buchanan, P. D.; Pollitzer, W.S. and Mootnick, A.R. (1983): *Bunopithecus*: A genus-level taxon for the hoolock gibbon (*Hylobates hoolock*). *American Journal of Primatology* 5: 83-87.

Raemaekers, J.J.; Raemaekers, P.M. and Haimoff, E.H. (1984): Loud calls of the gibbon (*Hylobates lar*): Repertoire, organization and context. *Behaviour* 91:146-189.

Remane, A. (1921): Beiträge zur Morphologie des Anthropoidengebisses. *Wiegmann-Archiv für Naturgeschichte* 87 (Abt. A) (11): 1-179.

Sarich, V.M. and Cronin, J.E. (1976): Molecular systematics of the primates. In: Goodman, M.; Tashian, R.E. and Tashian, J.H. (eds.), *Molecular Anthropology. Genes and Proteins in the Evolutionary Ascent of the Primates*, pp. 141-170. Plenum Press, New York.

Sawalischin, M. (1911): Der Musculus flexor communis brevis digitorum pedis in der Primatenreihe, mit spezieller Berücksichtigung der menschlichen Varietäten. *Morphologisches Jahrbuch* 42: 557-663.

Schultz, A.H. (1933): Observations on the growth, classification and evolutionary specialization of gibbons and siamangs. *Human Biology* 5: 212-255, and 385-428.

Schultz, A.H. (1973): The skeleton of the Hylobatidae and other observations on their morphology. In: Rumbaugh, D.M. (ed.), *Gibbon and Siamang, Vol. 2*, pp. 1-54. Karger, Basel.

Shafer, D.A. (1986): Evolutionary cytogenetics of the siabon (gibbon-siamang) hybrid apes. In: Taub, D.M. and King, F.A. (eds.), *Current Perspectives in Primate Biology*, pp. 226-239. Van Nostrand Reinhold Company, New York.

Sibley, C.G. and Ahlquist, J.E. (1984): The phylogeny of hominoid primates, as indicated by DNA-DNA hybridization. *Journal of Molecular Evolution* 20: 2-15.

Sibley, C.G. and Ahlquist, J.E. (1987): DNA hybridization evidence of hominoid phylogeny: Results from an expanded data set. *Journal of Molecular Evolution* 26: 99-121.

Stanyon, R.; Sineo, L.; Chiarelli, B.; Camperio-Ciani, A.; Haimoff, E.H.; Mootnick, A.R. and Sutarman, D. (1987): Banded karyotypes of the 44-chromosome gibbons. *Folia Primatologica* 48: 56-64.

Tenaza, R.R. (1976): Songs, choruses and countersinging among Kloss gibbons (*Hylobates klossi*) in Siberut island, Indonesia. *Zeitschrift für Tierpsychologie* 40: 37-52.

van Gulik, R.H. (1967): The Gibbon in China. An Essay in Chinese Animal Lore. E.J. Brill, Leiden.

Van Tuinen, P. and Ledbetter, D.H. (1983): Cytogenetic comparison and phylogeny of three species of Hylobatidae. *American Journal of Physical Anthropology* 61: 453-466.

Van Tuinen, P. and Ledbetter, D.H. (1989): New, confirmatory and regional gene assignments in the white-cheeked gibbon *Hylobates concolor*. *Cytogenetics and Cell Genetics* 51: 1094-1095 (Abstract only).

Wienberg, J. and Stanyon, R. (1987): Fluoroscent heterochromatin staining in primate chromosomes. *Human Evolution* 2: 445-457.

Wislocki, G.B. (1929): On the placentation of primates, with a consideration of the phylogeny of the placenta. *Contributions to Embryology* 20(111): 51-80, + 7 plates.

Wislocki, G.B. (1932): On the female reproductive tract of the gorilla, with a comparison of that of other primates. *Contributions to Embryology* 23(135): 163-204, + 12 plates.

Zhang, Y.; Quan, G.; Zhao, T. and Southwick, C.H. (1992): Distribution of primates (except *Macaca*) in China. *Acta Theriologica Sinica* 12: 81-95.

