Evolution of Communication in Gibbons (Hylobatidae)

Inaugural-Dissertation
zur Erlangung der philosophischen Doktorwürde
vorgelegt der Philosophischen Fakultät II
der Universität Zürich

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THOMAS GEISSMANN
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Begutachtet von den Herren
Prof. Dr. R.D. Martin
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Contents:

"Whether the species maintain their individuality through geographical segregation, or whether, if they were to meet and mix, sexual and social instincts would still maintain the present arrangement of species, are matters upon which no information has as yet been given. But the fact that certain of these species (*H. lar*, *H. pileatus*, and *H. hoolock*), if not all, have voices which can be distinguished, tends to show there is a physiological differentiation, and the colour markings are very constant."

(Keith, 1896)

"Um zu wissen, ob ein Gebiet von dieser oder jener Art bewohnt sei, ist es übrigens nicht immer nötig, ans Land zu gehen; man kann zuverlässig feststellen, welche Art hier vorkommt. Die Stimme der Hylebatiden ist nämlich sehr laut und bei den einzelnen Arten sehr verschieden."

(Volz, 1904)

1. Introduction

1.1 Introduction to Gibbons

The gibbons, or lesser apes (*Hylobates* spp.), are distributed throughout the tropical rain forests of Southeast Asia (Chivers, 1977; Groves, 1972; Marshall & Sugardjito, 1986). They are unusual among primates in several respects which can be summarised under three key complexes: locomotion, social structure, and communication.

Gibbons are strictly arboreal and mainly frugivorous (Chivers, 1984a; Leighton, 1987). Their arm-swinging form of locomotion (brachiation), unique suspensory behaviour and habitual erect posture represent extreme specialisations which evolved in connection with the animals' substrate and diet (Chivers, 1984b).

Gibbons live in monogamous, territorial family groups (Brockelman & Srikosamatara, 1984; Chivers, 1984b; Leighton, 1987). In the wild, single offspring are born at intervals of approximately 3 years. Offspring remain with their parental family group until attaining sexual maturity at about 8 years of age, at which time they usually leave the group in order to find a mate and a territory.

All species of gibbons are known to produce elaborate, species-specific and sex-specific patterns of vocalisation often referred to as "songs" (Haimoff, 1984a; Marshall & Marshall, 1976, 1978). 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, 1984a; Leighton, 1987).

1.2 Gibbon Ancestry

Various fossil primates have at some time or other been proposed as possible ancestors of gibbons, including genera from the Oligocene such as *Propliopithecus* (= *Aeolopithecus*) and from the Miocene such as *Crouzelia*, *Dendropithecus*, *Dionysopithecus*, *Laccopithecus*, *Limnopithecus*, *Micropithecus*, *Pliopithecus* (see e.g. Barry et al., 1986; Fleagle, 1984; 1988). Most of them are probably too primitive to be gibbon ancestors and probably precede the radiation of living hominoids; in others, the critical cranial and postcranial material is not available (Fleagle, 1984; 1988). In many cases, phyletic relationship with hylobatids has been assumed on the basis of dentition (5-cusped, ape-like molars) and small body size. A major problem in tracing gibbon ancestry is that modern gibbons are defined as a clade mainly by derived postcranial features related to brachiation (Andrews & Groves, 1976), whereas, so far as known, none of the previous candidates for hylobatid ancestors seems to exhibit such features (Barry et al., 1986; Fleagle, 1984). On the other hand, gibbon dentition apparently shows mostly primitive features which are not suited for tracing a possible ancestor (Barry et al., 1986; Szalay & Delson, 1979). As a result, none of the currently known fossil primates from the Oligocene and the Miocene can be clearly shown to be uniquely related to modern gibbons (Fleagle, 1988).

The fossil record of the genus *Hylobates* extends back only to the middle Pleistocene of China, Indochina and Indonesia. One of the most complete specimens was a fossil mandibular fragment from the Yangtze River (Sichuan Province, China) which has been described as *Bunopithecus sericus* by Matthew and Granger (1923). It was later referred to *Hylobates sericus* (Colbert & Hooijer, 1953), to *Hylobates hoolock* (Groves, 1972; Marshall & Sugardjito, 1986), and more recently to *H. concolor* (Gu, 1989). A number of additional Pleistocene specimens from China attributed to *Hylobates* are largely confined to individual teeth (Chang et al., 1975; Delson, 1977; Gu, 1989; Han, 1982; Lin et al., 1974; Wang et al., 1982; Zhao et al., 1981). While Chinese gibbons today are restricted to southern Yunnan and Hainan (Fooden et

al., 1987; Geissmann, 1989; Groves & Wang, 1990; Ma & Wang, 1986), their distribution range extended as far north as the Yellow River in historical times (Gao et al., 1981; van Gulik, 1967), thus including the range of known fossils.

Pleistocene teeth identified as *H. moloch* (= *leuciscus*) and *H. syndactylus* have been recorded from several fissure deposits in Java (Badoux, 1959; von Koenigswald, 1940). More recently, a partial cranium of *Hylobates* has been reported from Pleistocene deposits in a karst cave in northern Vietnam (Ciochon, 1988).

Fossil evidence apparently suggests that the great ape and human clade separated from the gibbon clade 17-20 myr ago (Andrews et al., 1987; Pilbeam, 1985). Recent molecular estimates of the dating of the divergence of gibbons from the hominoid lineage are quite variable and range between 12 and 25 myr ago (Cronin et al., 1984; Goldman et al., 1987; Hasegawa et al., 1984, 1985; Sibley & Ahlquist, 1984, 1987).

1.3 Gibbon Systematics

It is generally accepted that gibbons are the sister group of the great apes and humans and that, together with the latter, they form the monophyletic group Hominoidea. It has also been widely accepted in recent years that the gibbons constitute the most ancient branch within the Hominoidea and show the most primitive characteristics (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 & 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 & Cronin, 1976; Sibley & Ahlquist, 1984, 1987).

There is considerably less agreement on the phylogenetic relationships between gibbon species. Several authors suggest that among modern gibbons, the siamang (*H. syndactylus*) was the first species to split off from the main stem (Bruce & Ayala, 1979; Creel & Preuschoft, 1976, 1984). Others disagree and see the crested gibbons (*concolor* group) in that position (Groves, 1972; Haimoff, 1983a; 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 & 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 siamang, the *concolor* group and the hoolock (*H. hoolock*) are generally believed to be the earliest members of the gibbons to split off from the main stem, and it has been proposed that these three offshoots and the main stem should each be referred to a separate subgenus (i.e. *Symphalangus*, *Nomascus*, *Bunopithecus*, and *Hylobates*, respectively) (Marshall & Sugardjito, 1986; Prouty et al., 1983a). Each of the four groups is, among other characteristics, identified by a distinctive karyotype, the diploid number being 50, 52, 38 and 44, respectively.

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 & Preuschoft, 1976, 1984; Haimoff, 1983a; Haimoff et al., 1982, 1984). The remaining group of gibbons is commonly referred to as the *lar* group (Brockelman & Gittins, 1984; Groves, 1972, 1984; Haimoff et al., 1984; Marshall & Sugardjito, 1986; Marshall et al., 1984). Morphological differences within the *lar* group are slight (Groves, 1984), karyotypes are virtually identical (Stanyon et al., 1987) and phylogenetic relationships highly speculative (Creel & 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 & Preuschoft, 1984), in contrast to other recent studies which recognise 4 (Groves, 1984) or 5 species (Chivers, 1977; Chivers & Gittins, 1978; Haimoff, 1983a; Haimoff et al., 1982, 1984; Marshall & Sugardjito, 1986; Marshall et al., 1984).

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 colouration shows some similarities to *H. muelleri 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 & Gittins, 1984; Marshall & Sugardjito, 1986; Marshall et al., 1984). 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 *albibarbis* as yet another species, or combining *H. agilis*, *H. muelleri* and *albibarbis* into one species (Groves, 1984).

The main systematic divisions of the genus *Hylobates* are summarised in Table 1.1.

Table 1.1: Main divisions of the genus *Hylobates*.

Subgenus	Other divisions	Species
Hylobates	*Lar* group	*H. agilis*
(=44-chromosome gibbons)		*H. lar*
		H. moloch
		H. muelleri
		H. pileatus
		H. klossii
Bunopithecus		*H. hoolock*
Nomascus	*Concolor* group	*H. concolor*
		H. leucogenys
Symphalangus		*H. syndactylus*

1.4 Adopting a Systematic Framework

In order to discuss the phylogenetic relationships within any group of animals, it is necessary to define clearly the various taxa under comparison at the outset of the study. 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 25 years, several reviews of gibbon taxonomy have been published (Chivers, 1977; Chivers & Gittins, 1978; Groves, 1972, 1984; Marshall & Sugardjito, 1986; Napier & 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.

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 to this day also remains 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) 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 reference on gibbon classification at this time. With only slight modifications, this paper will be used here as the standard reference for the taxonomy of the

lesser apes. The major modification consists in recognising the light-cheeked gibbon (*Hylobates leucogenys*) as a separate species from the black crested gibbon (*H. concolor*), as proposed by Dao Van Tien (1983) and Ma and Wang (1986). These authors reported on anatomical differences between the black crested and the light-cheeked gibbon, most of which the present author was able to confirm. In addition, evidence from museum specimens suggest that areas of sympatry between the forms exist both in China and in Vietnam (Dao Van Tien, 1983; Ma & Wang, 1986).

During the present study, it became apparent that the systematics of crested gibbons, or *concolor* group, is still in need of revision: Considerable differences in the vocalisations were found in support of a species separation between *H. leucogenys* and *H. concolor*, but similar differences also exist between two forms of the light-cheeked gibbon *H. leucogenys*. These differences suggest that one subspecies of latter, the yellow-cheeked gibbon (*H. leucogenys gabriellae*), may deserve species status as well. In addition, vocalisations of one female *H. concolor* from Vietnam differed so radically from those of all Chinese females of that species as to suggest the existence of a previously unrecogised taxon at the species level. These possibilities will be evaluated in a future study. In the present study, the yellow-cheeked gibbon is provisionally kept as a subspecies of *H. leucogenys*, but results for both forms will be analysed separately.

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.

Hylobates agilis – Agile gibbon, black-handed gibbon
Hylobates concolor – Concolor gibbon, black 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 gibbon
Hylobates moloch – Javan gibbon, silvery gibbon
Hylobates muelleri – Müller's gibbon, Bornean gibbon, grey gibbon
Hylobates pileatus – Pileated gibbon, capped gibbon
Hylobates syndactylus – Siamang

Of these species, *H. concolor* and *H. leucogenys* constitute the *concolor* group 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.

The controversy about the phylogenetic affinities of the race *albibarbis* has been mentioned above. Following Marshall and Sugardjito (1986), this form will provisionally be kept with *H. agilis* in the present study, but its characteristics of fur colouration will be examined separately from those of other populations of *H. agilis*.

1.5 Aims of the Present Study

The primary aim of the present study was to trace the evolution of selected characteristics of gibbon communication. This included identifying, where possible, homology vs. analogy (i.e. convergent evolution) of characteristics, and primitive vs. derived character states across the various gibbon species. The second aim was to use these results for a reassessment of the gibbon radiation. This included the reconstruction of a cladogram based on both the characteristics of gibbon communication and more traditional characteristics collected from the relevant literature.

Characteristics from each of the following three communication modalities were analysed: Vocal, olfactory and visual communication. Results on each modality are presented in a separate chapter. The part of each communication channel that was analysed during the present study is briefly described below.

Vocal Communication:

The chapter on vocal communication is entirely devoted to gibbon singing behaviour. Gibbon songs are characterised by being loud, long, stereotyped and species-specific (Haimoff, 1983a, 1984a; Marler & Tenaza, 1977; Marshall & Marshall, 1976, 1978; Marshall & Sugardjito, 1986). 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 5kHz.

In recent years, vocal characteristics have been used to assess systematic relationships among hylobatids and to reconstruct their phylogeny (Creel & Preuschoft, 1984; Haimoff, 1983a; Haimoff et al., 1982, 1984; Marshall et al., 1984). Similar studies have also been carried out on other primates (e.g. Gautier, 1988; Oates & Trocco, 1983; Snowdon et al., 1986; Struhsaker, 1970; Wilson & Wilson, 1975). Such interpretations are based on the assumption

that homologous characteristics are concerned. Similar function, however, is thought to enhance the convergent evolution of vocalisations of similar structure and examples of this have been presented for both birds (Marler, 1957) and primates (Herzog & Hohmann, 1984; Vencl, 1977). The same effect has been held responsible for remarkable similarities between songs of gibbons and loud calls of other monogamous, territorial primates such as the the indri (*Indri indri*), the spectral tarsier (*Tarsius spectrum*), and the Mentawai langur (*Presbytis potenziani*) (Haimoff, 1986; MacKinnon & MacKinnon, 1984). Therefore, it is of particular importance to examine critically the justification for assuming homology of various gibbon song vocalisations. This has been largely neglected in previous studies that introduced vocal characteristics into the assessment of gibbon phylogenetic relationships, and the phylogenetic value of several of these characteristics has been said to be "questionable because of problems of homology (e.g. is a 'duet' the same in all populations?) or potential ease of convergence (pitch range, length of female great call)" (Creel & Preuschoft, 1984).

Of course, gibbons produce not only songs but also a number of other vocal signals. These have, however, been neglected in the present study (as well as in all previous studies on gibbon systematics). Songs were selected here because they are known to occur in all gibbon species, because they are relatively stereotyped (hence reducing the problem introduced by individual variability of a given characteristic), and because they are loud and frequently produced by gibbons, thus facilitating data collection. Only limited information is available on gibbon vocalisations uttered in an intra-group context (Boutan, 1913; Carpenter, 1940; Ellefson, 1974; Marler & Tenaza, 1977); such signals are apparently few in number and low in intensity in at least one species (*H. syndactylus*) and – in at least one further species (*H. leucogenys*) – may represent a graded system (Chivers, 1976; Deputte & Goustard, 1978), thus complicating a comparative analysis.

Olfactory Communication:

Whereas there is a growing number of studies dedicated to gibbon vocal communication (see reviews in Cowlishaw, 1992; Haimoff, 1983a; Leighton & Whitten, 1984; Tuttle, 1986), olfactory communication has remained unappreciated in virtually all studies and reviews of gibbon communication and social behaviour (see reviews in Marler & Tenaza, 1977; Tuttle, 1986). Although olfactory communication has been assumed to be of particular importance to prosimians (Klopfer, 1977), skin glands specialised for the production of olfactory signals have been described for many other primates as well (Epple, 1986). In gibbons, such glands were virtually unknown at the beginning of this study. Research in this direction appeared to be promising, however, because observations on captive siamangs (*Hylobates syndactylus*) made by the present author had indicated that these animals have a specialised glandular area on the chest. Initial results of the present investigation have been published in a preliminary report (Geissmann, 1987b) and in two abstracts (Geissmann, 1986b, 1987a). These early results chiefly concerned sternal glands in siamangs and have been considerably expanded for the following account.

Visual Communication:

This chapter is mainly confined to characteristics of fur colouration, but a comparison of various forms of sexual dimorphism (including body size) in gibbons is added.

Of course, gibbons also use facial expressions and gestures for communication. In spite of the large number of behavioural studies on gibbons, relatively detailed descriptions of such signals are available from ethograms of two species only: *H. lar* (Baldwin & Teleki, 1976; Ellefson, 1974) and *H. syndactylus* (Fox, 1977; Orgeldinger, 1989). As in intra-group vocalisations (see above), Chivers (1976) reported an unusual "paucity of communicative expressions and gestures" for at least one species (*H. syndactylus*). To collect reliable ethograms of the visual communicative repertoire for 10 species of gibbons would probably represent a long-term study in its own right.

In contrast to expressions and gestures, gibbons exhibit a considerable number of fur characteristics which are apparently of signal value. In addition, some species show distinct sex-specific colour characteristics, others show strong polymorphisms in fur colouration, and yet others undergo radical colour-changes during maturation (Fooden, 1969; Groves, 1972; Marshall & Sugardjito, 1986). Characteristics of fur colouration probably have the oldest tradition in the history of gibbon systematics (Elliot, 1913; Forbes, 1894; Kloss, 1929; Martin, 1841; Matschie, 1893; Pocock, 1927). As pointed out by Groves (1972), "when all is said and done, colouration remains the chief means of distinguishing between taxa for most authors, as well as the most convenient to use on living specimens."

2. Material and Methods

2.1 General Methods

The age classes for captive gibbons are here defined as follows: infants 0-2 years of age; juveniles 2.1-4 years; subadults 4.1-6 years; adults more than 6 years. These age classes differ considerably from those defined for wild gibbons and siamangs (Gittins & Raemaekers, 1980, p. 70), which assume a slower maturation rate. A modification of previous age classes was necessary, however, because the present author has demonstrated in an earlier study that – at least in captivity – gibbons can attain sexual maturity much earlier than previously assumed (Geissmann, 1991a). Animals up to an age of 7 days were considered to be neonates, following the definition used in Geissmann and Orgeldinger (in prep.).

In museum specimens, the exact age is usually not known; in these specimens, age estimates were based on dental eruption and dental wear (Schultz, 1944, p. 7). These estimates are rather crude, but for the present study it was usually only necessary to know whether a museum specimen was adult or not. This was particularly important for the analysis of gibbon body weight. Where possible, the author inspected the preserved skulls for all specimens included in the body weight analysis.

When writing scientific names of hybrids, the father's species is mentioned before the mother's.

Most statistical calculations, unless stated otherwise, were computed using StatView™ II statistics software (Abacus Concepts); near the end of the study, StatView™ 4.0 was used. All statistical tests are two-tailed.

2.2 Vocal Communication

2.2.1 Study Animals

Vocalizations were tape-recorded from gibbons kept in zoos, primate centers and from privately owned animals in China, England, France, Germany, Hong Kong, Italy, Switzerland and the United States. A list of all institutions visited and of the gibbon species kept in each is presented in Table 2.2.1. Vocalizations of free-ranging *H. concolor* were tape-recorded in August 1990 during a one-week field trip to the Ailao Mountain Reserve in Kunming Province (China). Additional tape-recordings used in the present study were kindly made available by Mr. Lan Daoying (*H. hoolock*), Dr. K.-H. Frommolt and Prof. G. Tembrock (various species), Mr. R. Gates (various species), Dr. M.M. Haraway (*H. muelleri* x *H. agilis*), Dr. M. Kappeler (*H. moloch*, *H. muelleri*), Mr. S. Kingswood (*H. agilis*, *H. muelleri*, and *H. agilis* x *H. muelleri*), Dr. J.T. Marshall (*H. pileatus* x *H. agilis*, *H. muelleri* x *H. agilis*), Mr. M. Perschke (various species), Dr. M. Schwarz (duet *H. lar* male and *H. moloch* female), Dr. R.R. Tenaza (*H. klossii*, *H. lar* x *H. muelleri*), Ms. B. Uphoff (*H. muelleri* x [*H. muelleri* x *H. moloch*]), and Ms. B. Wehrmann (*H. leucogenys*).

Descriptions and sonagrams of gibbon vocalizations have appeared in a large number of publications. Many of these data were used to supplement those collected during the present study: either in order to compile character states for a cladistic analysis of vocal communication in gibbons, or in order to compare hybrid vocalizations with those of the parental species. A list of the publications used in this study is presented in Table 2.2.2, arranged by species.

Table 2.2.1: Gibbon species tape-recorded in various institutions. [1]

Location	ag	co	ga	ho	kl	la	le	mo	mu	pi	sy	hy
China												
Gejiu Zoo		x		x			x					
Guangzhou Zoo	x			x								
Kunming Zoo				x								
England												
Banham Zoo						x			x		x	x
Bekesbourne, Howletts Zoo								x			x	
Bristol Zoo												x
Paignton Zoo	x					x		x	x			x
Rushden, Ravensden Farm												x
Southport Zoo						x						x
Twycross Zoo	x	x			x	x	x		x	x	x	x
France												
Asson Zoo	x					x	x					x
Clères Zoo			x				x					
Doué-la-Fontaine Zoo							x		x		x	
La Flèche Zoo			x									
Mazé, Mr. J. Bauné						x				x		x
Mulhouse Zoo			x			x	x					
Paris, Jardin des Plantes							x					
Paris, Vincennes Zoo						x	x					
Germany												
Berlin, Tierpark Berlin							x					
Berlin Zoo						x		x		x	x	x
Cottbus Zoo									x			x
Dortmund Zoo	x								x		x	
Duisburg Zoo						x	x				x	x
Eberswalde Zoo							x					x

[1] Abbreviations: ag – *H. agilis*; co – *H. conolor*; ga – *H. leucogenys gabriellae*; ho – *H. hoolock*; kl – *H. klossii*; la – *H. lar*; le – *H. leucogenys leucogenys* and *H. l. siki*; mo – *H. moloch*; mu – *H. muelleri*; pi – *H. pileatus*; sy – *H. syndactylus*; hy – inter-species hybrids.

Table 2.2.1: Continued. [1]

Location	ag	co	ga	ho	kl	la	le	mo	mu	pi	sy	hy
Frankfurt Zoo											x	
Gelsenkirchen, Ruhr Zoo												x
Hannover Zoo							x					
Hodenhagen, Serengeti Park												x
Kronberg, Opel Zoo										x		x
Leipzig Zoo			x									
München, Zoo Hellabrunn							x	x			x	
Münster Zoo									x			x
Nordhorn Zoo						x						x
Rheine Zoo						x						x
Rostock Zoo									x			
Hong Kong												
Hong Kong Zoo			x								x	
Italy												
Rome Zoo						x				x		
Switzerland												
Rapperswil, Knie's Kinderzoo						x						
Studen, Zoo "Seeteufel"						x					x	
Zürich Zoo										x	x	
United States												
Atlanta, Yerkes Regional Research Primate Center						x						x
Miami, Metro Zoo						x					x	
New York, LEMSIP Primate Center						x						
West Palm Beach, Lion Country Safari Park											x	x

[1] Abbreviations: ag – *H. agilis*; co – *H. conolor*; ga – *H. leucogenys gabriellae*; ho – *H. hoolock*; kl – *H. klossii*; la – *H. lar*; le – *H. leucogenys leucogenys* and *H. l. siki*; mo – *H. moloch*; mu – *H. muelleri*; pi – *H. pileatus*; sy – *H. syndactylus*; hy – inter-species hybrids.

Table 2.2.2: Publications on gibbon vocalizations used to supplement the present study.

H. agilis	Brockelman & Gittins (1984); Gittins (1978a; 1984b); Haimoff (1984b); Haimoff & Gittins (1985); Marshall (1981); Mitani (1987a; 1987b; 1988; 1990); Mitani & Marler (1989)
H. conolor	Demars et al. (1983)[1]; Haimoff (1984c)[1]; Haimoff et al. (1987)
H. hoolock	Choudhury (1989); Gittins & Tilson (1984); Haimoff (1985b)
H. klossii	Haimoff & Tilson (1985); Tenaza (1976); Whitten(1984; 1982)
H. lar	Brockelman & Schilling (1984); Caldecott & Haimoff (1983); Geissmann (1984a); Marshall (1981); Raemaekers & Raemaekers (1984a; 1984b; 1985; 1985); Raemaekers et al. (1984); (Schröpel, 1977); Tenaza (1985)
H. leucogenys leucogenys and *H. l. siki*	Demars et al. (1983)[1]; Deputte (1982); Deputte & Leclerc-Cassan (1981); Goustard (1979; 1980; 1982; 1984); Haimoff (1984c)[1]; Schilling (1984c)
H. leucogenys gabriellae	Adler (1991); Demars & Goustard (1972); Goustard (1965; 1969; 1976); Goustard & Demars (1971; 1973; 1974)
H. moloch	Geissmann (1984a); Kappeler (1984)
H. muelleri	Haimoff (1985a); Mitani (1984; 1985a; 1985b; 1985c; 1987a); Tenaza (1985)
H. pileatus	Brockelman & Schilling (1984); Geissmann (1983; 1984a); Haimoff (1986); Srikosamatara & Brockelman (1983; 1987)
H. syndactylus	Chivers (1974; 1976); Geissmann (1984b); Haimoff (1981; 1983b); Hess-Haeser (1971); Lamprecht (1970); Maples et al. (1989); Rühmekorf (1963); West (1982)
Various species	Chivers (1978); Demars & Goustard (1978); Gittins (1984a); Haimoff (1983a; 1984a; 1988); Haimoff et al. (1982; 1984); Marler & Tenaza (1977); Marshall &Marshall (1976; 1978); Marshall & Sugardjito (1986); Marshall et al. (1972; 1984); Tembrock (1974)

[1] Demars et al. (1983) and (Haimoff, 1984c) both referred to the same pair of crested gibbons as *H. concolor hainanus*. These animals were later identified by the present author as a male *H. concolor* cf. *concolor* and a female *H. leucogenys*, respectively (Geissmann, 1989).

Because the analysis of hybrid vocalisations represents an important part of this study, the proper identification of hybrid gibbons became a crucial pre-condition. Most of the hybrids were located and identified by the present author in zoos in England, France, Germany and the United States. The parents of all hybrids that were old enough to vocalise were carefully tracked down, sometimes through several animal dealers and zoos. Only hybrids for which both parents could reliably be identified were included in the analysis. All hybrids that were heard to participate in singing behaviour are listed in Appendix 10.1. The parents remained unknown for only 1 out of 34 (i.e. the last animal in the list). This animal was not included in the analysis, although – as a result of the present study – it can be identified *a posteriori* with reasonable accuracy (see Appendix 10.1). Most of the hybrids were first generation-hybrids (F1): only four F2-animals were old enough to produce songs. In adition, most hybrids combine species of the *lar* group: only one subgeneric hybrid was found (*H. muelleri* x *H. syndactylus*). Table 2.2.3 summarises the species combinations of the F1 hybrids within the *lar* group.

Table 2.2.3: Species combinations found in F1-hybrids of the *lar* group. Commas separate males (left) and females (right).

	Mother					
Father	*H. agilis*	*H. lar*	*H. moloch*	*H. muelleri*	*H. pileatus*	Total
H. agilis		–	–	1,2	–	3
H. lar	0,1		0,2	1,1	–	5
H. moloch	–	–		–	–	–
H. muelleri	0,2	2,3	2,2		–	11
H. pileatus	0,1	2,4	2,0	–		9
Total	4	11	8	5	–	10,18

2.2.2 Sound Analysis

Most of the tape-recordings were made with a Sony TC-D5M tape recorder equipped with a Sennheiser ME 80 (+K3U) directional microphone. At the beginning of this study only, vocalisations were recorded with an UHER 4200 Report Stereo tape recorder (with tape speed of 9.5 cm/s) and an AKG directional microphone (model CK9). The tape-recorded vocalisations were digitised on a Macintosh IIci computer using a Sound Recorder® device (Farallon). The sampling rate is defined as "the number of intervals per second used to capture a sound when it is digitized" (Schmidt et al., 1989) and determines the highest frequency the system can record. Unless otherwise stated, all sounds were sampled at a 11 kHz sampling rate, thus removing frequencies above 5.5 kHz. A detailed description of the method used here can be found in Schmidt et al. (1989). Sonagrams of digitised vocalisations were generated with the program the SoundEdit™ (version 2.0.1, Farallon).

2.2.3 Acoustic Terms and Definitions

A *note* is any single, continuous sound of any distinct frequency modulation, produced by either an inhaled or an exhaled breadth. A phrase is a larger and looser collection of notes identifying a single vocal activity. These definitions were developed by Haimoff (1984a) for the study of gibbon vocalisations. The term song is used here according to the definition of Thorpe (1961, p. 15): "What is usually understood by the term song is a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time", or shorter: a song consists of "Strophenfolgen mit nicht-zufälliger Folgewahrscheinlichkeit" (Tembrock, 1977, p. 33). Songs are separated by an arbitrarily defined interval of at least 5 minutes. A duet is defined as the joint vocalisation of two individuals, coordinated in time and/or in selection of distinct note-types (Wickler, 1974).

2.3 Olfactory Communication

2.3.1 Macroscopic Study

In order to collect reliable observations on skin glands in gibbons, a close examination of the animals was necessary. Although sternal glands of some animals were visible at a distance of several meters, their presence or absence in others could be detected only at close range. Close examination was also necessary in order to inspect skin areas that were covered with hair such as the axillary and inguinal regions, and in order to measure and photograph glands. Therefore, most of the observations reported below have been carried out on anaesthetised animals. A few additional findings stem from examination of particularly tame captive gibbons, and from fresh cadavers before they were fixed or otherwise preserved post-mortem. Appendix 10.3.1 summarises available information on the study animals and their life history.

It is important to note that the study animals were not sedated for the purpose of this investigation, but for management reasons (e.g. for veterinary checks, veterinary treatment, or in order to put them in transportation boxes). Several zoos were asked to indicate when such intervention was scheduled, and visits were timed accordingly. In a few instances, such an opportunity had not been prearranged but happened to coincide with the author's visit to a zoo.

The age of the animals in Appendix 10.3.1 was determined at the time when they were examined. The study animals were examined at the following institutions:

England: Bekesbourne: Howletts Zoo Park; Twycross Zoo.

France: Mulhouse: Parc Zoologique et Botanique; Paris: Ménagerie du Jardin des Plantes.

Germany: Duisburg Zoo; Eberswalde Zoo; Kronberg: Opel Zoo; Münster Zoo; Munich: Zoo Hellabrunn; Rostock Zoo; Schwerin Zoo.

Italy: Rome Zoo.

Switzerland: Bern: Naturhistorisches Museum Bern; Magliaso: Zoo Al Maglio; Studen: Zoo Seeteufel; Zürich: Anthropology Institute of Zürich University; Zürich: Tierspital of Zürich University; Zürich Zoo.

U.S.A.: Atlanta: Yerkes Regional Primate Research Center; New York: Laboratory for Experimental Medicine and Surgery in Primates (LEMSIP).

At the outset of this study, the author planned to examine large numbers of museum specimens (cadavers preserved in alcohol or phenoxetol and tanned skins) in order to estimate the frequency of skin glands in the various species of gibbons. After having examined a test sample of 52 specimens, it was discovered that the presence or absence of skin glands could often not be verified reliably in museum specimens (as will be demonstrated in the Results section), and the undertaking was discontinued. Similarly, estimating the frequency of skin glands in captive gibbons without close examination proved to be unreliable and was soon abandoned.

Because detailed observations of skin glands could be reliably made only on anaesthetised, tame or freshly dead animals, only individuals examined under these conditions are listed in Appendix 10.3.1. Occasional observations on other gibbons will also be presented in the Results section; information on the identity of these animals will be provided there. Specimens identified with an AIMUZ-number are preserved in the collection of the Anthropology Institute of Zürich University; those with an AHS-number are part of the A. H. Schultz collection, also housed at the Anthropology Institute in Zürich.

In early stages of the present study, animals were examined only in the sternal region. Later, a number of other areas of the skin were examined where possible; these include the axillary, clavicular and inguinal areas, the region of the lower, lateral ventrum, and the area between the scapulae.

Because anaesthetised animals were usually subjected to some medical treatment or checks before the author was allowed to examine them, the time available for examination (i.e. the time before the anaesthetic ceased to be effective) was usually of short duration, ranging

from a few seconds to several minutes. Therefore, it was not always possible to examine all skin regions of interest in the short time available. Documentary photographs of the various skin regions were made when time permitted. Photographs were made with a 100 mm macro-lens.

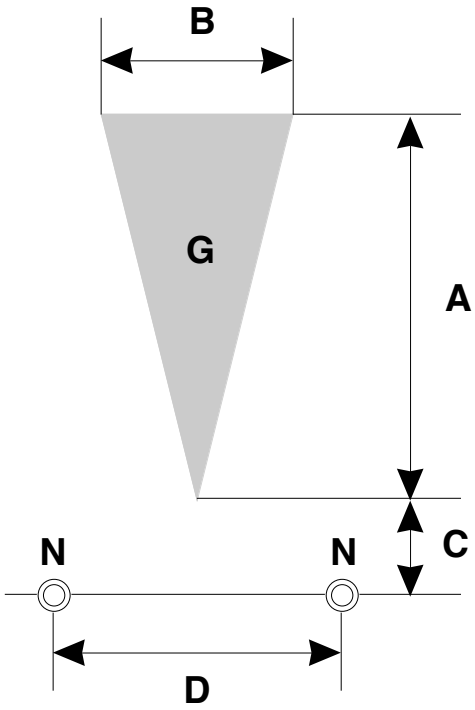

Figure 2.3.1: Schematic contour and measurements (A – D) taken of sternal glands in gibbons. G = glandular patch; N = nipples.

Where they occurred, sternal glands of gibbons were found to be relatively consistent in shape, usually resembling an inverted triangle. This made it possible to take standardised measurements of the glands' dimensions and location. Figure 2.3.1 illustrates the measurements. These measurements include: A, largest cranio-caudal length of the sternal gland; B, largest breadth of the gland; C, vertical distance of the caudal end of the gland from an imaginary line through the centres of the nipples; D, distance between the nipples. If the caudal apex of the sternal gland was situated above (i.e. cranial to) the nipples, measurement C had a positive value; if the gland's apex was situated caudal to the nipples, C was negative. Measurement D was recorded mainly in order to provide an indication of the animal's body size. Although the

distance between the nipples is probably no more than a crude substitute for body size, it is easily measured even in unsedated but relatively tame gibbons, whereas other measurements, such as body weight, were frequently not available.

In order to increase sample sizes, adult and subadult animals were pooled. Individuals which were repeatedly observed and which thus cover several age classes are counted once for each age class.

Most measurements were taken of captive gibbons listed in Appendix 10.3.1. A few sternal glands visible on preserved museum specimens (not included in Appendix 10.3.1) were measured for comparison. These specimens include one preserved cadaver of a newborn male siamang preserved at the Anthropology Institute of Zürich University (AIMUZ 7969), two skins of *H. muelleri abbotti* housed at the British Museum of Natural History in London (BM[NH] No. 20.12.4.5 and 33.6.6.1), one skin of *H. muelleri funereus* at the Field Museum of Natural History in Chicago (FMNH No. 88564), and two skins of *H. agilis agilis* at the American Museum of Natural History in New York (AMNH No. 106571 and No. 106572).

In several zoos, caretakers were interviewed about skin glands in gibbons and great apes. Specific questions included whether the caretakers were familiar with skin glands in gibbons and other apes, and whether they had made any observations relating to these skin glands (such as marking behaviour, animals manipulating skin glands, the occurrence of glandular secretions, the ontogeny of glands, etc.). Information gained from these interviews will be referred to as such.

2.3.2 Microscopic Study

For this study, a total of 58 skin samples taken from 23 animals were submitted to histological analysis. A short description of each animal and each sample is provided in Appendix 10.3.2; only a few individuals are identical to those examined in the previous section (see also Appendix 10.3.1). The sites on the body of the animal from which skin samples were taken are shown in Figure 2.3.2. These sites will be referred to as dorsal (interscapular), axillary, sternal, lateral abdominal and inguinal, respectively, throughout this study. When a sternal skin gland was macroscopically visible (usually of an oblong shape), the sternal skin sample was cut vertically to the glandular area, in a strip which was long enough to include parts both of the glandular area and of the adjacent, unmodified area. The latter area will be referred to as lateral chest in the following text.

Tissues were fixed in formol (4%) and embedded in paraffin. Histological preparations were made from vertical sections cut at 7 and 10 μm.

Three different methods were used to stain the sections: (1) Hematoxylin and eosin (HE); (2) Alcian blue with periodic-acid-Schiff reaction (AB-PAS reaction); and (3) Masson's trichrome. In addition, some of the HE-stains were stained with alcian yellow (for acid mucopolysaccharides). These histological techniques are described, for instance, in Burck (1981) and Romeis (1968). A large number of the histological sections and staining procedures in this study were carried out by Ms. A.-M. Hulftegger at the Institute for Veterinary Anatomy of Zürich University, the others were made by the author at the Zoology Museum of Zürich University.

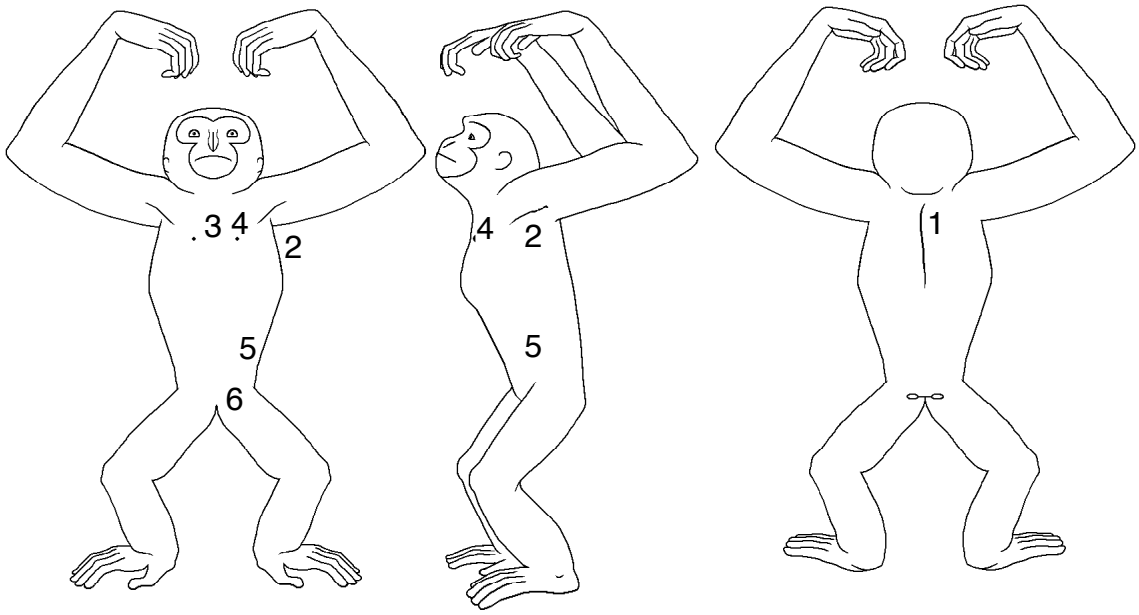

Figure 2.3.2: Sites from which skin samples were taken: 1. dorsal (interscapular); 2. axillary; 3. sternal; 4. lateral chest; 5. lateral abdominal; 6. inguinal.

2.3.3 Chemical Analysis

Between July 1986 and January 1991, a total of 138 samples (including 7 control blanks which will be described below) were collected for analysis using a radioimmunoassay technique. All radioimmunoassays (RIA) for this study were carried out by Ms. B. Manella at the Kinderspital Zürich. A detailed description and discussion of the radioimmunoassay technique can be found in Moss et al. (1976). For each sample, the three steroid hormones dehydroepiandrosterone (DHEA), androstenedione, and testosterone were analysed.

Most samples of skin secretions were collected from anaesthetised animals. The anaesthetised gibbons are mostly the same as those examined in the macroscopic study (Section 2.3.1, see also Appendix 10.3.1). As already pointed out there, the animals were not sedated for the purpose of this investigation, but were examined by the author when their sedation became necessary for management reasons.

The study animals are (or were) kept at the following institutions:

- Atlanta: Yerkes Regional Primate Research Center (U.S.A.)
- Duisburg Zoo (BRD)
- Mulhouse: Parc Zoologique et Botanique (F)
- Munich: Zoo Hellabrunn (BRD)
- New York: Laboratory for Experimental Medicine and Surgery in Primates (LEMSIP), (U.S.A.)
- Paris: Ménagerie du Jardin des Plantes (F)
- Zürich: Zoological Garden (CH)

Secretions were collected from 4 gibbon species and 2 great ape species. Table 2.3.1 lists the number of samples of every species collected at the various institutions. The individual study animals and the number of samples collected from each are listed in Appendix 10.3.3. Because animals are a subset of those used for the macroscopic study (see section 2.3.1 above),

information on the study animals' life history has already been summarised in Appendix 10.3.1 and is not repeated in Appendix 10.3.3.

Appendix 10.3.3 lists fewer individuals and samples than Table 2.3.1, because it includes only those individuals which have actually been used for the present analysis: Two different techniques for the collection of skin secretions were evaluated at the beginning of the study (see below). Because one of these failed to give meaningful results, some samples (and some individuals) had to be excluded from the final analysis.

Table 2.3.1: Number of samples of skin secretions collected for this study. (The numbers in brackets represent the number of individuals.)

Species	Institution [a]							Total
	Atlanta	Duisb.	Mulh.	Munich	N. Y.	Paris	Zürich	
Hylobates lar	12 (3)				4 (1)			16 (4)
H. leucogenys		13 (2)	6 (3)	14 (3)		6 (2)		39 (10)
H. pileatus							9 (5)	9 (5)
H. syndactylus				10 (2)			28 (4)	38 (6)
Pan troglodytes	8 (2)							8 (2)
Pongo pygmaeus	19 (6)						2 (1)	21 (7)
Control blanks						1	6	7
Total	39 (11)	13 (2)	6 (3)	24 (5)	4 (1)	6 (2)	39 (10)	138 (34)

[a] Only the cities appear in this list. See text for full names of institutions.

For most animals, secretion samples were collected in the sternal and axillary areas, but for some individuals additional samples were taken from other body regions. The latter regions are the same as those from which histological sections were made in the museum specimens (see above, Figure 2.3.2). All samples labelled as "dorsal" refer to the area between the shoulder blades in the midsagittal plane.

Unless otherwise stated, samples were collected in a standardised way: After the animal was sedated, sterile compresses (TELFA, ® Trademark Kendall Company Boston, USA) were

moistened with pure ethanol (per analysis, 99%) and rubbed with slight pressure twelve times over a selected spot of the animal's skin. In order to avoid contamination of the samples with human steroid hormones, a fresh pair of medical gloves was used for the collection of each sample.

Table 2.3.2 lists the hormone concentrations of the seven control samples used in this study. Not all controls served the same purpose. In the following paragraphs, the various types of controls and the way how they were collected will be described in detail.

Three unmanipulated TELFA compresses were used as control samples (Nos. 1-3, Table 2.3.2). The highest steroid concentrations found by RIA in any of the three control samples were then subtracted from the hormone values of (most) secretion samples (exceptions described below). By this means, the "background noise" introduced into our results by the sensitivity of the RIA technique was eliminated. This procedure will be referred to as "standard correction" in the following text.

Table 2.3.2: Hormone concentrations used as controls (ng/sample). [1]

Control No.	DHEA [2]	Androstenedione	Testosterone
1	0.82	0.72	0.83
2	1.12	0.64	0.44
3	0.83	0.82	0.39
4	–0.86	8.33	–2.97
5	0.66	3.00	2.16
6	13.88	5.33	3.40
7	0.00	0.33	0.02

1 See text for a description of the different types of controls and explanation for negative values in control No. 4.

2 DHEA = Dehydroepiandrosterone

In the following cases, special corrections were necessary: In a few instances, an opportunity for collecting secretion samples arose when no gloves where available (samples

Nos. 3-25). Although the author then washed his hands with great care before collecting every single sample, the TELFA compresses possibly became contaminated to some degree with human steroid hormones during the rubbing procedure. In order to measure the amount of possible contamination, two samples (Nos. 32 and 33) were collected from adjacent areas on the back of the same animal; one sample (No. 32) was collected with gloves, the other one (No. 33) without gloves. The difference in the hormone concentrations between the two samples (33 minus 32) is shown in Table 2.3.2 as control No. 4. In two hormone concentrations (DHEA and Testosterone), the value for the sample collected without gloves was lower than the value for the sample collected with gloves (resulting in negative values in Table 2.3.2), which is the opposite of what should be expected if the samples had been contaminated by the investigator. The sample collected without gloves had considerably higher concentrations only for androstenedione, probably as a result of contamination. This possible amount of androstenedione contamination was subtracted from all samples that had been collected without gloves.

In another control test, the author intensively manipulated one new TELFA compress with ethanol. The androstenedione and testosterone (but not the DHEA) levels measured on this control sample (No. 5, Table 2.3.2) are slightly higher than the "standard corrections" described above. The difference may be due to contamination. The testosterone concentration found in this control sample has accordingly been subtracted from all samples collected without gloves. For androstenedione, the higher correction value described above (control No. 5) has been used for samples collected without gloves. For DHEA, the "standard correction" measured on control sample 2 was the highest correction value found; therefore, it was also used for the samples collected without gloves.

Another unexpected opportunity for collecting secretion samples arose during a visit to the Ménagerie du Jardin des Plantes in Paris. Because neither gloves nor sterile TELFA compresses were available, samples were collected without gloves and on sterile gauze, not compresses (samples Nos. 62-67). Again, a control sample consisting of manipulated gauze and ethanol was

collected (control No. 6, Table 2.3.2), and its hormone levels have been subtracted from all samples collected in Paris, in order to correct for possible effects of contamination.

A small amount of pure exudate from the sternal gland was collected in a test tube directly from the fur of a study animal (No. 60). In this case, an empty test tube served as a control sample (control No. 7, Table 2.3.2).

At the beginning of this study, another method for collecting skin secretions from anaesthetised animals was tested. In this, pure ethanol was allowed to trickle from a sterile pipette directly onto the skin region of interest. After 30 seconds, the ethanol was sucked up from the skin, using the same pipette. Samples collected with this method (Nos. 3, 4, 6, 8, 10) did not contain enough steroid hormones to be detected by RIA, in contrast to samples collected (partly from the same animals) with the compress-rubbing method described above. Therefore, the method of directly applying ethanol on the skin with a pipette was abandoned at an early stage of this study, and the results gained from these samples have not been used in the results.

Although there are too few specimens for a statistical comparison of the RIA results between animals belonging to different subspecies, no such differences are suggested by the data available. Therefore, all animals of the same species (including hybrids between subspecies) have been pooled for interpretation of the RIA results.

Because the exact amount of secretion collected with the rubbing method could not be determined reliably, hormone concentrations are given in ng per compress, unless stated otherwise.

For the statistical comparison of hormone concentrations between species, the (two-tailed) Mann-Whitney U-test (Siegel, 1956) has been used with a significance level set at 5% ($\alpha = 0.05$).

2.4 Visual Communication

As mentioned in section 1.4, there is some controversy about the phylogenetic relationship of *H. agilis albibarbis* (Groves, 1984). Whereas vocal characteristics of this gibbon are virtually identical to those of other populations of *H. agilis*, its fur colouration shows some similarities to *H. muelleri muelleri* (one of three recognised subspecies of *H. muelleri*). *Hylobates agilis albibarbis* is not known to differ from other populations of *H. agilis* in any other aspect than fur colouration. Similarly, differences between the three subspecies of *H. muelleri* (*muelleri*, *funereus*, and *abbotti*) are confined to fur colouration. Therefore, these taxa are treated separately only in the chapter on Visual Communication.

Data on fur colouration and body weight of gibbons were collected in a number of museum collections which are listed in Appendix 10.7. The data set was supplemented with information from the literature, as mentioned in the text and in the tables on body weight (Appendix 10.9). Information gained from captive gibbons was used only for some aspects on fur colouration, but not for body weights.

When compiling data on body weight, only adult animals or animals reported to be adult where included in the analysis. "Young adult" specimens were also included, but "nearly adult" specimens (Lyon, 1908, p. 675) were not. All adult, wild-caught gibbon specimens of known weight are individually listed in Appendix 10.9. A list of the collectors and abbreviations for their names (used in Appendix 10.9) are presented in Appendix 10.8. Finally, a gazetteer of all collecting localities mentioned in Appendix 10.9 is provided in Appendix 10.10.

Multidimensional scaling (MDS) was computed using SYSTAT software (version 5.1, SYSTAT, Inc.). Because MDS operates directly on dissimilarities, a dissimilarity matrix had first to be calculated from the data set under study. This was accomplished by calculating a matrix of negative Pearson correlations. The matrix was then subjected to MDS following the Guttman method (Wilkinson, 1989).

2.5 Phylogenetic Evaluation

Phylogenetic analysis were conducted with the aid of the PAUP program version 3.0 (Swofford, 1990) and the MacClade program version 3.0 (Maddison & Maddison, 1992). Cluster analysis (UPGMA) was computed using SYSTAT software (version 5.1, SYSTAT, Inc.).

The bootstrap option (Felsenstein, 1985) of PAUP was used to examine the robustness of internal nodes. In this procedure, the data matrix is replicated *n* (here =100) times. For every replicate, some characters from the original matrix will be duplicated one or more times, and others will be omitted entirely. For each replicate, an estimate of the phylogeny is obtained using standard Wagner parsimony procedures, and a consensus tree is developed from these 100 phylogenies. If monophyly of a group of taxa occurs in 95% or more of the trees obtained from the replicates, the evidence for the monophyly of that group is thought to be statistically significant.

For comparison with the extant gibbon taxa, a hypothetical "ancestor" was used as an outgroup. This "ancestor" was assembled using primitive character states wherever they could be reconstructed or plausibly assumed. Where the primitive character state was unknown, the "ancestor's" state was coded as missing. This method of using a hypothetical "ancestor" is essentially equivalent to directly coding certain character states as ancestral in the input data file, as used in an earlier studies (e.g. Haimoff, 1983a; Haimoff et al., 1982, 1984). The "ancestor" method was preferred here, because this facilitated the removal of the assumptions which underlie the identification of primitive character states, and thus facilitated explorative data analysis.

The consistency index (CI) of a character is defined as the minimum conceivable number of steps for that character on any tree, divided by the number of reconstructed steps for that character on the particular tree in question (Maddison & Maddison, 1992). A CI of 1 would thus indicate a character with no homoplasy, and a CI of 0.5 would indicated that twice as many

steps as needed occur in this character. The CI for all characters on a tree can be defined as the minimum possible tree length divided by the observed tree length.

3. Vocal Communication

3.1 Introduction

3.1.1 Description of Gibbon Song Bouts

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 s. The shape of individual great call notes and the intervals between the notes follow a species-specific pattern (Haimoff, 1983, 1984; Marler & Tenaza, 1977; Marshall & Marshall, 1976; Marshall & 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 2 min. In the intervals, females usually produce so-called interlude sequences: short, variable phrases of relatively simple notes which in many species bear some resemblance to male phrases described below. The typical female song bout hence follows the sequential course *ABCBCBCBC…*, where *A* stands for the introductory sequence, while *BCBCBC…* represent the alternating great call sequences and interlude 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 min.

Male Song Contributions

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 & Tenaza, 1977; Marshall & Marshall, 1976; Marshall & Sugardjito, 1986).

Whereas mated males of most gibbons species may produce solo song bouts, mated males of *H hoolock*, *H. syndactylus* and of 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 2 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 & Tenaza, 1977; Marshall & Marshall, 1976; Marshall & 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. Thereafter, great call sequences and interlude sequences are produced in successive alternation. During interlude sequences, males usually progressively develop their phrases from short, 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 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 phrases, but is more stereotyped. It usually interrupts the progressive building-up of the male phrases described above by being more advanced in development than the male phrases 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 will be discussed below. Duet song bouts, like female song bouts, usually have a duration of less than 30 min.

At the climax of a great call, the female typically exhibits a locomotor display, usually accompanied by her mate in the duetting species, as shown in a male siamang in Fig. 3.1.1. The short and acrobatic bout of vigorous brachiation frequently includes branch shaking and (presumably intentional) breaking off dead branches (e.g. Carpenter, 1940; Chivers, 1974; Ellefson, 1968; Kappeler, 1981, 1984).

Figure 3.1.1: Adult male siamang (*H. syndactylus*) "Ingo" during a locomotor display exhibited immediately after the second climax of a great call sequence (Hellabrunn Zoo, Munich, 24 July 1982).

3.1.2 Inter-Species Comparison of Vocal Characteristics

The song repertoire is notably constant in structure and organisation for each species (see above). Species-specific characteristics of gibbon vocalisations have previously been listed for most gibbon species (Haimoff, 1983, 1984; Haimoff et al., 1982, 1984; Marler & Tenaza, 1977; Marshall & Marshall, 1976; Marshall & Sugardjito, 1986; Marshall et al., 1984). This study compiles a new matrix of characteristics which will be used for a cladistic analysis in Chapter 6. This matrix complements and – where necessary – corrects earlier lists. In addition, information on the distribution of vocal characteristics within the genus *Hylobates* and in other Old World primates in some cases permits to make some assumptions on whether a character state is ancestral to gibbons or derived.

3.1.3 Inheritance of Vocal Characteristics

The song repertoire had repeatedly been assumed to be largely genetically determined, although inheritance of song characteristics had not been conclusively assessed (Boutan, 1913; Brockelman, 1978; Carpenter, 1940; Marler & Tenaza, 1977; Tembrock, 1970). The observation that captive gibbons retain their species-specific song even in heterogeneous groups (Carpenter, 1940) does not explain how these animals acquired their particular song. Boutan (1913) raised a young gibbon in isolation from other gibbons, and this animal was eventually able to utter the song typical of this species (according to Boutan). The possibility cannot be precluded, however, that this animal learned the song from its parents prior to separation; moreover, it is not clear (from this otherwise detailed description) to what extent the song of this animal was in fact species-specific.

There remains the question of how the species-specific song traits can be passed on from one generation to the next. Critical evidence can, under particular circumstances which exclude the possibility of parental teaching, be expected from the analysis of the songs of hybrid gibbons compared with their parents. This circumstances are met if: 1.) the vocal repertoire of the parental species includes sex-specific vocalisations, and 2.) hybrids are reared only with their parents. Under these conditions, the potential template for a transfer of vocal characteristics from parents to hybrid is restricted to the female repertoire of the maternal and the male repertoire of the paternal species. In contrast, the template for a genetic transfer of vocal characteristics could include the full set of male and female repertoire of *both* species. Hence, a hybrid that produces female vocalisations which are specific to females of the paternal species cannot have heard these vocalisations from either parent. The same would be true for male vocalisations specific to males of the maternal species. Any such vocalisations in the repertoire of a hybrid gibbon must be inherited.

In fact, several gibbon species have been hybridised in captivity (see e.g. the records of 'species of wild animals bred in captivity', in: Int. Zoo Yearbook, 1962-1974, 1977-1982, 1986-1991); the most spectacular case describes a gibbon-siamang hybrid, *H. muelleri abbotti* x *H. syndactylus* (Myers & Shafer, 1978, 1979; Pellicciari et al., 1988; Rumbaugh et al., 1976; Shafer, 1986; Shafer & Myers, 1977; Shafer et al., 1984; Wolkin, 1977; Wolkin & Myers, 1980). In addition, evidence for some hybridisation in wild gibbons has been reported from three widely separated areas of sympatry: One each between *H. agilis* and *H. lar* in northern West Malaysia, between *H. lar* and *H. pileatus* in Khao Yai National Park in northeast Thailand, and between *H. agilis* and *H. muelleri* in central Kalimantan (Brockelman, 1978; Brockelman & Gittins, 1984; Gittins, 1978; Marshall & Brockelman, 1986; Marshall & Sugardjito, 1986; Marshall et al., 1984).

In a previous study, the present author has analysed the duet song of two hybrid offspring of a pileated and a lar gibbon (Geissmann, 1984a). In that study, he was able to demonstrate that the song of the hybrids differed from the songs of both parental species and that at least some of the hybrids' song characteristics were inherited.

That previous study, however, only referred to the song of two individuals. Additional studies on larger numbers of hybrids have now become available (Brockelman & Schilling, 1984; Marshall & Sugardjito, 1986; Tenaza, 1985). These studies mainly analysed songs which were tape-recorded in two of the natural hybrid zones mentioned above: one between the pileated and the lar gibbon in the Khao Yai National Park in Thailand, and one between the agile and Mueller's gibbon in Central Kalimantan (but see Tenaza, 1985). These studies found considerable differences in song structure between hybrid individuals which were thought to correspond to the proportion of genetic mixture between the two species contributing to each hybrid.

In individuals from a hybrid zone, however, the number of hybrid generations and the extent of admixture is usually not known. In most cases, an analysis of inheritance of song characteristics will depend on the validity of some preliminary assumptions: For instance, it has

been assumed that individuals that look like and sing like a pure species are in fact genetically pure species. This is not necessarily true in a hybrid population. Second, it has in several cases been assumed that young animals living with an adult pair represent the immediate offspring of that pair. However, several exceptions to this immediate family pattern have been found exactly in the hybrid zone between pileated and lar gibbons (Brockelman & Treesucon, 1986).

For the present study, songs of a large sample of captive hybrid gibbons of exactly known parentage are analysed (n=28). The sample includes mostly first generation hybrids as well as a few second generation hybrids. All study animals are hybrids between species of the *lar* group, with the exception of the one hybrid between a male *H. muelleri* and a female *H. syndactylus* mentioned above.

As a result of this study, the song pattern of several *true* first-generation hybrids can now be described in some detail for the first time, the variability or stereotypy of this hybrid pattern can now be assessed to some degree, and it can be shown whether some of the song characteristics passed on from parent to hybrid are based on genetic or learned processes (where the latter implies learning from the parents).

3.1.4 Comparison of Hybrid Calls

The vocalisations of hybrid gibbons are of additional interest for the present study. Vocalisations of F1 hybrids have been shown to combine vocal characteristics of both parental species (Brockelman & Schilling, 1984; Geissmann, 1984a; Marler & Tenaza, 1977; Marshall & Sugardjito, 1986). If species-specific parental characteristics are transferred to hybrids to form a combination which is specific to a certain hybridisation, then the following expectation can be formulated: Similar vocal characteristics shared by two species and submitted to the same type of hybridisation should result in similar hybrid vocalisations if they are *homologous* characteristics. Similarities based on convergent evolution are less likely to "behave" identically under hybridisation, especially if the characteristics are inherited and if they depend on more

than a single locus. Problems of homology obstructing the reconstruction of gibbon systematics using vocal characteristics have been mentioned previously (Creel & Preuschoft, 1984). Comparison of hybrid vocalisations can possibly help to resolve some of these problems.

3.2 Pure Species Vocalizations

In the present section, the vocal characteristics of each species and the type of call bout produced by mated animals are briefly described. A list of all characteristics available for cladistic analysis, including specifications of the character states for each species, is provided in Appendix 10.2.

Figure 3.2.1 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 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 & Marshall, 1976, 1978; Marshall & Sugardjito, 1986) are virtually identical to those recorded from captive gibbons during the present study.

The great call sequences in Figure 3.2.1 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 3.2.1 (see following page): 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.: 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, 17 May 1988); j. *H. l. gabriellae* (Mulhouse Zoo, 13 Sept. 1988); k. *H. syndactylus* (Metro Zoo, Miami, 31 July 1988).

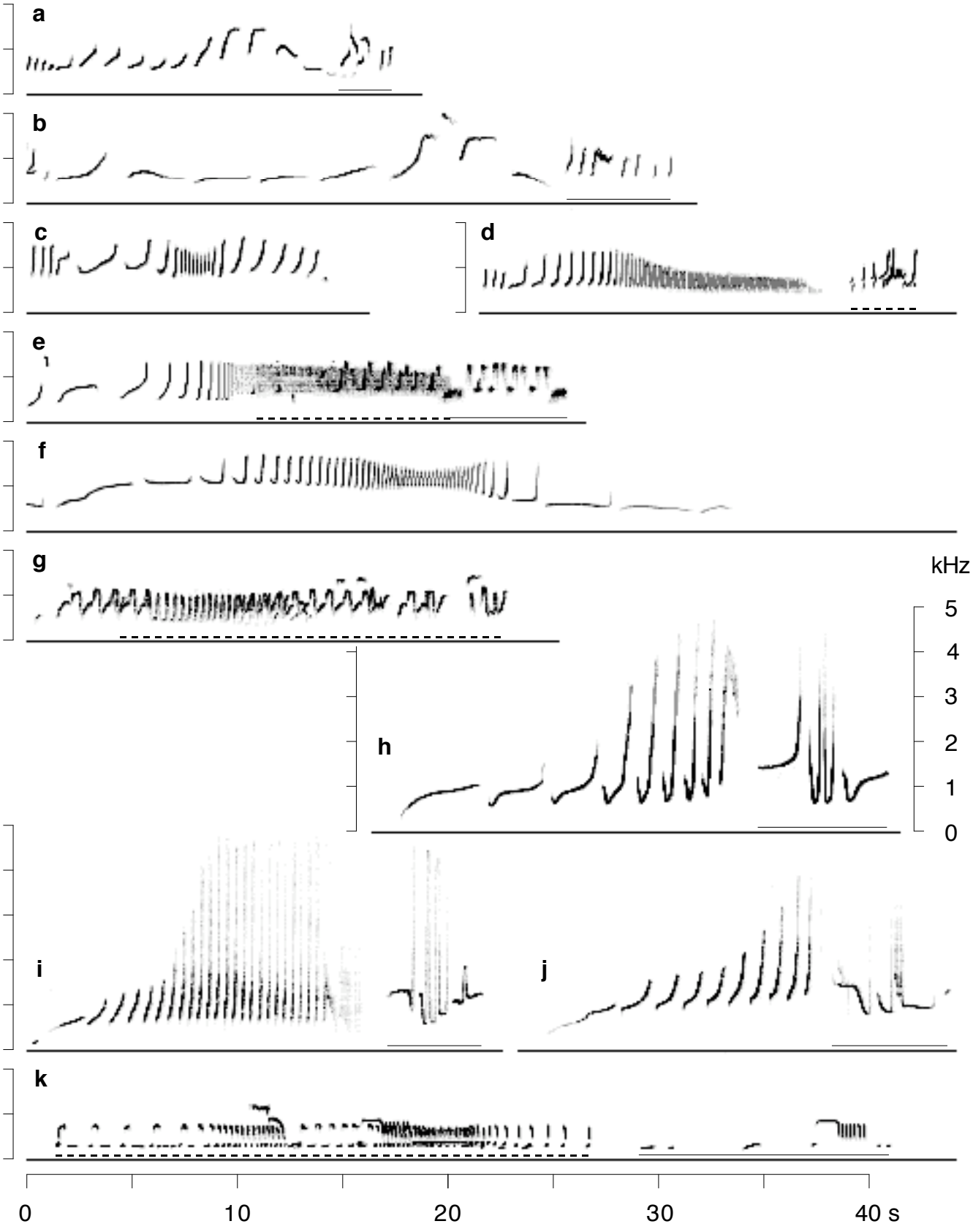
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Figure 3.2.2 provides sonagrams of fully developed male phrases of all gibbon species, all recorded from captive specimens by the present author, excepting the solo song of a male *H. concolor* (recorded in the Ailao Mountain Reserve in China by the 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 & Marshall, 1976, 1978; Marshall & Sugardjito, 1986).

The sonagrams in Figs. 3.2.1 and 3.2.2 had to be considerably reduced in size in order to accommodate sonagrams of all gibbon species on one page. Larger sonagrams of the species of the *lar* group will be presented in Section 3.3.

Figure 3.2.2 (see following page): 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: Lan Daoying); h. *H. concolor* (Gejiu Zoo, 2 Aug. 1990); i. *H. leucogenys* (Paris, Ménagerie, 17 May 1988); j. *H. l. gabriellae* (La Flèche Zoo, 29 May 1988); k. *H. syndactylus* (Howletts Zoo, 16 Oct. 1988).

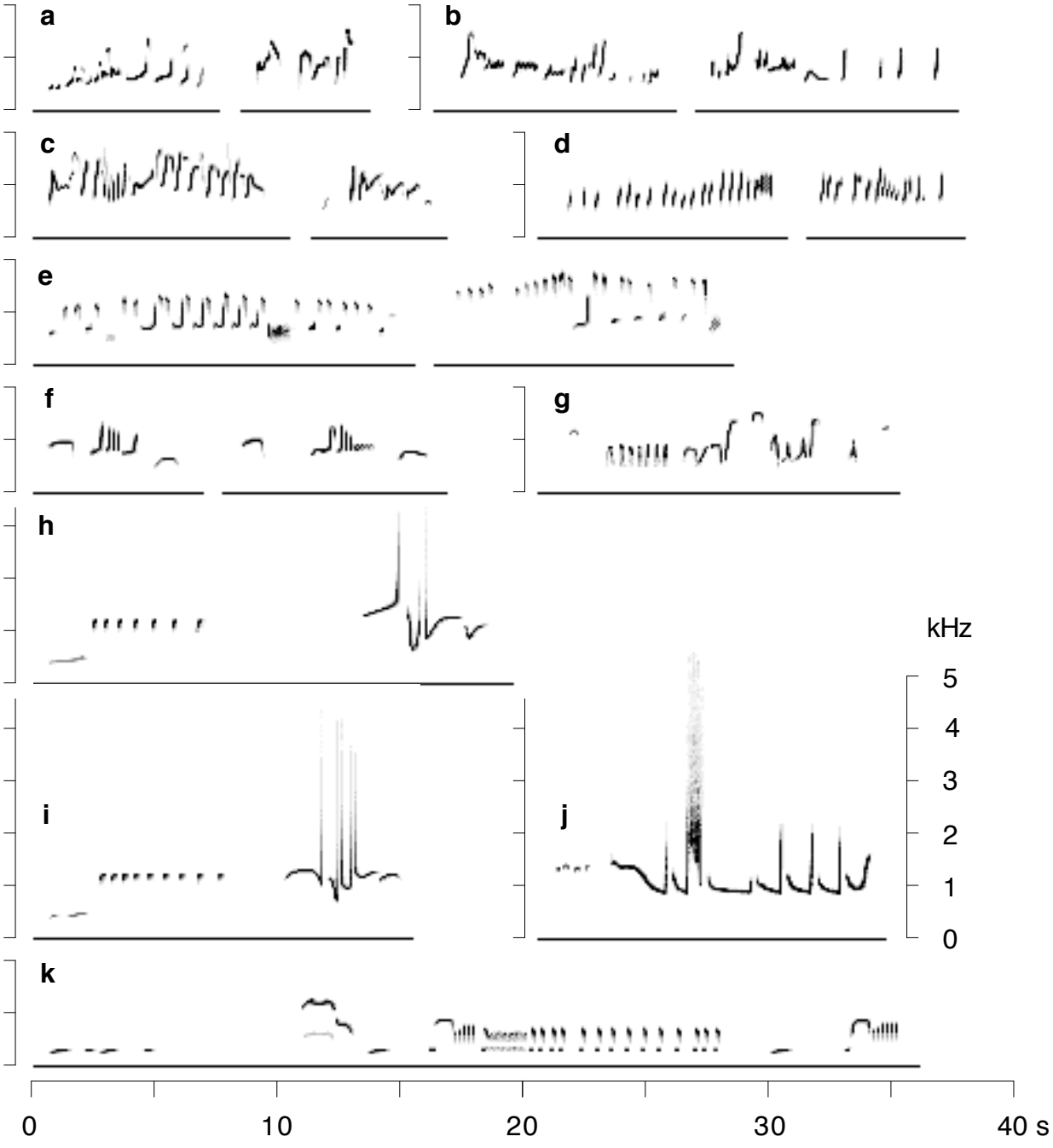


Figure 3.2.2: Legend see previous page.

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. 3.2.2a). 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. 3.2.1a). 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 closing of the mouth during long hoots (Fig. 3.2.2b). 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. 3.2.1b). 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. 3.2.2c). 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. 3.2.1c). Male solo song bouts and female solo song bouts. Duet songs uncommon or absent (see Discussion for a review of the surrounding controversy).

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. 3.2.2d). 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*. 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. 3.2.1d). Male solo song bouts *us*: 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. 3.2.2e). 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*. Male produces coda, beginning halfway through the great call (Fig. 3.2.1e). 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. 3.2.2f). 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. 3.2.1f). Male solo song bouts and female solo song bouts. Duet songs uncommon or absent (see Discussion for a review of the surrounding controversy).

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. 3.2.2g). 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. 3.2.1g). 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 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. 3.2.2.h). 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. 3.2.1h). 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. 3.2.2i). Females 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. 3.2.1i). Duet song bouts.

H. l. gabriellae: Fully developed male vocalisations similar to *H. concolor*, but booms usually missing, and series of short simple 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. 3.2.2j). 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. 3.2.1j). 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. 3.2.2k). 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 consisting of 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. 3.2.1k). Duet song bouts.

In most species, daughters living in the natal group sing great calls in synchrony with their mothers. During this study, examples of this were heard for *H. agilis*, *H. leucogenys*, and *H. syndactylus*. The synchronous production of great calls is not restricted to family groups. All adult gibbon females kept in adjacent cages were observed to produce their great calls in synchrony. This is not only true for females of the same species, but apparently for many, if not all combinations of gibbon species. Particularly impressive choruses were heard at the zoos of Asson (France) and Twycross (England), where large numbers of gibbon groups of various species are kept in adjacent cages. In Asson, synchronous mass great calls were observed to include females of *H. agilis*, *H. lar*, *H. leucogenys*, and two different female hybrids. In Twycross, such great calls were observed to include *H. agilis*, *H. lar*, *H. leucogenys*, *H. pileatus* and *H. syndactylus*. Many other combinations were heard in other zoos. In a few cases, neighbouring females were observed to abort great calls if another female failed to participate.

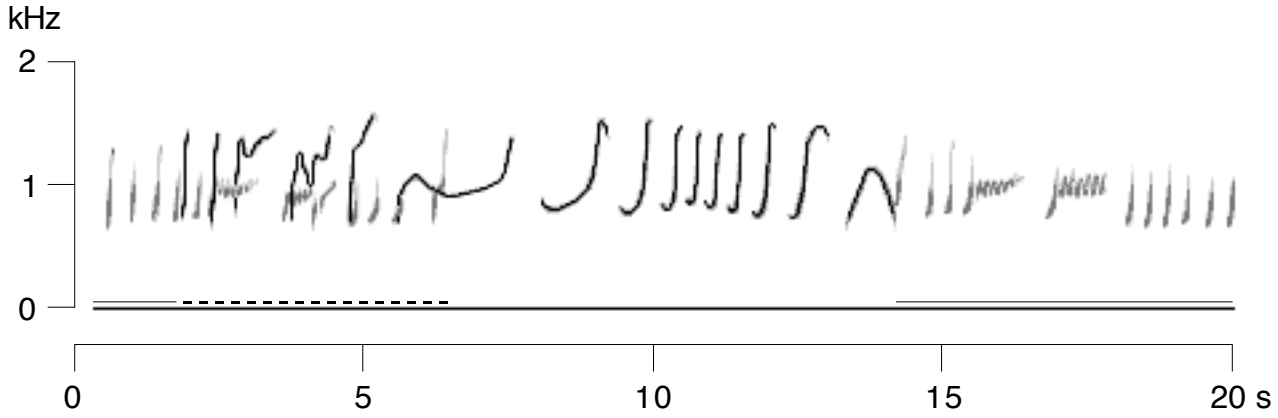


Figure 3.2.3: Sonagram of great call sequence of mixed pair *H. lar* (male) and *H. moloch* (female). Knie's Kinderzoo, Rapperswil, 30 April 1979 (rec. Dr. M. Schwarz). Male solo contributions are underlined with a solid line, synchronous male and female vocalisations are underlined with a dashed line.

In most species, males produce coda phrases to the great calls of their mates. In mixed pairs, males were observed to produce codas readily to females of other species. Such great call sequences were heard between a *H. pileatus* male and two different *H. lar* females, a *H. agilis* male and a *H. muelleri* female, and between a *H. lar* male and a *H. moloch* female (Fig. 3.2.3). In pure pairs, male codas are either typically inserted at the end of the great call in some species, or during the great call in others. In mixed pairs mentioned above, male codas were added to the great calls with the timing typical of the male's species: The male *H. pileatus* started to produce his codas already during the *H. lar* great calls, whereas the *H. agilis* and the *H. lar* males would add their codas at the end of their respective mates' great-calls (see Fig. 3.2.3). Likewise, in a mixed pair consisting of a male *H. pileatus* and a female hybrid (*H. pileatus* x *H. lar*), the male's coda would start before the end of the great call.

Mated males are not known to produce great calls, even in *H. hoolock* where the note repertoire does not appear to include sex-specific notes. In immature males of the *concolor* group, however, the situation is different. Like immature females, their song contribution contains short, great call-like phrases only, which are produced in synchrony with the great calls of their mother. This was heard with several immature males of *H. l. leucogenys* and *H. l.*

gabriellae. It probably occurs in *H. concolor* as well. Males of these species change from female to male repertoire at some time during their development, this event may be related to attainment of sexual maturity. Nothing similar has been described of other gibbon species. During the present study, however, one juvenile male *H. agilis* of less than 3.5 years of age was frequently heard to produce great calls. This male lived in Twycross zoo with his parental group, which included the breeding pair, a subadult daughter and a infant daughter. During the songs, the juvenile male would produce his great calls in synchrony with his mother and his subadult sister, whereas the breeding male of the group produced species-specific male phrases only.

3.3 Hybrid Vocalisations

3.3.1 Female Hybrids

Females:

In this section, the vocal characteristics of each female hybrid are briefly described. For each hybrid, a sonagram of a typical phrase is provided. In order to facilitate comparison with vocalisations of pure species, sonagrams of females of all species of the *lar* group are shown in Fig. 3.3.1.

Figure 3.3.1 (see following page): Sonagrams of great calls of all gibbon species of the *lar* group. a. *H. agilis* (Asson Zoo, 31 May 1988); b. *H. lar* (Al Maglio Zoo, 23 Nov. 1987); c. *H. moloch* (Munich Zoo, 16 July 1987), d. *H. muelleri* (Paignton Zoo, 22 Oct. 1988); e. *H. pileatus* (Rome Zoo, 7 Oct. 1987).

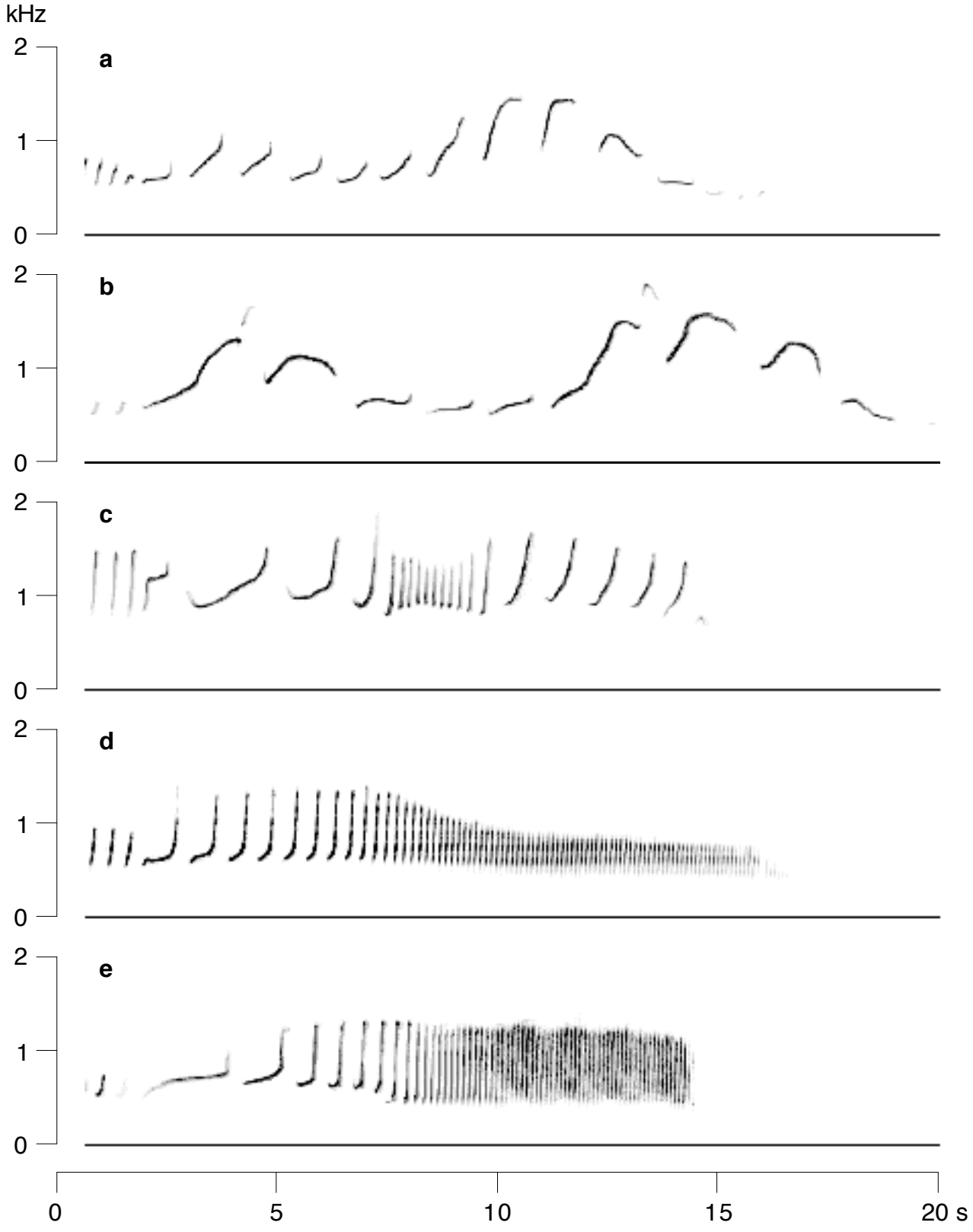


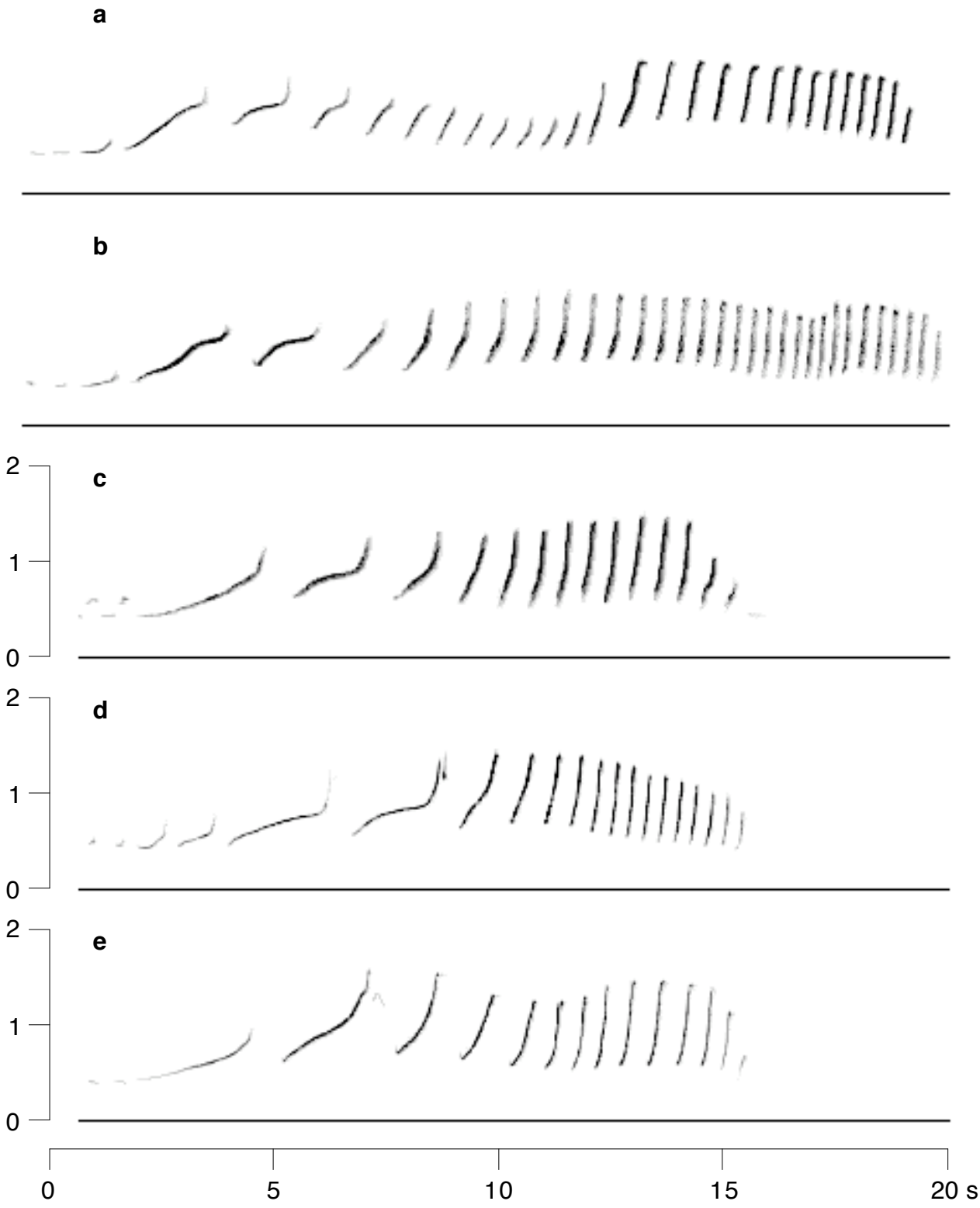
Figure 3.3.1 (Legend see previous page).

H. pileatus x *H. lar* (Fig. 3.3.2): The great call shows notes of increasing frequency only, and an acceleration-type climax. Speed of note presentation moderate, intermediate between parental species. Two climaxes occur frequently in all animals. Great calls of one of these hybrids ("Toni") tape-recorded in Sept. 1981 are virtually identical to those recorded of the same female in June 1987.

H. muelleri x *H. lar* and *H. lar* x *H. muelleri* (Fig. 3.3.3): The great call shows notes of increasing frequency only, and an acceleration-type climax. Speed of note presentation moderate, intermediate between parental species. Two climaxes optionally occur in all animals, excepting the female *H. lar* x *H. muelleri.*

H. muelleri x *H. agilis* and *H. agilis* x *H. muelleri* (Fig. 3.3.4): The great call shows notes of increasing frequency only, and an acceleration-type climax. Speed of note presentation moderate, intermediate between parental species. No great calls with two climaxes were observed in any of these hybrids. Both specimens of *H. muelleri* x *H. agilis* were singing in synchrony with their mother and possibly not fully mature when recorded on tape. This may be responsible for the shortness of their great calls.

Figure 3.3.2 (see following page): Sonagrams of great calls of hybrids *H. pileatus* x *H. lar*. a. "Toni", Opel Zoo Kronberg, 18 June 1987; b. "Johnny", Opel Zoo Kronberg, 18 June 1987; c. "Miss", Asson Zoo, 31 May 1988, d. "Suse" Ruhr Zoo, Gelsenkirchen, 30 June 1987; e. "Yoko", Southport Zoo, 10 Oct. 1988. Vertical scale in kHz.



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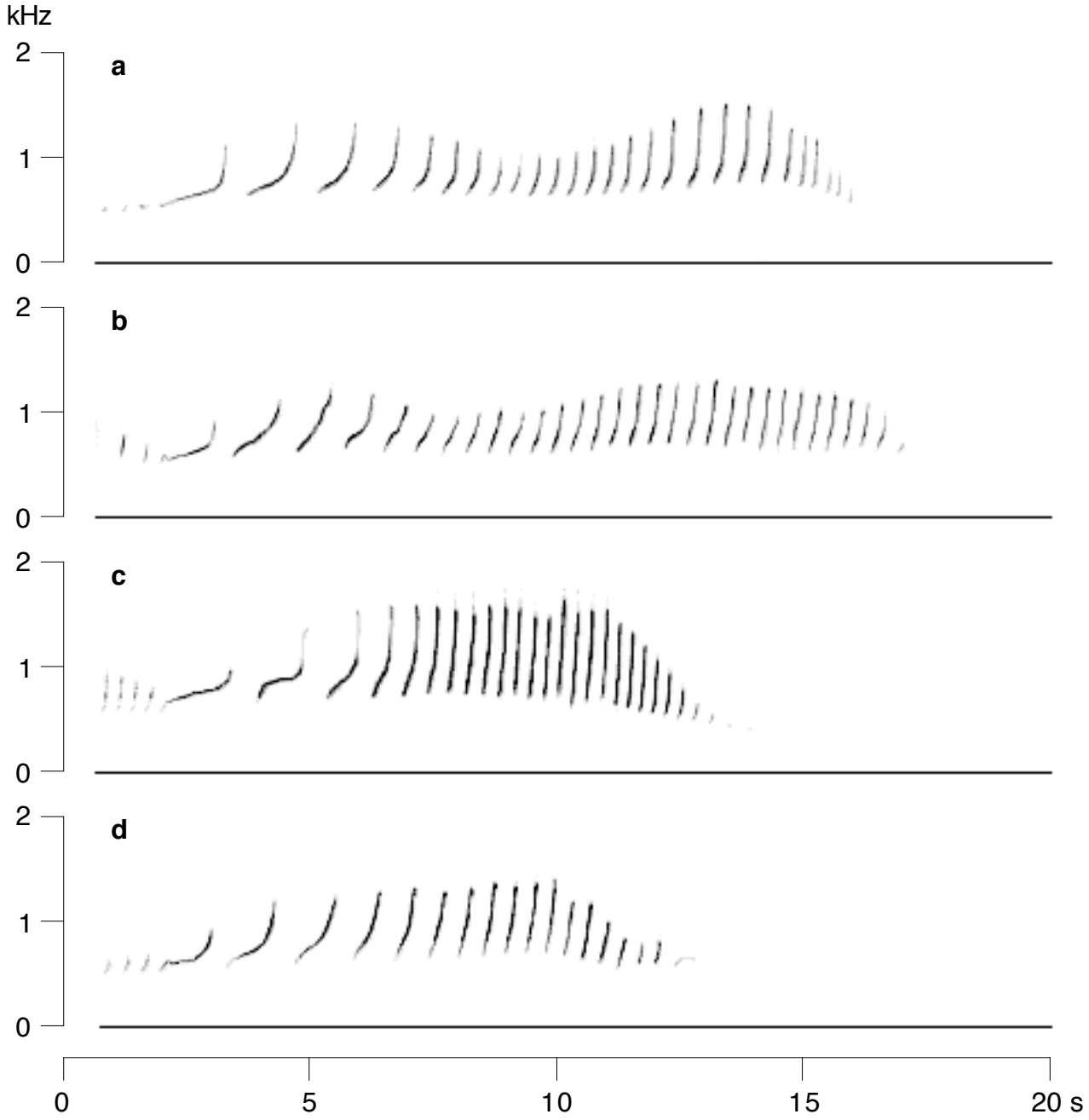


Figure 3.3.3: Sonagrams of great calls of hybrids *H. muelleri* x *H. lar* (a-c) and *H. lar* x *H. muelleri* (d). a. "Micky", Duisburg Zoo, 26 June 1987; b. no name, Mazé, 30 May 1988; c. "Tina", Ravensden Farm, Rushden, 13 Oct. 1988, d. no name, Micke Grove Zoo, 10 Feb. 1976 (rec. Dr. R.R. Tenaza).

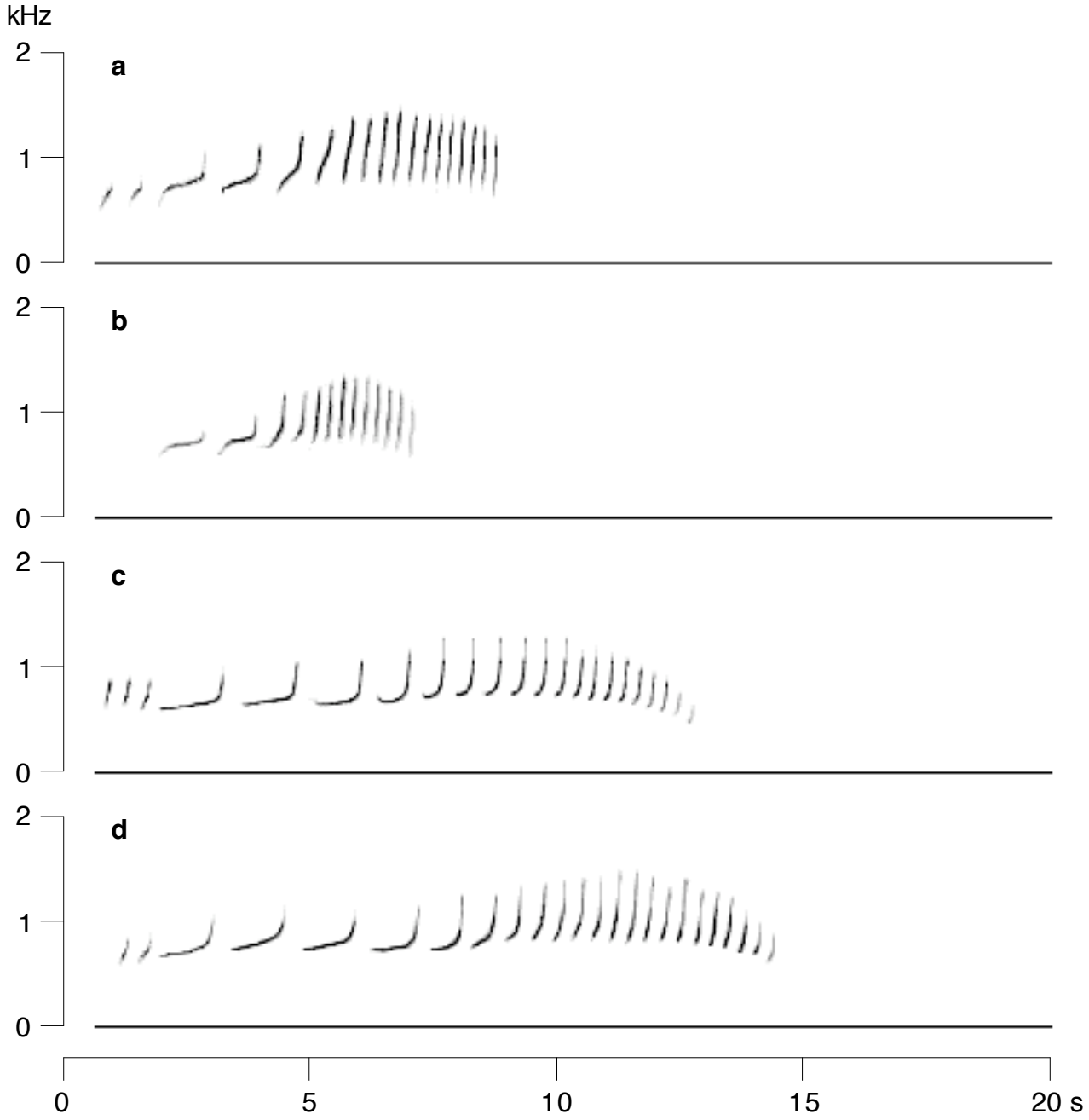


Figure 3.3.4: Sonagrams of great calls of hybrids *H. muelleri* x *H. agilis* (a-b) and *H. agilis* x *H. muelleri* (c-d). a. no name, older hybrid, Louisiana Zoo, Monroe, Sept. 1979 (rec. Mr. C. Welch); b. no name, younger hybrid, Louisiana Zoo, Monroe, 12 Nov. 1987 (rec. Dr. M.M. Haraway); c. "Bertha", Lion Country Safari Park, West Palm Beach, 2 Aug. 1988, d. "Bernice", Lion Country Safari Park, West Palm Beach, 2 Aug. 1988.

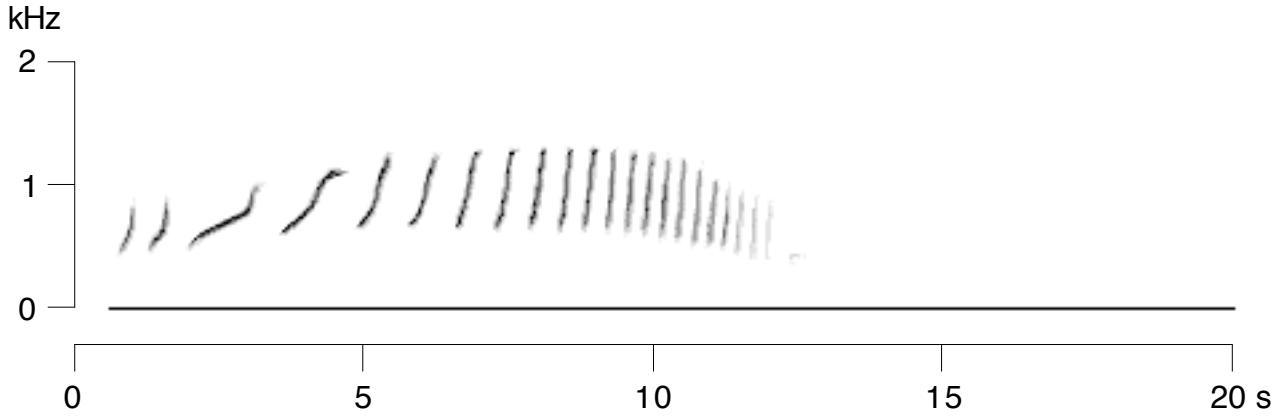


Figure 3.3.5: Sonagram of great call of hybrid *H. pileatus* x *H. agilis*: "Barbara", U.S: National Zoological Park, Washington, D.C., April 1979 (rec. Mr. D. Kessler, Mr. M. Roberts).

H. pileatus x *H. agilis* (Fig. 3.3.5): The great call shows notes of increasing frequency only, and an acceleration-type climax. Speed of note presentation moderate, intermediate between parental species. Only two great calls were tape-recorded from this animal, neither had two climaxes. The female was well over 34 years old when the tape-recordings were made.

H. lar x *H. moloch* (Fig. 3.3.6a-b): The great call shows notes of increasing frequency only in the first hybrid (Fig. 3.3.6a), and additional notes of relatively stable frequency at the end of the great calls of the second hybrid (Fig. 3.3.6b). Great calls clearly with acceleration-type climax in the first hybrid. This cannot be reliably ascertained in the second hybrid, mainly because of the brevity of its great calls. In both hybrids, notes frequently begin with a short descent in frequency and end with a short descent. These notes appear S-shaped in the sonagrams, similar to those of *H. moloch*. Speed of note presentation slow, intermediate between parental species in the first hybrid, but similar to *H. lar* in the other. Great calls with two peaks frequently occur in the first hybrid, but were not recorded in the second one.

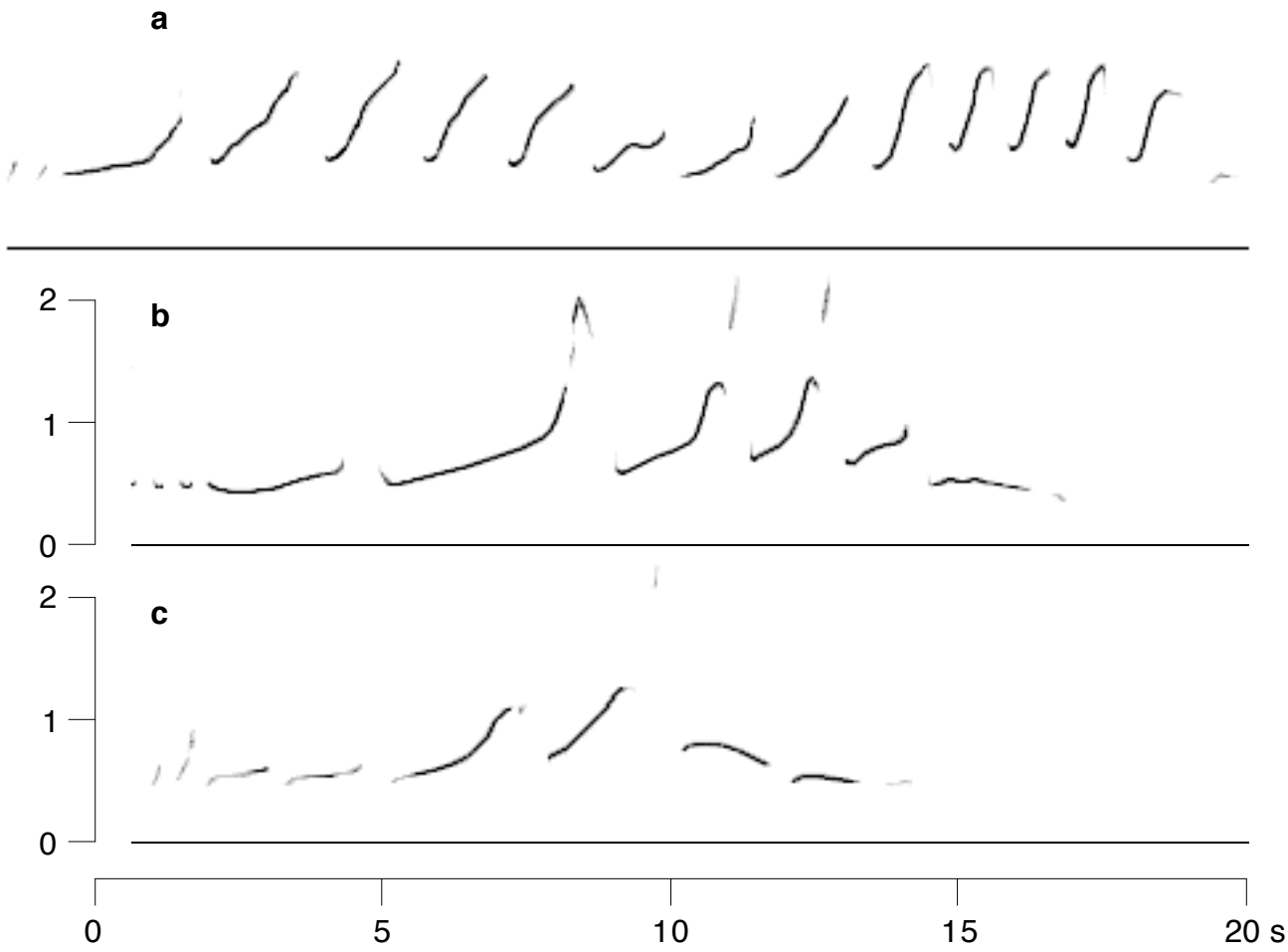


Figure 3.3.6: Sonagrams of great calls of hybrids *H. lar* x *H. moloch* (a-b) and backcross *H. lar* x (*H. lar* x *H. moloch*) (c). a. "Frieda", Serengeti Park, Hodenhagen, 9 July 1987; b. "Gipsy", Rheine Zoo, 4 July 1987; c. "Alice", Hasenmoor, 8 Nov. 1989 (rec. Mr. and Mrs. Manzke). Vertical scale in kHz.

H. lar x (*H. lar* x *H. moloch*) (Fig. 3.3.6c): The great call shows notes of increasing and of decreasing frequency, like *H. lar*. Climax of frequency-modulated type. Notes not S-shaped. Speed of note presentation slow, but apparently slightly faster than *H. lar*. Only two great calls available on tape, neither of which had two climaxes. Although the animal was nearly adult when recorded on tape, it may not have been fully mature; the female was kept in a peer group which included other gibbons of both sexes and was reported to vocalise only rarely. This may explain the brevity of this animal's great calls and, perhaps, the absence of two climaxes.

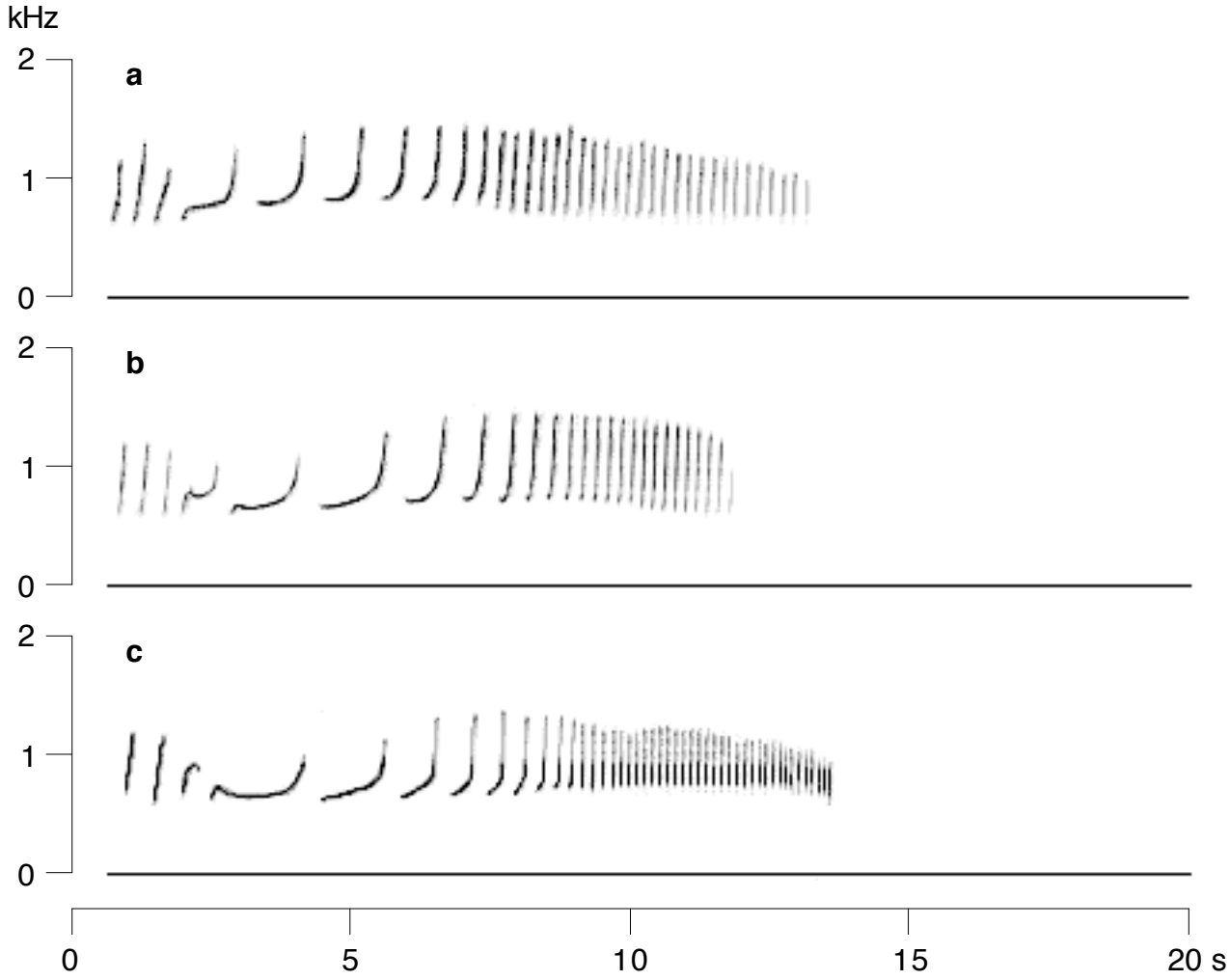


Figure 3.3.7: Sonagrams of great calls of hybrids *H. muelleri* x *H. moloch* (a-b) and backcross *H. muelleri* x (*H. muelleri* x *H. moloch*) (c). a. "Juvi", Bristol Zoo, 18 Oct. 1988; b. "Maria", Münster Zoo, 1 July 1987; c. "Bo", Münster Zoo, July 1990 (rec. Ms. B. Uphoff).

H. muelleri x *H. moloch* (Fig. 3.3.7a-b): The great call shows notes of increasing frequency only, and an acceleration-type climax. No S-shaped notes. Speed of note presentation relatively fast, intermediate between parental species. Great calls with one climax only.