Dr Thomas Geissmann, Anthropological Institute, University Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

Fig. 9. *H. agilis* cf. *agilis*, light phase: adult female, Singa (with infant, born on 20 Nov. 1987). Zoo Asson, France, 1 June 1988. The father of the infant was a nearly black male, similar to the one shown in Fig. 10.

Fig. 10. *H. agilis* cf. *unko*, dark phase: adult male, Singapore Zoo, 5 Sept. 1993. Notice the light cheek patches which frequently occur in males of this species.

Fig. 11. *H. agilis*, intermediate phase: adult female (Zoo No. 183/2A), Paignton Zoo, England, 22 Oct. 1988. Because the subspecies *H. agilis agilis* and *H. agilis unko* (sensu Marshall and Sugardjito, 1986) are apparently defined only by the higher proportion of light phase animals occurring in the former and of dark phase animals in the latter, captive individuals cannot be reliably identified, unless their provenience is known. In addition, many intermediate colour variants are known to exist in this species, whose subspecies identification is even more difficult. This dark animal exhibits areas of light fur coloration including the corona, lower legs and distal back (not visible).

Fig. 12. *H. agilis*, intermediate phase: adult male (Zoo No. 183/1A), Paignton Zoo, England, 22 Oct. 1988. This beautifully patterned animal is much lighter than the female in Fig. 11, but still completely different from the typical light phase shown in Fig. 9, the back showing a warm light brown colour, contrasting with dark brown ventral parts and inner sides the limbs. Notice again the light cheek patches and the light genital tuft, which is often contrastingly light coloured in males of intermediate phases (but apparently never in males of the black phase).

Fig. 13. *H. agilis albibarbis*: adult male, Guangzhou Zoo, China, 7 Sept. 1990. Note the contrasting coloration, the black hands (not visible) and feet, and the light genital tuft in males of this often very contrastingly patterned Bornean subspecies.

Fig. 14. *H. lar* cf. *carpenteri*, light phase: adult female, Priscilla (with infant, born on 13 July 1988), Metro Zoo, Miami, U.S.A., 31 July 1988. The long fur of this gibbon suggests a tentative identification as *H. lar carpenteri*, but subspecies identification in *H. lar* faces similar difficulties as in *H. agilis* (see legend to Fig. 11).

Fig. 15. *H. lar* cf. *entelloides*, dark phase: adult male, Vo, Southport Zoo, England, 10 Oct. 1988.

(*All photographs: Thomas Geissmann*)

494

Fig. 9

Fig. 10

Fig. 11

Fig. 12

Fig. 13

Fig. 14

Fig. 15

Fig. 16. *H. lar*, intermediate phase: adult male, Pupuce, Zoo Mulhouse, France, 14 Sept. 1988. In addition to light buffy coloured and black animals, many different colour variants are known to exist in this species, like in *H. agilis*. Unless the provenience of the animal is known, their subspecies identification is often unreliable.

Fig. 17. *H. moloch*: adult male, Iwanowitsch, Berlin Zoo, Germany, 1 July 1988.

Fig. 18. *H. moloch*: adult female, Paula, Berlin Zoo, Germany, 1 July 1988. This female exhibits a particularly contrasting black cap and a black belly. These characteristics may occur more frequently in females than in males.

Fig. 19. *H. muelleri muelleri*: adult male, Fridolin, Münster Zoo, Germany, 2 July 1987. Notice the black digits of this subspecies.

Fig. 20. *H. muelleri funereus*: adult male, Banham Zoo, 14 Oct. 1988. The digits are not usually black in this subspecies. This male is known to originate from Sarawak.

Fig. 21. *H. muelleri funereus*: adult female, Singapore Zoo, 5 Sept. 1993. Animals from the northern part of its distribution range often exhibit light hands and feet.

Fig. 22. *H. muelleri abbotti*: adult male, Cuckoo, Paignton Zoo, England, 22 Oct. 1988. The mouse-grey individuals of this subspecies sometimes resemble *H. moloch* (see Fig. 17). The latter usually exhibits a more silvery grey fur coloration and a more contrasting white goatee beard.