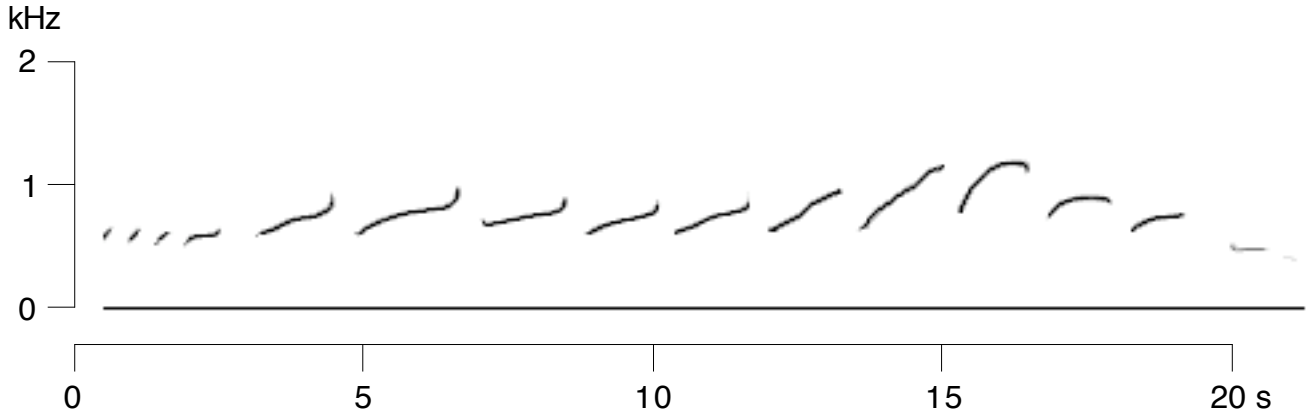


Figure 3.3.8: Sonagram of great call of hybrid *H. lar* x *H. agilis*: no name, Asson Zoo, 2 June 1988.

H. muelleri x (*H. muelleri* x *H. moloch*) (Fig. 3.3.7c): The great call shows notes of increasing frequency only, and an acceleration-type climax. No S-shaped notes. Speed of note presentation relatively fast, faster than in *H. muelleri* x *H. moloch*, but still not as fast as in *H. muelleri*. Great calls with one climax only. The great call shown in Figure 3.3.7c is part of songs recorded in July 1990, when the female was young adult (6 years old), but still living in its parental group and singing in synchrony with its mother. Great calls of the hybrid were previously tape-recorded in July 1987 when the animal was a juvenile; they are virtually identical to those of the young adult in speed, but of shorter duration (mean = 7.0 s vs. 10.9 s). It is possible that the great calls will eventually become even longer once the animal is older.

H. lar x *H. agilis* (Fig. 3.3.8): Great call very similar to both parental species, showing notes of increasing and of decreasing frequency, and two climaxes of frequency-modulated type. Speed of note presentation slow, similar to both parental species, but clearly slower than in *H. agilis* mother. Only three calls available on tape. The animal was not fully mature (less than 5 years old) when recorded on tape. It was kept with a male *H. lar* of similar age, but rarely produced great calls. This may explain the less developed frequency changes in this animal's climaxes, compared to those observed in both parental species.

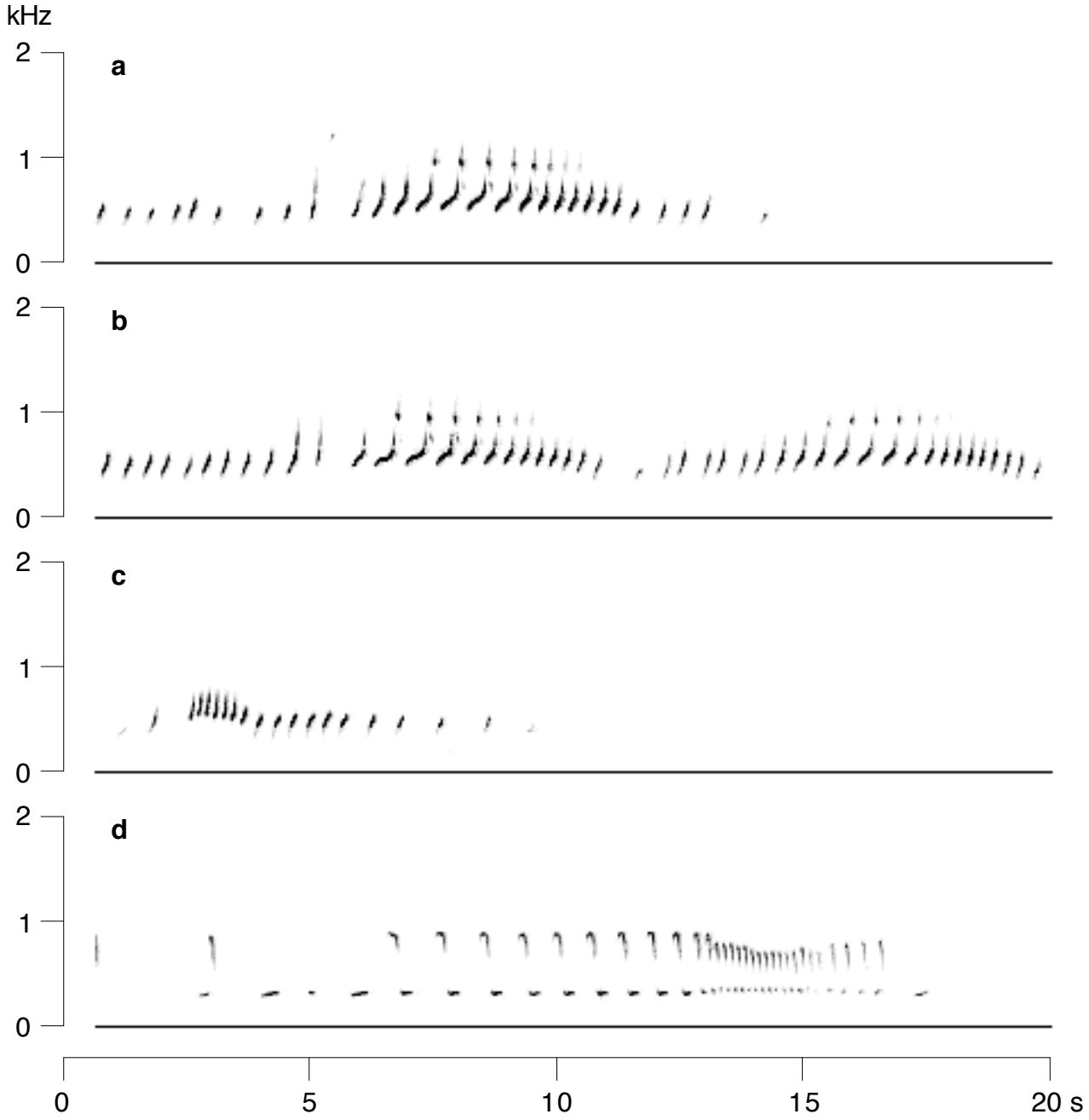


Figure 3.3.9: Sonagrams of great calls of hybrid *H. muelleri* x *H. syndactylus* (a-b), short phrase of the same hybrid (c), and great call of lone female *H. syndactylus* (d). a-c. "Shawn-Shawn", Yerkes Regional Research Primate Center, Atlanta, 5 Aug. 1988; d. "Gaspa", Zürich Zoo, 31 July 1981.

H. muelleri x *H. syndactylus* (Fig. 3.3.9a-b): Solitary female. The great call shows an acceleration-type climax, like those of both parental species. Speed of note presentation moderate, clearly slower than in both parental species. Great call notes bi-phasic during acceleration of great call. Bi-phasic notes consist of sounds alternatingly produced during exhalation and inhalation, like great calls of *H. hoolock*, but unlike either parental species. Great call optionally repeated immediately upon terminating previous great call, similar to the double acceleration in great calls of mated females of *H. syndactylus*. In solitary females of *H. syndactylus*, however, the great call apparently does not typically contain two accelerated series of barks, but one (Fig. 3.3.9d). Short phrases of hybrid female without bi-phasic notes, but frequently with trills (Fig. 3.3.9c), similar to – but slower than – short phrases of males of *H. muelleri*. Range of fundamental frequency similar to *H. syndactylus*, but much lower than in all other gibbon species.

As in pure species, hybrid females were observed to sing great calls in synchrony with their mothers or with other gibbon females kept in adjacent cages.

Most of the great calls of the various hybrids have been described above to occupy an intermediate position between the parental species in the rate of note emission. This impression can be verified by calculating the number of great call notes per great call duration for pure species and hybrids. These values are listed in Table 3.3.1 and support the impression gained from comparison of the vocalisations by ear or with sonagrams. The variability of the number of notes and the duration of the great call for pure species and hybrids of the *lar* group is shown in Figures 3.3.10-3.3.15.

In the following, great calls of *H. pileatus* x *H. lar* hybrids are discussed as an example. Considerable differences between these great calls (see above, Fig. 3.3.2) are obvious. The hybrid great calls differ in length, number of notes and number of accelerations. These differences are not individual-specific. For instance, each individual can produce great calls with one or two accelerations, and even rare great calls with three accelerations were observed. Such a degree of variability does not normally occur in pure pileated and *lar* gibbons.

Table 3.3.1: Number of notes, duration, and notes per second in great calls of pure species and hybrids of the *lar* group (SD = standard deviation). Taxa are ordered by the speed of their great call (notes/s).

Taxon	N great calls	Notes per great call		Duration (s) of great call		Notes / s
		Mean	SD	Mean	SD	
H. lar	85	9.6	1.9	18.4	3.5	0.5
H. lar x *H. moloch*	22	10.0	4.2	16.6	5.4	0.6
H. lar x *H. agilis*	3	11.3	1.5	17.1	1.8	0.7
H. agilis	42	9.7	1.7	14.8	2.7	0.7
H. lar x (*H. lar* x *H. moloch*)	2	8.8	0.3	11.9	0.4	0.7
H. pileatus x *H. lar*	53	19.3	7.0	14.8	2.9	1.3
H. moloch	39	15.1	2.8	11.5	1.9	1.3
H. lar x *H. muelleri*	13	16.3	2.3	10.0	1.0	1.6
H. pileatus x *H. agilis*	2	17.0	4.2	9.2	1.2	1.8
H. agilis x *H. muelleri*	14	21.9	1.8	11.3	0.8	1.9
H. muelleri x *H. lar*	32	28.7	6.0	13.5	2.4	2.1
H. muelleri x *H. agilis*	21	14.6	2.7	6.4	1.4	2.3
H. muelleri x *H. moloch*	21	28.6	4.5	10.5	0.8	2.7
H. muelleri x (*H. muelleri* x *H. moloch*)	8	40.5	9.2	9.7	1.8	4.1
H. pileatus	26	80.2	12.3	15.8	1.8	5.1
H. muelleri	35	66.8	17.5	12.0	2.6	5.6
Total	418					

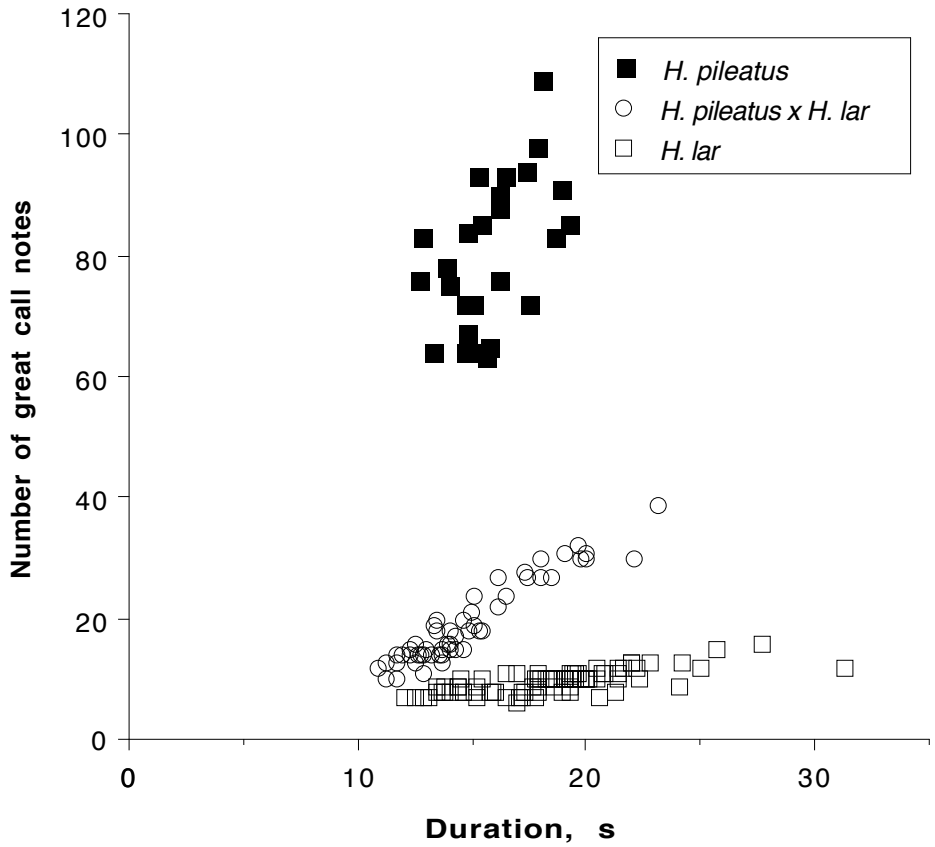


Figure 3.3.10: The number of notes in a great call plotted against its duration for *H. pileatus*, *H. lar* and *H. pileatus* x *H. lar*.

However, all great calls produced by the hybrids resembled each other in the rate of note emission. Whereas *lar* gibbons have a fairly low number of notes per second, pileated females produce a rapid trill consisting of a high number of notes. The rate of note emission in the F1-hybrids differs from that of both parental species, as can easily be seen in Figure 3.3.10: Here, the number of great-call notes is plotted against great-call duration. Each point represents one great-call. The three groups: i.e. *lar* gibbons, pileated gibbons and F1-hybrids, do not overlap, and the hybrids are about intermediate between both parental species in the rate of note emission.

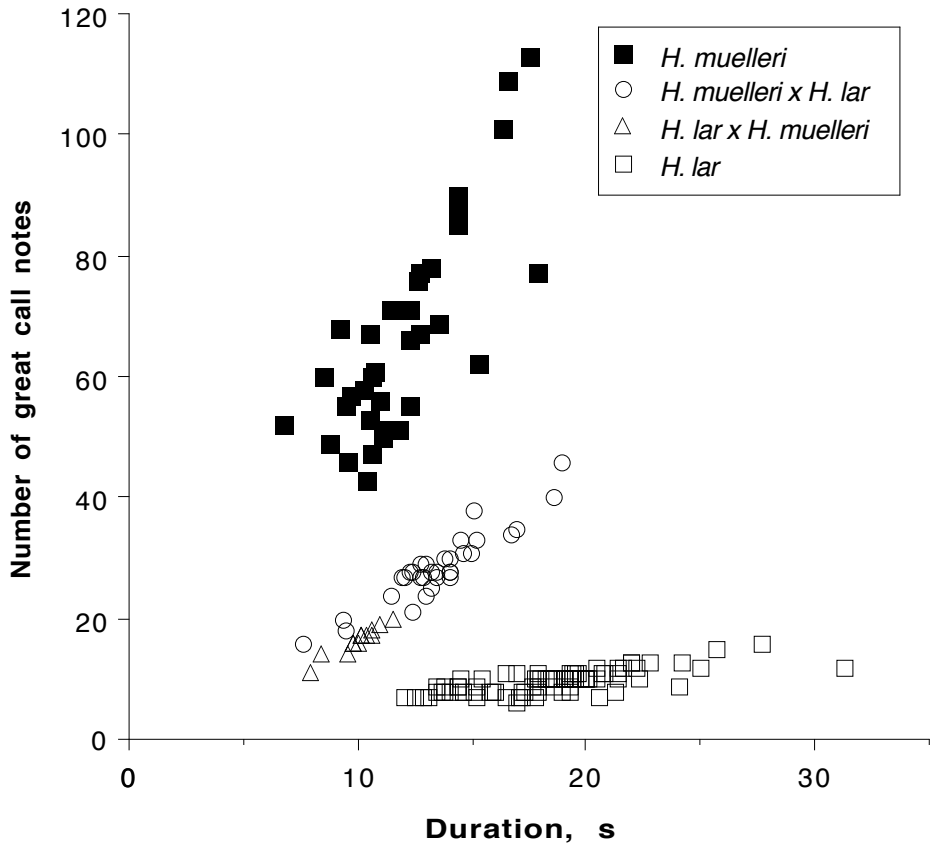


Figure 3.3.11: The number of notes in a great call plotted against its duration for *H. muelleri*, *H. lar*, *H. muelleri* x *H. lar* and *H. lar* x *H. muelleri* .

As a rule, hybrids of the *lar* group appear to be intermediate in the rhythm of their great calls between both parental species. This can most easily be seen in hybrids between species which differ most radically in this characteristic, such as hybrids between *H. agilis* or *H. lar* on the one hand, and *H. muelleri* or *H. pileatus* on the other (see Figs. 3.3.10-3.3.13). The resulting hybrid great call of a particular species combination is apparently unaffected by a reversal of paternal and maternal parental species: The note speed in *H. muelleri* x *H. lar* is about the same as in *H. lar* x *H. muelleri* (Fig. 3.3.11); and that of *H. muelleri* x *H. agilis* is about the same as in *H. agilis* x *H. muelleri* (Fig. 3.3.12).

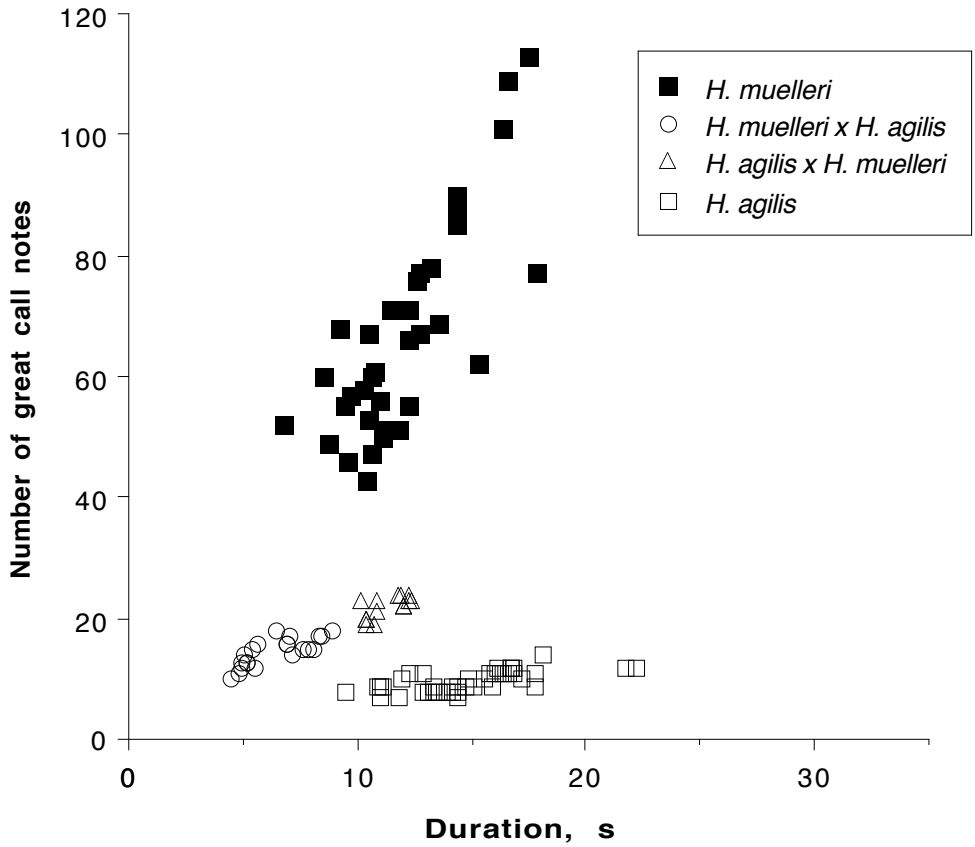


Figure 3.3.12: The number of notes in a great call plotted against its duration for *H. muelleri*, *H. agilis*, *H. muelleri* x *H. agilis* and *H. agilis* x *H. muelleri* .

The more parental great calls resemble each other, the more it becomes difficult to recognise the intermediate position of hybrid great calls. While *H. muelleri* and *H. lar*, for instance, differ radically in the speed of their great call, *H. moloch* is approximately intermediate between both of them in this respect, but slightly closer to the condition shown by *H. lar*. Consequently, hybrids between *H. muelleri* and *H. moloch* can still be well identified, but hybrids between *H. moloch* and *H. lar* show some overlap in the rhythm of their great call notes with the cluster of *H. lar* (Figure 3.3.14).

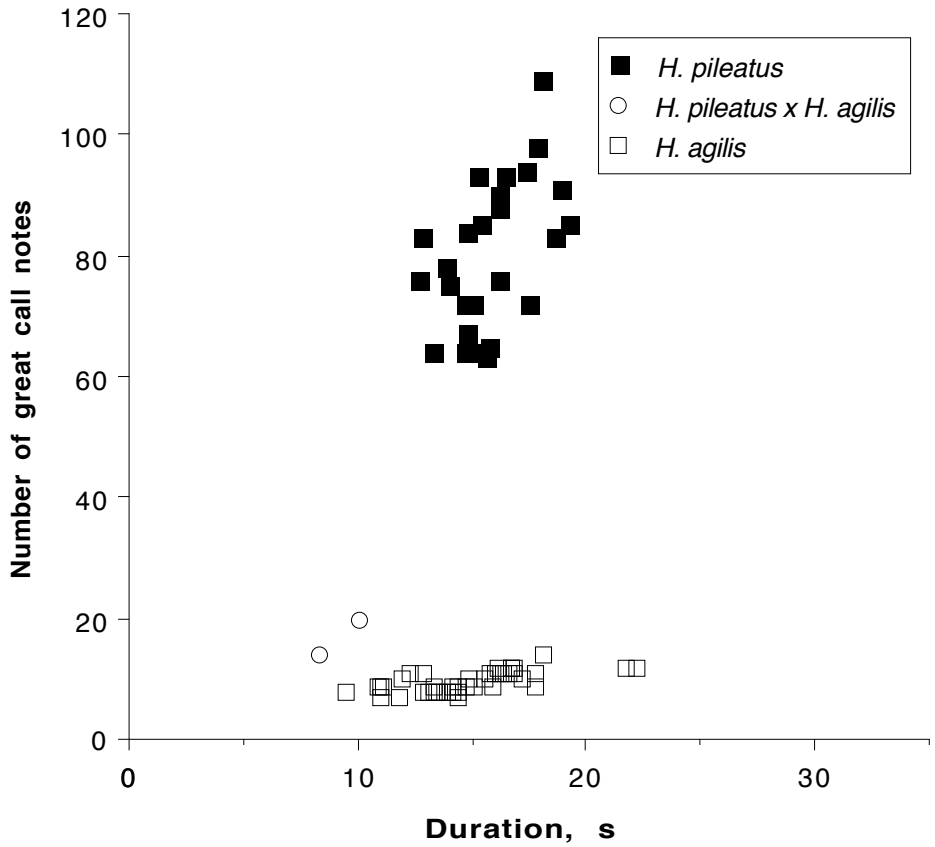


Figure 3.3.13: The number of notes in a great call plotted against its duration for *H. pileatus*, *H. agilis* and *H. pileatus* x *H. agilis*.

Even more difficult is the analysis of great calls of backcrosses. Those of *H. muelleri* x (*H. muelleri* x *H. lar*) show some overlap with *H. muelleri*, although their intermediate position can still be recognised (Figure 3.3.14). On the other hand, the available great calls of *H. lar* x (*H. lar* x *H. moloch*) are more similar to pure *H. lar* than to pure *H. moloch* . This unexpected position should be regarded with caution, because only two isolated great calls of this backcross were available. In such cases, individual variability may possibly obscure the position of a particular hybrid in the plot. In addition, this female may not have been old enough to produce its fully developed great calls.

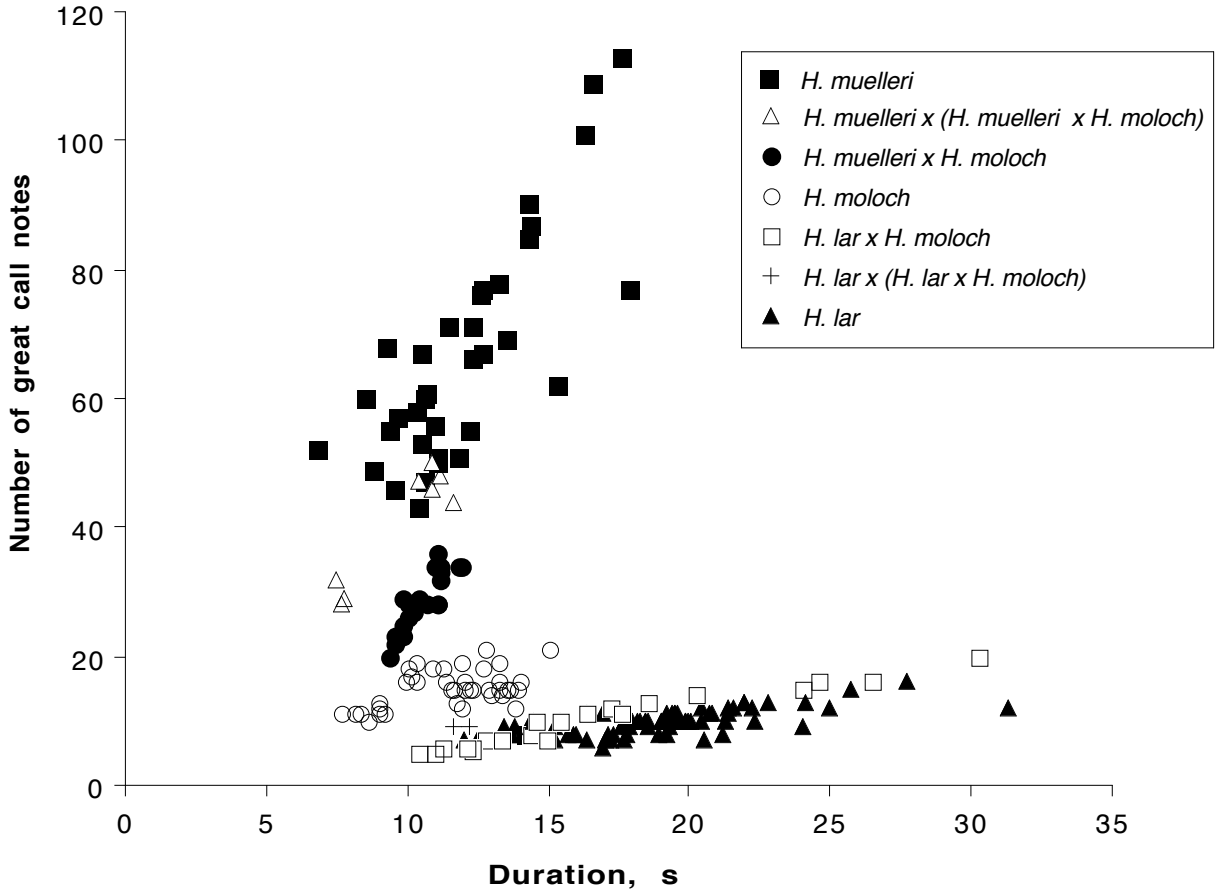


Figure 3.3.14: The number of notes in a great call plotted against its duration for *H. muelleri*, *H. lar*, hybrids and backcrosses with *H. moloch*.

Because the great calls of *H. agilis* and *H. lar* are already very similar, it was not surprising to find that the few great calls available of a young hybrid *H. lar* x *H agilis* were almost indistinguishable from those of both parental species (Fig. 3.3.15).

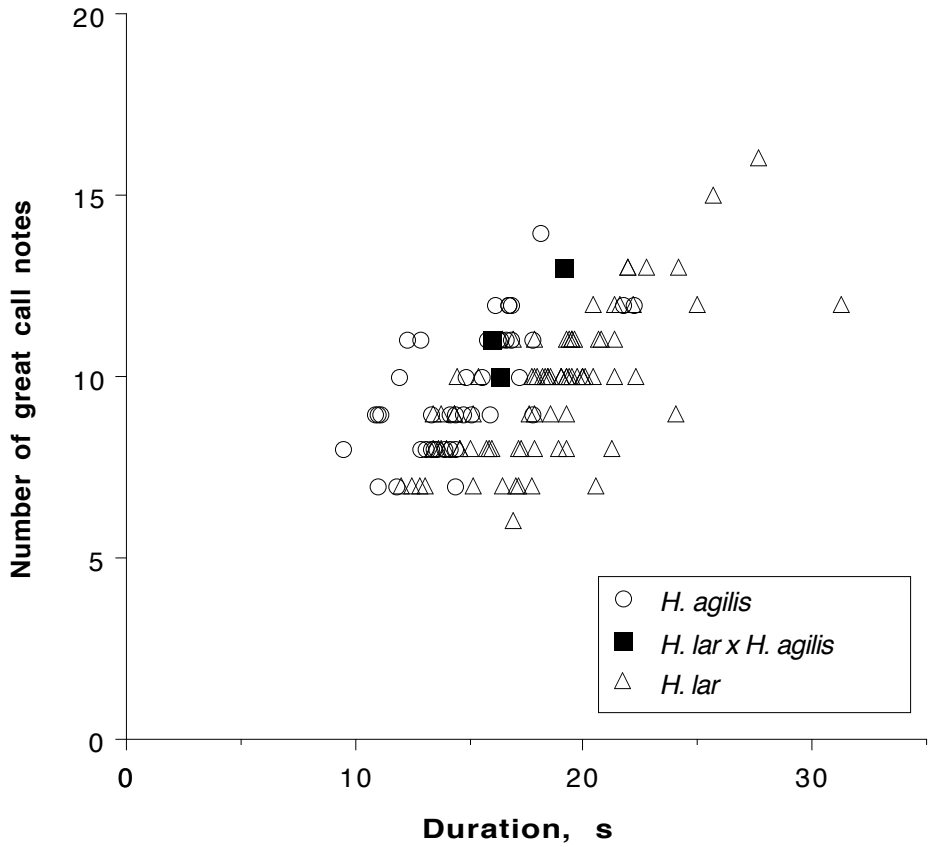


Figure 3.3.15: The number of notes in a great call plotted against its duration for *H. agilis*, *H. lar* and *H. lar* x *H. agilis*.

3.3.2 Male Hybrids

In the present section, the vocal characteristics of each male hybrid are briefly described. For each hybrid, a sonagram of a typical phrase is provided. In order to facilitate comparison with vocalisations of pure species, sonagrams of males of all species of the *lar* group are shown in Fig. 3.3.16.

Figure 3.3.16 (see following page): Sonagrams of fully developed male phrases of all gibbon species of the *lar* group. In order to show variability, sonagrams of two different individuals are provided for species a - d.
a. *H. agilis* (Dortmund Zoo, 20 June 1987; and Twycross Zoo, 2 Oct. 1988); 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).

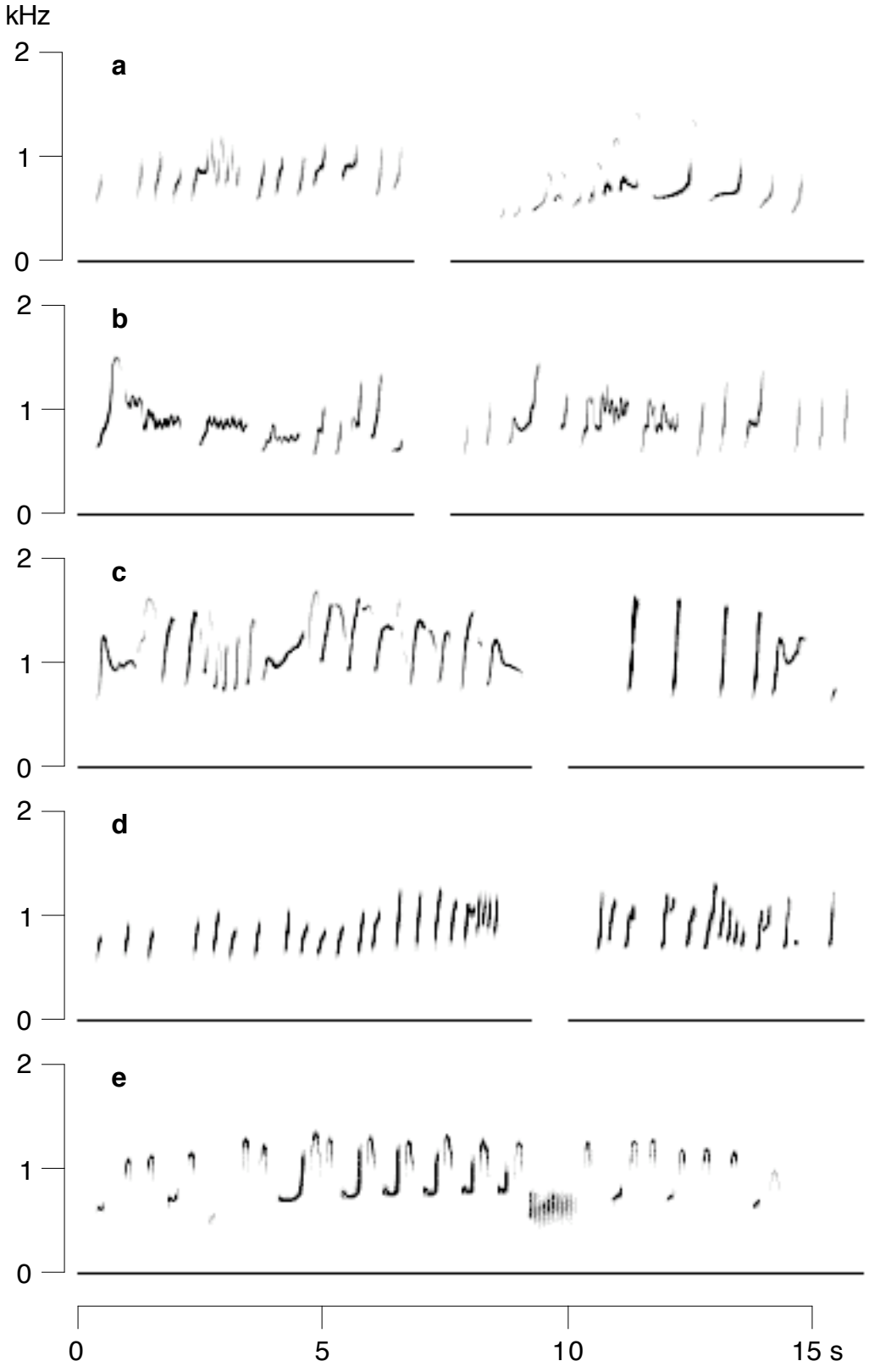


Figure 3.3.16 (Legend see previous page).

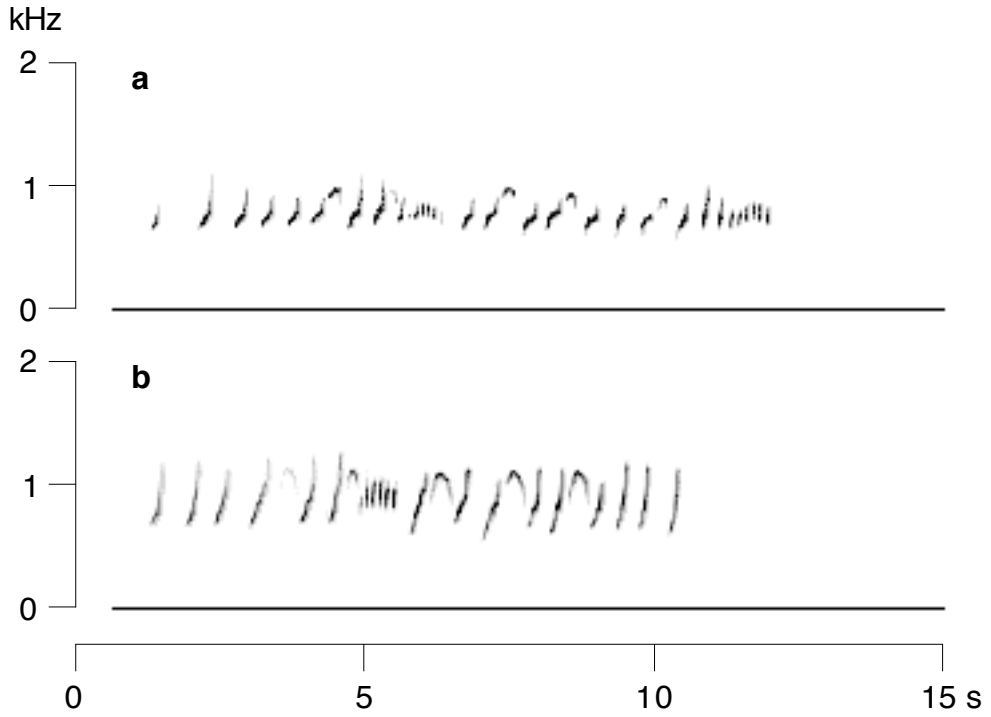


Figure 3.3.17: Sonagrams of male phrases of hybrids *H. pileatus* x *H. lar*: a. "Charly", Nordhorn Zoo, 6 July 1987; b. "Wombel", Opel Zoo, Kronberg, 18 June 1987.

H. pileatus x *H. lar* (Fig. 3.3.17): Male phrases with frequent bi-phasic notes, like *H. pileatus*. Exhalation notes are simple hoots of increasing frequency, i.e. no quaver notes or other complex hoots; unlike *H. lar*. Inhalation notes usually longer than in *H. pileatus*. Frequent short trills, like *H. pileatus*, but apparently of slower speed. Triplet figures consisting of an exhalation-inhalation-exhalation sequence frequently occur in both hybrids, but are not known to occur in any other gibbon species. Virtually identical short phrases (including trill and triplet figures) were also heard from a solitary female *H. pileatus* x *H. lar* (not shown on sonagram). During interlude sequences, another adult female *H. pileatus* x *H. lar* – kept as a pair with her adult brother – frequently produced short trills which were usually synchronised with those of the male hybrid.

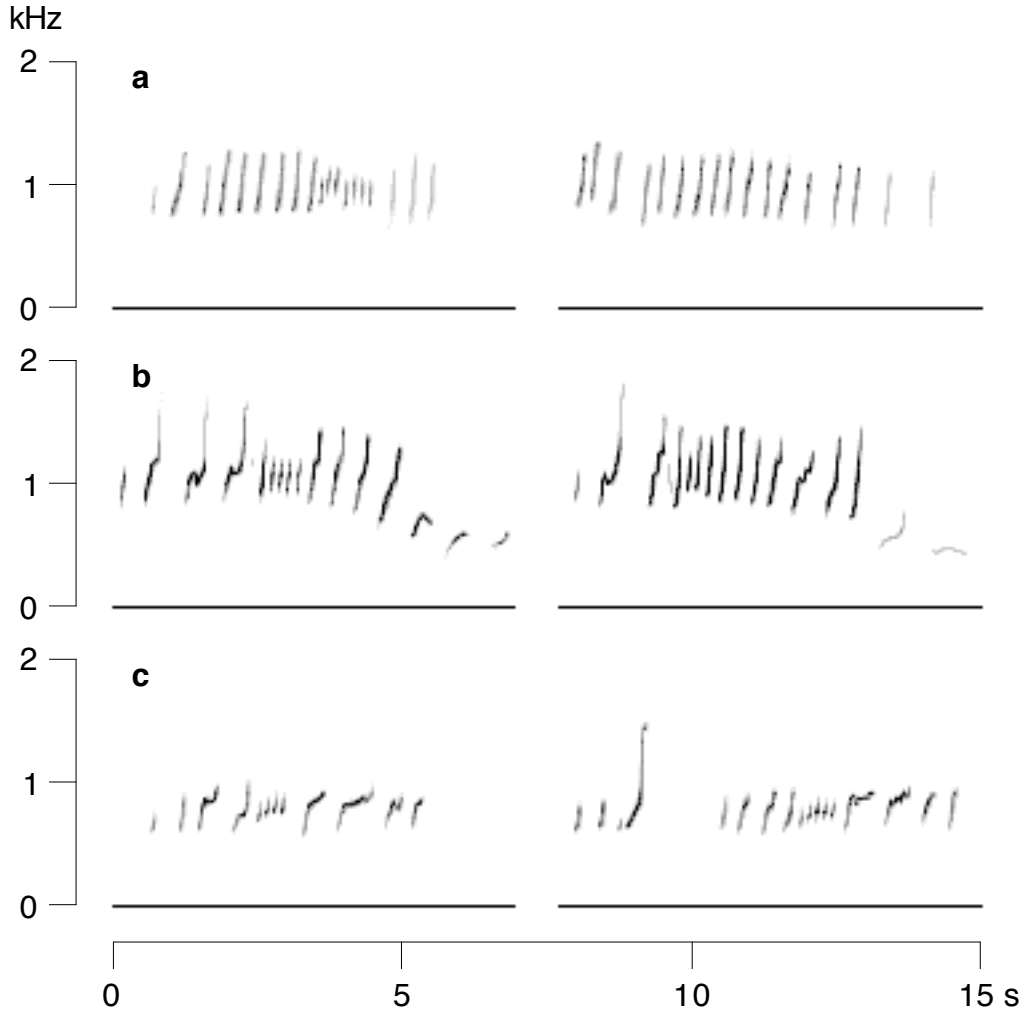


Figure 3.3.18: Sonagrams of male phrases of hybrids *H. muelleri* x *H. lar* (a-b) and *H. lar* x *H. muelleri* (c). a. "Barney", Banham Zoo, 15 Oct. 1988; b. "Frodo", Twycross Zoo, 2 Oct. 1988, c. no name, Micke Grove Zoo, Lodi, CA, Oct. 1977 (rec. Dr. R.R. Tenaza).

H. muelleri x *H. lar* and *H. lar* x *H. muelleri* (Fig. 3.3.18): Male phrases without bi-phasic notes. Simple hoots of increasing frequency only in the first hybrid (Fig. 3.3.18a), but more complex hoots and short, quavering notes in the other two hybrids (Fig. 3.3.18 b-c). Quavering not as pronounced as in *H. lar*. Frequent short trills occur in all three hybrids; like *H. muelleri*, apparently of similar speed.

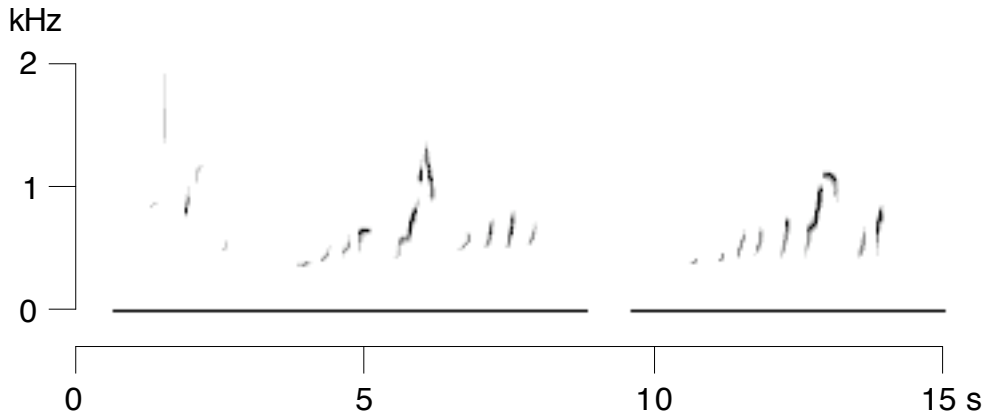


Figure 3.3.19: Sonagram of male phrases of hybrid *H. agilis* x *H. muelleri*: "Männlein", Duisburg Zoo, 24 June 1987.

H. agilis x *H. muelleri* (Fig. 3.3.19): Male phrases with frequent bi-phasic notes, like *H. agilis*. Exhalation notes are simple hoots of increasing frequency or more complex hoots ("whoo-aa"), but no quaver notes, unlike *H. lar*. No short trills, unlike *H. muelleri*. This male produced relatively soft, squealing sounds between its short phrases, similar to some males of *H. agilis* and *H. muelleri*. Some of these sqeals are faintly seen at the beginning of the first sonagram.

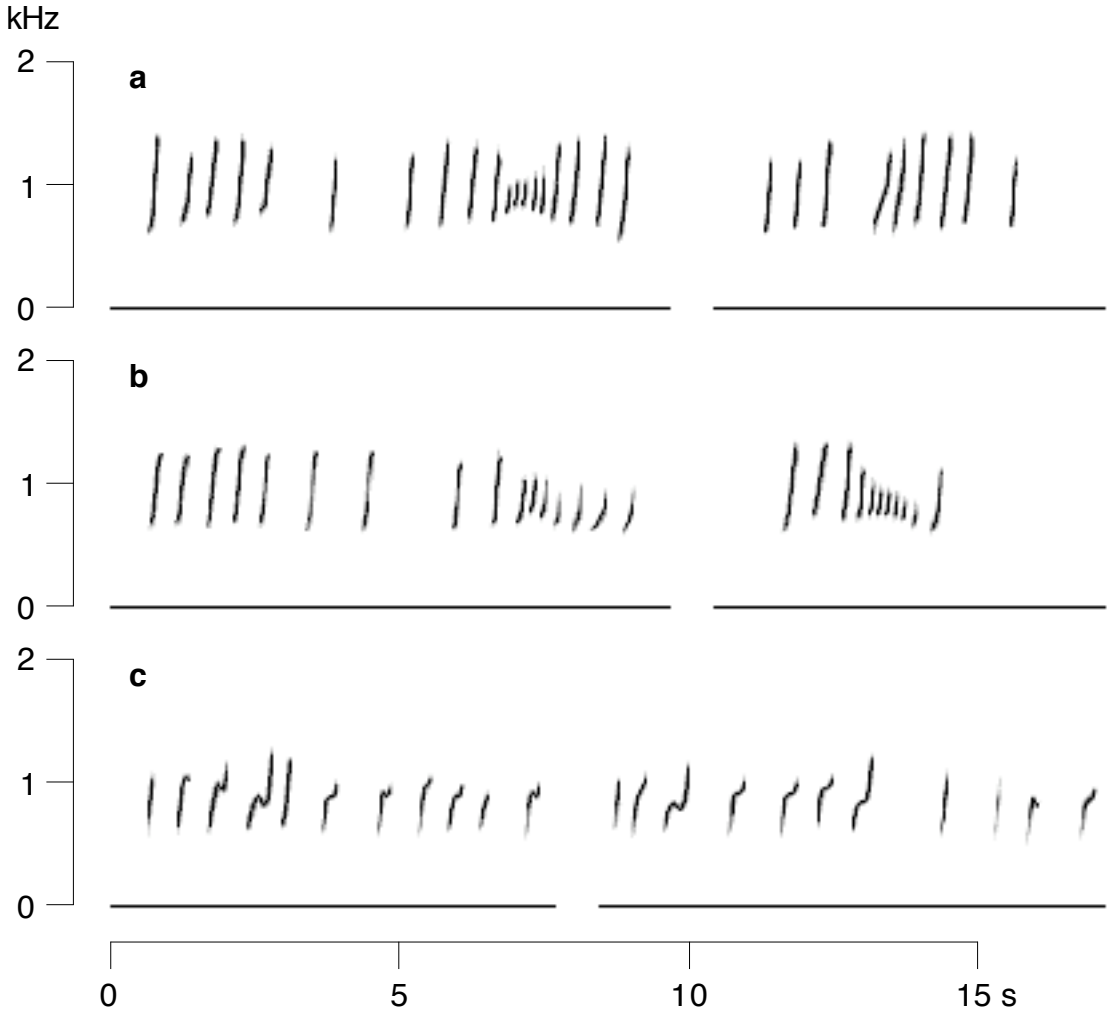


Figure 3.3.20: Sonagrams of male phrases of hybrids *H. muelleri* x *H. moloch* (a-b) and backcross *H. muelleri* x (*H. muelleri* x *H. moloch*) (c). a. "Adolf", Bristol Zoo, 19 Oct. 1988; b. "Mooli", Paignton Zoo, 22 Oct. 1988, c. "Fritzke", Eberswalde Zoo, 11 July 1988.

H. muelleri x *H. moloch* (Fig. 3.3.20a-b): Male phrases with simple hoots of increasing frequency and short trills of similar speed like *H. muelleri*. More complex hoots ("wa-oo") very rarely heard of first hybrid only (not shown in Fig. 3.3.20a), and not heard at all in second hybrid, unlike both parental species.

H. muelleri x (*H. muelleri* x *H. moloch*) (Fig. 3.3.20c): Male phrases with simple hoots of increasing frequency, and frequent more complex hoots ("whoo-aa"). No short trills recorded.

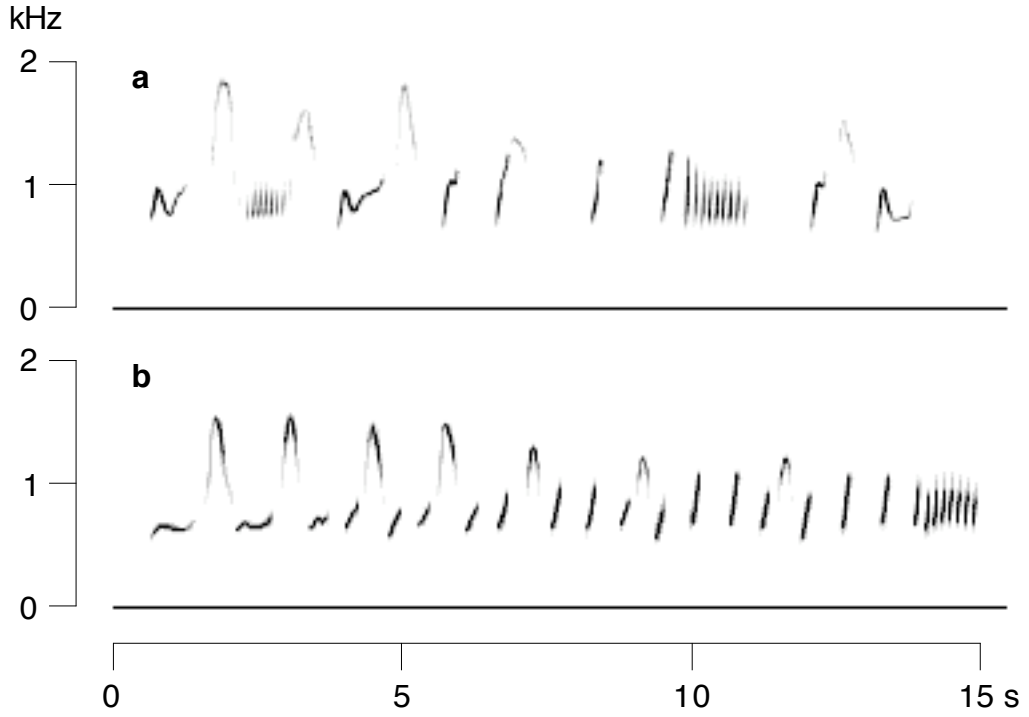


Figure 3.3.21: Sonagrams of male phrases of hybrids *H. pileatus* x *H. moloch*. a. "Peter", Ruhr Zoo, Gelsenkirchen, 30 June 1987; b. "Franz", Safari Park, Hodenhagen, 9 July. 1987.

H. pileatus x *H. moloch* (Fig. 3.3.21): Male phrases with simple hoots of increasing frequency, more complex hoots ("wa-oo", "wa-oo-wa") like *H. moloch*, and with frequent bi-phasic notes and short trills, like *H. pileatus*. Exhalation notes of chevron shape, as in *H. pileatus*, but of longer duration. Short trills apparently slower than those of *H. pileatus*.

As in pure species, hybrid males were typically observed to produce coda phrases to the great calls of their mates. The males differed in the timing of their coda insertion in relation to the great calls. Table 3.3.2 lists the type of codas used by each male. Three hybrid males are not included in the table, because they were kept solitary and, therefore, did not produce codas: one male each of *H. pileatus* x *H. lar*, *H. agilis* x *H. muelleri* and *H. muelleri* x (*H. muelleri* x *H. moloch*).

Table 3.3.2: Timing of coda insertion used by hybrid males.

Hybrid	Zoo	Mate	Coda insertion
H. pileatus x *H. lar*	Nordhorn Zoo	*H. lar*	immediately before end of great call
	Opel Zoo, Kronberg	*H. pileatus* x *H. lar*	variable: during second half of great call or immediately before end of great call
H. muelleri x *H. lar*	Banham Zoo	*H. lar*	no codas heard
H. lar x *H. muelleri*	Micke Grove Zoo, Lodi	*H. lar* x *H. muelleri*	variable: on last note of, or after great call
H. muelleri x *H. moloch*	Bristol Zoo	*H. muelleri* x *H. moloch*	after great call
	Paignton Zoo	*H. moloch*	well after great call
H. pileatus x *H. moloch*	Ruhr Zoo, Gelsenkirchen	*H. pileatus* x *H. lar*	variable: during second half of great call or immediately before end of great call (exceptionally after great call)
	Safari Park, Hodenhagen	*H. lar* x *H. moloch*	well after great call

Finally, one adult male *H. pileatus* x *H. lar* ("Charly", Nordhorn Zoo) was heard once to produce an accelerated great call-like phrase in synchrony with (i.e. during the first half of) the great call of his mate (*H. lar*). The phrase was much shorter than typical great calls of *H. pileatus* x *H. lar* (8 notes vs. a mean of 19.3 notes), but was otherwise identical to great calls of these hybrids. There were even soft pre-great call notes which typically announce the start of a great call in the female song. The speed of the phrase (1.5 notes/s) was similar to that of hybrid females (1.3 notes/s) and differed from that of the *H. lar* female (see Table 3.3.1). Immediately before the end of the great call of this female, the hybrid male also added the typical coda, as he did in the other great call sequences of this pair. This was the only great call-like phrase heard from a mated male during the present study. Six songs of this pair were recorded on tape, but no other great call-like phrases were heard from the male. In two other great calls, the male

produced a few hoots during the same part of the female's great call, but these hoots were not recognicable as a phrase, even less a great call.

Table 3.3.3a lists those hybrid males and females of the present study which grew up and always lived in a particular form of acoustic isolation. This meets the special condition referred to in section 3.1.5: These hybrids have never heard gibbon songs other than those of their parents, and – in a few cases – of other males of their father's species or of other females of their mother's species. Each deviation of these hybrids' songs from that of their same-sexed parent is a potential indication for an inherited song characteristic. Table 3.3.3b lists additional hybrids which experienced limited acoustical input throughout their lives. Although these hybrids have heard songs of some gibbon species other than those of their parents, they are listed here because none of their song characteristics shows a deviation in the direction of the additionally present gibbons.

Table 3.3.3: Hybrids which grew up and lived under some form of acoustic isolation (see text for explanation).

	Hybrid	Sex	Name	Zoo [1)]
a.)	*H. lar* x *H. moloch*	female	"Gipsy"	Rheine Zoo
	H. lar x *H. muelleri*	male	no name	Micke Grove Zoo, Lodi
		female	no name	Micke Grove Zoo, Lodi
	H. muelleri x *H. moloch*	male	"Adolf"	Bristol Zoo
		female	"Juvi"	Bristol Zoo
		female	"Maria"	Münster Zoo
	H. muelleri x (*H. muelleri* x *H. moloch*)	female	"Bo"	Münster Zoo
	H. pileatus x *H. lar*	male	"Charly"	Saarbrücken Zoo; Nordhorn Zoo
		male	"Wombel"	Opel Zoo, Kronberg
		female	"Toni"	Opel Zoo, Kronberg
		female	"Johnny"	Opel Zoo, Kronberg
b.)	*H. muelleri* x *H. agilis*	female	no name, hybrid 1	Louisiana Zoo, Monroe [2)]
		female	no name, hybrid 2	Louisiana Zoo, Monroe [2)]
	H. muelleri x *H. lar*	female	no name	Mazé [3)]
	H. muelleri x (*H. muelleri* x *H. moloch*)	male	"Fritzke"	Münster Zoo; Eberswalde Zoo [4)]
	H. muelleri x *H. syndactylus*	female	"Shawn-Shawn"	Atlanta Zoo; Yerkes Regional Research Primate Center [5)]
	H. pileatus x *H. lar*	female	"Yoko"	Southport Zoo [6)]

1) This column also lists all zoos where a hybrid was kept *before* its songs were tape-recorded for the present study.

2) A male siamang was present at the zoo, and, starting from 1985, a female siamang.

3) A male *H. pileatus* was present at the zoo.

4) A female *H. leucogenys leucogenys* was present at the Eberswalde Zoo.

5) Several *H. lar* were present both at the Atlanta Zoo and at the Yerkes Regional Research Primate Center.

6) A male *H. lar* was present at the zoo.

4. Olfactory Communication

4.1 Introduction

4.1.1 General Comments

This part of the thesis focusses on skin glands in gibbons. The following introductory sections review the occurrence of sternal and axillary glands in primates and other mammals. In subsequent chapters, macroscopic and histological characteristics of sternal and other skin glands in gibbons are described. In addition the possible production of certain chemical compounds (steroid hormones) in these glandular areas is examined, and observations on changes in glandular activity are discussed in relation to possible functions of the skin glands in gibbons. Finally, some phylogenetic implications of these new findings are explored.

4.1.2 Sternal Glands

Mammals have a large variety of cutaneous glands (e.g. Schaffer, 1940), and this is particularly true for primates (e.g. Montagna, 1972). Glandular concentrations are more common in some regions of the skin than in others. One of the most important of these regions, apart from the genital area, is the medial anterior part of the chest (Montagna & Ellis, 1963; Montagna & Yun, 1962; Sprankel, 1962), where concentrations of glands may actually form glandular organs commonly called sternal glands. Glands and glandular concentrations occur in the sternal region in many primate species, but are also known to occur in several other, only distantly related, orders of mammals. Table 4.1.1 gives an apparently exhaustive list of all primate species known to possess a sternal gland, and a representative sample of publications on sternal glands has been compiled in Table 4.1.2 for all other orders of mammals for which sternal glands have been described.

In addition to the sternal glands of the species listed in Table 4.1.1, accumulations of apocrine glands in the chest have also been described for the following primate species: *Cacajao rubicundus* (Perkins et al., 1968b), *Cebus albifrons* (Perkins & Ford, 1969); *Cercopithecus mitis* (Machida et al., 1964); *Macaca nemestrina* (Perkins et al., 1968a) and *Papio anubis* (Montagna & Yun, 1962). It was pointed out, however, that such fields "should not be confused with the sternal aggregations" in callitrichids and *Aotus* that consist of "circumscribed masses of gigantic apocrine coils" (Perkins & Ford, 1969, p. 6). Montagna and Ellis (1963, p. 194) also stated that the macaques and mangabeys have "rich concentrations of glands" in the region of the anterior chest, but histological evidence in support of this has apparently been published only for *Macaca nemestrina* (Perkins et al., 1968a).

Table 4.1.1: Occurrence of cutaneous glands on the medial anterior part of the chest in primate species (expanded from Geissmann, 1987b).

Species	Evidence [a]	Reference
A. Strepsirhini		
Microcebus coquereli	1	Petter et al. (1977)
Phaner furcifer	1,3,4	Petter et al. (1977); Rumpler & Andriamiandra (1971)
Varecia variegata	1, 3, 4	Petter et al. (1977); Rumpler & Andriamiandra (1971)
Hapalemur simus	3, 4	Petter et al. (1977)
Propithecus sp.	1	Petter (1965)
Propithecus diadema	3, 4	Petter et al. (1977); Rumpler & Andriamiandra (1971)
Propithecus verreauxi	1, 3, 4	Jolly (1966); Mertl-Millhollen (1979); Petter et al. (1977); Richard (1974); Rumpler & Andriamiandra (1971); Zeller (1984; 1986)
Galago crassicaudatus	1, 3	Bearder & Doyle (1974); Clark (1978; 1988); Sauer (1974)
Galago demidoff	3	Pitts (1988)
Galago garnettii	1, 3, 4	Clark (1986; 1988); Dixson (1976)
Galago moholi	1, 3	Bearder & Doyle (1974); Sauer (1974)
Tarsius bancanus	1, 3	Hill (1951); Hill et al. (1952); Niemitz (1984)
Tarsius syrichta	3, 4	Arao & Perkins (1969); Hill (1951; 1955); Hill et al. (1952)

[a] 1, marking behaviour on substrate; 2, other behaviours centering on sternal skin (e.g. rubbing or scratching glandular area with hands, rubbing strong-smelling substances or saliva on glandular area); 3, macroscopic modifications of skin and/or fur; 4, histological evidence.

Table 4.1.1: Continued.

Species	Evidence [a]	Reference
B. Haplorhini		
Callimico goeldii	1, 3	Carroll (1985); Epple & Lorenz (1967); Omedes & Carroll (1980); Perkins (1969b)
Callithrix argentata	1, 3, 4	Epple (1972); Epple & Lorenz (1967); Omedes & Carroll (1980); Perkins (1969a)
Callithrix humeralifer	1, 3	Epple & Lorenz (1967); Rylands (1982)
Callithrix jacchus	1, 3, 4	Box (1975; 1977); Epple (1972); Epple & Lorenz (1967); Sutcliffe & Poole (1978)
Callithrix kuhlii	1	Rylands (1982)
Cebuella pygmaea	1, 3, 4	Christen (1974); Epple & Lorenz (1967); Perkins (1968); Soini (1988)
Leontopithecus chrysomelas	1	Rylands (1982)
Leontopithecus rosalia	1, 2, 3	Epple (1972); Epple & Lorenz (1967); Kleiman (1977a); Kleiman & Mack (1980); Mack & Kleiman (1978); Omedes & Carroll (1980)
Saguinus fuscicollis	1, 3	Bartecki & Heymann (1990); Epple & Lorenz (1967)
Saguinus geoffroyi	1, 3	Epple (1972); Epple & Lorenz (1967)
Saguinus labiatus	3	Epple & Lorenz (1967)
Saguinus midas	1, 3	Epple & Lorenz (1967); Omedes & Carroll (1980)
Saguinus mystax	1, 3	Epple & Lorenz (1967); Heymann (1989)
Saguinus nigricollis	1, 3, 4	Epple & Lorenz (1967); Izawa (1978); Perkins (1966)
Saguinus oedipus	1, 3	Epple (1972); Epple & Lorenz (1967)
Aotus sp.	3, 4	Epple & Lorenz (1967); Hanson & Montagna (1962)
Aotus azarae	3	Hershkovitz (1983)
Aotus brumbacki	3	Hershkovitz (1983)
Aotus vociferans	3	Hershkovitz (1983)

[a] 1, marking behaviour on substrate; 2, other behaviours centering on sternal skin (e.g. rubbing or scratching glandular area with hands, rubbing strong-smelling substances or saliva on glandular area); 3, macroscopic modifications of skin and/or fur; 4, histological evidence.

Table 4.1.1: Continued.

Species	Evidence [a]	Reference
Cacajao rubicundus	3	Epple & Lorenz (1967)
Callicebus moloch	1, 2, 3	Epple & Lorenz (1967); Mason (1966); Moynihan (1966)
Callicebus torquatus	1, 3	Epple & Lorenz (1967); Kinzey (1981)
Cebus albifrons	1	Bernstein (1965)
Cebus apella	1, 3	Dobroruka (1972); Epple & Lorenz (1967)
Cebus capucinus	1, 3	Epple & Lorenz (1967)
Cebus nigrivittatus	3	Dobroruka (1972)
Pithecia monachus	3	Epple & Lorenz (1967)
Pithecia pithecia	1, 3, 4	Claussen (1982); Dugmore (1986); Epple & Lorenz (1967); Hill (1960); Sanderson (1949-1950)
Saimiri sp.	1, 3, 4	Epple & Lorenz (1967); Hill (1960); Machida et al. (1967)
Alouatta palliata	1	Eisenberg (1976); Young (1982)
Alouatta seniculus	1, 3	Epple & Lorenz (1967); Neville (1972); Sekulic & Eisenberg (1983)
Ateles sp.	3, 4	Schwarz (1937)
Ateles belzebuth	1, 3	Epple & Lorenz (1967); van Roosmalen & Klein (1988)
Ateles fusciceps	1, 2	Eisenberg (1976)
Ateles geoffroyi	1, 2, 3, 4	Epple & Lorenz (1967); Klein & Klein (1971); Wislocki & Schultz (1925)
Ateles paniscus	3	Wislocki & Schultz (1925)
Brachyteles arachnoides	3	Epple & Lorenz (1967)
Lagothrix lagotricha	1, 2, 3	Eisenberg (1976); Epple & Lorenz (1967); Schifter (1968); White et al. (1989)
Cercopithecus aethiops	1	Gartlan & Brain (1968)
Cercopithecus hamlyni	1	Loireau (1985); Loireau & Gautier-Hion (1988)

[a] 1, marking behaviour on substrate; 2, other behaviours centering on sternal skin (e.g. rubbing or scratching glandular area with hands, rubbing strong-smelling substances or saliva on glandular area); 3, macroscopic modifications of skin and/or fur; 4, histological evidence.

Table 4.1.1: Continued.

Species	Evidence [a]	Reference
Allenopithecus nigroviridis	1	Loireau (1985); Loireau & Gautier-Hion (1988)
Cercopithecus neglectus	1, 4	Gautier & Gautier (1977); Loireau (1985), Loireau & Gautier-Hion (1988)
Mandrillus leucophaeus	1, 2, 3, 4	Fiedler (1957); Hearn et al., (1988); Hill (1944; 1954; 1970)
Mandrillus sphinx	1, 3, 4	Feistner (1991); Fiedler (1957); Hill (1954; 1970); Jouventin (1975); Mellen et al. (1981)
Hylobates agilis	3	Geissmann, present study
Hylobates concolor	3	Geissmann, present study
Hylobates hoolock	3, 4	Geissmann, present study
Hylobates lar	3, 4	Geissmann, present study
Hylobates leucogenys	3	Geissmann, present study
Hylobates moloch	3, 4	Geissmann, present study
Hylobates muelleri	3, 4	Geissmann, present study
Hylobates cf. *muelleri*	3	Pocock (1925)
Hylobates pileatus	3, 4	Geissmann, present study
Hylobates syndactylus	3, 4	Geissmann (1987b), and present study
Pongo pygmaeus	3, 4	Brandes (1939); Schultz (1921); Wislocki & Schultz (1925)

[a] 1, marking behaviour on substrate; 2, other behaviours centering on sternal skin (e.g. rubbing or scratching glandular area with hands, rubbing strong-smelling substances or saliva on glandular area); 3, macroscopic modifications of skin and/or fur; 4, histological evidence.

Table 4.1.2: Occurrence of cutaneous glands on the medial anterior part of the chest in mammalian orders other than primates.

Order	Evidence [a]	Reference
Carnivora:	1, 3	Albignac (1969)
Chiroptera:	3, 4	Bradbury (1977); Hood & Smith (1984); Hall & Gordon (1982); Pandey & Dominic (1987); Schaffer (1940)
Marsupialia:	1, 2, 3, 4	Aslin (1974); Croft (1981a; 1981b); Fadem & Cole (1985); Green (1963); Mykytowycz & Nay (1964); Schaffer (1940); Schultze-Westrum (1965); Smith (1980)
Ruminantia:	3, 4	Meyer (1986)
Scandentia:	1, 3, 4	Aue & Fuchs (1986); Kaufmann (1965); Martin (1968); Sprankel (1962); von Stralendorff (1982; 1987); Vandenbergh (1963); Zeller et al. (1989)

[a] 1, marking behaviour on substrate; 2, other behaviours centering on sternal skin, where applicable (e.g. rubbing or scratching glandular area with hands, rubbing strong-smelling substances or saliva on glandular area); 3, macroscopic modifications of skin and /or fur; 4, histological evidence.

Among hominoids, a sternal gland has been reported only for the orang-utan, *Pongo pygmaeus* (Brandes, 1939; Schultz, 1921; Wislocki & Schultz, 1925). Wislocki and Schultz (1925, p. 242) published a "list of those primates which could be carefully examined, none of which showed a sternal gland," including the hylobatids "*Symphalangus klossi, S. syndactylus, Hylobates agilis, H. lar, H. concolor, H mülleri.*"

In contrast to the findings reported by Wislocki and Schultz, Pocock (1925; 1927) suspected that a sternal gland was present in two captive male gibbons. Both animals had a dark patch in the sternal region, in one animal covered with a dark, wet substance, and both were thought by Pocock to have originated from Borneo. Bornean gibbons may comprise more than one species (Chivers, 1977; Chivers & Gittins, 1978; Groves, 1984; Marshall & Marshall, 1976; Marshall & Sugardjito, 1986; Marshall et al., 1984). The identity of Pocock's animals is

therefore uncertain, even if their origin was correctly assigned. In addition, gibbons in zoos have frequently been misidentified as Bornean gibbons or, conversely, have frequently not been recognised as such (personal observations in several European zoos; see also Schilling, 1984a). For instance, Epple (1986, p. 542), in a recent review on communication by chemical signals in primates, cited Pocock's (1925) observation, but changed his original identification from "*Hylobates leuciscus muelleri*" to "*Hylobates moloch* (silvery gibbon)". This is difficult to justify, as the distribution range of *H. moloch* is restricted to Java, whereas Pocock's gibbons are reportedly from Borneo.

Weber and Abel (1928) stated, without providing anatomical evidence, that the sternal patch observed by Pocock did not consist of a glandular concentration:

> "Im dreieckigen nackten Brustfleck des Männchens von *Hylobates leuciscus* Mülleri, den Pocock (1925) beschreibt, handelt es sich nicht um gehäufte Drüsen" (Weber & Abel, 1928, p. 765).

Laîné (cited by (Dandelot, 1960) reported that perspiration in a captive male white-cheeked gibbon (*Hylobates leucogenys*) and a female pileated gibbon (*H. pileatus*) produced coloured droplets, but he did not mention on which region of the animals' bodies the droplets were observed:

> "Nous avons remarqué que la sudation chez le mâle (un Gibbon *concolor leucogenys*) produit un suint en gouttelettes colorées qui tachent le linge et l'eau des bains en jaune foncé. Ceci existe aussi chez la petite femelle (espèce *H. lar pileatus*) mais le suint est moins coloré" (Laîné, cited by Dandelot, 1960, p. 11).

Montagna and Yun (1962, p. 134) stated that "the gibbon" has "… a rich field of eccrine and apocrine glands on the anterior surface of the chest …." This statement was later repeated by Montagna and Ellis (1963, p. 194), and by Perkins and Ford (1969, p. 6). More recently, Montagna (1985, p. 18) reported that gibbons (and orangs) have a "scent-producing apparatus … located in a sternal pit, above the manubrium of the sternum." Of the various publications

produced by Montagna's research group, however, only one (Perkins & Ford, 1969) cites the source of evidence, a publication by Parakkal et al. (1962).

The only published study known to me in which histological examination of the chest skin of a gibbon is reported is that of Parakkal et al. (1962). The authors do not, however, mention a sternal gland or any concentration or enlargement of eccrine or apocrine sweat glands on any part of the body, and no such configuration can be seen in a figure showing a section of the skin from the chest (Fig. 8 in their report). However, they observed that "when under Sernyl anesthesia, … these animals perspired freely over the entire body, but particularly on the chest above the nipples" (see also Montagna, 1976, p. 56).

The subjects in the study quoted above, three young females, were said to be white-browed gibbons (*Hylobates hoolock*); however, in view of the extreme rarity of *H. hoolock* in captivity – only one individual in North America (Mootnick, 1984) and none in European zoos (Schilling, 1984a; Schilling, 1984b; personal observations) – this attribution may be incorrect, as previously suggested by Geissmann (1987b). Subsequently, additional evidence supporting this suggestion has been found in a publication by Montagna (1976) which contained a photograph of a gibbon identified as "a crested gibbon (*Hylobates hoolock*)" (Montagna, 1976, p. 42, his Fig. 20). This gibbon is obviously not a *Hylobates hoolock*; it can be clearly recognised as a female *Hylobates leucogenys gabriellae*.

Finally, Montagna and Yun (1963, p. 193 and 196) reported that apocrine glands are numerous and larger in the gular region of *Pan troglodytes*. This finding has apparently never been associated with the sternal glands of other primates.

The review presented above demonstrates that, prior to the present study, the only unequivocal evidence for a sternal gland in hominoid primates had been provided for the orang-utan.

4.1.3 Axillary Glands

Among hominoids, specialised and massive concentrations of mainly apocrine glands in the axillary region, the so-called axillary organs, have been described for the genera *Gorilla* (Brinkmann, 1909; Ellis & Montagna, 1962; Klaar, 1924; Straus, 1950), *Pan* (Brinkmann, 1909, 1923-1924, 1926; Ford & Perkins, 1970; Klaar, 1924; Montagna & Yun, 1963; van Gelderen, 1962), and *Homo* (Montagna, 1982; Schiefferdecker, 1922; Talke, 1903). None of these genera has been reported to possess a sternal gland.

It is generally accepted that axillary organs are present only in the African apes and in humans: "The axillary organs of chimpanzees and gorillas are very similar to those of man, despite some peculiarities of the latter. The axillae of other primates are not noteworthy; none have special glands there" (Montagna, 1972). In an earlier publication, however, Montagna and Ellis (1963, p. 194), without providing direct evidence, had stated that the orang-utan also has an axillary organ "to a lesser extent", and that, apart from apes and humans, "other primates have no such accumulation of eccrine and apocrine glands in the *cavum axillae*." Parakkal et al. (1962, p. 172) explicitly stated that an axillary organ was absent in the three gibbon females that were the subjects of their histological study.

4.1.4 Chemical Constituents of Scent Secretions in Primates

In this section, previous studies of the chemical components of sternal and axillary glands in primates will be briefly reviewed.

In spite of the wide distribution of sternal glands among primates (see above, Table 4.1.1), the chemical constituents of sternal glandular secretions have apparently been analysed for only one species, the greater galago (*Galago crassicaudatus*)*:* Secretion was analysed with a gas chromatograph-mass spectrometer (GC-MS), revealing three major components, all aromatic

compounds: benzyl cyanide, p-hydroxybenzyl cyanide, and 2-(p-hydroxyphenyl) ethanol (Crewe et al., 1979; Wheeler et al., 1977; see also Katsir & Crewe, 1980).

Non-sternal glandular secretions used for marking behaviour have been chemically analysed for several other primate species:

A large number of publications deal with the complex scent marks, consisting mainly of the secretions of specialised circumgenital skin glands and some urine, in callitrichid monkeys of the genus *Saguinus*. Chemical studies included GC-MS analysis for the volatile components and gel electrophoresis for proteins. These studies revealed that the scent marks of four *Saguinus* species are very complex in chemical composition and that they share certain components. *Saguinus fuscicollis, S. o. oedipus, S. leucopus* and *S. labiatus* all produce squalene and a series of butyric acid esters, albeit in very different concentrations (Belcher et al., 1988; Epple et al., 1979, 1981, 1987a, 1987b; Smith et al., 1976; Yarger et al., 1977). In addition, the scent material from all four species contained a number of proteins in the molecular weight range between 6,000 and 66,000 daltons (Belcher et al., 1990; Epple et al., 1987a).

Schilling (1980) has demonstrated that Coquerel's mouse lemurs (*Microcebus coquereli*) were able to discriminate between urine of two male conspecifics. About 40 volatile compounds in the urine were identified by GC-MS. Addition of two of these (short-chained-saturated fatty acids, hexanoic and decanoic) to the total urine modified the behavioural response (Schilling, 1980, quoted in Epple, 1986).

The exudates from brachial glands of the slow loris (*Nycticebus coucang*) and the pygmy loris (*Nycticebus pygmaeus*) have been resolved into several major components by HPLC. Fractions from both species contain several acid-soluble toxins (Alterman, 1989, 1990; Alterman & Hale, 1991). One of these components has been identified by mass spectrometry (MS) as a steroid (Alterman, 1989).

Although tree shrews (family Tupaiidae) are not included in the order Primates by most modern workers, the possibility of their phylogenetic relationship with primates has been controversial for a long time (e.g. Martin, 1990). A study of the chemical composition of urine

scent marks of *Tupaia belangeri* (Stralendorff, 1987) will be mentioned here only for comparative purposes. Urine of tree shrews was fractioned by TLC and GC-MS, and more than 30 urinary components have been identified. The GC profile of males is distinguished by certain pyrazine compounds (not detected in the profiles of females) and some volatile monocarboxylic acids (present at higher concentrations in male than in female urine). When presented to tree shrews, these compounds elicited strong responses ("chinning", i.e. one form of marking behaviour) from both males and females.

Several studies deal with the chemical composition of glandular secretions that are possibly involved in olfactory communication but not in marking behaviour: For instance, vaginal aliphatic acids have been found in several primate species such as *Saimiri sciureus, Papio anubis, Macaca fascicularis, M. mulatta, M. nemestrina, Erythrocebus patas, Pan troglodytes* and humans (see review in Epple, 1986). There is some evidence that male rhesus monkeys (*M. mulatta*) are able to assess these aliphatic acids as olfactory cues to determine the female's sexual attractiveness and that they may become sexually aroused by these odours.

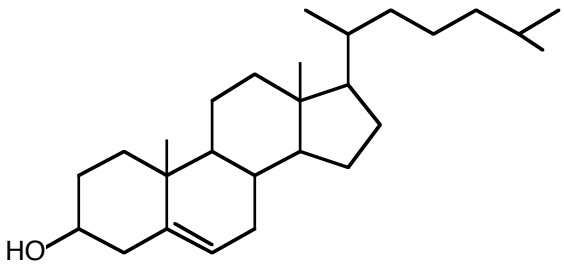
In humans, the axillary organ is probably the most conspicuous scent-producing specialisation of the skin. The composition of axillary secretions has been reviewed, for instance, by Gower et al. (1985; 1988), Labows et al. (1982), and Labows (1988). Axillary secretions contain lipids (mainly fatty acids and steroids) and approximately 10 per cent protein (including a number of enzymes).

Of the various steroid substances which have been identified in samples from the axilla, cholesterol makes up about 1 per cent by weight (Gower et al., 1988). A list of steroids found in human axillae is presented in Table 4.1.3. The chemical structures of some of these steroids are shown in Fig. 4.1.1.

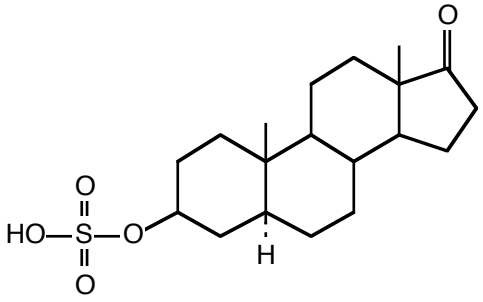
Table 4.1.3: Steroids found in human axillae (collated from reviews of Gower et al. (1988, p. 59), Labows et al. (1982, p. 200) and Labows (1988, p. 325).

Sample	Steroid
Axillary sweat and/or hair:	Cholesterol
	4, 16-androstadien-3□-one
	5, 16-androstadien-3(□)□-ol
	Androst-4-ene-3, 17-dione
	5□-androst-16-en-3(□)□-ol
	5□-androst-16-en-3□-one
	Androsterone (and sulfate)
	Dehydroepiandrosterone (DHEA) (and sulfate)
	Pregn-5-en-3□-ol-20-one
Sterile apocrine secretion:	Cholesterol
	Androsterone (and sulfate)
	Dehydroepiandrosterone (DHEA) (and sulfate)

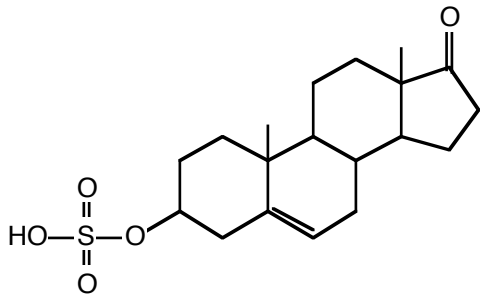
Much of the musk-like or urine-like smell which is reported from the human axilla (see e.g. review in (Stoddart, 1990) is caused by the presence there of at least two odorous Δ^{16}-androgen steroids: 3□-androstenol (5□-androst-16-en-3□-ol) and 5□-androstenone (5□-androst-16-en-3-one) (Brooksbank et al., 1974; Claus & Alsing, 1976; Gower et al., 1985). The former, an alcohol, has a musky odour and "is not altogether unpleasant", whereas the latter, a ketone, confers the disagreeable and dominant odour which has been labelled as "urine", "sweaty" and "perspiration" in odour description studies (Labows et al., 1982, p. 199f). Studies utilising radioimmunoassay techniques have demonstrated significant differences in concentration of 5□-androstenone in male and female subjects (Bird & Gower, 1981; Gower et al., 1985).



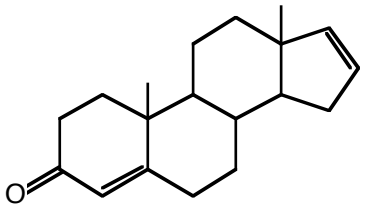
Cholesterol



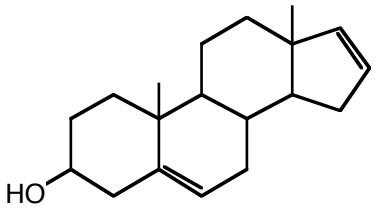
Androsterone sulfate



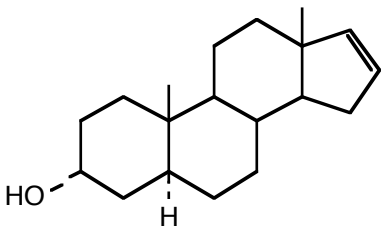
Dehydroepiandrosterone sulfate (DHEA sulfate)



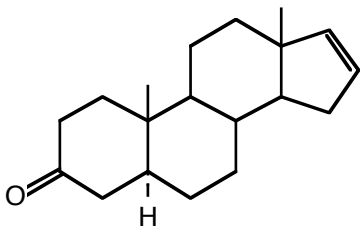
Androstadienone
(4, 16-androstadien-3-one)



Andien-β
(5, 16-androstadien-3β-ol)



3β-androstenol
(5β-androst-16-en-3β-ol)



5β-androstenone
(5β-androst-16-en-3-one)

Figure 4.1.1: Chemical structures of selected steroids found in human axillae.

Freshly-secreted apocrine sweat is odourless (Hurley & Shelley, 1960; Shelley et al., 1953); it contains little or no 3α-androstenol or 5α-androstenone, but cholesterol, dehydroepiandrosterone sulfate, and androsterone sulfate are present (Labows et al., 1979). Although the two sulfated steroids are closely related to the odorous steroids in their chemical structure, it is unknown whether either of these is a precursor of the latter (Labows et al., 1982).

There is strong evidence indicating that axillary odour is associated with a coryneform-dominated axillary microflora (Jackman, 1982; Jackman & Noble, 1983; Leyden, 1988). Incubation of apocrine sweat with coryneform bacteria produced the typical axillary odour (Leyden et al., 1981), whereas sterile eccrine sweat produced no odour when incubated with bacteria (Hurley & Shelley, 1960; Shelley et al., 1953). Coryneform bacteria are present especially in the axillae of men and this could explain the higher levels of 5α-androstenone found in men compared with those of women (Gower et al., 1985; Jackman, 1982). These observations are also consistent with the more pronounced "musky" or "strong" smells of male axillary extracts compared to those of woman (Gower et al., 1985). Taken together, these findings suggest that the odorous Δ^{16}-steroids are formed by the action of coryneform bacteria on apocrine secretion in the axillae, and that these bacteria are, therefore, mainly responsible for the phenomenon of human axillary odour. The mechanistic link between these factors, however, still requires more direct experimental evidence (Jackman, 1982), and the biochemical pathways by which coryneform bacteria produce the odorous materials are unknown (Leyden, 1988).

Other substances in the axilla originating from the sebaceous, eccrine and apocrine glands may contribute indirectly to the total odour profile. Sebum intermingles with apocrine secretion in the infundibulum of hair follicles and contains about 10% squalene, a material which fragrance formulators use as a "fixative" to make the odour more durable (Labows et al., 1982, p. 200; Leyden, 1988, p. 317).

4.2 Macroscopic Study

4.2.1. General Comments

Macroscopic evidence for the occurrence of specialised skin glands in gibbons was first documented by Pocock (1925; 1927), who described a dark patch in the sternal region of two captive gibbons, possibly *Hylobates muelleri* (see section 4.1.2). Other authors, however, were unable to confirm Pocock's findings (Weber & Abel, 1928; Wislocki & Schultz, 1925).

A different kind of observation relating to skin glands in gibbons was reported by Laîné (cited in Dandelot, 1960), who noticed that coloured droplets were produced by two captive gibbons (*H. leucogenys* and *H. pileatus*) under perspiration. Similarly, Parakkal et al. (1962) observed distinct perspiration in three anaesthetised gibbons of unknown species. These observations have been reviewed in more detail above (see section 4.1.2).

For the present study, a large number of captive individuals of all species of gibbons and have been examined. Although museum specimens have also been studied, the latter are of limited value in this context (see Material and Methods). For comparative purposes, a few individuals of two species of great apes have also been examined.

4.2.2. Results

Aspect of Sternal Glands

Macroscopic evidence for the presence of sternal glands was found in all 10 gibbon species except the Kloss gibbon (*H. klossii*), which was not available for macroscopic examination. Sternal glands occur in both male and female gibbons. Figures 4.2.1 and 4.2.2 show sternal glands of an adult female pileated gibbon and a juvenile male siamang.

The macroscopic evidence of sternal glands usually consists of a distinctly coloured patch in the midline of the sternal region. There, the skin is often stained with coloured secretion or hairs are matted together with dried, or pasted with fresh, secretion. An example of the latter characteristic can be seen in the adult female siamang shown in Fig. 4.2.3. In some individuals, dried secretion along the border of the sternal gland appeared to include little crystal-like structures.

As a rule, the outer borders of sternal glands were sharply demarcated by the features described above. The patch is of elongated shape. The broader end is situated cranially; distally, the patch is thinner and ends about at the level of a straight line drawn through both nipples. In white-cheeked gibbons, the patch tended to be situated slightly higher up on the neck, but was often less clearly visible.

The colouration of the sternal patch is probably produced by glandular secretions and can be removed. The colour of dried secretion ranged from yellow through orange, red and brown to blackish-brown. The fresh secretion of siamangs is a yellowish substance, somewhat similar in aspect to human earwax, and of pungent odour, which I found to be typical for the siamang (see below). The smell was found to be faintly similar to blossoms of the vetch *Lathyrus odoratus*. In one female white-cheeked gibbon, the fresh secretion was of milky-reddish colouration. No smell was noticed here.

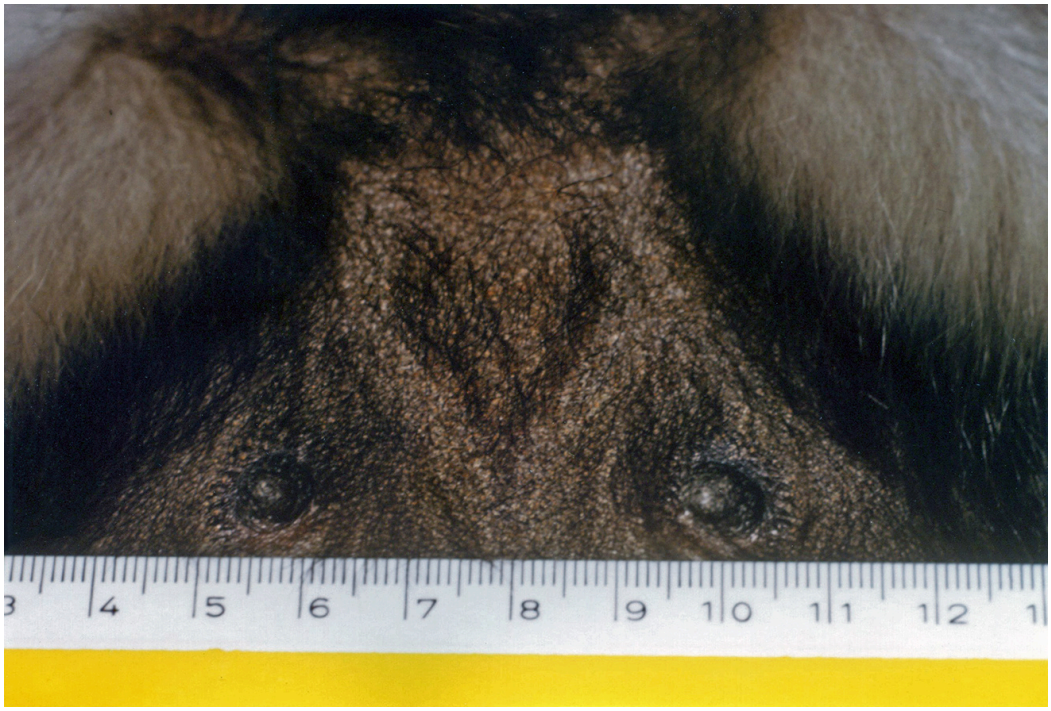


Figure 4.2.1: Sternal gland of adult female pileated gibbon (*H. pileatus*) "Gray". Photograph taken on anaesthetised animal at Zürich Zoo on 18 May 1987.

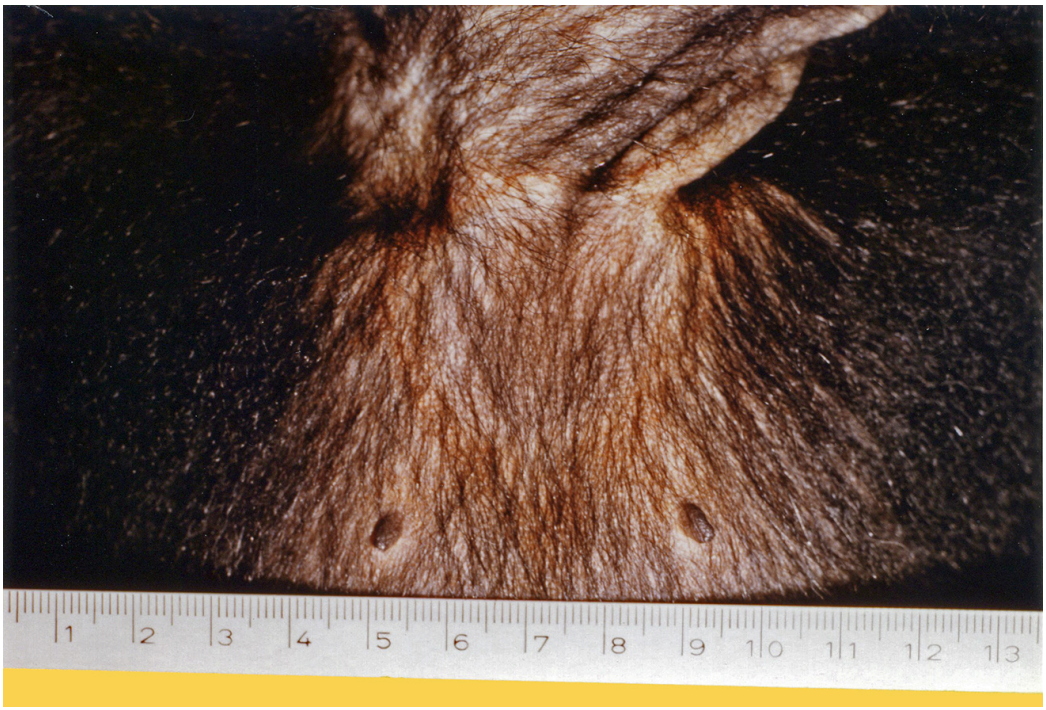


Figure 4.2.2: Sternal gland of infant male siamang (*H. syndactylus*) "Layang", 1.51 years old. Photograph taken on anaesthetised animal at Zürich Zoo on 18 May 1987.

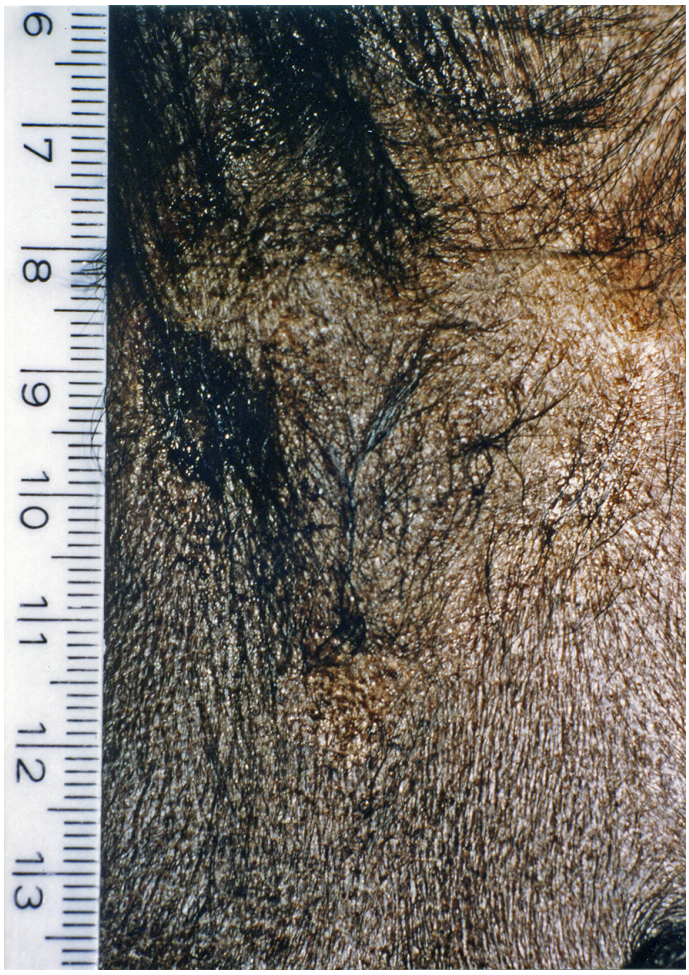


Figure 4.2.3: Sternal gland of adult female siamang (*H. syndactylus*) "Gaspa", showing hairs "glued" together from secretion. Photograph taken on anaesthetised animal at Zürich Zoo on 30 August 1989.

The sternal gland is most distinctly developed in siamangs. In this species, the gland has, in addition, the very strong smell mentioned above. It can be recognised in outdoor enclosures at a distance of several meters. In all other gibbon species examined, sternal glands can be smelled only at close range, if any smell can be recognised at all. In pileated gibbons, in particular, the odour of the sternal gland resembled that of the siamangs, although it was weaker. In white-cheeked gibbons and *lar* gibbons, the odour was not perceived as being similar to that of the siamang. Orang-utans and gorillas, which exhibit very strong body odours, each have their own, distinctive aroma which can easily be recognised.

Some animals did **not** show a distinct sternal gland. Among the adult gibbons available for close examination, the sternal gland was clearly demarcated in 100% of the siamangs and pileated gibbons, in only 50% of the *lar* gibbons, and almost invisible in all white-cheeked gibbons (Table 4.2.1, column A). Some white-cheeked gibbons **do** have a distinct sternal gland, but these individuals were not available for close examination (Table 4.2.1, column B). Apparently, the sternal gland is reduced in white-cheeked gibbons and, possibly, in other gibbons of the *concolor* group as well.

In Table 4.2.1, the frequency of sternal glands found among gibbons under close examination is much higher than in museum specimens (sign test, $N = 6$, $x = 0$, $p = 0.031$). The macroscopic characteristics signalling the presence of a sternal gland may often be destroyed in the process of preserving the specimens. This may explain why some previous authors failed to find sternal glands in gibbons (Weber & Abel, 1928; Wislocki & Schultz, 1925). Possibly, they were relying on tanned skins or preserved cadavers.

Although skin glands can sometimes be observed in captive gibbons without close examination (i.e. at a distance of several meters), negative findings do not necessarily imply absence of such glands, because the relevant characteristics may sometimes be hidden under the animals' fur. In a few captive gibbons which were first thought to lack a sternal gland, distinct glands were later discovered when the anaesthetised animals were examined.

The measurements taken of gibbon sternal glands, separated by sex, are summarised in Table 4.2.2. One male pileated gibbon ("Pipin Fabian") was measured both as a juvenile and as an adult; both measurements have been entered separately in Table 4.2.2 because they represent two different age classes. Two sets of measurements were also collected each of an adult female pileated gibbon ("Gray") and an adult female siamang ("Gaspa"). In these cases, only the average values were used for Table 4.2.2.

Table 4.2.1: Numbers of individual gibbons observed to possess a distinct sternal gland versus the number of individuals without sternal glands (only the former are listed under observation type B). [1]

Taxon	Age	Sex	Type of observation [2]		
			A	B	C
Hylobates agilis	ad.	m			2/2
H. agilis	ad.	f	1/0	1	0/4
H. agilis Total			1/0	1	2/6
H. klossii	ad.	f			0/1
H. lar	ad.	m	1/1		1/0
H. lar	ad.	f	2/2	1	
H. lar	juv.		1/1		0/1
H. lar	inf.				0/2
H. lar	neo.				0/3
H. lar	fet.				0/1
H. lar Total			4/4	1	1/7
H. moloch	ad.	m	1/0	1	1/0
H. moloch	ad.	f		1	
H. moloch	juv.			1	
H. moloch Total			1/0	3	1/0
H. muelleri	ad.	m	1/1		3/4
H. muelleri	ad.	f	1/0		0/3
H. muelleri	juv.				1/0
H. muelleri Total			2/1		4/7

1 Individuals which are included in data column 1 and for which data would have been available for columns 2 and 3 as well are not repeated there. Age classes "adult" and "subadult" are pooled. Individuals which were repeatedly observed and which thus cover several age classes are counted once for each age class. Abbreviations: ad. = adult; juv. = juvenile; inf. = infant; neo. = neonate; fet. = fetus; m = male; f = female.

2 A = close examination (anaesthetised or tame animal, or fresh cadaver), B = animal not seen at close range, C = museum specimen (tanned skin or preserved cadaver).

Table 4.2.1: Continued. [1]

Taxon	Age	Sex	Type of observation [2]		
			A	B	C
H. pileatus	ad.	m	2/0		0/1
H. pileatus	ad.	f	2/0		
H. pileatus	juv.		1/0		
H. pileatus	inf.		1/0	1	
H. pileatus	neo.		0/3		
H. pileatus	fet.				0/2
H. pileatus Total			6/3	1	0/3
H. sp. (*lar* group)	inf.				0/2
hybrids *lar* group	ad.	m	1/0	2	
hybrids *lar* group	ad.	f	2/0	1	
hybrids *lar* group	inf.				0/1
hybrids *lar* group	neo.				0/1
hybrids *lar* group	fet.				0/1
hybrids *lar* group Total			3/0	3	0/3
lar group Total			17/9	9	8/29
H. concolor	ad.	f		2	
H. concolor x *H. leucogenys*	ad.	f		1	
H. leucogenys	ad.	m	0/5		
H. leucogenys	ad.	f	0/4	4	
H. leucogenys	inf.		0/1		
H. leucogenys	fet.				0/1
H. leucogenys Total			0/10	4	0/1
concolor group Total			0/10	7	0/1

[1] Individuals which are included in data column 1 and for which data would have been available for columns 2 and 3 as well are not repeated there. Age classes "adult" and "subadult" are pooled. Individuals which were repeatedly observed and which thus cover several age classes are counted once for each age class. Abbreviations: ad. = adult; juv. = juvenile; inf. = infant; neo. = neonate; fet. = fetus; m = male; f = female.

[2] A = close examination (anaesthetised or tame animal, or fresh cadaver), B = animal not seen at close range, C = museum specimen (tanned skin or preserved cadaver).

Table 4.2.1: Continued. [1]

Taxon	Age	Sex	Type of observation [2]		
			A	B	C
H. hoolock	ad.	m		1	
H. hoolock	ad.	f		3	
H. hoolock Total				4	
H. syndactylus	ad.	m	4/0	2	0/7
H. syndactylus	ad.	f	5/0	4	1/1
H. syndactylus	juv.		2/0		
H. syndactylus	inf.		4/0	1	0/2
H. syndactylus	neo.		2/0		2/0
H. syndactylus	fet.				1/0
H. syndactylus Total			17/0	7	4/10

[1] Individuals which are included in data column 1 and for which data would have been available for columns 2 and 3 as well are not repeated there. Age classes "adult" and "subadult" are pooled. Individuals which were repeatedly observed and which thus cover several age classes are counted once for each age class. Abbreviations: ad. = adult; juv. = juvenile; inf. = infant; neo. = neonate; fet. = fetus; m = male; f = female.

[2] A = close examination (anaesthetised or tame animal, or fresh cadaver), B = animal not seen at close range, C = museum specimen (tanned skin or preserved cadaver).

Table 4.2.2: Average dimensions (cm) and standard deviations of gibbon sternal glands. The numbers of individuals measured are given in brackets. [1]

Species	Age	Sex	A	B	C	D
H. agilis [2]	ad.	m	6.3±0.4 (2)	2.2±1.2 (2)	0.0 (2)	–
H. agilis	ad.	f	3.6 (1)	1.4 (1)	2.0 (1)	2.8 (1)
H. lar	ad.	m	9.0 (1)	2.2 (1)	–2.5 (1)	5.6 (1)
	ad.	f	3.9±1.4 (3)	1.8±1.0 (3)	1.7±0.6 (3)	4.1±0.9 (3)
H. moloch	ad.	m	3.5 (1)	1.5 (1)	0.9 (1)	3.2 (1)
H. muelleri	ad.	m	6.0 (1)	3.5 (1)	0.0 (1)	3.3 (1)
H. muelleri [2]	ad.	m	5.3±0.8 (3)	1.5±0.2 (2)	0.0 (2)	2.9±0.1 (2)
H. pileatus	ad.	m	8.5±0.7 (2)	4.3±1.8 (2)	–1.5±1.4 (2)	5.0±0.0 (2)
	ad.	f	4.6±3.7 (2)	2.5±1.1 (2)	–1.1±0.1 (2)	4.2±0.6 (2)
	juv.		6.5 (1)	3.3 (1)	–1.7 (1)	4.4 (1)
	inf.		4.7 (1)	3.5 (1)	–1.7 (1)	3.5 (1)
Hybrids, *lar* group	ad.	m	5.0 (1)	4.0 (1)	0.0 (1)	6.0 (1)
	ad.	f	4.1±1.2 (2)	3.1±0.1 (2)	1.6 (2)	4.3±1.1 (2)
Total, *lar* group	ad.	m	6.3±1.8 (11)	2.7±1.4 (10)	–0.46±1.1 (10)	4.2±1.3 (8)
	ad.	f	4.1±1.7 (8)	2.3±0.9 (8)	1.0±1.4 (8)	4.0±0.8 (8)
H. leucogenys	ad.	m	6.5±3.5 (3)	4.9±2.5 (5)	3.9±2.8 (4)	5.1±0.8 (4)
	ad.	f	6.5±2.6 (3)	3.2±1.1 (3)	7.2±1.4 (3)	6.6±1.0 (3)
	inf.		5.0 (1)	1.0 (1)	6.0 (1)	3.5 (1)
H. syndactylus	ad.	m	8.9±0.6 (2)	4.1±1.3 (2)	0.6±0.8 (2)	4.5 (1)
	ad.	f	6.5±0.4 (2)	4.7±0.2 (2)	1.4±0.9 (2)	5.3±0.8 (2)
	juv.		5.3±1.1 (2)	2.1±1.3 (2)	0.3±1.8 (2)	4.3 (1)
	inf.		5.0±1.2 (2)	2.7±2.9 (2)	–0.4±0.6 (2)	3.0±1.2 (2)
	neo.		1.9±0.0 (2)	0.6±0.1 (2)	0.7±0.1 (2)	1.4±0.4 (2)
	neo.[3]		2.3 (1)	0.7 (1)	0.6 (1)	1.1 (1)

1 Measurements (see Figure 2.3.1): A, largest cranio-caudal length of the sternal gland; B, largest breadth of the gland; C, vertical distance of the caudal end of the gland from an imaginary line through the centres of the nipples; D, distance between the nipples. Abbreviations: ad. = adult; juv. = juvenile; inf. = infant; neo. = neonate; m = male; f = female.