(*All photographs: Thomas Geissmann*)

Fig. 16

Fig. 17

Fig. 18

Fig. 19

Fig. 20

Fig. 21

Fig. 22

497

Fig. 23. *H. pileatus*: adult male, Blacky, Zoo Zürich, Switzerland, 28 Oct. 1987. Notice the grey corona, the light digits and the white genital tuft of this sexually dichromatic species.

Fig. 24. *H. pileatus*: adult female, Iba (with infant, Khmer, born on 28 Nov. 1984), Zoo Zürich, Switzerland, 15 July 1986. Notice the contrasting black cap and ventral field, and light temple fringes hanging down over the black cheek region and ears.

Fig. 25. *H. klossii*: adult male, Bilou, Twycross Zoo, England, 4 Oct. 1988. This species differs from other black gibbons by its smaller size and the absence of an external throat sac (as compared to *H. syndactylus*, Fig. 36) and by the absence of an occipital crest (as compared to males of *H. concolor*, Fig. 28).

Fig. 26. *H. hoolock leuconedys*: subadult male, Jian-Jian, Kunming Zoo, China, 30 Aug. 1990. In adult males of this subspecies, the long genital tassel usually becomes contrastingly lighter.

Fig. 27. *H. hoolock leuconedys*: adult female, Gui-Gui, Kunming Zoo, China, 5 Aug. 1990. This species also exhibits strong sexual dichromatism. Notice the light cap and white stripe below eyes and across the ridge of the nose.

Fig. 28. *H. concolor*: adult male, Dong-Dong (with female in the background), Gejiu Zoo, China, 3 Sept. 1990. This species, like all crested gibbons, exhibits strong sexual dichromatism.

Fig. 29. *H. concolor*: adult female, Hong-Hong, Gejiu Zoo, China, 3 Sept. 1990. Notice the black belly; females of other crested gibbon species have a light ventral area.

(*All photographs: Thomas Geissmann*)

Fig. 23

Fig. 24

Fig. 25

Fig. 26

Fig. 27

Fig. 28

Fig. 29

Fig. 30. *H. gabriellae*: adult male, Arthur, Zoo La Flèche, France, 29 May 1988. Notice the brown chest and the yellow cheek patches.

Fig. 31. *H. gabriellae*: adult female, Dak Lua Market, Nam Bai Cat Tien National Park, Vietnam, 27 Sept. 1993. Notice the lateral direction of the fur on the cheeks: The hairs spread out from the corners of the mouth like a fan. Females of this species usually have a less pronounced whitish face ring than this individual, in contrast to *H. leucogenys* (see Figs. 33 and 34).

Fig. 32. *H. leucogenys leucogenys*: adult male, Ménagerie du Jardin des Plantes, Paris, France, 18 May 1988. Notice the particularly high crest and the large white cheek patches of this subspecies.

Fig. 33. *H. leucogenys leucogenys*: adult female, Bronx Zoo, New York, U.S.A., 18 Aug. 1988. The bright orange fur coloration may be paler in some individuals and undergo periodical changes in others (see Geissmann, 1993). Females of this species usually have a whitish face ring.

Fig. 34. *H. leucogenys siki*: adult female, Charlotte, Zoo Clères, France, 24 May 1988. Adult females of the two subspecies leucogenys and siki cannot be reliably identified by their fur coloration, at present. This female shows particularly extensive white fur in the facial area and an unusually weak cap, although she had a very large black cap only few years before this photograph was taken (see photograph in Geissmann, in press).

Fig. 35. *H. leucogenys siki*: adult male, Charly, Tierpark Hellabrunn, Munich, Germany, 24 July 1982. Notice the black chest and white cheek patches (in comparison to *H. gabriellae*, Fig. 28).

Fig. 36. *H. syndactylus*: adult female, Püppi II (left) and adult male, 'Piet' (right, father of, Püppi II), Duisburg Zoo, 21 June 1987. The whitish brow band in this female is a very rare trait of males and females of this species. Its occurrence suggests that ancestral forms had a white face ring (see Geissmann, 1993).

(*All photographs: Thomas Geissmann*)

Fig. 30

Fig. 31

Fig. 32

Fig. 33

Fig. 34

Fig. 35

Fig. 36