2 Museum specimens: tanned furs.

3 Museum specimen: preserved in fixative.

As a trend, males appear to have slightly larger glands than females. The samples were, however, too small for a statistical comparison between male and female glandular dimensions. The size of the sternal gland shows little variation between gibbon species. In adult animals, the cranio-caudal length of the gland clusters around 3.5-8.0 cm, and its breadth around 1.5-4.5 cm. Figure 4.2.4 shows mean values and standard errors of these two measurements for each species. Males and females have been pooled.

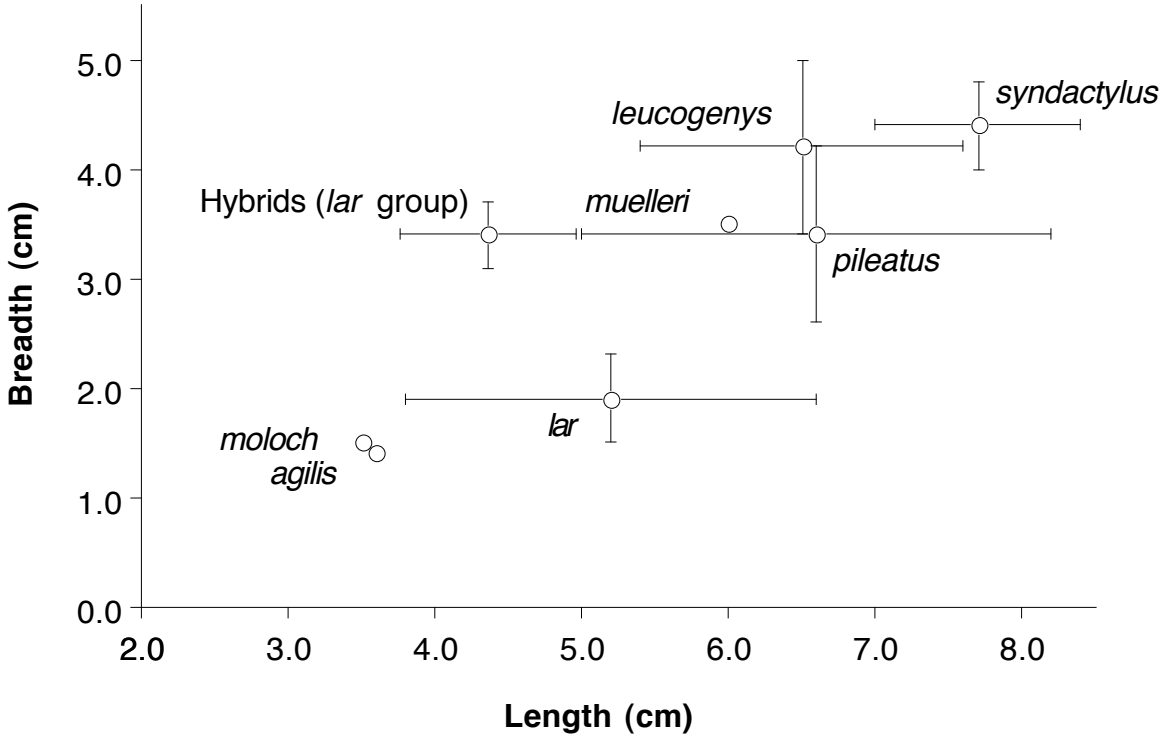


Figure 4.2.4: Cranio-caudal length and breadth of sternal glands in adult gibbons (mean values and standard errors).

Non-sternal Glandular Concentrations

Fields of coloured pores may occur in other areas of the skin. The axillary region of a female *lar* gibbon and the inguinal region in a male *lar* gibbon are shown in Figure 4.2.5 and 4.2.6, respectively. Dried glandular secretion of red-brown colouration can clearly be seen near the hair roots.

These concentrations of coloured pores preferentially occur in the clavicular, axillary and inguinal regions of the skin. Figure 4.2.7 shows the distribution and density of these glandular concentrations in four adult gibbons. They differ from the sternal glands in that they are not sharply delimited. Instead, glandular density gradually changes over the surface of the skin. The extent of these fields is subject to considerable individual variability, and differences between the animals shown in Fig. 4.2.7 need not reflect species-specific conditions.

Fields of coloured pores are probably responsible for areas of reddish or orange colouration sometimes observed in the otherwise pale-yellow or buff fur of females of the *concolor* group (see below).

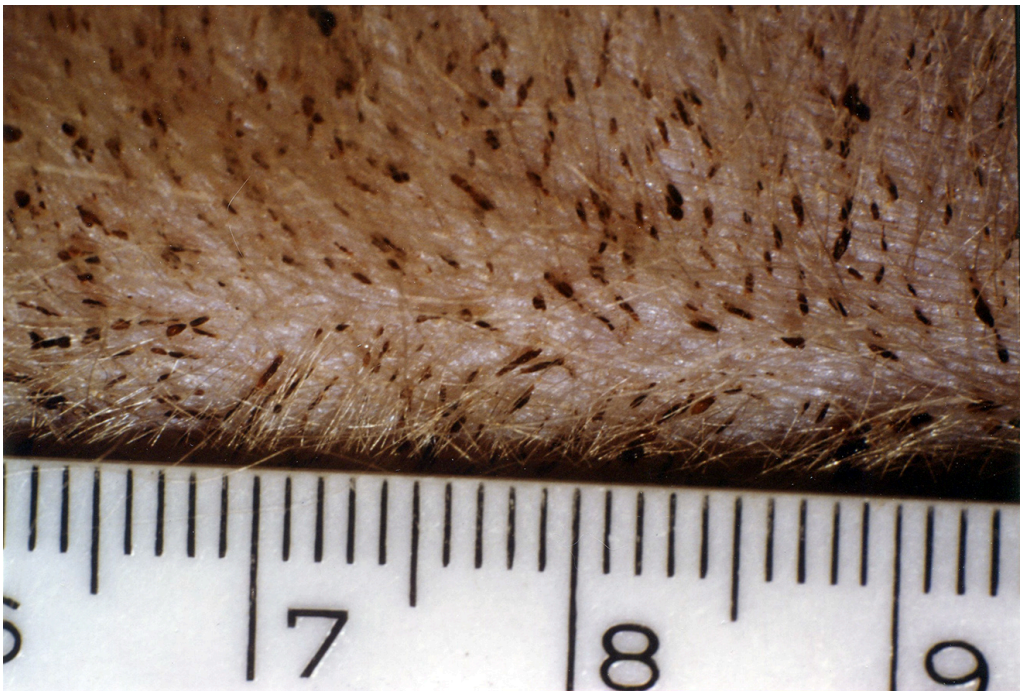


Figure 4.2.5: Axillary concentration of coloured pores in an adult female *lar* gibbon (*H. lar*) "Virgo". Photograph taken on anaesthetised animal at LEMSIP Primate Center in New York, on 15 August 1988.

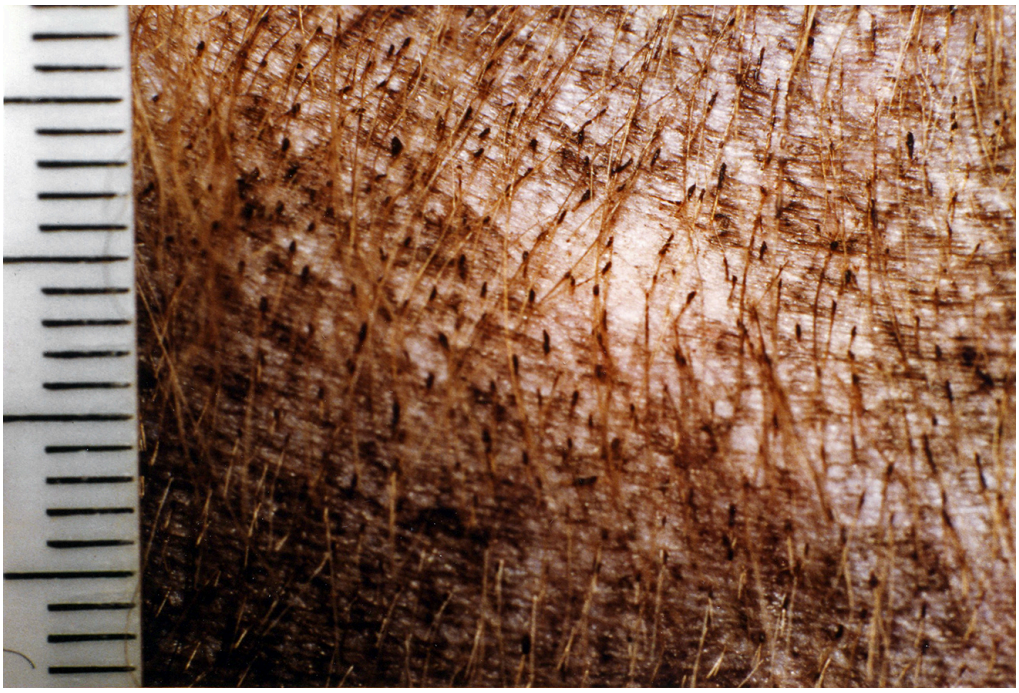


Figure 4.2.6: Inguinal concentration of coloured pores in an adult male *lar* gibbon (*H. lar*) "Buddy". Photograph taken on anaesthetised animal at Yerkes Regional Primate Research Center in Atlanta, on 10 August 1988.

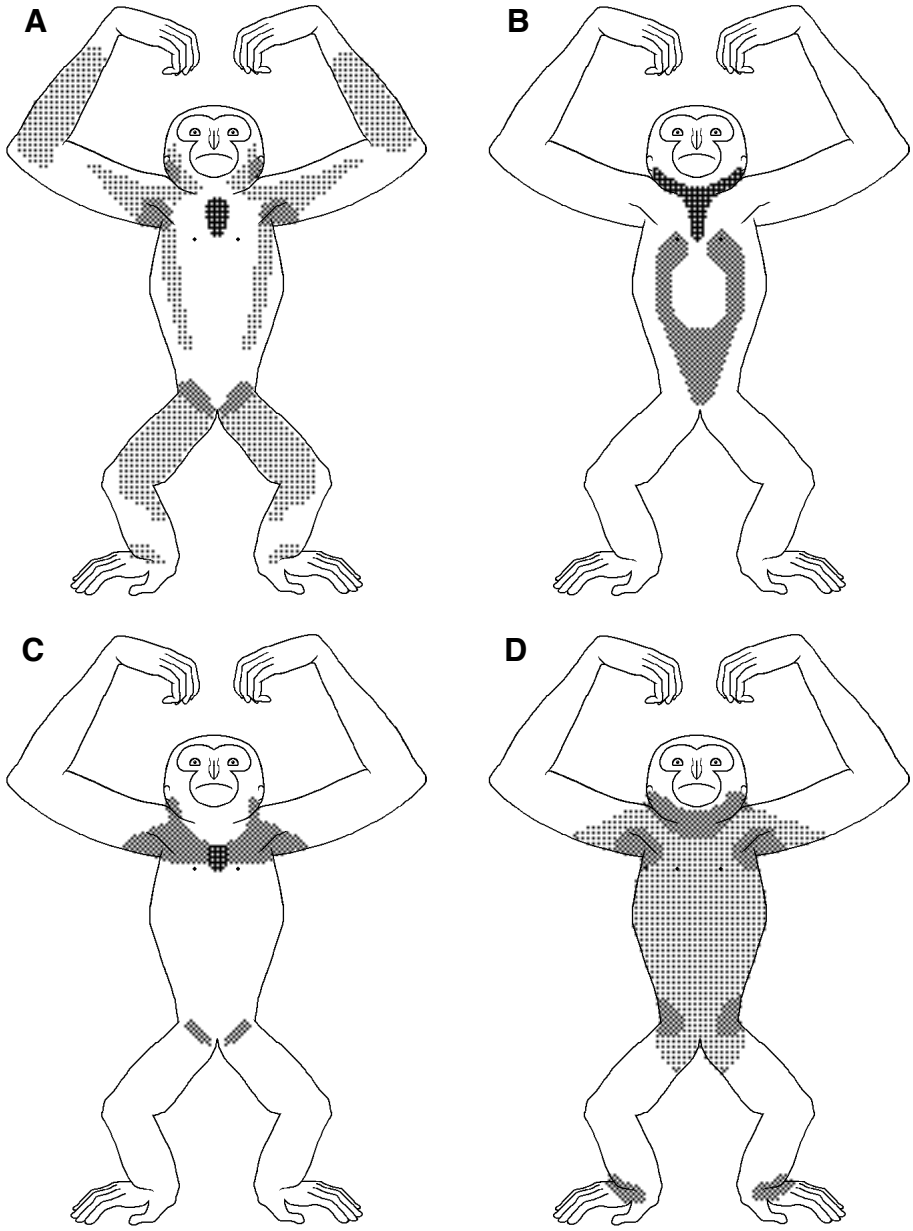


Figure 4.2.7: Fields of coloured pores on the skin of four adult gibbons. Density of pores is indicated by three different intensities of grey shading (darker shading represents higher concentration of pores).

A: *H. lar*, male "Buddy" (Yerkes Regional Primate Research Center, Atlanta, 10 Aug. 1988);

B: *H. pileatus*, male "Pipin Fabian" (Tierspital , Zürich University, 14 June 1992);

C: *H. syndactylus*, female "Mücke" (Munich Zoo, 11 Feb. 1988);

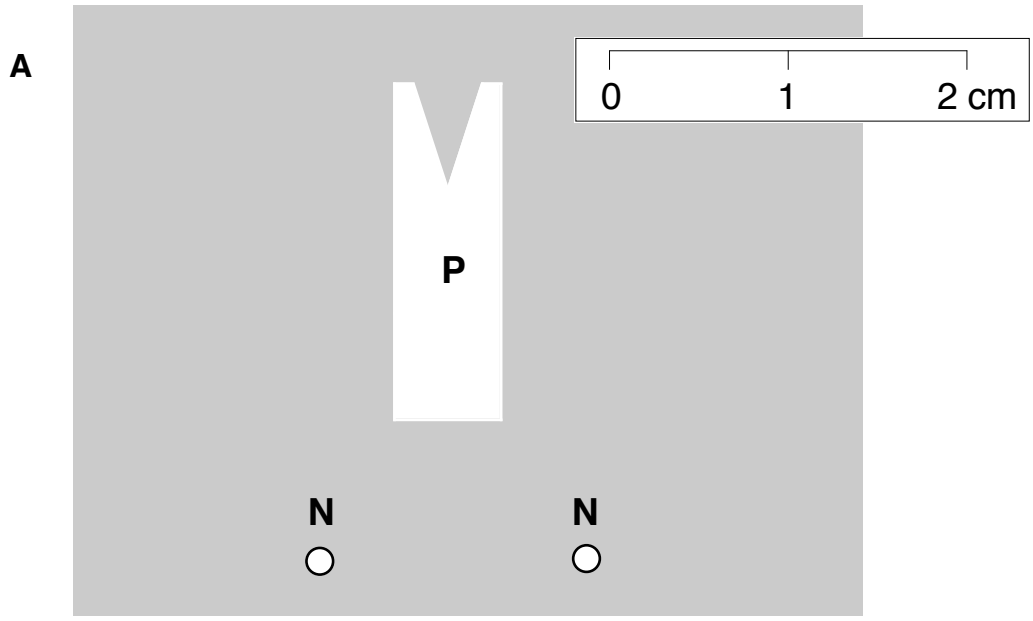
D: *H. leucogenys*, female "Püppi" (Duisburg Zoo, 1 March 1988).

Ontogenetic Changes

Newborn siamangs show a peculiar feature in the skin of the sternal region: a distinct whitish patch which can easily be seen, because the skin of newborn siamangs is quite heavily pigmented and of grey-brown colouration (Figure 4.2.8 A and B). The whitish patch is of a cranio-caudally elongated shape, with a length of about 2 cm and a breadth of about 0.6 cm. The cranial end of the patch is bifurcated and ends directly below the throat sac. The patch consists of an apparently unpigmented skin area, and the marking cannot be washed off. Therefore, verification of its presence in preserved cadavers of newborn siamangs may be more reliable than that of the sternal glands in older siamangs (see above).

The whitish patch described above was observed in all newborn siamangs of this study (n = 4, including two preserved cadavers AIMUZ No. 7969 and No. 8395), and occurs in both males and females. It was also found in some (n = 3) of the infant siamangs, but was absent in others (n = 4). All siamang infants that had the patch were younger than one year, the two oldest were 0.64 and 0.67 years old, respectively. Of those which lacked the patch, two were older than one year (1.07 and 1.52 years, respectively). The remaining two infants were preserved cadavers (AIMUZ No. 7293 and No. 10064). The exact age of both of them was unknown, but both may be more than one year old, to judge from their physical appearance and size. Live animals older than one year were found to have an (apparently functional) sternal gland of dark colouration resembling that of adult animals.

Finally, the presence of the whitish skin patch was also checked on one preserved cadaver of a female siamang fetus (AIMUZ No. 9346). This animal was a premature breech birth to a primiparous mother. The weight of the fetus was recorded as 152 g (Geissmann, 1984b), whereas neonatal siamangs have an average body weight of about 540 g (Geissmann & Orgeldinger, in prep.). In this animal, the white patch was already present, although less distinct than in full-term births.



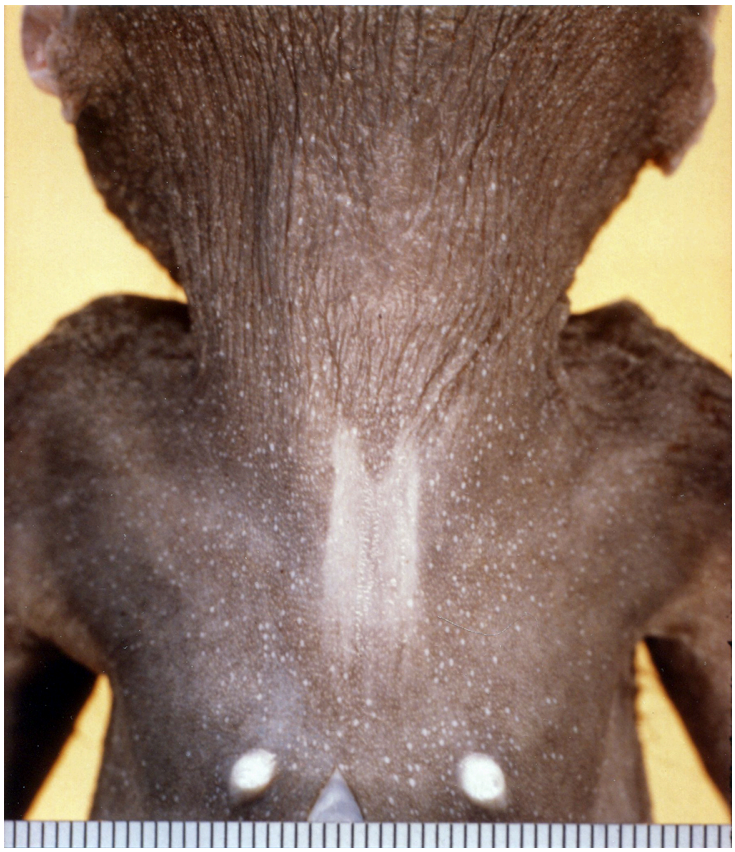


Figure 4.2.8: A.) Schematic contour and dimensions of whitish sternal patch in newborn siamangs. P = sternal patch; N = nipples. **B**.) Sternal region of newborn male siamang; photograph taken of fresh cadaver. Specimen born and died on 21 Jan., 1985; AIMUZ No. 9795 (see Appendix 10.3.1). Divisions of scale on photograph in mm.

Because the whitish skin patch occurs on exactly the same site as the typical sternal gland of older siamangs, the patch may represent a precursor of the sternal gland, although no glandular secretion, dark staining of the skin, or hairs sticking together were observed in the neonates and young infants that had the whitish patch. This hypothesis was tested by a histological analysis of the white skin patch (chapter on microscopic analysis, see below).

No sign of a white skin patch could be found in fetal, neonatal and infant animals of a number of other gibbon species, including *Hylobates lar*, *H. pileatus* and *H. leucogenys*, and hybrids of the *lar* group (see Table 4.2.1). This finding must be regarded with some caution, however, because in these species neonates and infants lack the heavy skin pigmentation found in siamangs of the same age. An unpigmented sternal area (i.e. the whitish patch) would certainly be less conspicuous in these animals and could perhaps have escaped detection.

Several caretakers, several of whom had hand-raised zoo gibbons, were interviewed about skin glands in gibbons and apes (see Material and Methods). In one question they were asked whether they had made any observations relating to the ontogeny of skin glands in gibbons. The results of this part of the interviews are summarised below.

Mrs. U. Rathfelder (formerly of Zürich Zoo) reported that the sternal gland in siamangs became functional near the end of the first year of life. From that time on, secretion is produced, which leads to a dark staining of the site. In one hand-reared siamang infant ("Tawar", 1.2 years old, male), Mrs. Rathfelder had removed the dark stain in the sternal region with body lotion. The sternal skin then had the same colouration as the skin surrounding the sternal area. The dark stain reappeared after 10 days (pers. comm., 31 March, 1984).

Mrs. E. Schramke (c/o Duisburg Zoo, Germany) reported that the sternal gland in a hand-reared siamang male ("Elliott") had started to smell at the age of 4-5 months (pers. comm., 24 June, 1987).

Ms. S. Fowmes (c/o Twycross Zoo, England) had noticed that hand-reared hybrid crested gibbons (*H. concolor* x *H. leucogenys*) started to produce coloured secretion from skin glands

at the age of about 6 weeks: at that time, the animals' nappies and clothes began to show reddish staining (pers. comm., 8 Oct., 1988).

Mrs. G. Adler (formerly in Leipzig, Germany) also reported that several hand-reared infant white-cheeked gibbons (*H. leucogenys*) had produced a reddish skin secretion which stained their diapers. She remembered that she had first considered this to be a pathological condition. The reddish staining was found only in infants that still retained their light natal coat (personal communication, 3 July, 1988). Crested gibbons are known to change from light yellow to black fur colouration near the end of the first year of life (Groves, 1972) or during the second year of life (Dittrich, 1979).

These observations on infant gibbons of the *concolor* group probably refer to the fields of coloured pores which have been described above and which are sometimes very prominent in adult females of the same species.

Changes in Glandular Activity and Other Behavioural Observations

In siamangs, the sternal patch was often wet and sticky from fresh secretion of the gland. This could be taken as a rough indicator of "high secretory activity" and was observed chiefly in two situations: on hot days and during arousal (evoked by loud noises, unfamiliar people near the animals' sleeping cage, or during siamang song bouts). In these situations, the characteristic body odour of the siamang is especially strong and conspicuous and carries over distances of several meters.

A case of unusually profuse sternal secretion was once observed in an adult male siamang "Bohorok", which had been hand-reared at the Zürich Zoo, and was more than 11 years old in October 1986, when the following observation was made in front of the outdoor cage. The male was observed to exhibit both sudden agitation and a discharge of sternal exudate, probably caused by the sight of its former caretaker (Mrs. U. Rathfelder) carrying an infant siamang (which also had to be hand-reared). The adult male alternatingly bit into the wire-mesh of his

cage and stared at Mrs. Rathfelder, who was standing a few meters away from the cage talking to other staff members. The typical odour of the siamang became very strong, and sternal secretion could actually be seen trickling down from the male's sternal gland. This was the only situation in which pure, fresh secretion from the sternal gland of a gibbon was collected during this study (section 4.4.3).

As described above, gibbons may exhibit concentrations of coloured pores in various parts of the skin. Fields of coloured pores are particularly pronounced in gibbons of the *concolor* group, where glandular secretion is apparently responsible for an apparently undocumented feature. Figure 4.2.9 shows an adult female of the white-cheeked gibbon with very pale, almost whitish fur colouration. Figure 4.2.10 shows the same female some time later. By then, the animal's fur had turned a bright orange colour in some regions: around the neck, on the shoulders, in the inguinal area and on the lower legs. This is apparently the result of glandular activity in these regions. Female gibbons of the *concolor* group have repeatedly been observed to switch back and forth between whitish and orange fur colouration.

The same phenomenon cannot be directly observed in males of the *concolor* group, because their fur is black. But sometimes, when grooming males of the *concolor* group, the author's hands became stained in red or reddish-brown, probably from dry secretion. In these males, small reddish particles were visible in the fur, but only at a very close range (Fig. 4.2.11). Nothing similar has been observed in other gibbon species.

Figure 4.2.9: Adult female *H. leucogenys* "Schopfeline", with pale fur colouration (Munich Zoo, 24 July 1982).

Figure 4.2.10: Same adult female as in Fig. 4.2.9, but with reddish glandular areas (Munich Zoo, 17 July 1987).

Figure 4.2.11: Adult male *H. leucogenys siki* "Mohrle"; close-up view of dorsal fur showing small reddish particles (Tierpark Berlin, 14 Sept. 1988).

The timing of the colour changes in females of the *concolor* group is unclear. No consistent pattern emerged from interviews with staff members in several zoos or from my own observations. Some females were said to change **seasonally**, others were said to change to saturated colouration when **giving birth**, others were observed to show this change upon being **separated from their mate**, and in other females still, **no** colour changes had been noticed.

In one zoo (Duisburg), two adult female white-cheeked gibbons were kept together. The author was present when both had to be caught with a net for a veterinary check. One female ("Sophie") was easily caught at the first trial, and no fresh glandular secretion was observed in this individual. The other female ("Püppi") was very elusive and it took the staff about three capture sessions, each of about fifteen minutes duration, until they succeeded in catching the female. The exhausted animal was heavily transpiring over the whole body. The very fine sweat droplets were of reddish colouration, and stained the table upon which the sedated animal was examined.

The author failed to find any kind of marking behaviour in spite of having spent thousands of hours observing gibbons of all species in captivity. Interviews with staff members in many zoos revealed only two observations relevant in this respect:

Mr. and Mrs. H.J. and G. Adler (formerly in Leipzig, Germany) reported on an infant female *H. leucogenys* ("Minnie") which was being hand-reared. This infant would exhibit a peculiar behaviour in situations when it was believed to be jealous (for instance when Mrs. Adler was busy taking care of a baby orang-utan). The gibbon would first bite and afterwards rub its ventral region against Mrs. Adler's face, or rub first and bite afterwards (pers. comm., 3 July, 1988). One such sequence was recorded on a short video film by Mr. Adler and was shown to the present author.

Mr. K. Rathfelder (Zürich Zoo) reported that one of the adult siamangs kept in Zürich had a particularly shiny nose. The reason for this characteristic became obvious after Mr. Rathfelder had observed that this female ("Ratana") would alternatingly rub her hand over the sternal gland and over her nose. By doing so, she was probably transferring sternal secretion to her nose. This behaviour was very intense when the animal was under stress. Such situations were particularly frequent when there where two breeding pairs of siamangs at the zoo. No other siamang at the zoo was ever observed to exhibit a similar behaviour (pers. comm., 31 March, 1984, and 3 July, 1986).

4.3 Microscopic Study

4.3.1. General Comments

Previous to the present study, only one publication has apparently been dedicated to the histology of the gibbon skin (Parakkal et al., 1962). These authors did not mention any concentration of eccrine or apocrine sweat glands in any part of their subjects' bodies. Their study animals were said to be white-browed gibbons (*H. hoolock*). Uncertainties regarding this identification have already been discussed by Geissmann (1987b) and, in more detail, in section 4.1.2 of the present study (see above).

Histological sections of gibbon skin have also been carried out in two earlier studies, but these were strictly concerned with axillary glands in primates (Brinkmann, 1909; Klaar, 1924). Both authors had a specimen of "*Hylobates leuciscus*" at their disposal (the name "*leuciscus*" has been used for several gibbon species, but most frequently for *H. moloch*); these gibbons were not adult. No axillary organs were found in the two specimens, but small apocrine glands were observed in the axillary region of one of them (Klaar, 1924).

This study presents a histological analysis of skin samples of 21 individual gibbons representing eight species. Results based on two of the animals (sample nos. 1 and 2) of the siamang (*H. syndactylus*) have already been presented in a preliminary report (Geissmann, 1987b). For comparative purposes, skin samples of two species of great apes (one male gorilla and one male orang-utan) have also been examined.

4.3.2. Results

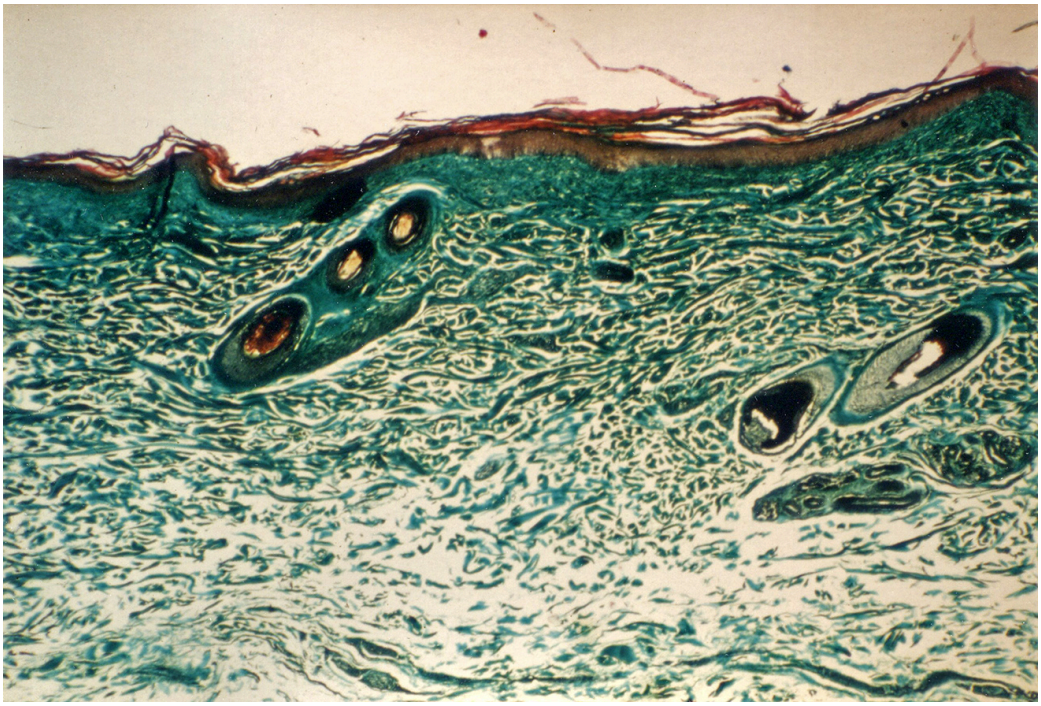
Six skin samples from the lateral chest have been examined (comprising the species *H. lar, H. pileatus, H. muelleri,* and *H. syndactylus*). In these sections, no or very few and small tubular glands were found (Figure 4.3.1a). Sebaceous glands, attached to hair follicles, were more abundant, but also relatively small.

In contrast to the situation found in the lateral chest, most samples from the sternal skin contained, in addition to sebaceous glands, a very conspicuous concentration of coiled tubular glands, thus forming a specialised glandular field (Figure 4.3.1b). Such was the case with most samples of the gibbon species *H. hoolock, H. lar, H. moloch*, *H. muelleri*, *H. pileatus*, and in all seven specimens of *H. syndactylus* (including a neonate individual). In the two sternal samples of the great apes, and in some sternal samples of the gibbons (including *H. klossii*, *H. hoolock*, *H. leucogenys*, *H. lar*, and *H. muelleri*), no significant glandular concentration was detected. It should be mentioned, however, that a large piece of skin was missing from the sternal area of the specimen of *H. klossii*; it may have contained a glandular concentration.

Five of the samples consist of a continuous piece of skin extending from the lateral chest to, and including, the sternal gland (including *H. lar*, *H. muelleri*, *H. pileatus*, and *H. syndactylus*). In these sections, the transition between the unspecialised skin of the chest and the glandular area can be seen to be abrupt rather than graded.

In the specialised sternal fields, the tubular glands are not only more numerous, but also more voluminous (as compared to the skin on the lateral chest) and form a veritable carpet of considerable thickness, which is separated from the more superficially situated layer of smaller sebaceous glands. In the tubular coils, two types of segments, similar to apocrine sweat glands and their ducts, can be distinguished: segments composed of cuboidal or columnar epithelium and with wide lumina often containing granular secretion, and very narrow segments composed of two layers of cuboidal epithelium.

a.



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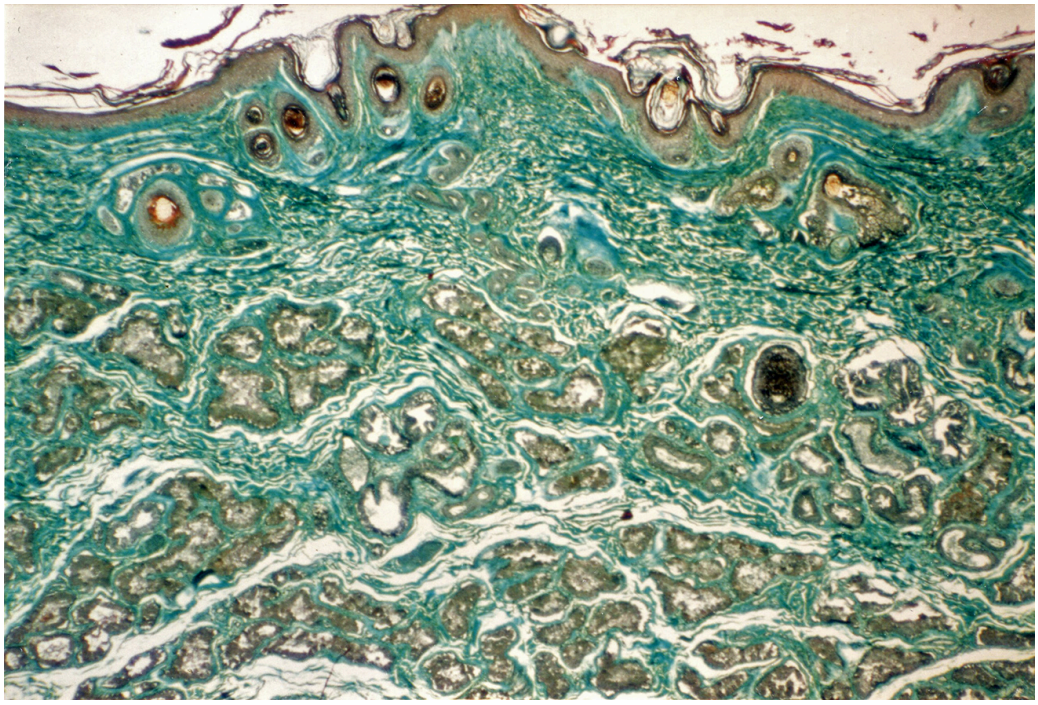


Figure 4.3.1: Photomicrographs of vertical sections through the skin of an adult siamang (wild-shot specimen, preserved at the Anthropological Institute of Zürich University, AIMUZ 7297). Sections stained with Masson's Trichrome technique. a: Lateral chest, showing hair follicles associated with sebaceous glands, but no tubular glands. b: Sternal gland, showing the superficial layer of sebaceous glands and the deeper layer of densely packed, coiled tubular glands.

The histological structure of the axillary organ of the male gorilla of this study was virtually identical to that of the sternal gland in gibbons, except that the layer of tubular glands was thicker in the gorilla and extended well into the subcutis.

Some variability was observed in the sternal glandular structure among the gibbons: For instance, in the adult female *H. moloch* and in the juvenile male *H. pileatus* the lumina of the coils were particularly wide, with a very thin epithelium. The juvenile female *H. syndactylus* represented the opposite extreme: here, the epithelium of the coils was especially high and columnar. Only in the female *H. moloch* were some of the coils deeply embedded in the subcutaneous tissue, whereas in other specimens the coils were restricted to the dermis, of which they usually occupied the deeper part. Among the sternal samples examined, the adult female *H. muelleri* is exceptional in that the tubular coils appear to be especially crowded, filling out almost the whole depth of the dermis. In the two juvenile siamangs, not only the tubular glands, but also the sebaceous glands appeared to be more numerous and larger than in other areas of the skin. In the neonate and the infant siamang, the coils of the tubular glands appeared to be smaller than in the older animals.

In several sternal samples (e.g. *H. moloch*, *H. muelleri*, *H. syndactylus*), but also in the axillary area of the juvenile female *H. syndactylus*, two distinct types of tubular glands could be seen to coexist. The dominant type is very abundant and forms large coils with relatively wide lumina. It possibly corresponds to apocrine glands in humans. The second, less frequent type, consists of very small coils with much narrower lumina; this type may correspond to human eccrine glands.

In gibbons, distinct glandular specialisations similar to those in the sternal regions did not occur in the skin sections from other parts of the body. Nevertheless, some skin sections showed moderate concentrations of tubular glands. In general, the axillary and inguinal samples tended to contain more tubular glands than the samples from the lateral abdomen and from the back. These tubular glands were considerably smaller and their density lower than in the sternal sections of the same individuals. Only the axillary area of one male siamang and the inguinal

area of the juvenile female siamang contained a distinct layer of tubular glands. Again, these were smaller than those found in the sternal samples, but larger than those in other areas of the body.

The axillary sample of the male gorilla contained huge bundles of tubular glands, which were concentrated on the subcutaneous skin layer. They could easily be seen even in unmagnified (but stained) sections.

The above findings on the occurrence of skin glands in gibbons are summarised in Table 4.3.1. In this table, the density of tubular glands is indicated by a scale ranging from −− to ++, with −− indicating no glands, (+) few glands, and ++ a massive concentration of glands.

Table 4.3.1: Occurrence of tubular glands in the skin samples of various gibbon specimens examined. [1]

Species	Age	Sex	Body area					
			lateral chest	sternal	axilla	lateral abdominal	inguinal	dorsal
H. hoolock	ad.	M		(+)	–			
	ad.	F		+ +			+	
H. klossii	ad.	F		––	–	X	–	––
H. lar	ad.	M		+	––		(+)	
	ad.	F	––	+ +	(+)		(+)	
	ad.	F		+	–		(+)	––
	juv.	M		(+)	–	–	(+)	––
H. leucogenys	ad.	F					–	
	inf.	F		(+)		–		
H. moloch	ad.	M		(+)	––		–	
	ad.	F		+	–		–	
H. muelleri	ad.	F		+ +	(+)			
	juv.	M	––	+ +	(+)		––	
H. pileatus	juv.	M	–	+ +	––	––	––	(+)
H. syndactylus	ad.	M		+ +				
	ad.	M	––	+ +	+			
	ad.	F		+ +				
	juv.	M	––	+ +				
	juv.	F		+ +	(+)		+	
	inf.	M	–	+				
	neo.	M		+ +				
Gorilla gorilla	ad.	M		–	+ +	+		
Pongo pygm.	ad.	M		+ +	(+)	(+)		

[1] ad. = adult; sad. = subadult; juv. = juvenile; inf. = infant; neo. = neonate; M = male; F = female; X = quality of histological section unsufficient for analysis.

4.4 Chemical Analysis

4.4.1 Why Radioimmunoassays?

The techniques which have been used in most previous studies on skin glands in primates (see above) are high performance liquid chromatography (HPLC) or gas chromatograph-mass spectrometry (GC-MS). They permit determination of an extensive profile of compounds contained in a secretion sample as well as the relative proportions of individual compounds.

Because it would be an extremely time-consuming task to check all possible compounds in a sample of unknown composition such as gibbon skin secretion, it became necessary to restrict this analysis to just a few compounds. As is explained below, it seemed particularly promising to check for the presence of certain steroid hormones. Radioimmunoassay (RIA) kits and commercial antibodies of high quality are available for several steroid hormones of clinical interest (Gammill, 1976). In addition, the RIA technique offers several advantages over other methods (Boyd & Herzberg, 1976). The single most important advantage is provided by its *sensitivity*, that is the ability of a measurement system to detect small amounts of substances. This characteristic made RIA the technique of choice for the present study.

4.4.2 Why Steroid Hormones?

Although there was no a priori knowledge of the chemical components of gibbon skin gland secretions, checking for the presence of steroid hormones appeared to be a useful initial procedure, for the following reasons:

Steroid hormones and derivates of them had previously been found in human axillary secretions (see above). Some gibbon skin glands have been found in this study to show a

histological structure similar to the axillary glands in humans, and similarity in function may also exist, as will be discussed below. In addition, gibbons are relatively closely related to humans. Moreover, radioimmunoassays of steroid hormones are routinely carried out on human urine samples at the Kinderspital of Zürich. Among these hormones, the following three have been analysed for this study: dehydroepiandrosterone (DHEA; 3β-hydroxy-5-androstene-17-one), androstenedione (4-androstene-3,17-dione), and testosterone (17β-hydroxy-4-androstene-3-one). A simplified view of the position of these three compounds within the network of steroid biosynthesis is shown in Fig. 4.4.1. Detailed discussions of steroid biosynthesis, metabolism and mechanisms of action can be found, for example, in Orten and Neuhaus (1982), and Träger (1977).

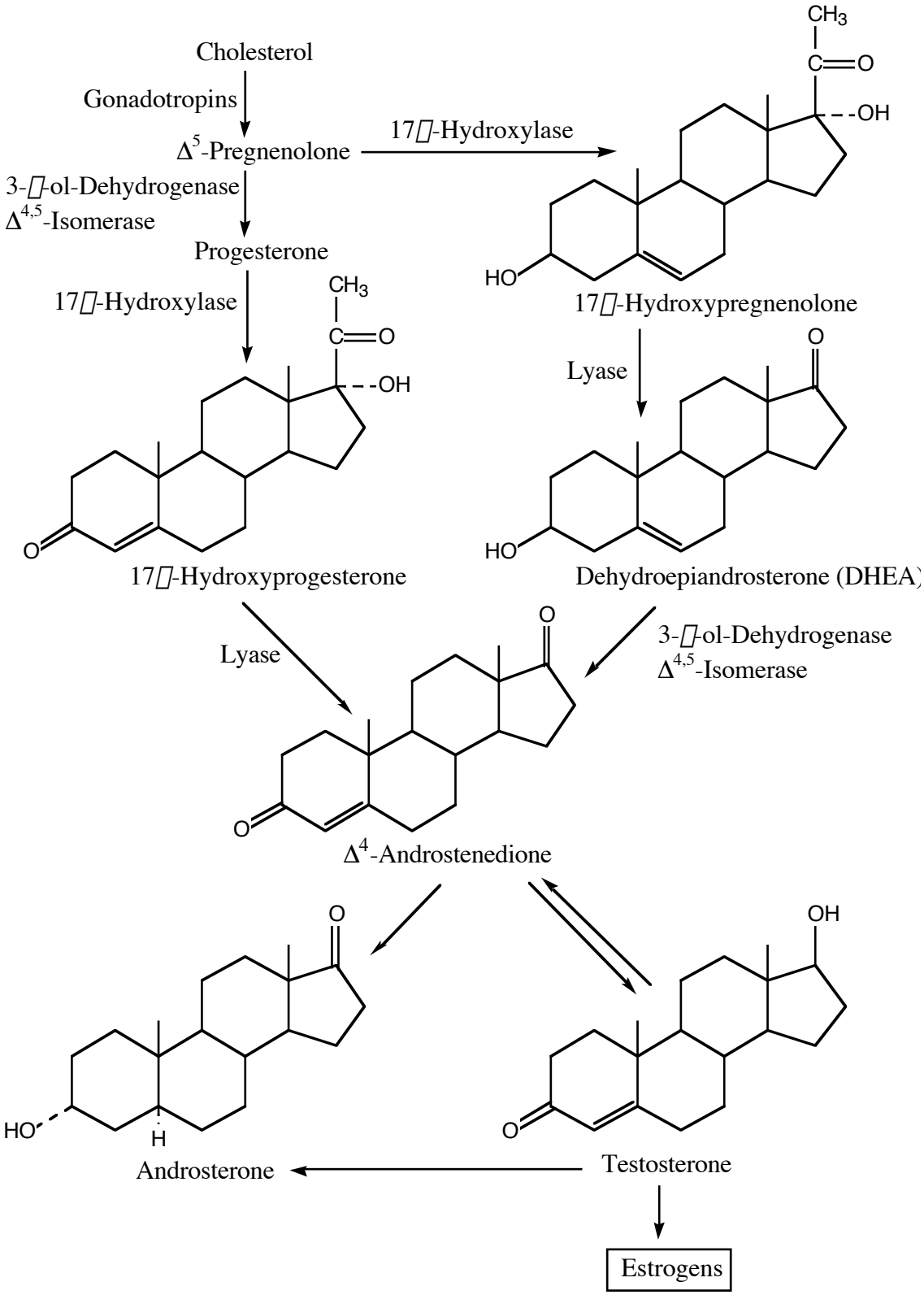


Figure 4.4.1: Pathways showing biosynthesis of androgens and estrogens (after Orten & Neuhaus, 1982; their Figure 18-17, changed).

4.4.3 Results

The hormone concentrations determined in each sample are listed in Appendix 10.4. All hormone concentrations given there and in the following text have been corrected, as described in section 2.4.3. Tables 4.4.1 and 4.4.2 present summary statistics (mean value, standard error, minimum and maximum value) of the hormone concentrations in the sternal region and the axillary region, respectively, for each species and sex separately. Within most species sex classes consisting of more than one individual, considerable variation in the hormone concentrations is apparent from comparison of the minimum and maximum values. This variation makes the interpretation of hormone concentrations difficult for species sex classes containing only one individual (samples from *Hylobates lar*, *H. pileatus* and *Pan*). By contrast, the larger samples available for *H. leucogenys*, *H. syndactylus* and *Pongo* permit more reliable comparisons to be made.

Figures 4.4.2 and 4.4.3 show the average proportions of the three hormones in each species sex class. Particularly high concentrations occur in the sternal samples of *H. syndactylus*, of male *H. pileatus* and of female *Pan*. The sternal values for *H. lar* and *H. leucogenys*, on the other hand, are very low, and the remaining sternal samples occupy a more intermediate position. In the axillary samples, high concentrations are found in *Pan* and the males of *Pongo*, whereas the values for *H. lar* and *H. leucogenys* are again particularly low.

Table 4.4.1: Species means of hormone concentrations in the sternal samples (ng/sample) of adult and subadult animals [1].

Species	Males					Females				
	N	Mean	SE	Min.	Max.	N	Mean	SE	Min.	Max.
DHEA										
H. lar	1	3.14				1	2.79			
H. leucog.	5	6.72	1.61	1.62	11.48	4	2.55	0.40	1.46	3.38
H. pileatus	1	34.83				1	24.18			
H. syndact.	2	21.35	1.27	20.08	22.63	3	25.93	2.96	22.21	31.78
Pan trogl.	1	18.59				1	90.3			
Pongo pyg.	3	9.36	1.48	7.37	12.26	2	14.49	9.73	4.76	24.21
Androstenedione										
H. lar	1	1.59				1	1.78			
H. leucog.	5	1.50	1.10	0	5.82	4	1.91	0.77	0.55	3.48
H. pileatus	1	207.17				1	0			
H. syndact.	2	161.38	93.80	67.58	255.18	3	177.62	95.59	0	327.68
Pan trogl.	1	10.05				1	15.81			
Pongo pyg.	3	17.83	9.67	0	33.25	2	7.68	3.98	3.7	11.65
Testosterone										
H. lar	1	0.57				1	0.37			
H. leucog.	5	0.39	0.19	0	0.97	4	0.78	0.33	0	1.50
H. pileatus	1	8.04				1	1.78			
H. syndact.	2	12.73	2.24	10.48	14.97	3	14.80	7.70	2.67	29.07
Pan trogl.	1	3.36				1	7.00			
Pongo pyg.	3	2.44	1.07	0.47	4.17	2	1.55	0.30	1.25	1.84

[1] Abbreviations: N = number of individuals; SE = standard error.

Table 4.4.2: Species means of hormone concentrations in the axillary samples (ng/sample) of adult and subadult animals [1].

Species	Males					Females				
	N	Mean	SE	Min.	Max.	N	Mean	SE	Min.	Max.
DHEA										
H. lar	1	2.72				1	3.11			
H. leucog.	3	1.1	0.49	0.12	1.60	4	2.46	0.20	2.00	2.84
H. pileatus	1	29.21				1	24.63			
H. syndact.	2	7.55	0.47	7.08	8.02	3	14.15	7.06	6.17	28.23
Pan trogl.	1	28.52				1	130.48			
Pongo pyg.	3	19.44	1.87	16.25	22.71	2	22.28	17.72	4.56	39.99
Androstenedione										
H. lar	1	1.49				1	2.18			
H. leucog.	3	0.50	0.27	0	0.94	4	2.28	0.80	0.40	4.13
H. pileatus	1	0				1	0			
H. syndact.	2	12.52	2.36	10.16	14.88	3	7.73	3.87	0	11.79
Pan trogl.	1	85.35				1	116.28			
Pongo pyg.	3	51.43	34.38	0	116.68	2	6.58	3.37	3.21	9.95
Testosterone										
H. lar	1	1.32				1	0.44			
H. leucog.	3	0.20	0.11	0	0.36	4	1.12	0.31	0.70	2.04
H. pileatus	1	0.42				1	0			
H. syndact.	2	1.43	0.73	0.69	2.16	3	1.21	0.70	0.38	2.61
Pan trogl.	1	7.64				1	44.00			
Pongo pyg.	3	5.47	2.37	0.81	8.54	2	1.71	0.53	1.18	2.24

[1] Abbreviations: N = number of individuals; SE = standard error.

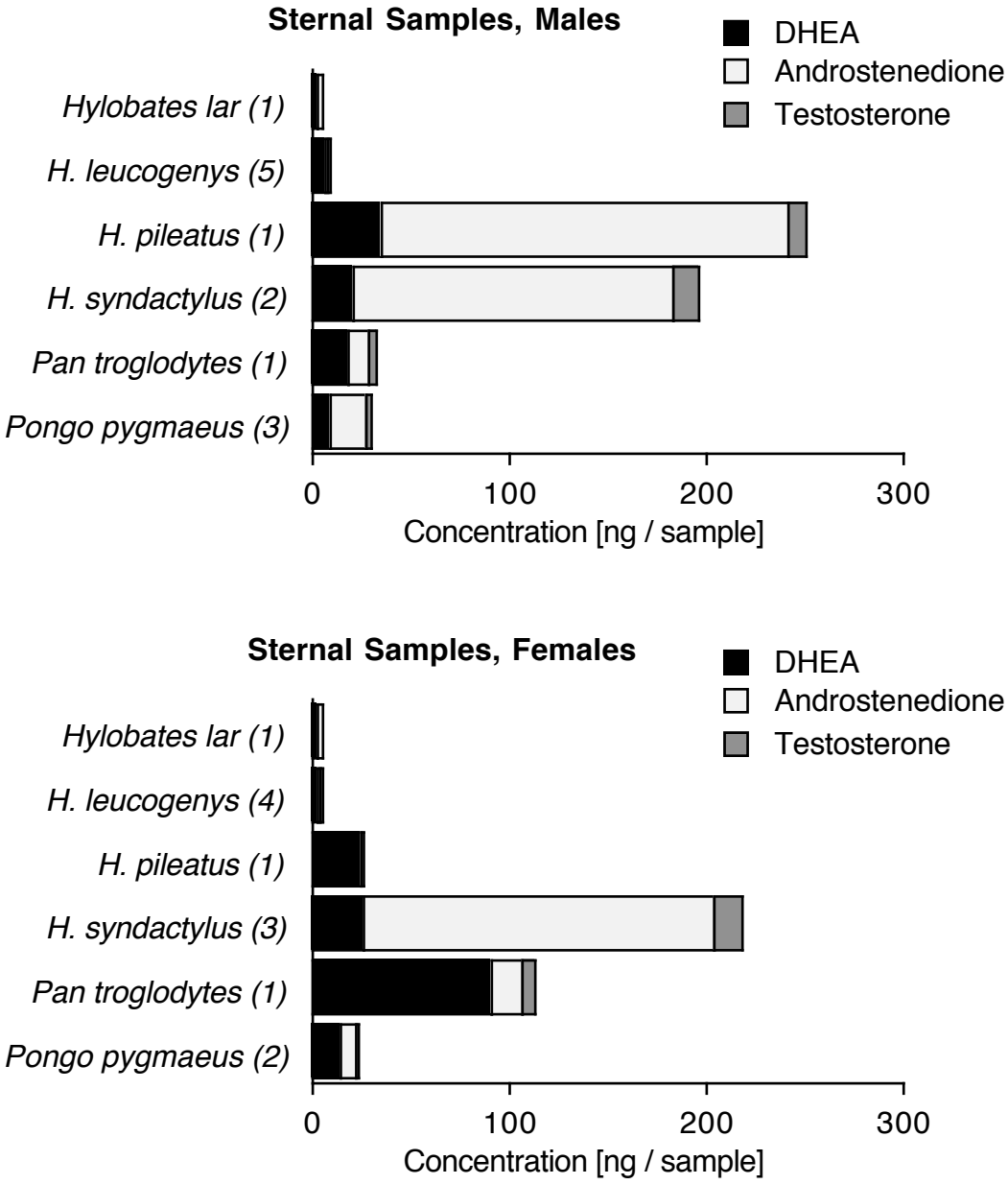


Figure 4.4.2: Stacked bar graphs showing the proportions of the three steroid hormones (average values) in the samples collected from the sternal region. (The number of individuals studied for each species is shown in brackets.)

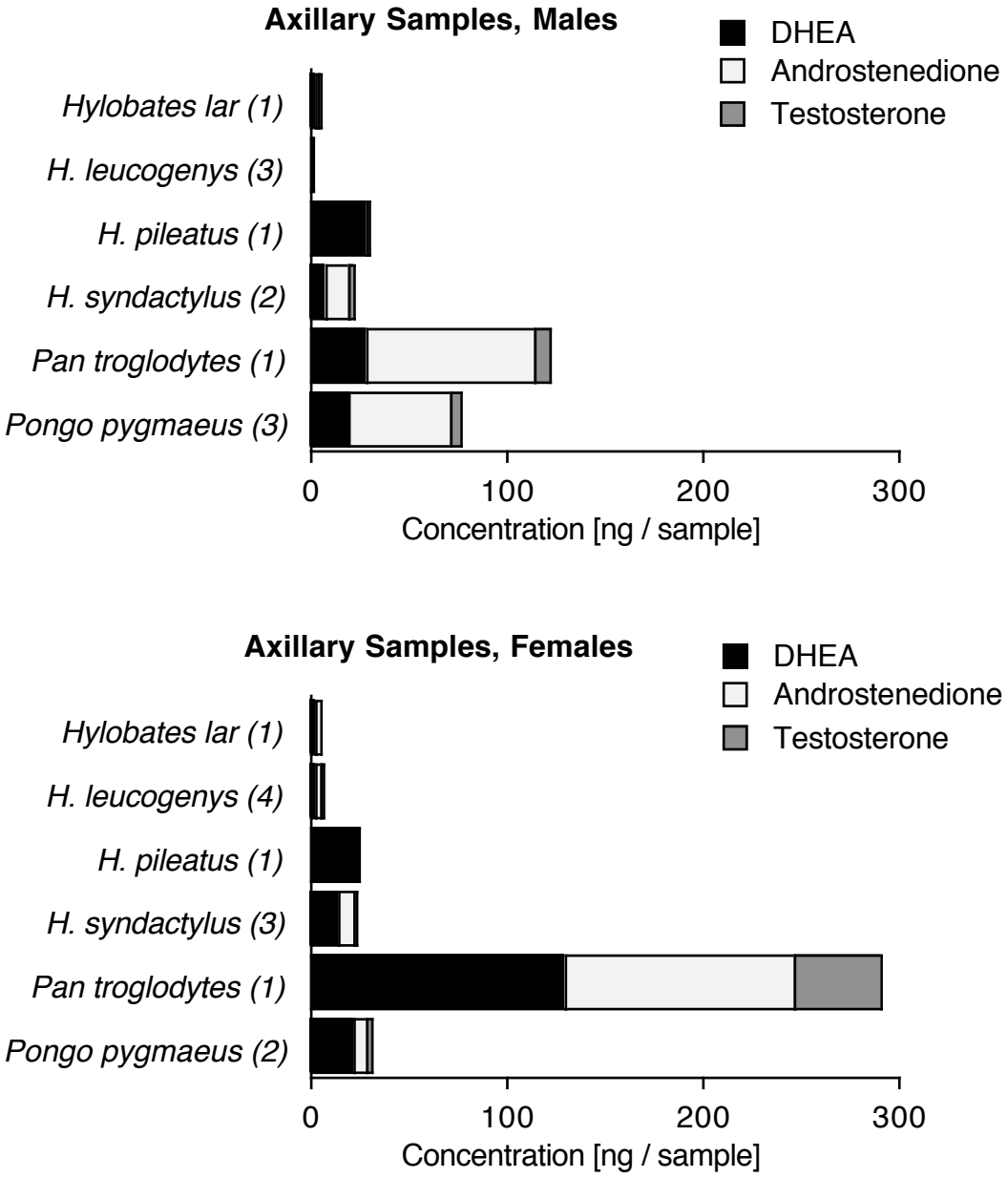


Figure 4.4.3: Stacked bar graphs showing the proportions of the three steroid hormones (average values) in the samples collected from the axillary region. (The number of individuals studied for each species is shown in brackets.)

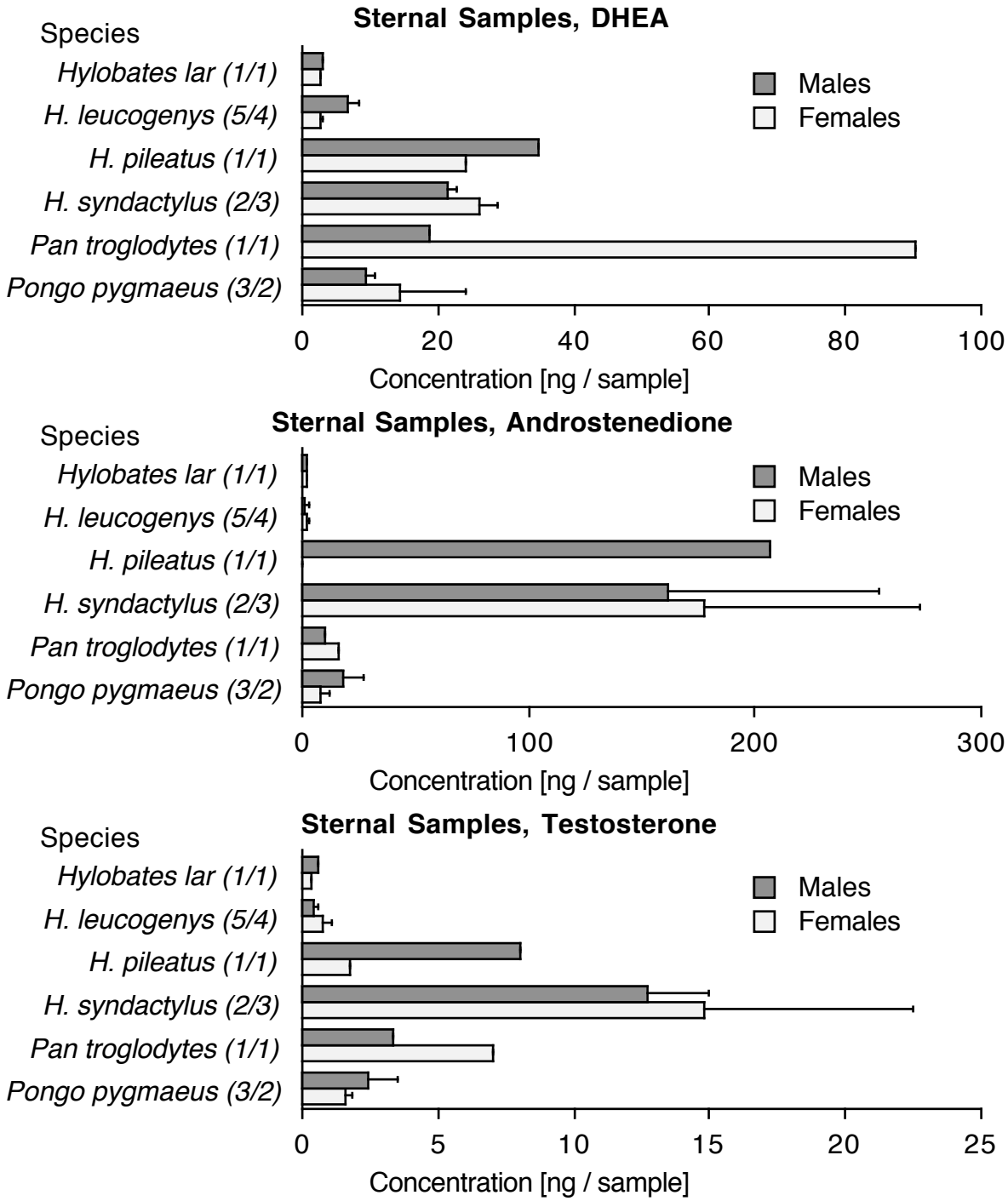


Figure 4.4.4: Comparison between the hormone concentrations of males and females of different ape species in samples collected from the sternal region. The numbers of individuals studied for each species are shown in brackets: (males / females). Note different scale for each graph. Error bars represent standard error.

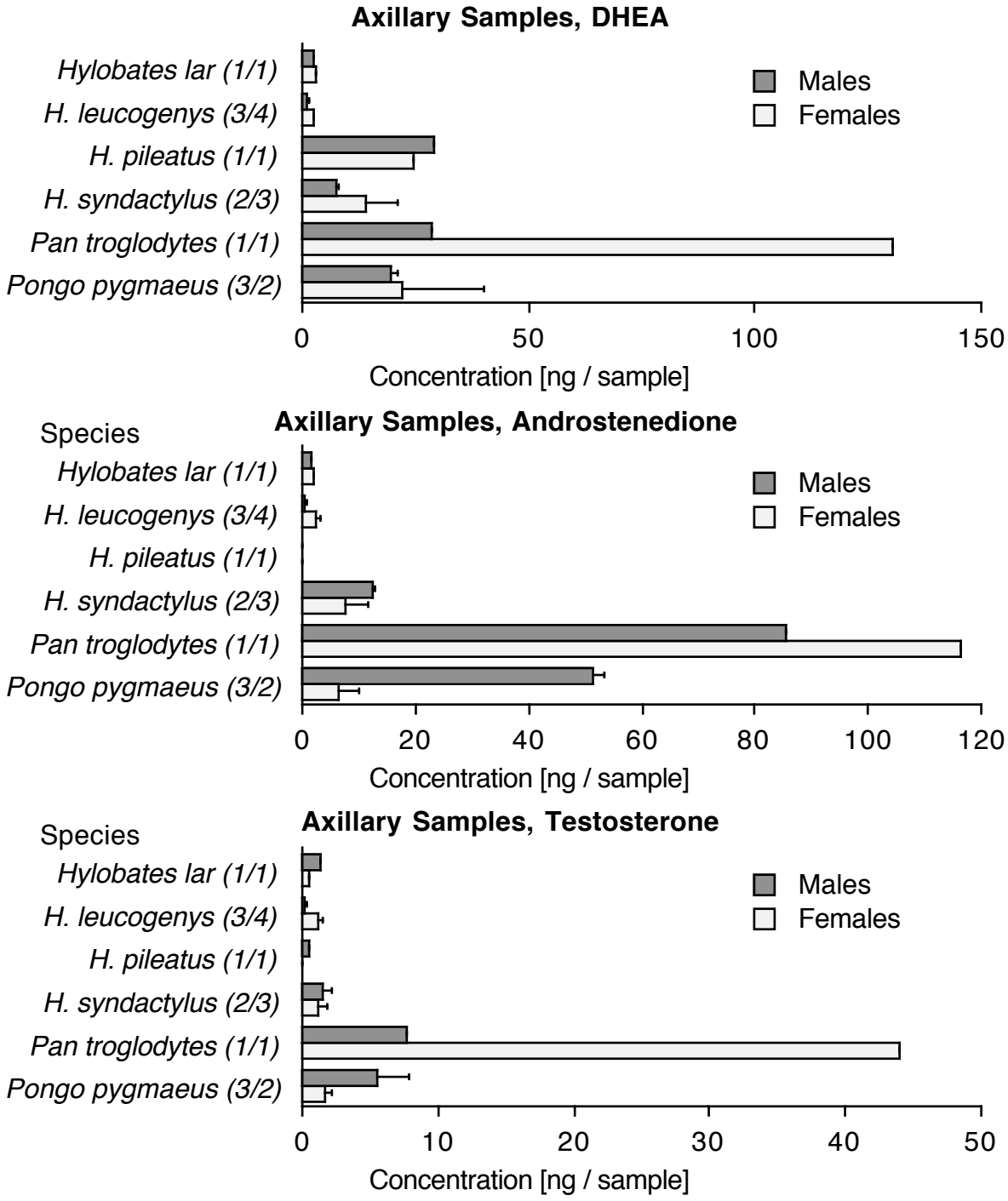


Figure 4.4.5: Comparison between the hormone concentrations of males and females of different ape species in samples collected from the axillary region. The numbers of individuals studied for each species are shown in brackets: (males / females). Note different scale for each graph. Error bars represent standard error.

Figures 4.4.4 and 4.4.5 permit a visual comparison between male and female hormone concentrations. Although the samples are too small to permit a statistical test for sex differences, the figures at least suggest such differences in several cases: In *Pongo pygmaeus*, axillary androstenedione and testosterone appear to be higher in males than in females; in *H. leucogenys*, sternal DHEA may be higher in males, whereas axillary androstenedione may be higher in females. Finally, in *H. syndactylus*, both sternal and axillary DHEA appear to be higher in females.

Table 4.4.3: Comparison of hormone concentrations between three species (sexes pooled) with the Mann-Whitney U-test.

Skin area	Steroid Hormone	*Pongo pygm.* vs. *H. leucogenys*	*Pongo pygm.* vs. *H. syndactylus*	*H. leucogenys* vs. *H. syndactylus*
Sternal	n	5 vs. 9	5 vs. 5	9 vs. 5
	DHEA	n.s.	n.s.	* *
	Androstenedione	n.s.	n.s.	n.s.
	Testosterone	*	*	* *
Axillary	n	5 vs. 7	5 vs. 5	7 vs. 5
	DHEA	* *	n.s.	* *
	Androstenedione	n.s.	n.s.	n.s.
	Testosterone	*	n.s.	n.s.

* = $p<0.05$; ** = $p<0.005$; n.s. = not significant; n = number of individuals.

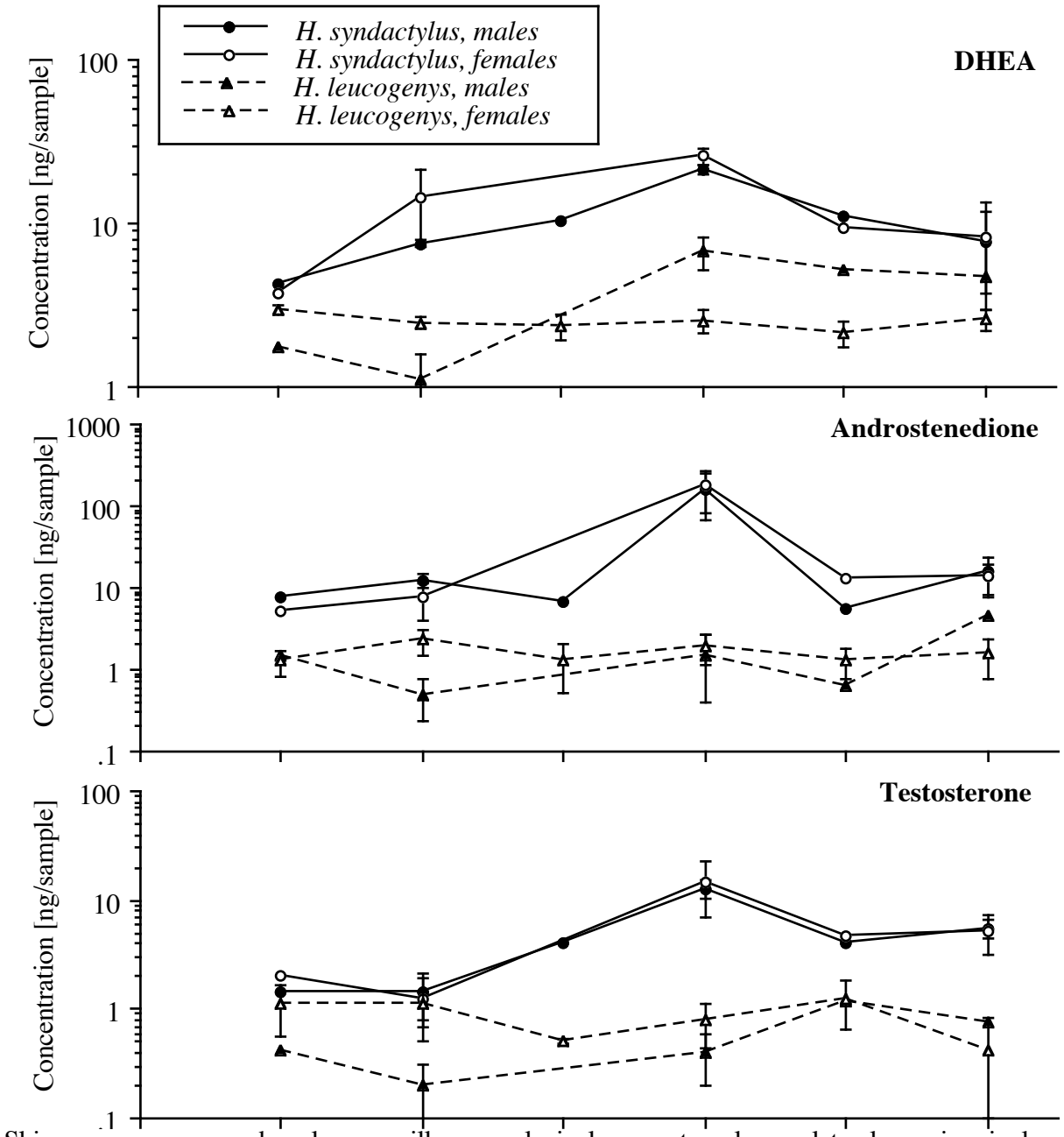
If the samples for males and females are pooled, a statistical comparison between three of the larger species samples (*H. leucogenys*, *H. syndactylus*, and *Pongo*) becomes possible. Table 4.4.3 lists the results of each pairwise comparison with the Mann-Whitney U-test. For the sternal samples, testosterone differs significantly between all three species, whereas only *H. leucogenys* and *H. syndactylus* differ in DHEA concentrations. Three significant differences are also found in the axillary samples: DHEA concentrations differ both between *Pongo* and *H. leucogenys*, and between *H. leucogenys* and *H. syndactylus*, respectively. In addition,

testosterone concentrations differ between *Pongo* and *H. leucogenys*. It is noteworthy that all significant differences follow a consistent trend: Hormone concentrations are highest in *H. syndactylus*, and lowest in *H. leucogenys*, with *Pongo* occupying an intermediate position. In addition to fully adult animals, these statistical comparisons include two subadult males: one *H. leucogenys gabriellae x H. l. siki* ("Charlot 2"), and one *H. syndactylus* ("Floh"). It should be noted, however, that all comparisons remain statistically significant even if the two subadults are removed from the analysis.

The findings on skin secretions presented in the previous paragraphs refer only to secretions collected in the sternal and the axillary areas. In several individuals of *H. leucogenys* and *H. syndactylus*, a few secretion samples were also collected in other areas of the skin.

In order to increase the sample size for each area, samples collected in the clavicular area and the lateral neck were pooled. Likewise, the samples from the inguinal area include one sample collected in the circumgenital area. Thus, the following skin areas were examined: 1) dorsal area (in the mid-saggittal plane, between the shoulder blades), 2) axilla, 3) clavicular area (and lateral neck), 4) sternal area, 5) lateral abdomen (ventral area), and 6) inguinal area. Figure 4.4.6 shows the average hormone concentrations in all 6 skin areas, with species and sex plotted separately. The sample size for each skin area is also provided at the bottom of the figure. Only adult and two subadult animals are included.

All average hormone concentrations for *H. leucogenys* are lower than those for *H. syndactylus*, independent of sex. The difference between the species is statistically significant (sign test, $N = 6$, $x = 0$, $p = 0.031$) In *H. syndactylus*, by far the highest concentrations are found in the sternal area (this finding is somewhat obscured by the logarithmic scale). In *H. leucogenys*, a similar sternal peak is apparently present in male DHEA concentrations, but no clear sternal peak can be seen in the other hormone levels.



n (males/females):						
H. syndactylus	1/1	2/3	1/0	2/3	1/1	2/2
H. leucogenys	1/3	3/4	0/2	5/4	1/4	1/3

Figure 4.4.6: Average concentrations of three steroid hormones in six skin areas of male and female *H. leucogenys* and *H. syndactylus*. Error bars are standard errors.

Of particular importance for the interpretation are the hormone concentrations determined for the sample of pure sternal secretion (sample No. 9) of the adult male siamang "Bohorok". This male had been hand-reared at the Zürich Zoo. In this male, a sudden charge of sternal exudate was observed during an incident which has been described in detail above (section 4.2.2).

It was possible to collect one to three droplets of pure exudate through the wire-mesh directly from the tame animal's fur with a piece of fresh paper nappy. The number of caught droplets is more likely to be one than three, because only one spot could afterwards be seen on the tissue. The hormone concentrations determined from this sample are shown in Table 4.4.4 (line 1). Although the exact amount of secretion is not known, the quantity of one to three droplets was determined to correspond to $2 \cdot 10^{-4} - 9 \cdot 10^{-4}$ dl. This range is a maximum estimate obtained by repeatedly measuring drops of water that were large enough to fall down from a syringe opening of 1 mm in width. The collected exudate droplets of the male siamang were, if anything, smaller than that. With the above estimate of exudate quantity, the hormone concentrations in the exudate can be calculated (Table 4.4.4, line 2). These are conservative values, because the quantity of exudate may be smaller (but certainly not larger) than assumed here.

For comparison, three samples of siamang blood plasma were collected. One of the samples stems from the same male as the pure sternal secretion. The hormone concentrations in the plasma samples show some variation (Table 4.4.4, line 3), but even the highest concentrations in the plasma samples are several times lower than the most conservative concentration estimate of the sternal sample. The difference amounts to a factor of at least 2.4 for testosterone, but up to 250.5 for androstenedione (Table 4.4.4, line 4).

On the other hand, the hormone concentrations in the siamang plasma samples are roughly similar to those of humans (adapted from Labhart et al., 1986, p. 523), except for the relatively high concentrations of androstenedione in the siamangs (Table 4.4.4, line 5).

Table 4.4.4: Determination of hormone concentration in the sternal secretion in an adult male siamang ("Bohorok").

			DHEA	Androstene-dione	Testosterone
1.	Concentration in secretion sample (ng / sample), ad. siamang male "Bohorok"		5.22	143.18	2.15
2.	Concentration in secretion sample (ng / dl), estimate, ad. siamang male "Bohorok"	Maximum	26 100	715 900	10 750
		Minimum	5 800	159 089	2 389
3.	Concentration in peripheral plasma (ng / dl):				
	ad. siamang female "Gaspa"	22.1.1987	280	238	82
	ad. siamang female "Gaspa"	30.8.1989	481	288	144
	ad. siamang male "Bohorok"	30.8.1989	694	635	992
4.	Accumulation factor, ad. siamang male "Bohorok"	Minimum	8.4	250.5	2.4
5.	Concentration in peripheral plasma (ng / dl), (Labhart et al., 1986, p. 523)				
	Men (20-40 years)		130-1270	60-230	300-1300
	Women (20-40 years)		140-1250	50-330	4-70

Pure exudate was also collected from an adult female *H. leucogenys* ("Püppi", Sample No. 59). This exudate was produced by the animal under a state of extreme stress and exhaustion. The incident has been described above (see Section 4.2.2). Reddish sweat was produced profusely all over the animal's body. This fresh secretion did not contain any measurable amount of steroid hormones, in contrast to the fresh sternal secretion of the male siamang. This result further supports the significant differences in hormone concentrations found in various skin areas of *H. leucogenys* and *H. syndactylus* (see above).

5. Visual Communication

5.1 Description of Visual Characteristics

In the present section, the visual characteristics of each gibbon species are briefly described. A list of all characteristics available for cladistic analysis, including specifications of the character states for each species, is provided in Appendix 10.6. Some previous publications have provided detailed descriptions of gibbon species and subspecies (Groves, 1972; Marshall & Sugardjito, 1986), drawings of facial markings and photographs of all species (Chivers, 1977; Chivers & Gittins, 1978), and colour plates of their fur characteristics (Chivers, 1984; Marshall & Marshall, 1976; Marshall & Sugardjito, 1986).

H. agilis: Coat colouration polymorphic, light buff, yellow, brown or blackish brown. Light individuals sometimes with contrasting darker brown ventral fur, sometimes extending on to inner side of limbs, and occasionally with dark cap. Blackish-brown individuals sometimes with brown lower back, occasionally with brown corona and brown distal limbs. Facial markings: White brow band in males and females, white or pale brown cheek patches (often joined under chin) occur mainly in males. White face ring in young animals. Facial markings do not contrast in very pale specimens. White brow band may be separate in females, and lacking in old females. Hands and feet: Usually not contrasting with distal limb colouration (except in *H. a. albibarbis*, see below). Genital area: Prominent genital tuft in males. In brown animals often of contrastingly buff or light grey colouration, but not in blackish-brown males. Tuft does not contrast in light specimens. In females, hair in genital region has same colour as the ventral fur.

H. agilis albibarbis: Dorsal side greyish brown, contrasting with blackish brown or black ventral fur and inner side of limbs. Transition between both colours on lateral rump, often golden brown there. Contrasting dark brown cap and buff or light grey corona and buff or light grey distal limbs. Facial markings: White brow band in males and females, white or cream cheek

patches (often joined under chin) occur in males and in about 50% of the females, according to Marshall and Sugardjito (1986). White face ring in young animals. Hands and feet: Fur on digits black, contrastingly coloured. Genital area: Prominent genital tuft in males of contrastingly buff or light grey colouration. In females, hair in genital region has same colour as the ventral fur.

H. lar: Coat colouration polymorphic, light buff, yellow, brown, blackish brown or black. Light individuals in Sumatra sometimes with contrasting brown ventral fur, inner side of limbs and cap. Black individuals absent in Sumatra (*H. l. vestitus*). Facial markings: White face ring in males and females. White face ring often much broader in young animals. Facial markings do not strongly contrast in very pale specimens. Hands and feet: White, contrasting with distal limb colouration (except in very pale specimens). Genital area: No prominent genital tuft in males. In light individuals, especially in males, hair in genital region often coloured contrastingly, darker brown or blackish.

H. moloch: Coat colouration silver grey, rarely light grey brown. Sometimes with contrastingly coloured dark grey or black chest and cap. These dark patches may occur more frequently in females than males, and are usually absent in young animals. Facial markings: White brow band in males and females, and white, forward projecting goatee beard, both sharply demarcated. Hands and feet: Not contrasting with distal limb colouration. Genital area: No prominent genital tuft in males. Hair in genital region usually contrastingly black, occasionally grey.

H. muelleri: Coat colouration mouse grey (*H. m. abbotti*), grey brown or brown (rarely blackish brown). Usually with contrastingly coloured dark brown or black chest, ventral fur, inner side of limbs, and cap. These dark areas are usually absent or much reduced in *H. m. abbotti*. Facial markings: White brow band in males and females, sometimes with light grey or whitish cheeks or chin, but usually not sharply demarcated. Young animals often with broad whitish or grey face ring. Hands and feet: Not contrasting with distal limb colouration in *H. m. abbotti* and most *H. m. funereus*. Feet paler than legs (but not white) in 24% of *H. m. funereus*

(Marshall & Sugardjito, 1986). Contrasting dark digits or whole hands and feet in *H. m. muelleri*. Genital area: No prominent genital tuft in males. Hair in genital region black.

H. pileatus: Coat colouration sexually dimorphic. Males black, with white or light grey corona, sometimes interrupted in occipital region. Lower back sometimes more or less intermingled with grey hairs (see syntype B.M. 60.4.20.1 for an extreme example). Females light buff grey, with contrasting black ventral fur (shaped like an inverted triangle), black cap, sides of head and throat, all black areas are sharply demarcated. Whitish corona in females does not contrast with the pale back. Juvenile animals similar to female, but sides of head and throat are pale. Facial markings: Contrasting thin white rim completely surrounds facial area in males. Rim thickest above eyes and lateral to eyes, where connected to corona. In females only a thin white brow band, optional, apparently rare in old females. Young animals often with broad whitish face ring. Hands and feet: White, contrasting with distal limb colouration in males, but not contrasting in females and young animals. White colouration usually less extended than in *H. lar*. Genital area: Prominent genital tuft of contrasting white colouration in males. In females, hair in genital region buff grey, not contrastingly coloured. Natal coat: Light buff grey, with no facial or other markings.

H. klossii: Coat colouration black. No facial or other markings.

H. hoolock: Coat colouration sexually dimorphic. Males black, sometimes blackish brown on back (*H. h. leuconedys*). Females pale brown, with darker brown ventral fur (not sharply demarcated), darker brown throat and sides of the head, and with cream cap, contrasting with sides of the head. Juvenile animals similar to male. Facial markings: Contrasting white brow band in males and females. In females, a contrasting thin white rim completely surrounds not only the facial area but also each eye. White goatee beard on the chin in some males and young animals (*H. h. leuconedys*). Hands and feet: Not contrasting with distal limb colouration in males and most females, but some lightening on hands and feet may occur in females of *H. h. leuconedys* (Groves, 1972). Genital area: Prominent genital tassel in males. Tassel of contrastingly lighter yellow, grey or white colouration in adult males of *H. h. leuconedys*, but

black in *H. h. hoolock*. In females, hair in genital region brownish, not contrastingly coloured. Natal coat: Pale brown, like adult females.

H. concolor: Coat colouration sexually dimorphic. Males black, with small crest of erect hairs on top of the head. Females yellow to pale grey brown, with dark brown or blackish ventral fur (often sharply demarcated and often interspersed with lighter hairs), throat sometimes dark. (No darkening on ventral fur in females of *H. c. hainanus*.) Females with no crest, but with black cap. Distinct small black tuft on ears. Juvenile animals similar to male. Facial markings: No markings in males. In females, a contrasting black patch on chin (absent in *H. c. hainanus*), and sometimes, a contrasting white patch below eyes. Light brow band rare, but below eyebrows, a distinct rim of black hairs commonly occurs (absent in *H. c. hainanus*). Hands and feet: Not contrasting with distal limb colouration in males, but contrasting black distal digits in females (optional in *H. c. hainanus*). Genital area: No prominent genital tuft in males. Hair in genital region usually contrastingly black in females (absent in *H. c. hainanus*). Natal coat: Light yellow or buff grey, like adult female, with no facial or other markings.

H. leucogenys: Coat colouration sexually dimorphic. Males black, with relatively big crest of erect hairs on top of the head (small in *H. l. siki*). Females pale yellow to golden yellow, without dark hairs on ventral fur. Females with no crest, but with black cap. Small black tuft on ears often indistinct. Juvenile animals similar to male. Facial markings: Contrasting white cheek patches in males. In females, contrasting white brow band, and frequently, a thin white rim completely surrounding the facial area. Rim extends to contrasting white patch below eyes. Hands and feet: Not contrasting with distal limb colouration, females frequently without black distal digits. Genital area: No prominent genital tuft in males. Hair in genital region usually contrastingly darker brown or rusty in females. Natal coat: Light yellow or golden yellow, like adult female, with no facial or other markings.

H. l. gabriellae: Coat colouration sexually dimorphic. Males black, with small crest of erect hairs on top of the head and orange-brown lightening on chest. Females yellow to orange-yellow, without dark hairs on ventral fur. Females with no crest, but with black cap. Distinct

small black tuft on ears. Juvenile animals similar to male. Facial markings: Contrasting creamy orange, light yellow or whitish cheek patches in males. In females a contrasting white patch below eyes sometimes occurs. Light brow band rare, but below eyebrows a distinct rim of black hairs commonly occurs. Hands and feet: Not contrasting with distal limb colouration in males, but contrasting black distal digits in females. Genital area: No prominent genital tuft in males. Hair in genital region usually contrastingly black in females. Natal coat: Light yellow or golden yellow, like adult female, with no facial or other markings.

H. syndactylus: Coat colouration black. No facial or other markings, but some exceptions are described below. Genital area: Prominent genital tassel in males.

5.2 Circumfacial Markings in Siamangs

5.2.1 Introduction

One of the most conspicuous and well-known characteristics of gibbon fur colouration is the white or at least bright circumfacial pattern. In some species, this pattern consists of a closed band bordering the whole contour of the dark and almost naked facial area. It is then usually called a face ring (Figure 5.2.1a). In other species, the circumfacial pattern may be reduced to a brow band (Figure 5.2.1b), and in yet other species the pattern may be reduced to the cheek region (Figure 5.2.1c). In the black crested gibbon (*Hylobates concolor*), the circumfacial pattern is absent in adult males, but traces of it sometimes occur in adult females. In two species, the facial pattern is completely absent in both sexes: in the Kloss gibbon (*H. klossii*) and in the siamang (*H. syndactylus*) (Figure 5.2.1d).

Groves (Groves, 1972) mentioned having seen a captive siamang with a face ring, and other siamangs with traces of face rings. Unfortunately, he did not document this in more detail, and it is difficult to decide how far his observations can be compared with the facial markings of other gibbons. In contrast to Groves, Haimoff *et al.* (1982, p. 222) stated:

> "Male siamang and Kloss gibbons have no face markings, and although Groves [1972] mentions some siamang specimens with a very faint face ring, this phenomenon is rare and equated with old age [Chivers, personal observation; Haimoff, personal observation]. … The females are generally the same…"

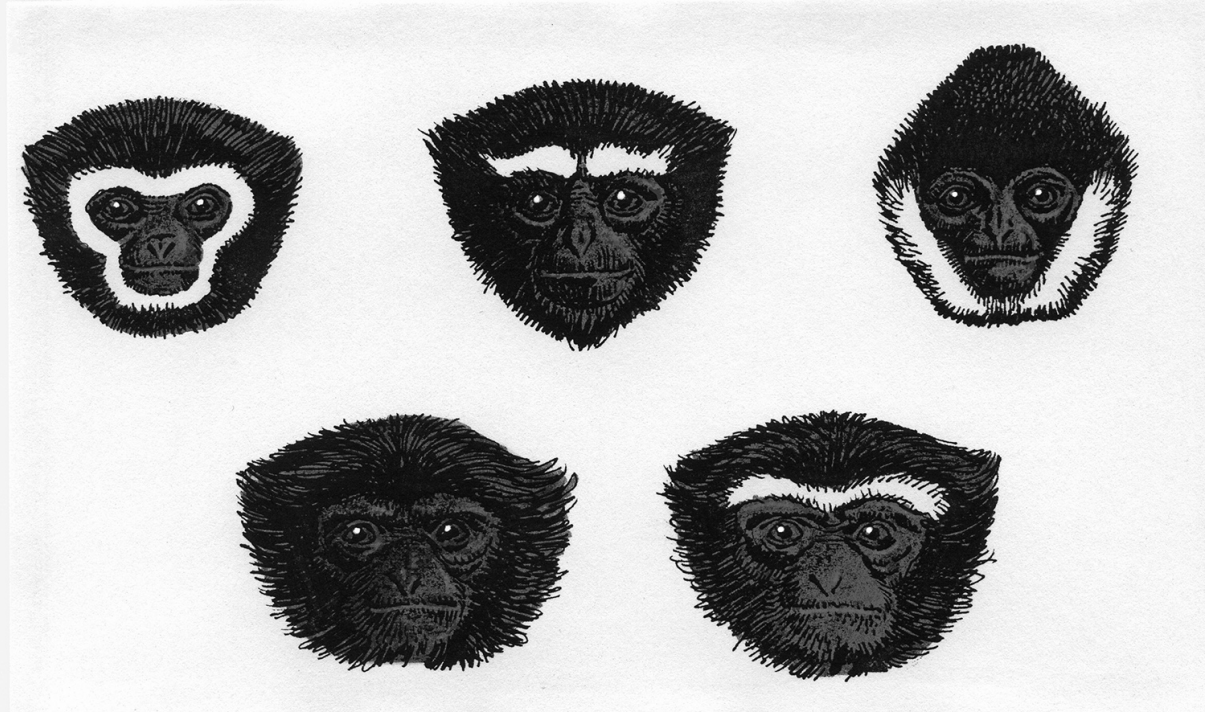


Figure 5.2.1: Drawings of various circumfacial patterns in gibbons: a) *Hylobates lar*; b) *H. hoolock hoolock*, male; c) *H. leucogenys leucogenys*, male; d) *H. syndactylus*; e) *H. syndactylus*, female with brow band.

In the dark face of the siamang, some short white hairs are usually present, especially in the lower half of the face. These hairs may become gradually more dense toward the periphery of the face. I have observed this facial hair in about 50 captive siamangs of various ages. It can also occur in other gibbons. It is unclear whether these white facial hairs are in any way related to the face ring pattern of other gibbon species. It is possible that one or both of the two studies mentioned above were actually referring to such facial hair when discussing the occurrence of face ring markings in the siamang.

In this section, the occurrence of a white brow band in a captive population of siamangs is reported for the first time. Based on the following description and photographic documentation, it can be shown that this brow band differs from the "faint face ring" observed by Chivers and by Haimoff in siamangs of old age (Haimoff et al., 1982). In addition, the brow band can be demonstrated to be probably related to the face ring pattern of other gibbon species.

5.2.2 Study Animals

The animals with the white brow bands were discovered in a siamang family of the Duisburg Zoo in West Germany. This family is maintained at the zoo in the fourth generation. A pedigree of the siamang colony at the Duisburg Zoo could be reconstructed with the help of members of the zoo staff (Figure 5.2.2).

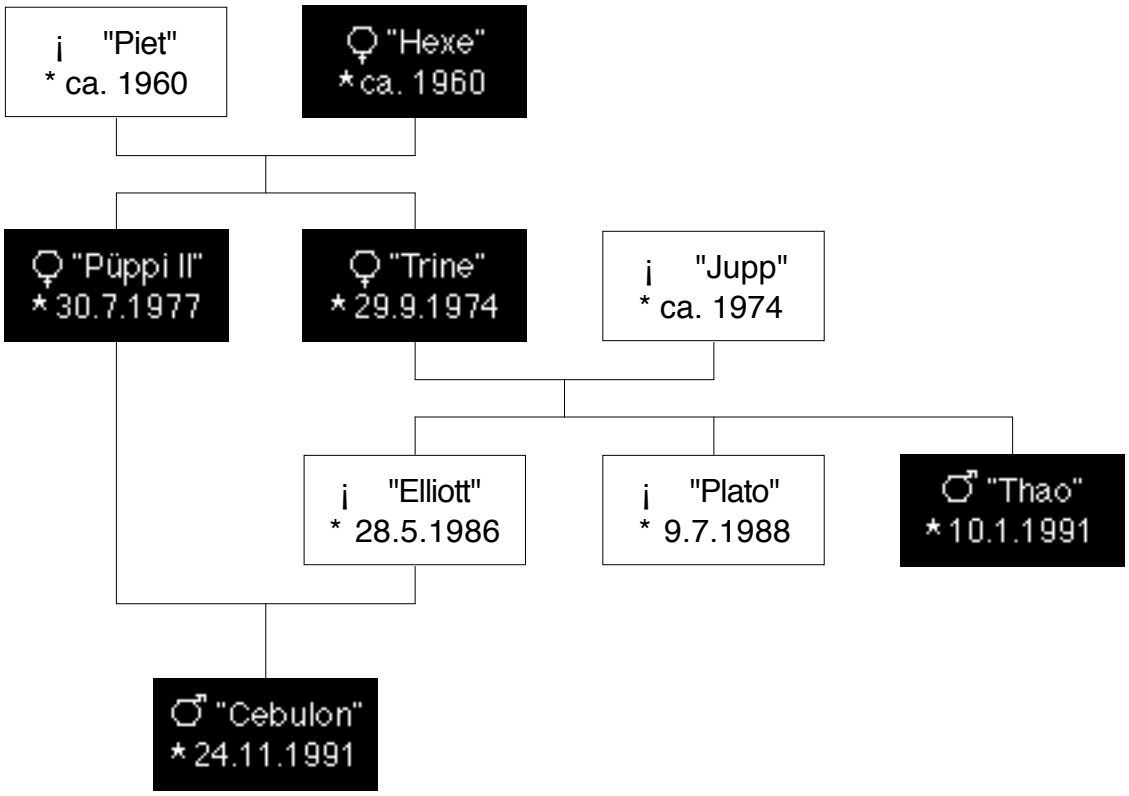


Figure 5.2.2: Family tree and birth dates of the siamangs at the Duisburg Zoo. Black rectangles indicate individuals with the brow band characteristic.

When first visited, the group consisted of seven siamangs living in two groups. Three of the siamangs were assumed to be wild-born: Two of these (the male "Piet" and the female "Hexe") arrived at the zoo before the beginning of record-keeping in 1967. According to a caretaker at the zoo, these two animals were already present in 1964 and were at least subadult at

that time (Mrs. E. Schramke, personal communication). The pair was kept on an island, and had their first offspring on 29. Sept. 1974, the female "Trine". A second female offspring "Püppi II" was born on 30. July 1977. While the second daughter was mother-raised and thereafter remained with her parents, the first-born daughter was hand-reared and later paired with an unrelated male, "Jupp". This supposedly wild-born siamang had arrived from an animal dealer on 13. May 1975 as a juvenile. The younger pair ("Jupp" & "Trine") had five offspring, so far, three of which survived. All three were males and were hand-raised.

The second daughter was not peripheralised by her parents, possibly because none of their subsequent offspring survived for more than one and a half year. The last offspring of the pair was stillborn on 17. July 1985. During the present author's observations in 1987 an 1988, the old female of the trio was apparently increasingly peripheralised by her adult daughter. Usually, the mother kept some distance to the other two siamangs. In 1988, she was frequently reluctant to enter the small indoor cage in the evening, possibly for fear of being bitten by her daughter (Mrs. Schramke, pers. comm.). In contrast, father and daughter pair were usually close together, and they sometimes embraced each other during the songs of the trio. The male "Piet" died on 10. May 1989, probably of old age. After introducing the two females with a young adult male ("Elliott", related to both females), the old female was increasingly attacked by her adult daughter and had finally to be removed from the group, while the remaining pair successfully started to breed.

Photographs and drawings of most of these siamangs were made during two visits at the Duisburg Zoo on 23-26 June 1987 and on 2-3 March 1988. Photographs and descriptions of animals born subsequently were kindly made available by Mr. M. Orgeldinger and Mr. J. Hammes.

5.2.3 Description of Animals

Five of the nine siamangs at Duisburg show the brow band characteristic (e.g. Figs. 5.2.3 and 5.2.4). The characteristic consists of a whitish band situated above the eyes, clearly outside but adjacent to the facial area. The brow band is slightly narrower in the middle part, but not separated, and it is thicker at the lateral ends. The brow band characteristic in the siamang is quite similar to the facial markings occurring in male hoolock gibbons or in female agile gibbons (compare Figs. 5.2.1b and 5.2.1e).

One individual showing the brow band characteristic ("Hexe") probably grew up at the Duisburg Zoo together with another siamang which does not show the characteristic ("Piet"). The hand-reared individuals comprise one animal with and two animals without the brow band characteristic. This makes it likely that the brow band characteristic in siamangs is controlled by genetic factors rather than by other factors such as environmental influences.

The pedigree revealed that all animals with the brow band are related to each other. Unfortunately, the mode of inheritance cannot be reliably determined from the small pedigree available at present. If the inheritance was recessive, all breeding females must be homozygous for the characteristic, because they all show the white brow band. Likewise all breeding males must be heterozygous, because they all produce offspring with the brow band characteristic. In view of the rarity of the characteristic, this seems to be relatively unlikely. Dominant inheritance appears to be more probable than the recessive form. Here, all breeding males must be homozygous non-carriers of the hypothetical brow band allele, because none of them shows the characteristic. The first breeding female ("Hexe") could either be homozygous or heterozygous for the characteristic (one allele is enough for phenotypic expression), but in any case her daughters are heterozygous, because they can only inherit one allele for the characteristic from their mother.

The three females at Duisburg are not the only brow-banded siamangs, however: Subsequent to this finding, the author systematically tried to find additional animals with this characteristic. About 50 animals in various zoos, about 60 furs in museum collections, and an undetermined number of published photographs were checked. As a result, four additional brow-banded siamangs were discovered:

- 1 adult female "Vreneli", wild-born about in 1963. Living in the "Seeteufel" Zoo in Studen (Switzerland) since about 1967.
- 1 adult female "Gaspa", wild-born about in 1963. Living since about 1967 in the "Seeteufel" Zoo in Studen (Switzerland), since 21 July 1980 in the Zoological Garden of Zürich (Switzerland), transferred to Thrigby Hall Zoo (Great Yarmouth, England) on 30 August 1989, died on 21 Sept. 1990.
- 1 adult female, skin and skull at the American Museum of Natural History, New York, AMNH 102723, collected by J.J. Menden on 2 June 1934 at "Moeara Doewa" (=Muara Dua), Palembang, Sumatra. Original field number 121. Skull of very old animal, teeth worn to basins.
- 1 female, skin at the Museum für Naturkunde der Humboldt-Universität, East Berlin, ZMB 38576, collected by W. Volz in Sumatra.

Several photographs of the two captive females were made during a study on siamang vocalisations in 1981 and 1982 (Geissmann, 1986). The pale brow band in these two females from Switzerland is less distinct than in the animals from Duisburg. Similarly, the specimen at the Museum für Naturkunde in Berlin has a relatively thin white brow band. In contrast, the specimen at the American Museum has a very distinct brow band, about 1.2 cm thick. In addition, a few short pale hairs also occur above the ears of this animal.

Figure 5.2.3: Adult female (left) and adult male siamang ("Piet", right) at the Duisburg Zoo (21. June 1987). Note the conspicuous white brow band in the female, and the absence of the characteristic in her father.

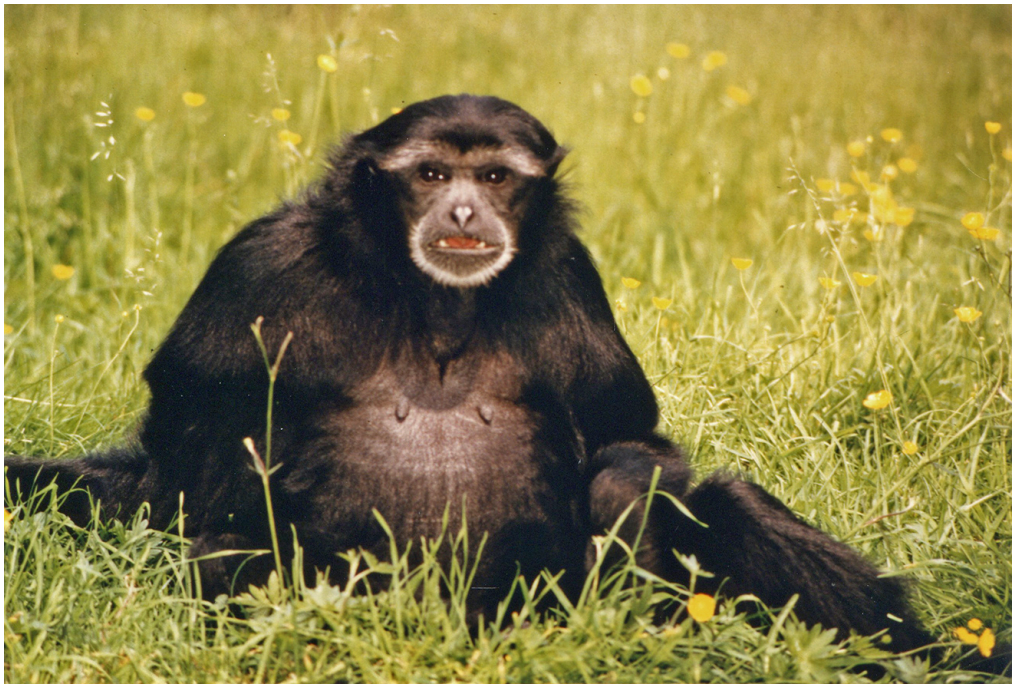


Figure 5.2.4: Adult female siamang "Hexe" at the Duisburg Zoo (21. June 1987). The distinct white brow band of this female is slightly broader at the lateral ends than the brow band of her daughter in Figure 5.2.3.

Only one additional male was found with white hairs outside the facial area: the adult male "Kajang", born about in 1964, living at Banham Zoo (England) before being transferred to Twycross Zoo (England) on 15 March 1971 (Badham, 1988; Badham & Richards, 1991). Photographs and drawings of the male were made by the author during a visit to Twycross Zoo on 2.-9. October 1988. This siamang had whitish hairs interspersed in the black fur on the forehead, on the ventral fur of the thighs, and on both sides laterally and distally on the belly. The whitish area on the animal's forehead was separated from the facial area by a stripe of black fur which was broadest (about 2 cm) in the midsaggittal plane. As the brow band area itself was black in this male, its unusual whitish colouration on the forehead and on other parts of the body may not be related to the brow band characteristic described for the Duisburg females.

The photographs presented above (Figs 5.2.3 and 5.2.4) appear to represent the first detailed documentation of facial patterns occurring in the siamang. These photographs show adult animals. However, it was possible to unearth some additional photographs in the archives of the Duisburg Zoo: Figure 5.2.5 shows one of the three females in Duisburg ("Trine") at the age of about 8 months. It unequivocally documents the presence of the brow band characteristic in the infant. This evidence clearly shows that the brow band characteristic is not a phenomenon restricted to old siamangs, as with the face pattern described by Haimoff and Chivers (Haimoff et al., 1982).

One of the males ("Thao") more recently born at Duisburg Zoo did not have a distinct brow band when about 6 months old, as documented by photographs kindly provided by Mr. M. Orgeldinger. The pattern did, however, start to develop when the animal was about 9 months old and has become very distinct since then (Mr. J. Hammes, pers. comm.). In another male ("Cebulon"), the pattern developed soon after birth and was much more pronounced than in the male mentioned above, and at least as distinct as in the female "Trine" (see Figure 5.2.5) (Mr. J. Hammes, pers. comm.).

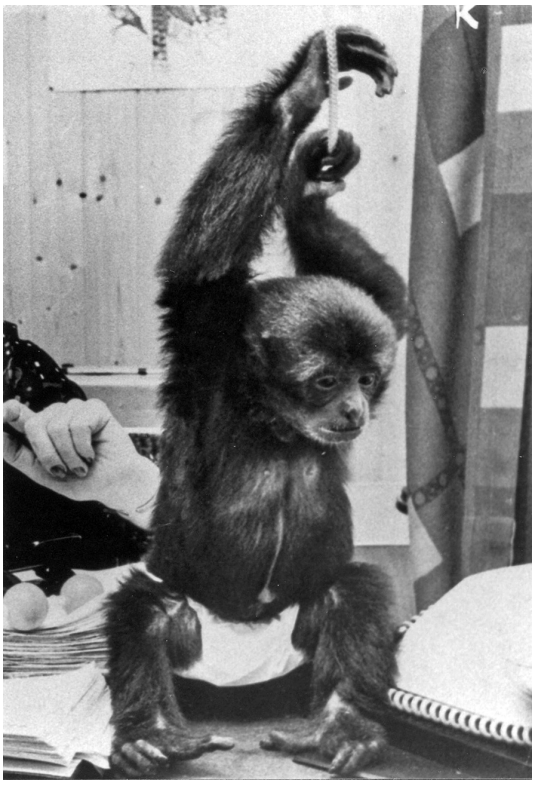


Figure 5.2.5: Siamang female "Trine" at the age of about 8 months (in May 1975) at the secretariat of the Duisburg Zoo (Photo Rolf Preuss). Notice the two separate patches of white fur laterally above the eyes. Only later did the patches become connected to form a continuous brow band.

In one of the Duisburg females, "Trine", white hair can be found on other parts of her body: This animal has a distinct tuft of long white hair above each ear (Figure 5.2.6). In addition, the big toes are covered with pure white fur (Figure 5.2.7) and the medial phalanges of hands and feet also carry white hair, but the latter parts are also intermixed with dark hair, especially on the hands. No hairs occur on the distal phalanges.

The photographs found in the archives of the Zoo contain evidence on the origin of the white tufts over the ears in the siamang female: Figure 5.2.8 clearly demonstrates that the same female, at the age of about 8 months, had a fully developed bright corona. Only when the animal became older was its crown reduced, but the tufts above the ears remained.

Figure 5.2.6: Tuft of white hairs above the ear of the adult female siamang "Trine" at the Duisburg Zoo (1. March 1988).

Figure 5.2.7: Right big toe of adult female siamang "Trine" at the Duisburg Zoo (1. March 1988). The toe is covered with pure white fur.

Figure 5.2.8: Siamang female "Trine" at the age of about 8 months at the Duisburg Zoo (Photo Dr. Hans Jesse). Note the broad white corona of the infant.

5.3 Body Weight

Table 5.3.1 lists mean values and standard deviations calculated from the individual body weights in Appendix 10.9. These body weights were collected from wild-shot museum specimens. The data set has also been evaluated for subspecies (and local populations for *H. lar*); these values are listed in Table 5.3.2. Figure 5.3.1 shows the degree of sexual dimorphism in body weight. In all species, males are slightly heavier than females, except in *H. klossii*. This exception may be due to the small sample size.

Table 5.3.1: Body weights in kg (mean and standard deviation) of gibbon species.

Species	Males					Females				
	Mean	SD	Count	Min.	Max.	Mean	SD	Count	Min.	Max.
H. agilis	5.88	0.74	19	4.42	7.37	5.82	0.67	10	4.54	6.80
H. lar	5.90	0.86	84	3.86	8.39	5.34	0.70	66	3.86	7.25
H. moloch	6.58	–	1	6.58	6.58	6.25	–	1	6.25	6.25
H. muelleri	5.71	0.66	20	4.65	6.80	5.35	0.69	19	4.11	6.58
H. pileatus	5.50	–	1	5.50	5.50	5.44	–	1	5.44	5.44
H. klossii	5.67	0.65	2	5.21	6.12	5.89	0.53	4	5.21	6.46
H. hoolock	6.87	0.83	13	5.30	8.50	6.88	0.83	5	6.01	8.00
H. concolor	7.77	1.69	7	5.50	10.00	7.62	1.27	13	5.75	10.00
H. leucogenys	7.41	1.24	8	5.70	10.00	7.32	0.57	4	6.50	7.80
H. syndactylus	11.88	1.81	7	9.50	15.12	10.71	1.50	10	8.40	12.70
Total	6.36	1.59	162	3.86	15.12	6.14	1.72	133	3.86	12.70

Table 5.3.2: Body weights in kg (mean and standard deviation) of gibbon subspecies and local populations.

	Males					Females				
	Mean	SD	Count	Min.	Max.	Mean	SD	Count	Min.	Max.
H. agilis										
agilis	6.44	0.29	2	6.24	6.65	4.54	–	1	4.54	4.54
albibarbis	5.71	0.61	5	4.88	6.50	6.30	0.35	5	5.90	6.80
unko	5.85	0.82	12	4.42	7.37	5.55	0.38	4	4.99	5.78
H. lar										
lar	5.37	0.39	3	5.00	5.78	4.90	0.55	3	4.31	5.40
carpenteri	5.80	0.68	46	4.08	7.37	5.31	0.55	37	3.86	6.80
entelloides (northern)	5.89	0.60	15	4.97	7.03	5.35	0.83	9	4.40	6.35
entelloides (central penins.)	6.83	0.98	14	4.99	8.39	5.67	1.00	12	4.31	7.25
vestitus	4.82	0.65	6	3.86	5.56	4.96	0.59	4	4.08	5.33
yunnanensis	–	–	0	–	–	5.00	–	1	5.00	5.00
H. moloch	6.58	–	1	6.58	6.58	6.25	–	1	6.25	6.25
H. muelleri										
muelleri	5.44	0.77	5	5.00	6.80	5.27	0.63	7	4.20	5.90
abbotti	6.01	0.70	6	4.65	6.46	5.82	0.24	3	5.56	6.01
funereus	5.65	0.57	9	4.99	6.40	5.24	0.80	9	4.11	6.58
H. pileatus	5.50	–	1	5.50	5.50	5.44	–	1	5.44	5.44
H. klossii	5.67	0.65	2	5.21	6.12	5.89	0.53	4	5.21	6.46
H. hoolock										
hoolock	7.32	0.62	3	6.69	7.94	6.35	–	1	6.35	6.35
leuconedys	6.96	0.96	7	5.30	8.50	7.74	0.36	2	7.48	8.00
H. concolor										
concolor	7.60	1.98	2	6.20	9.00	8.80	1.39	4	7.50	10.00
furvogaster	5.50	–	1	5.50	5.50	6.88	1.59	2	5.75	8.00
hainanus	8.25	2.47	2	6.51	10.00	6.62	1.24	2	5.75	7.50
cf. *hainanus*	8.50	–	1	8.50	8.50	7.00	–	1	7.00	7.00
jingdongensis	8.70	–	1	8.70	8.70	7.45	0.26	4	7.20	7.80
H. leucogenys										
leucogenys	7.27	0.44	6	6.80	8.00	7.65	0.21	2	7.50	7.80
siki	7.85	3.04	2	5.70	10.00	7.00	0.71	2	6.50	7.50
H. syndactylus										
syndactylus	11.88	1.81	7	9.50	15.12	10.71	1.50	10	8.40	12.70
Total	6.36	1.59	162	3.86	15.12	6.14	1.719	133	3.856	12.70

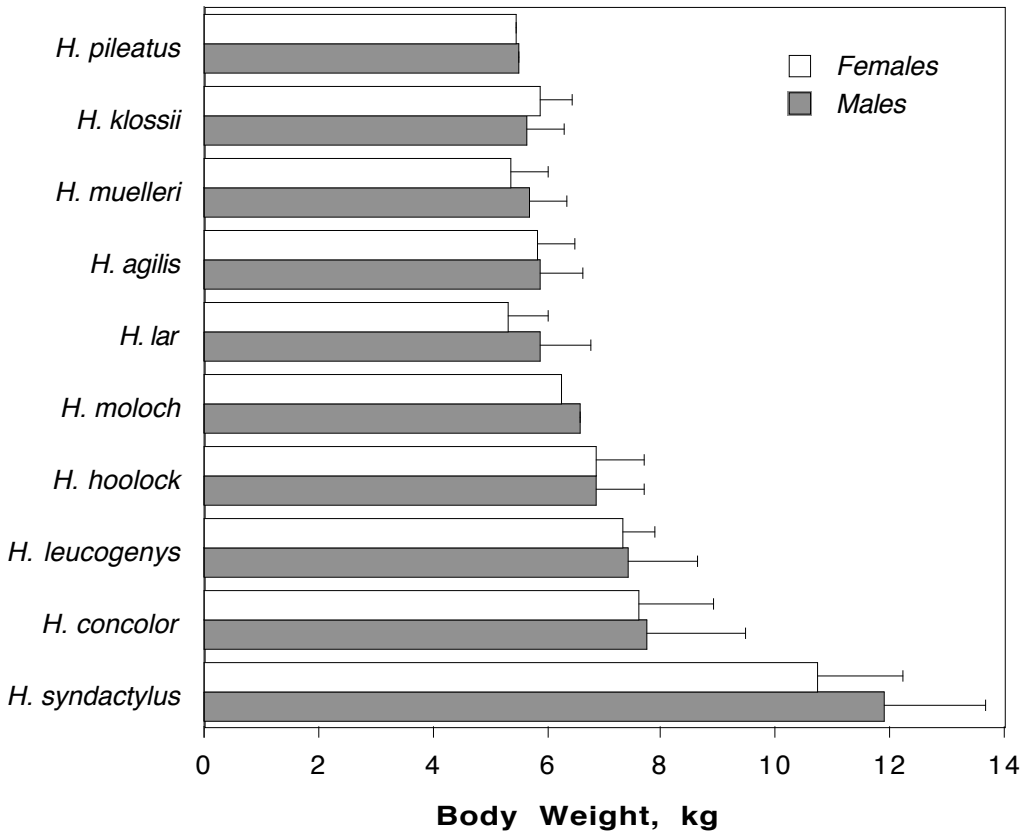


Figure 5.3.1: Sexual dimorphism in gibbon body weights. Species are arranged by male body weight. Error bars are standard deviations.

In order to search for correlates of various forms of gibbon sexual dimorphism, a multidimensional scaling (MDS) analysis was carried out. The variables and character states that were used are briefly described as follows:

A: Male body weight.

B: Female body weight.

C: Relative weight dimorphism: male body weight per female body weight (f/m).

D: Relative weight dimorphism: residuals of log male body weight plotted against log female body weight of a taxon. (This parameter of sexual dimorphism has been discussed in Martin et al., in press).

E: Sample size: number of individual body weights in a sample (see Tables 5.3.1 and 5.3.2).

F: Colour dimorphism. Absent, low, and strong sexual dichromatism were coded as 0, 1, and 2, respectively.

G: Song repertoire dimorphism. Absent, low, and strong sexual dichromatism were coded as 0, 1, and 2, respectively.

H: Occurrence of male solo songs: Mated male typically does not produce solo songs, does produce solo songs and duet songs, and typically produces solo songs only (coded as 0, 1, and 2, respectively).

I: Occurrence of female solo songs in mated females: absent and present (coded as 0 and 1, respectively).

J: Geographical latitude.

K: Geographical longitude.

L: Island endemism: Mainland distribution only, island distribution with subspecies on mainland, and island distribution only (coded as 0, 1, and 2, respectively).

M: Number of neighbouring or sympatric other species.

N: Annual rainfall in main area of distribution for each species: 100-200cm, 200-300cm, and over 300cm were coded as 0, 1, and 2, respectively (data from Istituto Geografico De Agostini S.p.A., 1979, p. 131).

O: Annual temperature amplitudes in main area of distribution for each species: 0-5°C, 5-10°C, and 10-15°C were coded as 0, 1, and 2, respectively (data from Imhof, 1965, p. 136).

The body weights used were those of the species listed in Table 5.3.1, except for the samples of *H. agilis*, *H. lar* and *H. muelleri*, which were large enough to permit the use of the subspecies samples from Table 5.3.2. Geographical latitude and longitude had to be converted to the decimal system. The data set used for the MDS analysis is presented in Table 5.3.3.

Table 5.3.3: Data used for multidimensional scaling analysis. Variables A, B and G (male and female body weight, and sample size) are listed in Tables 5.3.1 and 5.3.2.

	Variable											
	C	D	F	G	H	I	J	K	L	M	N	O
H. agilis agilis	0.70	0.11	1	1	1	0	0.78	99.28	1	2	2	0
H. a. albibarbis	1.10	-0.06	1	1	1	0	-1.99	110.12	1	1	2	0
H. a. unko	0.95	-0.01	1	1	1	0	0.55	102.56	1	2	1	0
H. lar lar	0.91	0.01	0	1	1	0	2.90	102.85	0	2	1	0
H. l. carpenteri	0.92	0.01	0	1	1	0	18.58	98.53	0	3	0	1
H. l. entelloides (northern)	0.91	0.01	0	1	1	0	15.74	98.90	0	1	0	0
H. l. entelloides (central peninsular)	0.83	0.05	0	1	1	0	9.80	98.90	0	2	1	0
H. l. vestitus	1.03	-0.05	0	1	1	0	4.02	97.87	1	2	1	0
H. moloch	0.95	0.00	0	1	2	1	-6.58	106.78	2	0	1	0
H. muelleri muelleri	0.97	-0.02	0	1	1	0	-2.29	116.38	2	1	2	0
H. m. abbotti	0.97	-0.01	0	1	1	0	0.36	110.10	2	1	2	0
H. m. funereus	0.93	0.00	0	1	1	0	5.51	118.18	2	0	2	0
H. pileatus	0.99	-0.03	2	1	1	0	12.00	103.00	0	2	1	0
H. klossii	1.04	-0.04	0	1	2	1	-3.00	100.33	2	0	2	0
H. hoolock	1.00	-0.02	2	0	0	0	23.35	96.82	0	2	0	2
H. concolor	0.98	0.00	2	2	0	0	22.26	103.69	0	3	0	2
H. leucogenys	0.99	-0.01	2	2	0	0	20.34	103.67	0	3	1	1
H. syndactylus	0.90	0.05	0	1	0	0	1.40	99.22	1	2	1	0

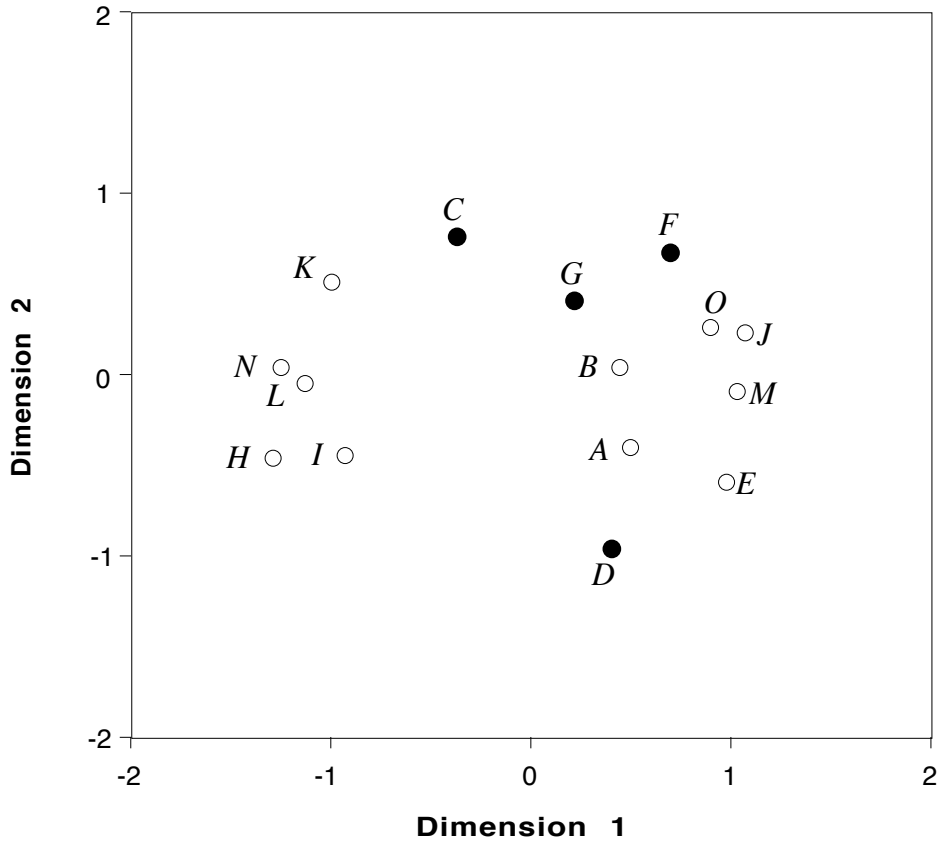


Figure 5.3.2: Multidimensional scaling (Guttman method) of various forms of sexual dimorphism in gibbons (black dots) and a number of other variables (see text). Variables of sexual dimorphism include body weight (C, D), fur colouration (F), and song repertoire (G).

The result of the MDS analysis is shown in Figure 5.3.1. Different types of sexual dimorphism do not appear to be closely related to each other, nor are they particularly closely linked to most other variables. Exceptions are the relatively proximity of the variable for vocal dimorphism (G) to the variables for female body weight (B), for colour dimorphism (F) and for annual temperature amplitude (O). A closer inspection of the correlation matrix (not shown) suggests that the former association (G-B) may result from the distortion of the MDS plot, because the two variables are not closely related ($r = 0.20$). On the other hand, the second possible association (F-O) shows the highest correlation found between any variable of sexual dimorphism and another variable ($r = 0.64$), suggesting that distinct dimorphism in fur colouration tends to occur in regions with higher annual temperature amplitudes.

None of the other correlations between a variable for sexual dimorphism and another variable is high (only in four of them – and only with dimorphism in four colouration – is *r* higher than 0.5: F-J = 0.58, F-H = -0.57, F-M = 0.52, F-O = 0.64). Whereas the two variables corresponding to weight dimorphism (C, D) are highly correlated with each other (r = -0.97), correlations between different types of sexual dimorphism are low ($r < |0.23|$).

6. Phylogenetic Evaluation

6.1 Description of the Data Matrix

The data matrix used for this analysis combines characters of vocal communication (n=29), olfactory communication (n=4), and visual communication (n=33). Most of these characters have been discussed in the three previous chapters. For this analysis, a fourth subset has been added. Its contains 26 "non-communicatory" characters describing various aspects of gibbon skull morphology, dentition, postcranial anatomy, soft part anatomy and karyology. Most of these data have been collected from the literature. For each subset, short descriptions of the characters and character states, and the scorings of each gibbon taxon, are listed in Appendices 10.2, 10.5, 10.6, 10.11, respectively.

The complete character by taxon matrix is shown in Appendix 10.12. It consists of 92 characters and 15 taxa. The latter contain 14 actual gibbon taxa and one hypothetical "ancestor" (as explained in section 2.5). As shown in the three previous chapters, the ancestral character state for many characters of gibbon communication could not be reconstructed with any reliability, mainly because many characters are absent in potential outgroups of the gibbons. As a result, the "ancestor" scores unknown in 53% of 66 characters of gibbon communication, but only in 19% of the 26 "non-communicatory" characters. Overall, 43% of the 92 characters are missing for the "ancestor".

6.2 Analysis of the Complete Data Matrix

Figure 6.2.1 shows a 50% majority-rule consensus tree calculated with the bootstrap option of PAUP (Swofford, 1990). Bootstrap values for 100 replicates are shown above internal

branches. They reflect the percentage of bootstrap trees in which that branch was found. Most of these values are very low (below 80%), except for the branch combining *agilis* and *albibarbis* (87%) and for the one combining the *concolor* group (i.e. the taxa *concolor*, *gabriellae*, and *leucogenys*: 100%). The consistency index of 0.416 is relatively low.

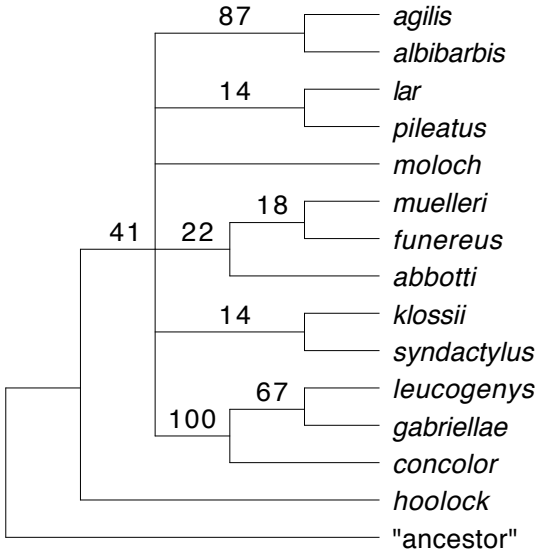


Figure 6.2.1: Bootstrap 50% majority-rule consensus tree, using the complete data matrix of Appendix 10.12. Bootstrap values for 100 replicates are shown above internal branches. Tree length = 363, consistency index = 0.416.

A branch-and-bound search of the same matrix in PAUP yielded a single most parsimonious cladogram of 314 steps and a consistency index of 0.481 (Figure 6.2.2a). It should be noted that none of the gibbon taxa, traditionally thought to be the earliest to split off from the main stem (such as *H. syndactylus*, *H. hoolock* or the *concolor* group) does so in this tree. Instead, this position is occupied here by members of the *lar* group. There are two trees that are one step less parsimonious. Interestingly, one of the latter (Figure 6.2.2b) resembles the traditional view much more closely than does the most parsimonious tree (Figure 6.2.2a).

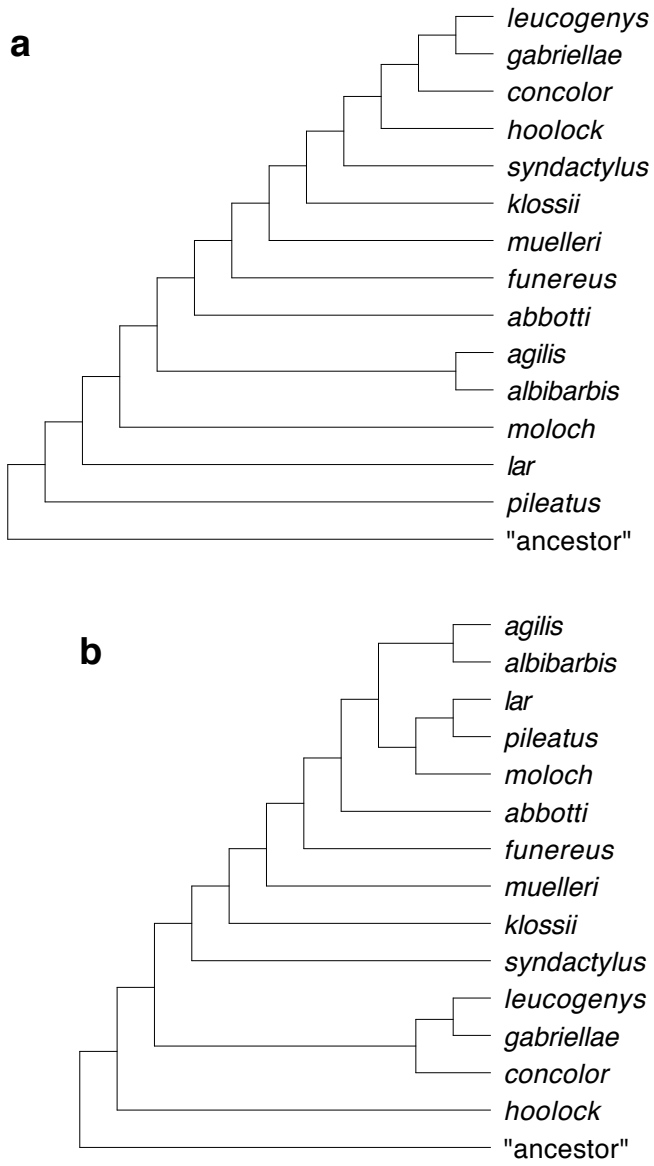


Figure 6.2.2: a) Most parsimonious tree, using the complete data matrix of Appendix 10.12. Tree length = 314, consistency index = 0.481. b) One of two trees which are one step longer than the most parsimonious tree. Tree length = 315, consistency index = 0.479.

Figure 6.2.3 shows the same two trees as Figure 6.2.2, but here the branch lengths are drawn proportional to the amount of change on each branch. Tree "a" appears to be an almost exact inversion of "b".

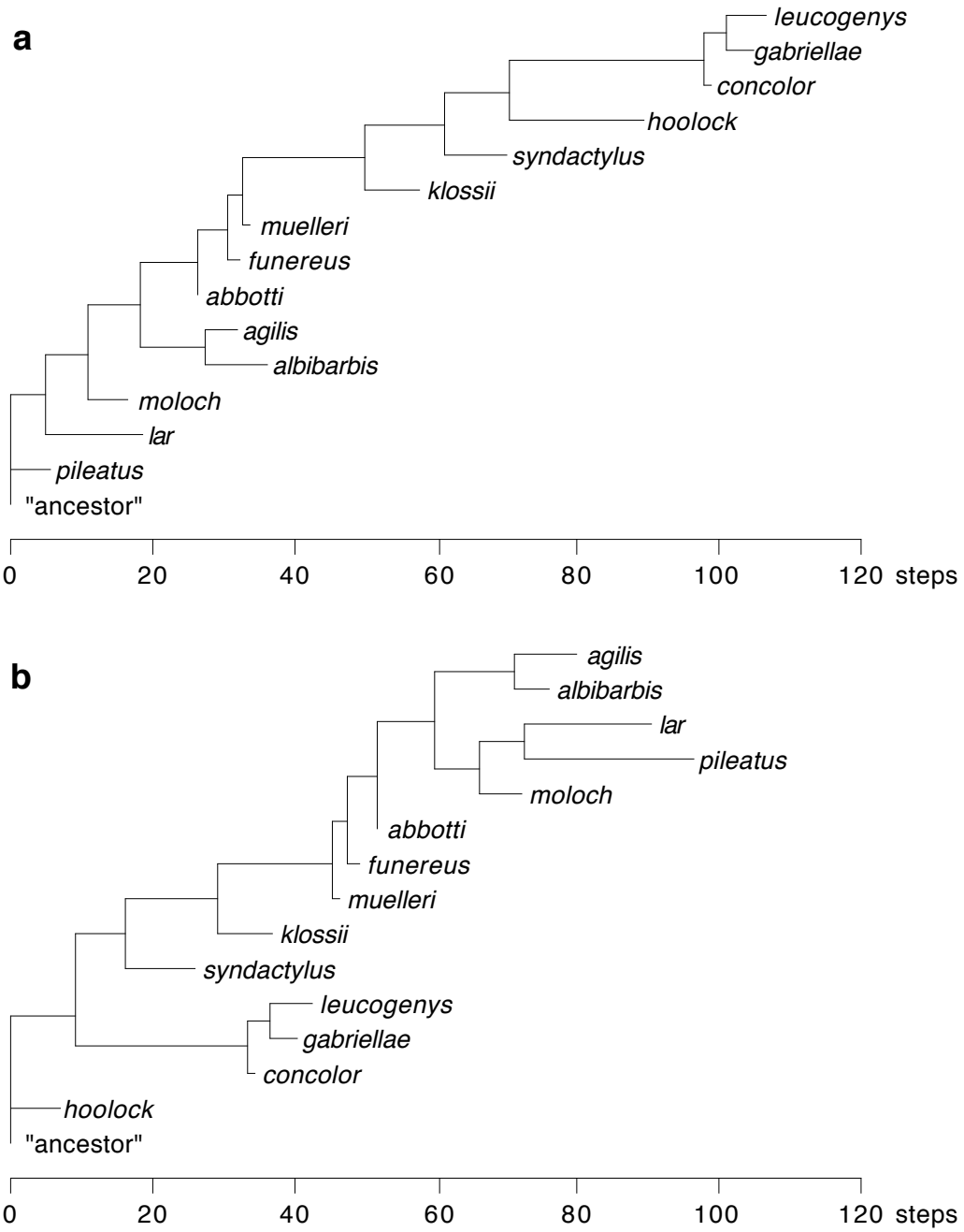


Figure 6.2.3: The same trees as in Figure 6.2.2, showing branch lengths proportional to inferred number of steps.

Finally, the same data matrix has been subjected to a cluster analysis. Although the hypothetical "ancestor" does not occur in an outgroup position in this type of analysis, the resulting dendrogram fairly closely resembles the bootstrap cladogram shown in Fig. 6.2.1. In both trees, the following groups occur: 1. *funereus*, *abbotti* and *muelleri*; 2. *agilis* and *albibarbis*; 3. *syndactylus* and *klossii*; and 4. *leucogenys*, *gabriellae* and *concolor*.

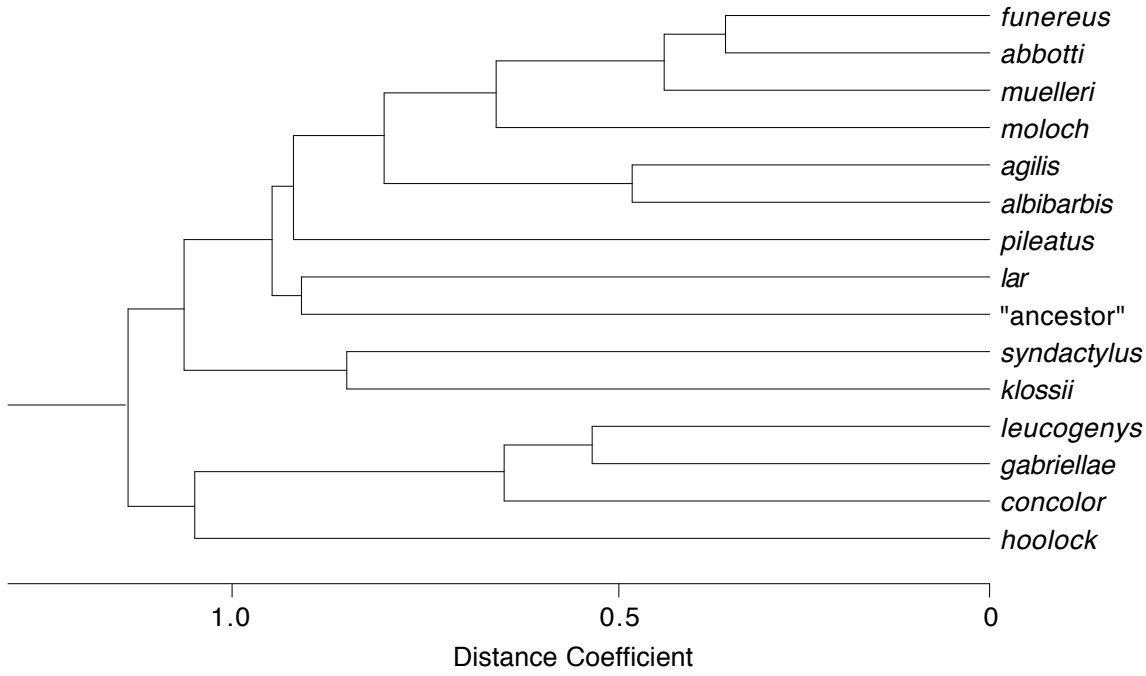
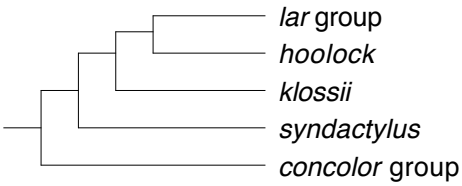


Figure 6.2.4: Cluster analysis, average linkage (UPGMA), using the complete data matrix of Appendix 10.12. Distance metric is normalised Euclidean distance (root mean squared distance).

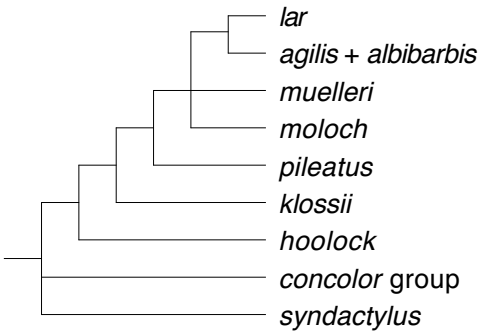
Several gibbon phylogenies have been proposed in previous studies (Chivers, 1977; Creel & Preuschoft, 1984; Garza & Woodruff, 1993; Groves, 1972; Haimoff, 1983a; Haimoff et al., 1982, 1984; the last three references propose the same phylogeny). These were compared with the data of the present study (Fig. 6.2.2a) by mimicking their tree topologies in the MacClade program, using the data matrix of the present study (Appendix 10.12). This method of comparison between a new data set and published phylogenies has been proposed by Kay et al. (1992). Taxa not included in a published phylogeny were removed from the data matrix, but the

hypothetical "ancestor" of the present study was retained. The tree length and the consistency index of the mimicked published tree were then compared with the tree length and consistency index of the most parsimonious tree of the present study. Because these authors did not all include the same taxa in their analyses as the present study, an exhaustive search for the most parsimonious cladograms was executed for their subsets of taxa. Phylogenies, tree lengths and consistency indices are summarised in Figure 6.2.5. In each comparison, a shorter tree with a higher consistency index than the published one was found using the data matrix of the present study.

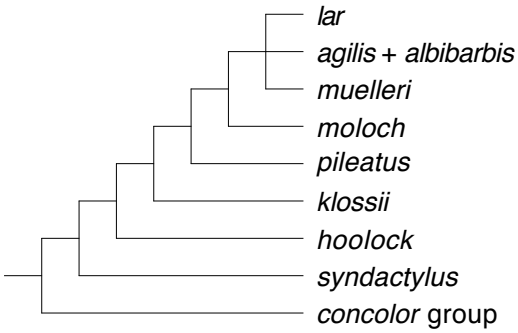
Groves (1972)
length 335, CI 0.45
shortest length 314, CI 0.48



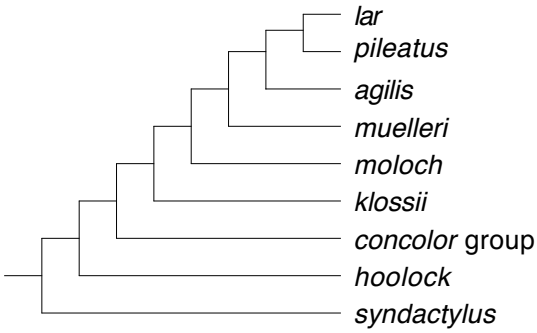
Chivers (1977)
length 331, CI 0.46
shortest length 314, CI 0.48



Haimoff et al. (1982)
length 324, CI 0.47
shortest length 314, CI 0.48



Creel and Preuschoft (1984)
length 326, CI 0.46
shortest length 305, CI 0.50



Garza and Woodruff (in press)
length 281, CI 0.53
shortest length 261, CI 0.57

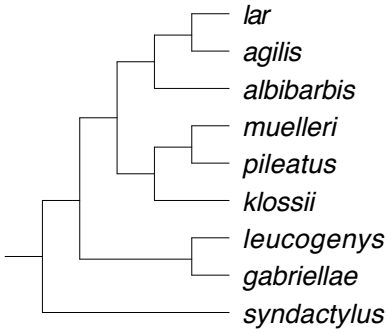


Figure 6.2.5: A comparison of five published representations of the phylogenetic relationships among gibbon taxa. Each phylogeny was mimicked in MacClade, using the data matrix of Appendix 10.12. The resulting tree lengths and consistency indices (CI) are compared with those of the most parsimonious trees calculated with the same data set in PAUP. Notice that "*muelleri*" in this Figure represents the species *H. muelleri*, i.e. it combines the three taxa (subspecies) "*muelleri*", "*funereus*" and "*abbotti*" otherwise used in the present study.

6.3 Analysis of Subsets of the Data Matrix

6.3.1 Vocal Communication

In the following sections, the subsets of the data matrix, as represented by Appendices 10.2, 10.6, 10.11, are analysed separately, i.e. separate parsimony analyses are carried out with characters describing vocal communication, visual communication, and "non-communicatory" characters, respectively. No similar analysis was carried out with characters describing olfactory communication (Appendix 10.5), because only four characters were available in that subset.

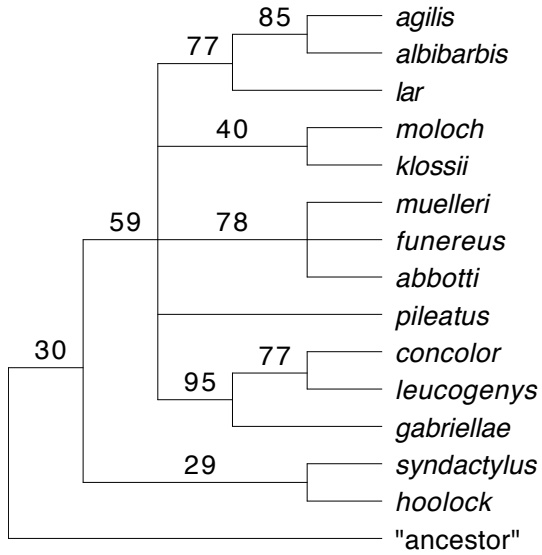


Figure 6.3.1: Bootstrap 50% majority-rule consensus tree, using the data on vocal communication (i.e. characters 1-29 of Appendix 10.12). Bootstrap values for 100 replicates are shown above internal branches. Tree length = 87, consistency index = 0.517.

Figure 6.3.1 shows a 50% majority-rule consensus tree calculated with the bootstrap option of PAUP, using the data subset on vocal communication (Appendix 10.2). Although bootstrap values for 100 replicates – as shown above the internal branches – are fairly low, they are higher on average than those in the bootstrap analysis using the whole data matrix (see Figure 6.2.1), and the consistency index is slightly higher, too, if only vocal characters are

analysed (0.517 vs. 0.416). The groups with the highest bootstrap values (above 80%) are the same as in the previous analysis: *agilis* and *albibarbis* (85%) and *concolor*, *gabriellae* and *leucogenys* (i.e. the *concolor* group: 95%).

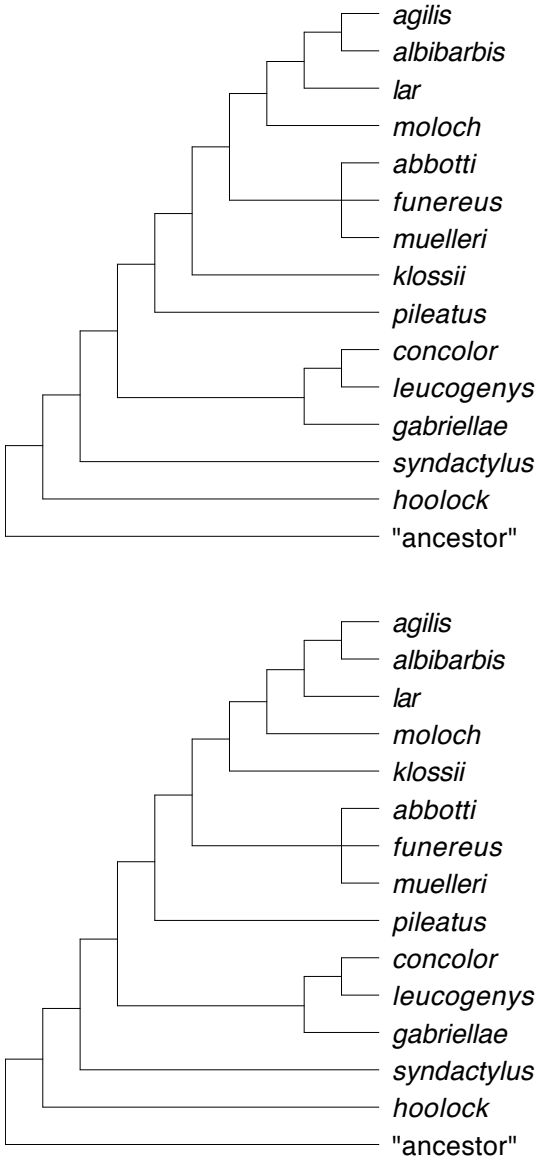


Figure 6.3.2: The two most parsimonious trees, using the data on vocal communication (i.e. characters 1-29 of Appendix 10.12). Tree length = 80, consistency index = 0.562.

The two most parsimonious trees found with the same subset are shown in Figure 6.3.2. They have a length of 80 steps and a consistency index of 0.562. A polytomy for *abbotti*,

funereus and *muelleri* occurs in both trees, because no vocal differences between these taxa are known. In both trees, *hoolock* is the first taxon to split off from the main stem, followed by *syndactylus*, then followed by the *concolor* group, and in both trees the 44-chromosome gibbons appear as a monophyletic group. The difference between the trees concerns the position of *klossii*. Its position close to *moloch* in one of the two most parsimonious trees (and in the bootstrap analysis, see above) probably reflects the absence of duetting in these two taxa, as will be discussed below, see section 7.1.3).

6.3.2 Visual Communication

Figure 6.3.3 shows a 50% majority-rule consensus tree calculated with the bootstrap option of PAUP, using the data subset on visual communication (Appendix 10.6). All bootstrap values for 100 replicates – as shown above the internal branches – are low (<70%), as is the consistency index (0.414).

A branch-and-bound search of the same subset yielded four most parsimonious cladograms of 144 steps and a consistency index of 0.451. A consensus tree of the four cladograms is shown in Figure 6.3.4. Similar to the most parsimonious tree obtained when analysing the complete data matrix (Figure 6.2.2a), and quite in contrast to the traditional view, members of the *lar* group are the first to split off from the main stem in each of the four most parsimonious trees of the present analysis (three times *lar*, once *pileatus*). All four trees show the *concolor* group (*concolor*, *gabriellae* and *leucogenys*), and *klossii* with *syndactylus*, respectively, as monophyletic groups, and three of the trees unite *agilis* and *albibarbis*. The monophyletic grouping of *klossii* and *syndactylus* obtained in this analysis of visual characters probably reflects the completely black fur colouration of both taxa.

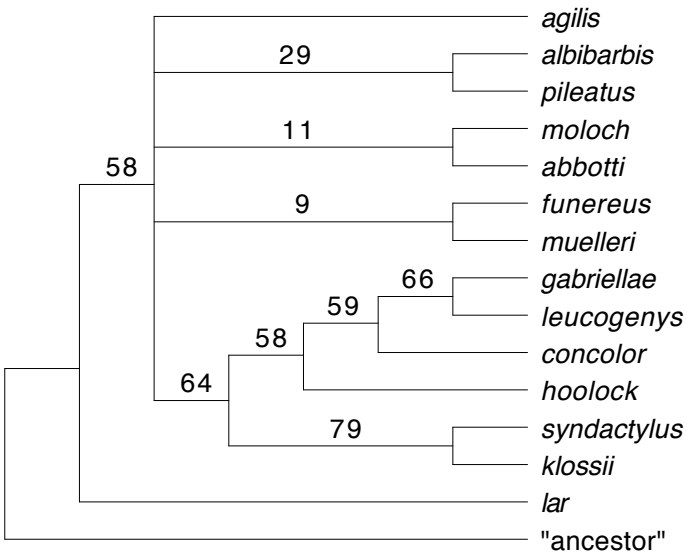


Figure 6.3.3: Bootstrap 50% majority-rule consensus tree, using the data on visual communication (i.e. characters 34-66 of Appendix 10.12). Bootstrap values for 100 replicates are shown above internal branches. Tree length = 157, consistency index = 0.414.

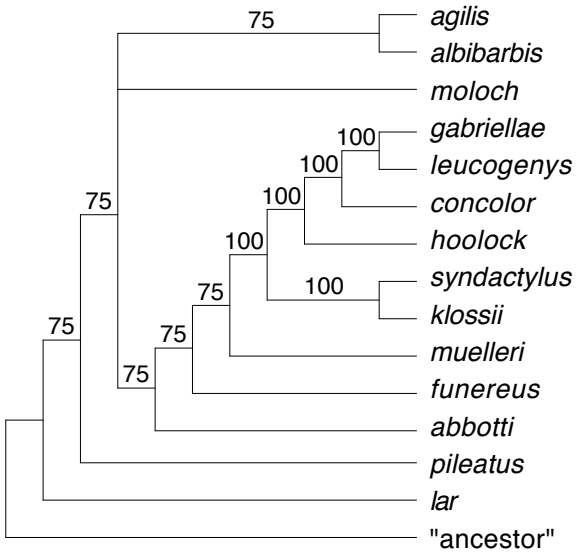


Figure 6.3.4: 50% majority-rule consensus of the four most parsimonious trees, using the data on visual communication (i.e. characters 34-66 of Appendix 10.12). The frequencies of each group in the four most parsimonious trees are shown above the internal branches of the consensus tree. Tree length of each of the four shortest trees = 144, consistency index = 0.451.

6.3.3 "Non-communicatory" Data

The bootstrap analysis of the subset of "non-communicatory" data (Appendix 10.11) was beyond the limits of the PAUP software. A branch-and-bound search of the same subset yielded as many as 156 most parsimonious cladograms of 56 steps and a consistency index of 0.661. A consensus tree of these 156 shortest cladograms is shown in Figure 6.3.5. All shortest trees show both the *concolor* group and the 44-chromosome gibbons as monophyletic groups. In contrast to all trees presented above, all 156 most parsimonious trees of this analysis also combine *syndactylus* and the *concolor* group to a monophyletic group.

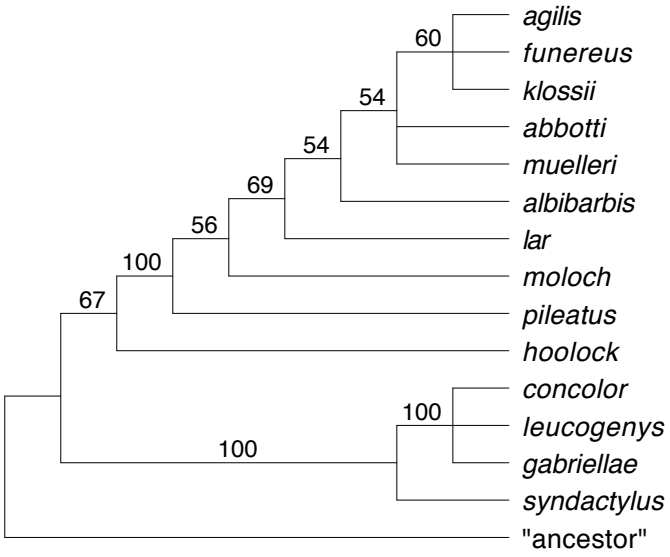


Figure 6.3.5: 50% majority-rule consensus of the 156 most parsimonious trees, using "non-communicatory" data (i.e. characters 67-92 of Appendix 10.12). The frequency of each group in the 156 most parsimonious trees are shown above the internal branches of the consensus tree. Tree length of each of the 156 shortest trees = 56, consistency index = 0.661.

7. Discussion

7.1 Vocal Communication

7.1.1 Comparison of Pure Species Great Calls

Each gibbon species can be shown to have its own, specific characteristics in both male and female song repertoires, as shown in section 3.2. The various species can easily be distinguished by their songs. In this respect, the comparison of pure species vocalisations carried out in the present study supports and expands the results of earlier studies (Haimoff, 1983a, 1984; Marler & Tenaza, 1977; Marshall & Marshall, 1976, 1978; Marshall & Sugardjito, 1986).

In spite of the species-specific differences mentioned above, a comparison of the various songs reveals similarities shared by all species. All gibbon females exhibit a spectacular, stereotyped phrase known as the great call. In all species, the great call consists of a series of notes, uttered with increasing speed (although the acceleration is barely noticeable in *H. agilis* and *H. lar*). In most species, a rise in frequency also occurs during the great call. During their song bouts, females repeat great calls at intervals of a few minutes.

In all gibbon species, the males abruptly stop any ongoing song contributions at the start of their mate's great call, and remain silent during the build-up of the great call. The start of a great call hence appears to act as an inhibitory signal with respect to the song of male gibbons.

In the great calls of all gibbon species, one or two climaxes can be recognised. A climax is here defined as the part of a great call where the female's note production reaches its highest speed and/or pitch. In many species, the climax is further distinguished by a peak in intensity. It is at this point of the great call that the males of most gibbon species resume vocalising and insert a phrase of their own. Thus, the great call of the female and the additional phrase of the

male, inserted near to or immediately after the climax of the great call, combine to produce a well coordinated duet.

Furthermore, at the climax the vocalising gibbons typically add a conspicuous visual component to the acoustical performance: At this point, they suddenly engage in vigorous brachiation: a highly spectacular acrobatical display which frequently includes branch shaking and breaking off of dead branches. As a result, the gibbon song is not only an acoustical but also a locomotor duet. In those species which have two climaxes in a great call, the typical locomotor display occurs only during the second climax. During the first climax, locomotion is confined to a simple change of position or a limited movement in *H. syndactylus*, or it is usually absent altogether in *H. agilis* and *H. lar*. In the latter two species, the first climax is also acoustically less pronounced than the second one (see also section 3.2).

All gibbon species produce long, uninterrupted vocal bouts, consisting of series of female great calls (with or without a male coda), uttered in successive alternation with interlude sequences which are produced either by the male, the female, or both.

The similarities in song structure mentioned above suggest that the songs of all gibbon species are based on a single ancestral pattern, which is apparently not shared with other apes or monkeys (this will be discussed further below). It is highly probable that the song structure common to all gibbon species may be interpreted in terms of homology, that is as synapomorphic (derived) characteristic relative to other apes.

The next question to be addressed is whether great calls in gibbon species are homologous. Several characteristics common to great calls of all species have been mentioned above in this section and appear to support the interpretation of homology. The observation that captive gibbons of various species, if kept in adjacent cages, tend to synchronise their great calls suggests that gibbon females experience great calls of other species as something with which to synchronise their own great calls. The additional observation of males in mixed pairs producing codas to great calls of females of another species suggests that males, like females, are able to "recognise" great calls other than those of their own species. It is unlikely that great calls

evolved similar characteristics in order to enable gibbons of different species to call together. To the contrary, these observations suggest that great calls of different species are homologous phrases.

Finally, the gradual development of increasingly complex phrases is common to solo songs of mated males of all species, although this build-up phase was relatively short in the pileated gibbons heard during the present study. This common characteristic suggests that male solo songs are a homologous characteristic in these species. In some species, mated males are not known to produce solo songs, but solitary males do (*H. concolor*, *H. hoolock*, *H. leucogenys* and *H. syndactylus*). A build-up phase also occurs in male solo songs of these species, with the possible exception of *H. hoolock*, for which no complete male solo was available for analysis. Probably, a build-up phase also occurs in male solos of *H. hoolock*.

7.1.2 Comparison with other Old World Primates

The great apes and humans are usually recognised as being the phylogenetic sister group to the gibbons. Among members of this group, some vocalisations can be discerned that at least in part resemble elements of the gibbon song (i.e. the great call) in their presumed functions and, to a lesser degree, in structure. These vocalisations are thought to be used primarily in inter-individual or inter-group spacing.

In orang-utans (*Pongo pygmaeus*), long calls are given by males only, and are often accompanied by pilo-erection and branch-shaking displays. Calls last up to 1 min in Sumatra and up to 3 min in Borneo. Their frequency is concentrated below 0.7 kHz in Sumatra, and below 1.3 kHz in Borneo. Long calls begin with a short series of low-frequency, low-intensity bubbling notes, which build up to a long series of evenly spaced high-intensity roars, then tail off gradually in another series of bubbling notes. The number of notes is rarely more than 25 in Sumatra, but sometimes up to 50 in Borneo. Long calls are mostly produced during the night in Sumatra, but during the daytime in Borneo, with a peak between 9:00 and 10:00 a.m. Long calls are the only orang-utan vocalisation that can be heard over long distances and have been hypothesised to mediate inter-individual spacing among males (Brandes, 1931; Galdikas, 1983; Hofer, 1972; MacKinnon, 1974; Mitani, 1985; Rijksen, 1978).

In gorillas (*Gorilla gorilla*), hoot-series are most frequently given by silverback males, and may be terminated by chest-beating, branch-breaking or runs through thick foliage. Hoot-series last only a few seconds. Their frequency is concentrated between 1 and 1.8 kHz. Hoot-series typically consist of 2 to 20, but exceptionally up to 84, hoots which may become slurred at the end, blending into a growling sound. Hoots may sometimes be presented in accelerated series. They are fairly loud and have been hypothesised to be primarily utilised in long-range inter-group communication (Fossey, 1972, 1983; Hess, 1988; Schaller, 1963).

In common chimpanzees (*Pan troglodytes*), a distinctive loud call known as the pant-hoot is uttered by both sexes and all ages, but most often given by males. Pant-hoots last from 2 to 23 s. Their fundamental frequency ranges from 0.2 to 1 kHz. In pant-hoots, four distinct phases have been identified: Calls may begin with a brief "introduction" consisting of a series of unmodulated tonal elements of low frequency. A progressively louder "build-up" follows, containing elements that are typically shorter than those in the introduction and produced both on inhalation and exhalation. Some further acceleration in rhythm may occur during this phase. The third phase, the "climax", is characterised by one or several long, frequency-modulated elements resembling a scream in acoustic properties. Frequency reaches its peak in this phase. The climax section is frequently present during pant-hooting of male chimpanzees, but typically absent in females. Pant-hoots conclude with a "let-down" portion, which includes unmodulated tonal elements of low frequency, similar to those of the build-up section. Pant-hooting is given in several contexts, including in response to other pant-hooting individuals, after rejoining other community members, in response to strange conspecifics, upon arriving at a particularly rich food source, during agonistic displays, upon capture of prey items, and during the night. It can be heard over long distances and its functions have been hypothesised to include long-range announcement of an individual's presence and sex, hence mediating inter-individual spacing among some individuals and groups, and reunion of others (Marler, 1969; Marler & Hobbett, 1975; Marler & Tenaza, 1977; Mitani et al., 1992). In bonobos (*P. paniscus*), apparently homologous vocalisations are known under the term "hooting complex" and occur in similar contexts as pant-hooting of common chimpanzees (de Waal, 1988).

Characteristics of these great ape calls resembling at least some gibbon songs include loudness (in all species except gorilla), a hypothetical function in long-distance inter-individual or inter-group communication (in all species), acceleration of note rhythm (common in chimpanzees, variably in gorillas, apparently absent in orang-utans), higher intensity in central section of call (apparently in all species of great apes, but variable in orang-utans), bi-phasic notes consisting of alternating exhalation and inhalation (chimpanzee only), higher frequency in

the central section of the call (common in chimpanzees, at least sometimes in gorillas, possibly absent in orang-utans) and pure tone of notes (chimpanzees only).

Among members of the Old World monkeys, too, certain vocalisations can be discerned that at least in part resemble elements of the gibbon song (i.e. the great call) in function and, to a lesser degree, in structure. In most species, these characteristics are restricted to loudness and a hypothetical function in long-distance inter-individual or inter-group communication (Gautier, 1988; Herzog & Hohmann, 1984; Horwich, 1976; Oates & Trocco, 1983; Tilson & Tenaza, 1976; Vogel, 1973; Waser, 1977, 1982). Other characteristics mentioned above are frequently absent. In several species (such as *Cercocebus galeritus*, *Lophocebus* spp., *Macaca silenus*, *Presbytis johnii*, *P. potenziani*) the occurrence of bi-phasic notes consisting of alternating exhalation and inhalation has been reported. In some species (*Macaca silenus, Presbytis entellus, Presbytis johnii*) notes are remarkably pure in tone, and in some species (*Cercocebus galeritus, Presbytis johnii*) notes are produced with accelerating rhythm (Herzog & Hohmann, 1984; Horwich, 1976; Tilson & Tenaza, 1976; Vogel, 1973; Waser, 1982).

Among great apes, chimpanzee pant-hooting apparently shares most similarities with gibbon great calls; among Old World monkeys, similarities with great calls are particularly prominent in the whooping display of the Nilgiri langur (*Presbytis johnii*). These similarities do not necessarily imply homology, but it is tempting to assume that loud calls with an accelerated rate of note emission and bi-phasic notes represent the ancestral condition of hominoids, and perhaps even of Old World monkeys.

Long, uninterrupted vocal bouts which correspond to the definition of "songs" (as defined in section 2.2.3) are, however, not known from any of these species. The sequential nature of female solo song bouts and duet song bouts, as well as the gradual development of increasingly complex phrases observed in male solo song bouts, appear to be synapomorphic characteristics of gibbons not reported from other Old World primates. It should also be noted that the loud calls of most Old World monkeys and great apes described above are mainly male-specific vocalisations, whereas their main structural similarities to gibbon songs are concentrated on

great calls, which are essentially female-specific. The occurrence of female loud calls may, however, be related to some degree to the monogamous mating system of gibbons (see section 7.3). In addition, the gap is reduced to some extent by the observation that pant-hooting also occurs in female chimpanzees (see above), whereas male gibbons of the *concolor* group typically produce great call-like phrases before reaching adulthood (see section 3.2). Moreover, loud calls of male Mentawai langurs (*Presbytis potenziani*) directed towards adjacent groups have been reported to be supplemented by a coda of 3 to 4 loud, apparently pure tones produced by the female, hence forming a simple duet (Tilson & Tenaza, 1976).

7.1.3 Non-Duetting Gibbons, and Female Solo Songs?

Hylobates moloch and *H. klossii* are unusual in that males of these species are not known to produce codas. Although it is generally accepted that males of these two species do not contribute vocally to the great call sequences, there is some controversy about whether these two species produce duet song bouts at all, as mentioned above (section 3.2.1). In his paper on vocalisations of the Kloss gibbon, Tenaza (1976) mentions that "¡¡ utter short, soft whistles during 25-50 % of the intervals between successive ™ songs" and explains further below in the same paper: "Unlike other gibbons that have been studied, in which mated ¡¡ and ™™ sing duets with their mates, Kloss' gibbons sing in all-¡ and all-™ choruses."

In contrast to this view, other authors have since reported that Kloss gibbons perform duets in a substantial proportions of their interlude sequences (Cowlishaw, 1992; Haimoff, 1983a, 1984; and Whitten, cited in all three publications). Subsequent to his publication (1976) on the singing behaviour of Kloss gibbons on Siberut Island, Tenaza (pers. comm., Nov. 1992) was able to supplement the results of his earlier study by additional observations made on Kloss gibbons in the Pagai islands. His more recent observations apparently confirm that Kloss gibbons do not duet. On occasion, a late morning male chorus would overlap a female chorus, but a male and a female from the same pair were never heard to participate in these overlapping choruses. The short, soft, monosyllabic whistle often produced by males between great calls of their mates does not necessarily represent a song contribution. "Rarely if ever did a male whistle more than once between songs [i.e. great calls] of his mate" (Tenaza, pers. comm., Nov. 1992). Similar whistles precede male song (Tenaza, 1976), but also occur when undisturbed gibbons are simply travelling or foraging (Tenaza, pers. comm., Nov. 1992).

The same authors who recognise duetting in the songs of Kloss gibbons also recognise it in the songs of moloch gibbons, quite in contrast to the results of Kappeler's field study (Kappeler, 1981; 1984). During 130 full days of listening scattered over the whole year, none of

the five resident mated males in Kappeler's study area ever performed a song bout: "it appears that territorial male moloch gibbons do not sing" (Kappeler, 1984). The only male song bouts heard were produced by an unmated individual on the border between two territories and by an unidentified individual singing outside of the study area. The present author had the opportunity to listen to all of Kappeler's many original tape-recordings, and found no evidence for duetting. There was no vocal contribution of the males to the female songs.

As evidence for duetting in moloch gibbons, Haimoff (1983a) cites his tape-recordings made of a captive gibbon pair at Bristol Zoo, and Cowlishaw (1992) cites a tape-recording made by Marshall and Marshall (Marshall & Marshall, 1976) in Java. Duetting of the pair at Bristol Zoo should not be cited for this purpose, however, because the male of this pair was not *H. moloch* but *H. muelleri abbotti*. The male was identified by the present author on the basis of a photograph kindly made available by Dr. C. West and of the sonagrams shown in Haimoff (1983a, his Fig. 6.8).

Some kind of communal calling appears to occur, however, during the interlude sequences of the Marshalls' tape-recording of wild moloch gibbons (later published on a phonograph disc (Marshall & Marshall, 1978). The present author witnessed one similar song spontaneously produced by the family group at the Berlin Zoo, consisting of the breeding pair and a juvenile male. All three members of the group contributed loudly to the interlude sequences, which consisted of brief outbursts of loud series of simple "wa"-notes. The males abruptly stopped vocalising each time the female started a great call, but did not add a coda at its end. On the following day, this tape-recording was played back to the group. The animals reacted by producing the same communal "wa"-phrases in synchrony with those presented on the tape-recording. At the Munich Zoo, a pair of *H. moloch* was repeatedly heard to produce solo songs only (male and female solos) during repeated visits, but once a song was recorded which appeared to be a male solo interrupted by female great calls. At Howletts Zoo, a pair of *H. moloch* with an infant offspring was observed to produce two introductory sequences which

included both male and female vocalisations. Both songs were aborted after few minutes, before any great call sequences were produced.

In conclusion, it appears that Kloss gibbons and silvery gibbons, as a rule, produce only solo songs. Silvery gibbons may occasionally engage in duetting, but it is unknown whether this is an individual characteristic or whether it occurs in specific situations. Similarly, solo songs of mated males appear to be rare in this species; the typical song bout seems to be the female solo song.

There is also some uncertainty as to whether female solo songs occur in mated *H. muelleri*. One early description of *H. muelleri* songs identified solo songs and female solo songs only (Marshall & Marshall, 1976); another described song bouts of this species as duet songs during which the male does not contribute to the interlude sequences, but simply adds a brief coda to the end of the female's great call (Marler & Tenaza, 1977). Later, singing behaviour of this species was described as including male solo songs and duet song bouts, and occasional solo songs of females (Mitani, 1984). More recent reports on songs of Mueller's gibbon fail to mention female solo songs altogether (Haimoff, 1985; Marshall & Sugardjito, 1986) or explicitly state that they do not occur in this species (Leighton, 1987). Only one pure pair of *H. muelleri* was available for the present study, and no female solo songs were observed in this pair. With the information available at present, it appears reasonable to assume that female solo songs do not typically occur in *H. muelleri.*

7.1.4 Song-Splitting and Duet-Splitting

Wickler and Seibt (1982) outlined three alternative routes in order to explain how duet songs could have evolved: "(a) through song merging: two individuals combine their respective songs in a more or less complicated manner; or (b) through song copying: individuals copy their partner's song; or (c) through song-splitting: a given song is divided up between the partners."

Only routes (a) and (c) would be expected to lead to duets with sex-specific repertoire of the mates, as is typical of most gibbon species. In contrast, route (b) necessitates that at least parts of the song repertoire of one pair partner be learned from the other. There is no evidence of gibbons learning parts of their repertoire from other gibbons; instead, the present study provides evidence that the gibbon song repertoire is largely inherited (see below: section 7.1.5). Therefore, routes (a) and (c) are more likely candidates to explain the evolution of gibbon duets.

In route (a), mates with basically different repertoires may combine them in a duet. This is the song-merging hypothesis. At no transitional stage along this evolutionary route would one expect a mate to be able to sing the other's repertoire. This is more likely to occur in song-splitting (c), where a basic song is divided into two subrepertoires, each becoming increasingly confined to one sex. The observation that both typical male and typical female duet parts can be sung by individuals of the opposite sex (section 3.2, and Caldecott & Haimoff, 1983; Geissmann, 1983; Srikosamatara, 1982) suggests that song-splitting rather than song merging occurred during the phylogeny of duetting in gibbons of the *lar* group, and perhaps in other gibbons, too.

The songs of the various gibbon species can be linearly arranged according to similarity of vocabulary available to both sexes and to the degree to which partners preferentially confine themselves to specific parts of that vocabulary, similar to the stages of song-splitting proposed by Wickler and Seibt (1982) to document the evolution of duetting in some species of birds.

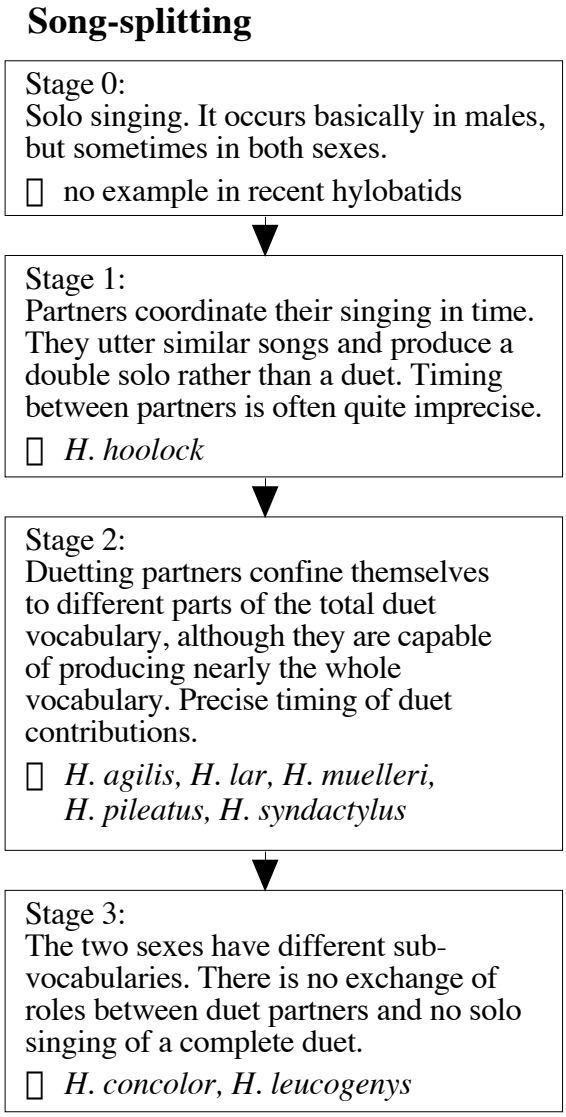


Figure 7.1.2: Gibbon species arranged according to the song-splitting hypothesis. See text for explanation.

It should be noted that the vocal characteristics mentioned in Figure 7.1.2 refer to mated adult gibbons. This hypothetical arrangement leads from duets in which both pair partners sing virtually identical duet contributions, through pairs in which the repertoires of both sexes overlap partially, and finally to pairs where the repertoires are completely sex-specific, because each sex confines its vocalisations to only one part of the whole song. This linear arrangement is interpreted as representing an evolutionary trend from solo singing to full partner dependence

and increasing song-splitting. The direction of evolutionary change is suggested because the more complex structure is more likely to be derived. Duet songs of recent gibbon species are likely to have evolved according to the song-splitting hypothesis as set out by Wickler and Seibt (1982).

The specialisation of the sexes on different parts of the whole song must probably be seen in connection with the frequently proposed possibility that the song contributions of each sex serve different functions and therefore are under different selective pressures (Cowlishaw, 1992; Geissmann, 1983; Gittins, 1978; Marshall & Marshall, 1976). It should be noted, however, that the arrangement of species presented in Figure 7.1.2 does not necessarily represent a phylogeny. Different species could independently have reached the same stage of song-splitting independently.

Two species are missing from the arrangement shown in Figure 7.1.2: *H. klossii* and *H. moloch*. Their position within the framework of the song-splitting hypothesis will be discussed below.

In some gibbons, another trend can be recognised in addition to the trend of song-splitting. In *H. lar* and *H. pileatus*, mated males produce extended solo songs in addition to the duet song bouts common to most gibbons. Solo songs in these two species are sung at about the same time of day as duet songs. In *H. muelleri* and *H. agilis*, however, the first peak of singing activity occurs before sunrise. At this time, the males are reported to produce solo songs on their sleeping trees. The second peak is somewhat later in the morning, at about 7 or 8h, after a first feeding bout. At this time, the females usually join the males in duet songs.

Two gibbon species, *H. klossii* and *H. moloch*, are exceptional in that the pair partners are reported to sing solo songs only (but see the discussion about this point above). At first sight, the logical conclusion would be to interpret this condition as a primitive trait, which would perfectly fit into the hypothetical stage zero of Wickler and Seibt's (1982) song-splitting hypothesis (see Fig. 7.1.2). In the following discussion, however, three arguments are presented

which support the alternative view, that is, solo singing in these two species has derived secondarily from duet singing.

1.) Several different phylogenies have been proposed for hylobatids; some of them are presented in Figure 7.1.3. They are mostly based on morphological and some behavioural characters. Although differing in several details, they share basic similarities. They all agree in the following point: Several duetting species, such as *H. concolor*, *H. syndactylus* and *H. hoolock*, split off from the main stem of hylobatids *before* the two non-duetting species did, and several duetting species split off *afterwards*, such as *H. muelleri*, *H. agilis* and *H. lar*.

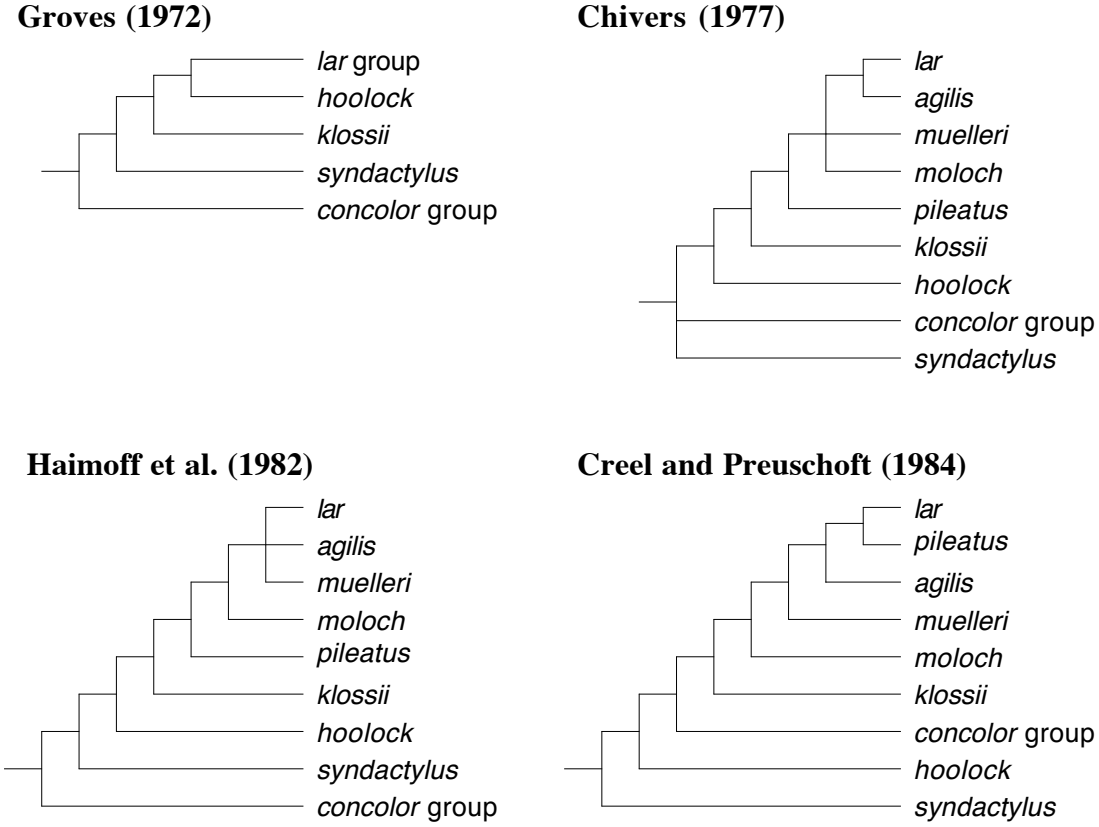


Figure 7.1.3: A comparison of phylogenies of gibbons constructed by different authors.

The conclusion of this comparison is: If duetting is primitive and non-duetting is derived, non-duetting must have evolved at least once in gibbons, but maximally twice if the trait has been developed independently in *H. klossii* and in *H. moloch*. If non-duetting is primitive and

duetting derived, however, duetting must have evolved *at least* twice in gibbons, or four to five times if any one of the phylogenetic trees shown in Fig. 7.1.3 is realistic. It has been described above that gibbon duets consist of a considerable number of characteristics which are shared by all duetting gibbon species. The complexity of the duet pattern renders convergent evolution very unlikely.

2.) In *H. klossii*, only the males sing before dawn in the sleeping trees, whereas the females sing their solos later in the morning. These completely separated singing periods of males and females appear to be the logic consequence of the previously mentioned trend of *H. agilis* and *H. muelleri* to produce male solo songs earlier in the morning than duet song bouts. The gibbon species whose pair partners always duet and those species which do not duet can be linked with these intermediate stages, in which duets are usually separated in time from solo songs. The occurrence of the intermediate stages 2a and 2b supports the view that the non-duetting species should be placed in a new, derived position into the evolutionary framework of the song-splitting hypothesis, as shown in Figure 7.1.4. The term "duet-splitting" which is used in the Figure will be explained below.

3.) A final, perhaps not very strong, argument results from the observation described in section 3.2, that the male of a duetting species (*H. lar*) was able to produce a typical duet with the female of a non-duetting species, *H. moloch* (see Fig. 3.2.3). The two gibbons produced a well coordinated duet; the organisation of their interaction in the great call sequence is virtually identical to that of duetting gibbon species. Apparently, the female song of *H. moloch* fulfils all the requirements for duetting, although this species is not known to duet during the great call sequence. This observation provides additional support for the hypothesis that this non-duetting species has evolved from a duetting one.

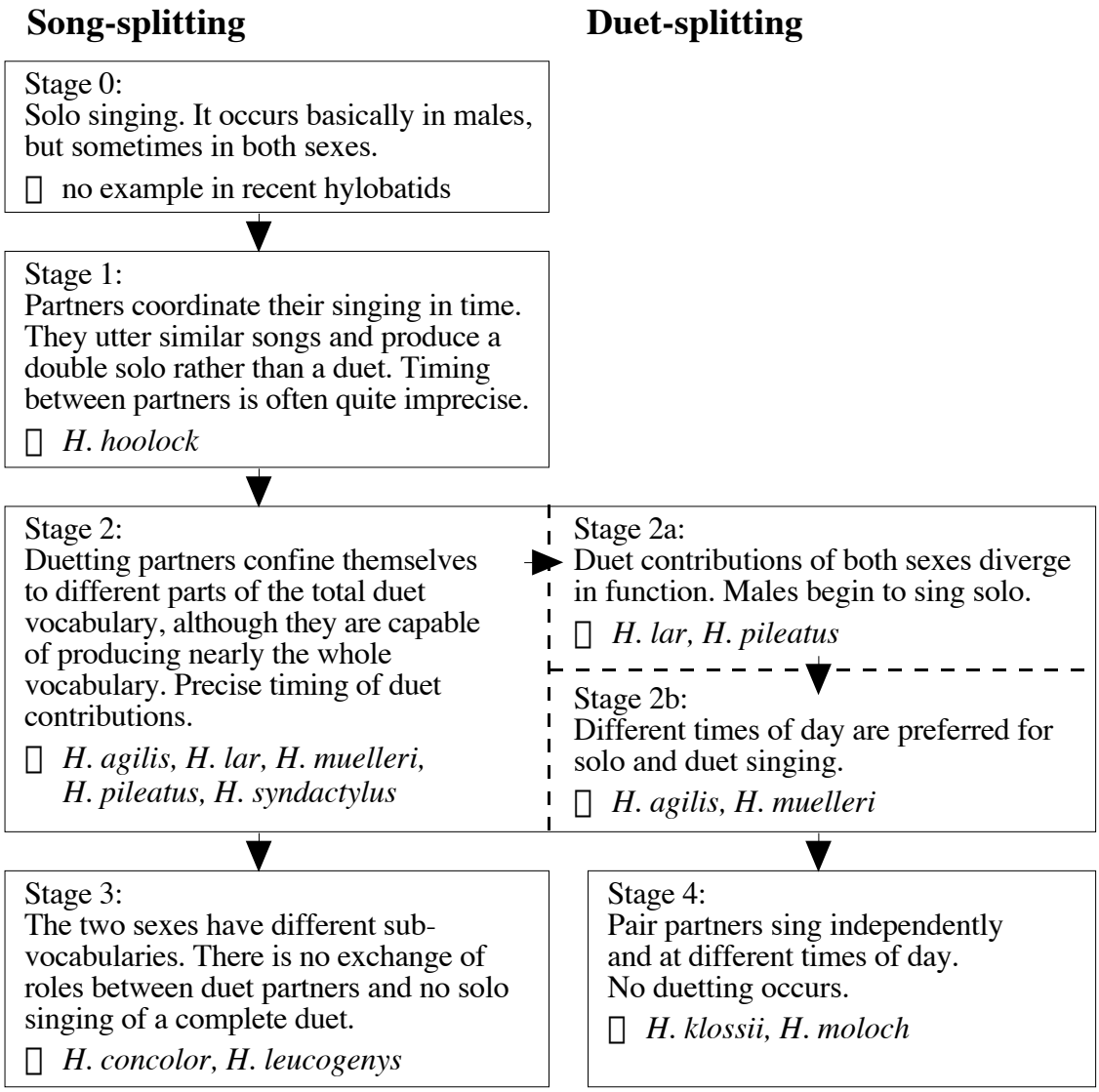


Figure 7.1.4: Gibbon species arranged according to the song-splitting hypothesis and the duet-splitting hypothesis. See text for explanation.

Previous studies disagreed on whether the absence of duetting represented the primitive condition in gibbons (Creel & Preuschoft, 1984), or whether duetting represented the primitive condition (Groves, 1984; Haimoff, 1983a; Haimoff et al., 1982). The former hypothesis was based on "the assumption that evolution normally proceeds from simple, unspecialized states to complex, specialized ones" (Creel & Preuschoft, 1984, p. 603), whereas the reasons supporting the latter hypothesis were either not explicitly formulated (Haimoff, 1983a; Haimoff et al., 1982)

or explained on the basis that "It is evidently a primitive characteristic for gibbons to duet, as all species do it except for *klossii*" (Groves, 1984, p. 558).

The arguments presented in the present study suggest that *H. moloch* and *H. klossii* only secondarily abandoned duetting behaviour, and that the common ancestor of all recent hylobatids did produce duet songs. Only subsequently did the duet contributions of each sex become increasingly independent. This appears to be the first time that a non-duetting animal can be shown to be derived from a duetting form. This process is tentatively called "duet-splitting", in analogy to the term song-splitting of Wickler & Seibt (1982).

The position of *H. moloch* and *H. klossii* together at the same stage of duet-splitting does not necessarily indicate a synapomorphic character state. Whereas males and females of *H. klossii* tend to sing at different times of the day, no evidence for this is yet available for *H. moloch*.

Of course it would be interesting to know which evolutionary constraints may have favoured the occurrence of duet-splitting. The present author failed to find a satisfying answer to this question. One obvious approach to this problem is to scan all gibbon taxa for other characteristics shared by the non-duetting species but absent in duetting gibbons, or vice-versa. Aspects from ecology, geography and ethology of the various species were taken into consideration. As a result, it appeared that the non-duetting gibbons are unique in having no common border with other gibbon species. Whereas *H. moloch* is restricted to the western half of Java, and *H. klossii* occurs only on the small Mentawai islands, all duetting gibbon species are in contact with at least one other species, and all presently occupy larger areas of distribution than the non-duetting species (Chivers, 1977; Chivers & Gittins, 1978; Groves, 1972; Marshall & Sugardjito, 1986). Some authors have suggested that the acoustical differences between gibbon species evolved as a consequence of selection against hybridisation (Marshall & Marshall, 1976; Mitani, 1987). But, in spite of this, it is difficult to imagine how the benefits of *duetting* may have diminished as a consequence of isolation; a causal relationship between speciation and duetting is unknown.

7.1.5 Inheritance of Vocal Characteristics

Hybrid Combinations:

Among captive-born F1 hybrids in the *lar* group (see above, Table 2.2.3), some species show a peculiar preference to be the paternal species, such as *H. muelleri* (11 vs. 5) and *H. pileatus* (9 vs. 0), whereas other species more frequently occupy the maternal position, such as *H. lar* (11 vs. 5) and *H. moloch* (8 vs. 0). Only in *H. agilis* is the frequency of paternal vs. maternal involvement nearly equal (3 vs. 4). The reason for this unequal distribution of hybrid fathers and mothers (Chi-square test, p=0.0002, df=4) is unclear and cannot simply be the result of the unequal numbers of animals of each species kept in captivity.

Inheritance of Female Vocal Characteristics:

Most of the hybrid great calls described in this study appeared to occupy an intermediate position between the parental species in the rate of note emission. This impression was verified by calculating the number of great call notes per great call duration for pure species and hybrids.

Great calls in most gibbon species contain only one climax. Two species of the *lar* group, *H. agilis* and *H. lar*, produce great calls with two climaxes, but in both species the first climax is weaker than the second and sometimes hardly recognisable in *H. agilis*. In general, hybrids with *H. lar* also produce two climaxes, but each hybrid (except *H. lar* x *H. agilis*) produced great calls with only one climax as well. In this regard, hybrids with *H. lar* are more variable than their parental species. The various hybrids with *H. agilis*, on the other hand, were not observed to produce great calls with two climaxes (except *H. lar* x *H. agilis*). Because all hybrids which produced two climaxes either have had a *H. lar* mother or other females of this species as potential templates during their youth, it cannot be decided whether this vocal characteristic was learned or inherited.

Hybrids between a species of the *lar* group with a frequency-modulated type of climax (such as *H. agilis* or *H. lar*) and a species of the *lar* group with a acceleration type climax (such as *H. moloch*, *H. muelleri* or *H. pileatus*) as a rule produce great calls with an acceleration type of climax. In these hybrids, all great call notes are of increasing frequency, whereas species with a frequency-modulated type of climax produce notes of other shapes (for instance notes of decreasing frequency) after a climax.

It should be noted that at least nine of these hybrid females never heard great calls of any species other than their mothers', which means that they lived in partial acoustic isolation. These hybrids could not have learned the note rhythm of their great calls from any gibbon. Four of the same hybrid females had a *H. lar* mother (i.e. which produced frequency-modulated climaxes), but these hybrids still uttered acceleration type climaxes and notes of increasing frequency only. Their failure to produce the mother's type of climax and note shapes (i.e. their failure to learn from the only available template) must be the result of the genetic input from their father. This demonstrates that note speed, note shape and the type of climax in great calls of the *lar* group are inherited characteristics, thus confirming the present author's earlier study on inheritance of song characteristics in hybrid gibbons (Geissmann, 1984a). In addition, it was possible to compare the great calls of one female with those tape-recorded from the same animal for the previous study, revealing that the hybrid pattern in this individual had remained stable over a time span of six years.

Inheritance of Male Vocal Characteristics:

Like vocalisations of female hybrids, most of the song phrases of male hybrids described above (section 3.3.2) combined species-specific parental note types in a unique way, not seen in pure species. For instance, hybrid male *H. pileatus* x *H. lar* were found to utter bi-phasic notes of lower frequency during exhalation and of higher frequency during inhalation, similar to pileated males. Males of *H. lar* do not normally produce inhalation notes. On the other hand, the hybrids do not produce quaver type notes typical of *lar* gibbons. Finally, pileated gibbons

produce very rapid short trills, which are apparently lacking in *H. lar* males. The hybrid males produce trills, but at a slower rhythm than pileated gibbons.

As a rule, hybrid males produced bi-phasic notes if at least one of the parental species exhibited this characteristic (i.e. if one parental species included *H. agilis* or *H. pileatus*). Because females of these species may also occasionally produce short phrases with bi-phasic notes, all hybrids in question could have had access to a template, and it cannot be decided how the characteristic was transferred from the parental to the hybrid generation.

The quaver-notes of *H. lar* were either absent in hybrid offspring of this species (e.g. in all *H. pileatus* x *H. lar*), or less developed and sometimes absent (e.g. in of the *H. muelleri* x *H. lar* and *H. lar* x *H. muelleri*). The latter cases do not present evidence for inheritance of the characteristic, because weak quaver notes are also produced occasionally by *H. muelleri*.

The short trills typical of male phrases of *H. muelleri* and *H. pileatus* occurred in all hybrids which had at least one of these species as a parent. At least one of these hybrids (*H. lar* x *H. muelleri*) had never heard songs with trills. He probably inherited this characteristic from his mother, as has previously been suggested for the same animal by Tenaza (1985). It is not clear why the trills of all hybrids with *H. pileatus* (i.e. *H. pileatus* x *H. lar* and *H. pileatus* x *H. moloch*) were slower than those of *H. pileatus*. A possible template was not available. Males of *H. lar* and *H. moloch* do not usually produce trills, although one male of the latter species was repeatedly heard to utter slow trills. It is tempting to speculate that trills, which occur in male songs of many species, are a primitive characteristic still genetically present in *H. moloch* and *H. lar*, but not usually expressed in the phenotype. These trills could originally have been slower in *H. moloch* and *H. lar* than in *H. pileatus*. This could result in a slowed-down trill in hybrids as compared to the *H. pileatus* father.

Hybrid male *H. pileatus* x *H. lar* and (to a lesser extent) *H. pileatus* x *H. moloch* show a curious preference for a combination of three notes. This figure of three notes consists of a sequence of exhalation-inhalation-exhalation, and has previously been described for a hybrid *H. pileatus* x *H. lar* (Geissmann, 1984a). Such a three-note figure is not typical for any other

gibbon species. Its occurrence in the hybrids cannot be explained by simple combination of parental song characteristics. It is unclear why this figure occurs in the hybrids.

Of particular interest are the vocalisations of the female *H. muelleri* x *H. syndactylus*. This hybrid has become known as "siabon" (Kortlandt, 1981; Rumbaugh, 1981; Rumbaugh et al., 1976), and for the sake of brevity this name will be used in the following discussion. The siabon is the only hybrid available for the present study which included a parental species outside of the *lar* group. This solitary female produced great calls which resembled *H. syndactylus*, not *H. muelleri*, in frequency. Since a potential template for this song characteristic was available to the hybrid, it cannot be decided whether the characteristic was learned or inherited from the mother.

Frequently, two great calls would be uttered with one immediately following the other. In this respect, the siabon also resembles *H. syndactylus*: Mated females of this species typically produce two accelerated series of long barks during a great call series. The only isolated female *H. syndactylus* available for study differed in usually producing one series per great call. It is not known whether all isolated females of *H. syndactylus* drop the second bark series (perhaps due to a lack of feedback from the mate's vocalisations typically occurring at the first climax), or whether this female siamang was simple exhibiting an individual trait. The former interpretation is more likely to be correct, because the same female had been mated before and after isolation and had been observed to produce regular great call sequences with two bark series with her mates. It would be interesting to see whether the siabon would also begin to utter great calls preferentially with two climaxes if mated with a pure siamang male (and great calls with one climax if mated with a duetting male of the *lar* group), or whether the variability of her great calls would remain unchanged.

It was particularly surprising to discover that the siabon produced bi-phasic notes during her great calls. This characteristic is absent in both parental species and made her great calls somewhat similar to those of *H. hoolock*. Bi-phasic notes (consisting of an exhalation and an inhalation sound) are a typical characteristic of *H. hoolock* great calls. In great calls of other species, inhalation notes were only recorded for individual climax notes of *H. lar* and –

occasionally – *H. agilis*. The occurrence of these notes throughout most of the siabon's great call cannot be explained as being learned either from the songs of her parents or from the songs of the *lar* gibbons with which she was familiar. It must either have been developed *de novo* by the hybrid, or else it may represent a primitive characteristic inherited from one of the parental species, where it may have been present without any phenotypic expression. It is impossible to test either hypothesis with only one such hybrid available.

Bi-phasic notes also occur in *male* songs of several species such as *H. agilis*, *H. hoolock*, *H. pileatus* and occasionally *H. moloch* (only one case known). It cannot be determined whether this is a homologous characteristic in all species or whether it has evolved several times within gibbons. It is even less clear whether the characteristic is homologous to the bi-phasic notes observed in the female siamang hybrid. But since bi-phasic notes are also known to occur in pant-hooting of chimpanzees and in long calls of a number of Old World monkeys, it may well represent a primitive condition in gibbons.

In another characteristic, i.e. the rhythm of her great call notes, the siabon resembled neither parental species, but was distinctly slower than either. The relatively slow speed of the hybrid's great call is difficult to explain. It may be an individual *de novo* development or an ancestral characteristic. Finally, it may be mentioned that the siabon's short phrases produced during the interlude sequences included a short trill similar to those produced during the male song of *H. muelleri*. For this characteristic, learning from the father cannot be excluded.

The results of the present study corroborate and considerably expand those presented in earlier studies (Brockelman & Schilling, 1984; Geissmann, 1984a; Marshall & Sugardjito, 1986; Tenaza, 1985), and can be summarised as follows:

1.) First-generation hybrid gibbons produce songs with hybrid-specific repertoire and structure which differ from the songs of both parental species.

2.) The song characteristics of F1-hybrids appear to be stable over several years.

3.) Gibbon song characteristics are at least in part genetically determined.

4.) In many respects, song characteristics of hybrids are intermediate between those of the parental species.

5.) Some characteristics can be shown to be more variable in hybrids than in the pure species.

6.) Some vocal characteristics of hybrids are not known from either parental species, and some are even not known from pure species at all. The origin of such characteristics is a matter of speculation.

7.1.6 Homology of Great Call Types

Whereas great calls are very distinct and highly species-specific in some species, they are remarkably similar in others. In gibbons of the *lar* group, there are basically two extreme forms of great calls: they have frequently been named the soaring or wailing type and the bubbling or trilling type by previous authors (e.g. Marshall et al., 1984). Whereas the great calls of *H. agilis* and *H. lar* consist of different, frequency-modulated note types which increase and decrease in frequency and are produced at slow speed with only slight variation in rhythm, those of *H. muelleri* and *H. pileatus* consist of notes of increasing frequency only; these notes are produced with a pronounced acceleration in rhythm until ending in a long, bubbling trill. The great call of a fifth species, *H. moloch*, is somewhat intermediate between the two extremes, because "it neither soars nor trills" (Marshall et al., 1984). It consists of notes of mainly increasing frequency uttered with an acceleration in rhythm. Only a moderate speed is reached, however, and the note rhythm becomes slower again at the end of the great call.

Systematically, the particular similarities between the great calls of *H. agilis* and *H. lar*, and between *H. muelleri* and H. *pileatus* have been interpreted as an index of a closer relationship between *H. agilis* and *H. lar* on the one hand, and between *H. muelleri* and *H. pileatus* on the other (Haimoff, 1983a; Haimoff et al., 1982, 1984; Marshall et al., 1984). Although this interpretation appears plausible, the basis for adopting it has never been properly discussed. This is not trivial: even if the great calls in all species are probably a homologous characteristic – as discussed above – this does not imply that individual great call characteristics shared by a subgroup of the gibbons are homologous as well; they might not, as has been suggested for the similarities shared by *H. agilis* and *H. lar*: "… the wailing great call of *lar* can be interpreted as mimicking the great call of *agilis* with whose distribution *lar* is intermittent in the south and not necessarily reflective of a close phylogenetic relationship between these species as many authors have inferred" (MacKinnon, 1978, p. 329).

The hypothesis that gibbon songs are largely genetically determined has been suggested repeatedly and is supported by convincing evidence presented above. If similarity in great call structure between two species is based on homology, then this structure should in both species be under similar genetic regulation, and hybridisation with a third species should result in similar hybrid great call in both cases. Similar great calls should be similarly affected by hybridisation if their similarity is based on homology. The same genetic substrate of a particular great call structure is unlikely to have evolved twice. If similarity in great call structure was the result of convergent evolution, one should not expect similar great calls to react the same way to hybridisation.

This theoretical framework can now be applied to great calls of the *lar* group. Great calls of different hybrids between various species of this group have been described above (section 3.3.1). All hybrids between a species with slow, frequency-modulated type of great call (*H. agilis* or *H. lar*) and a species with a fast, acceleration-type great call (*H. muelleri* or *H. pileatus*) show similarities in their great calls. Similarities include the structure (shape) of the notes, the number of notes, rhythm of notes, intensity of acceleration, and duration of the great call. As a result, the rhythm of their great call notes is intermediate between the parental species and somewhat similar to *H. moloch*, as has been mentioned previously (Geissmann, 1984a; Marshall et al., 1984).

It appears that similar great calls of two species in the *lar* group are affected in very much the same way under hybridisation to a third species and are under the same or at least similar genetic control. For example, great calls of *H. agilis* x *H. pileatus* and *H. lar* x *H. pileatus* hybrids are nearly identical. Therefore, the similarities between great calls of *H. agilis* and *H. lar* are probably based on homology. The same applies to the similarities between great calls of *H. muelleri* and *H. pileatus*.

Because only *H. agilis* and *H. lar* produce a frequency-modulated type of great call, this possibly represents a derived condition with respect to the acceleration-type of great call of other gibbon species. This view is further supported by the common occurrence of accelerated loud

calls in other species of apes and Old World monkeys. It is not clear, however, which rate of note emission may be more similar to the ancestral state: the faster rate of *H. muelleri* and *H. pileatus*, or the slower rate of *H. moloch*. Marshall et al. (1984) opted for the latter view. Comparison with other gibbon species reveals that all are closer in the rate of note emission to *H. moloch* than to *H. muelleri* and *H. pileatus* (excepting *H. klossii*, whose great calls are approximately intermediate between the two rates in question). Loud calls of all species of great apes are also closer to *H. moloch* in the rate of note emission. In view of this evidence, it appears more likely that the common ancestor of all gibbons produced a great call with a note rhythm similar to that of *H. moloch*.

This comparison between great calls of gibbons of the *lar* group and their hybrids can be developed one step further. In Figure 7.1.5, the number of notes per second in a great call (on a logarithmic scale) are shown for each category of great call type. If the slow great calls of *H. agilis* and *H. lar* are arbitrarily given class "0" and the fast great calls of *H. muelleri* and *H. pileatus* class "1", then the hybrids between both categories are consequently coded as class "1/2", i.e. they are situated half-way between the parental species. As the great call of *H. moloch* resembles that of the hybrids in note rhythm, it is put into the same category. All remaining hybrids are then inserted in categories situated half-way between the parental categories. A similar presentation has previously been used by Brockelman and Schilling (1984) to show the relationship between great calls of the hybrids between *H. lar* and *H. pileatus*.

Figure 7.1.5 shows that great calls of hybrids occupy an intermediate position between those of parental taxa in the rate of their note emission. Hybrids and backcrosses are situated on a more or less straight line between the extreme points represented by the great calls of categories "0" and "1".

Only the point for *H. lar* x *H. moloch* is slightly out of line. Two females of this particular type of hybrid were available for the present study. The misalignment of the point is due to only one of the females ("Gipsy"), which produced unusually short and very slow great calls. If the other hybrid ("Frieda") is plotted alone, she comes to lie in the expected position

between the parental great calls. Possibly, the great calls of "Gipsy" are atypical. Unless more hybrids of this type are discovered, this possibility must remain speculative.

Figure 7.1.5 not only provides support for the view that "genes for great call pattern are inherited in a quantitative fashion" (Brockelman & Gittins, 1984) and that similarities between great calls of the *lar* group are based on homology (as discussed above), but also suggests that the rate of note emission in hybrids is predictable. Figure 7.1.5 can serve as a model: Any type of hybrid can be inserted in its appropriate category (i.e. half-way between the parental categories), and the note rhythm of its great call can be expected to be situated on a line connecting the parental positions in the graph. Thus, the rate of note emission could be predicted for hybrids which were not available for the present study, such as *H. moloch* x *H. pileatus*, but also for backcrosses such as (*H. agilis* x *H. muelleri*) x *H. agilis* or more complex second generation hybrids *H. muelleri* x (*H. lar* x *H. moloch*).

The genetic mechanisms underlying this model are not clear, however. According to the rules of Mendelian inheritance, parental vocal characteristics should be expected to occur during the second hybrid generation (Hartl, 1983), but no evidence for this is available for the few backcross individuals studied so far. The rate of note emission in gibbons of the *lar* group does not show an obvious pattern of simple Mendelian inheritance, and its genetic determination is likely to be multifactorial.

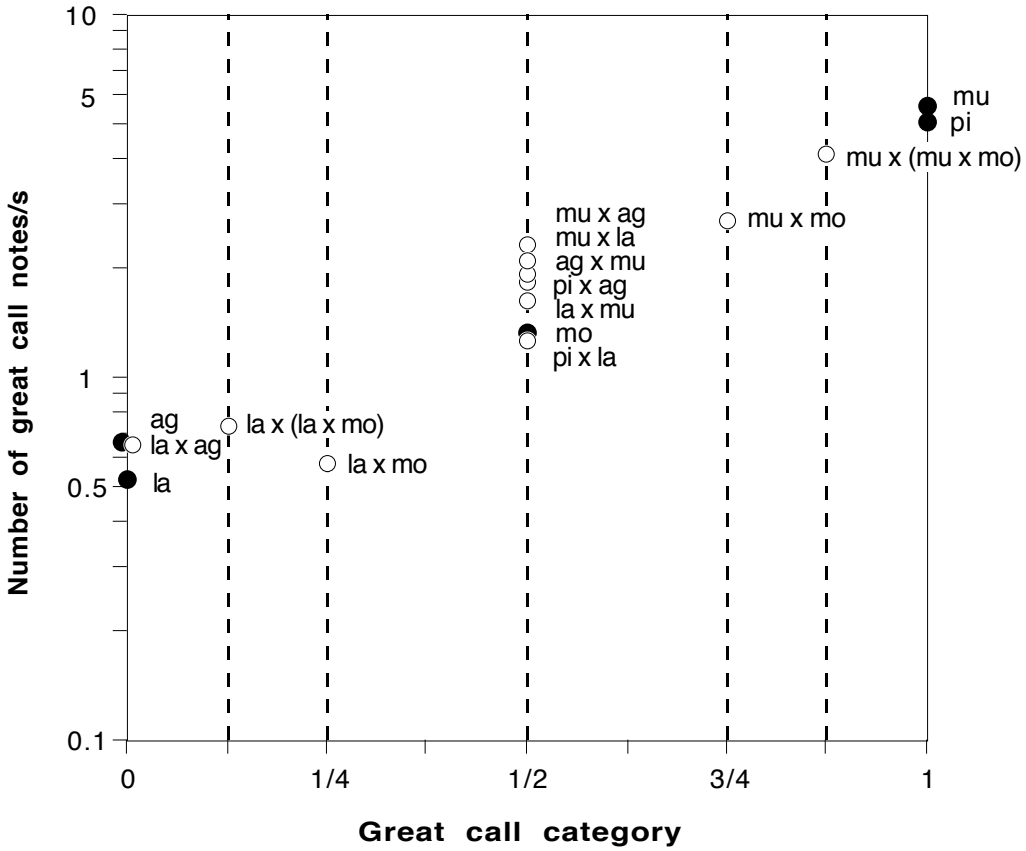


Figure 7.1.5: The number of notes per s in a great call, on a logarithmic scale in relation to genetic parentage, for all species of the *lar* group, their hybrids and backcrosses. Black points represent pure species, circles represent hybrids. See text for explanation of horizontal axis. Abbreviations: ag – *H. agilis*; la – *H. lar*; mo – *H. moloch*; mu – *H. muelleri*; pi – *H. pileatus*.

7.1.7 Summary: Evolution of Gibbon Songs

Long and complex song bouts have been described for all gibbon species. Comparison of their singing behaviour supports the following conclusions concerning the evolution of gibbon songs:

1. The recent hylobatids represent a monophyletic group whose common ancestor produced *duet* songs, although not all recent species are known to do so.
2. Duet songs of recent gibbon species are likely to have evolved according to the song-splitting theory: Gibbon duets probably evolved from a song which was common to both sexes and which only later became separated into male-specific and female-specific parts.
3. In the evolution of gibbon songs, a process tentatively called "duet-splitting" is suggested to have secondarily led from a duetting species to a non-duetting species, in that the contributions of the pair partners split into temporally segregated solo songs.
4. The analysis of hybrid vocalisations supports the view that gibbon songs are largely genetically determined.
5. Great calls of all gibbon species are probably a homologous song phrase. The fast, bubbling trills of *H. muelleri* and *H. pileatus* are probably homologous features, as are the slower, frequency-modulated great calls common to *H. agilis* and *H. lar*. The acceleration of the rate of note emission during the great call is probably the ancestral condition. The ancestor of modern gibbons probably produced great calls with a rate of note emission similar to that of *H. moloch.*
6. The gradual development of increasingly complex phrases from initially more simple phrases probably represents the primitive condition for male songs in gibbons.
7. The use of bi-phasic notes (alternate production of exhalation and inhalation sounds) during the song probably represents a primitive characteristic for gibbon vocalisations.

7.2. Olfactory Communication

7.2.1 Macroscopic Study

Sternal glands were found to occur in all gibbon species of this study, except perhaps the Kloss gibbon (*H. klossii*), for which no reliable data could be collected. Sternal glands are most prominent in siamangs (where they appear to be responsible for the typical body odour of this species) and least prominent in gibbons of the *concolor* group.

Additional, less sharply defined fields of coloured pores occur in other areas of the skin. They were found in several species, but are especially conspicuous in gibbons of the *concolor* group. In females of the latter, the reddish secretion of these glandular concentrations occasionally produces patches of reddish or bright orange fur colouration. The colouration of females may reversibly switch between saturated and unsaturated states, apparently depending on glandular activity. The timing and function of these changes in colouration is unclear (but see below).

Neither the occurrence of sternal glands nor the presence of fields of coloured pores is sex-specific. Both types of specialised glandular areas may be visible in very young gibbons. The early glandular activity of the field of coloured pores in 4-5 weeks old gibbons of the *concolor* group suggests that the ontogeny of their colour glands follows a timing different from that of the sternal gland in siamangs, where secretion reportedly starts in the second half of the first year of life. The onset of secretion in the fields of coloured pores of gibbons of the *concolor* group (and perhaps other gibbons) thus appears to be much earlier than that of the sternal gland in siamangs (and perhaps other gibbons).

A distinct patch of unpigmented skin in the sternal region appears to occur in siamang infants only and disappears (i.e. becomes pigmented) near the end of the first year of life. Its significance is unknown.

7.2.2 Microscopic Study

The histological analysis demonstrates that the macroscopical skin structures observed in the sternal area of gibbons are really glandular specialisations. They consist of an accumulation of tubular glands, mostly of the apocrine type, but frequently interspersed with some smaller, probably eccrine glands.

In five samples (sample No. 6 of *H. pileatus* and 4 samples of *H. syndactylus*), the transition between the unspecialised skin of the chest and the glandular area can be seen. This transition is abrupt rather than graded. This corresponds to the macroscopic appearance of the sternal glandular fields, which are usually quite clearly demarcated, especially on their lateral borders (see section 4.2).

Specimens of different age and sex classes are available for *H. syndactylus*. The glandular concentrations occur both in males and females, and in all age classes examined. Even a neonate siamang and an infant of 0.67 years of age clearly show the sternal glandular specialisation, but the coils appear to be smaller in these specimens than in the older animals. It should be mentioned that the macroscopic appearance of the sternal gland in these two individuals was different from that found in older animals: These very young animals had the peculiar patch of white skin in the sternal region that has been discussed above. The concentration of tubular glands corresponded exactly to the area of the white patch of the young siamangs. This supports the view that the white patch is the earlier equivalent of the typical sternal glands of older animals.

Although the histological sections showed that the majority of gibbons had distinct glandular concentrations in the sternal region, in some gibbons no such concentration was observed. There are three possible explanations for this finding: 1.) some gibbon species may lack the sternal gland; 2.) some individuals of a species may permanently or periodically lack the gland, 3.) the gland was missed in some sections. The correct explanation(s) can only be

determined by analysing additional specimens. Explanation 1 can be ruled out for *H. hoolock*, *H. moloch* and *H. lar*, because some individuals of each of these species clearly do have a sternal gland, but were not available for histological analysis. Explanation 3 may apply to the adult female of *H. klossii*, the subadult male of *H. lar* and the adult male *H. moloch* which were histologically examined. In each of these specimens, a large piece of the skin was missing on the anterior surface of the neck and the chest, and the author was not able to determine whether some skin of the sternal gland was left. In the latter two specimens, the sternal gland was probably not included in the piece of sternal skin analysed. For *H. klossii* and *H. leucogenys*, all three explanations have to be considered, because only one sternal skin sample of each species was available for analysis. Therefore, the possibility exists that these two species do not develop a sternal gland.

The microscopic structure of gibbon sternal glands appears to follow partly the same design as skin glands in many primates and other mammals: Sebaceous glands occupy a more superficial layer, and a deeper layer of the glandular organ consists of mainly apocrine tubular glands. In many skin glands, the layer of sebaceous glands represents the most voluminous part, as compared to the layer of tubular glands. This contrasts with the findings for gibbon sternal glands. As a few examples of this condition, the sternal glands of *Tupaia* (Sprankel, 1962) and the orang-utan (Schultz, 1921; Wislocki & Schultz, 1925) or the maxillary gland of *Avahi laniger* (Bourlière et al., 1956) may be mentioned. In other cases, the main body of the glandular organ consists of tubular glands; such is the case for instance in the sternal glands of *Ateles* (Schwarz, 1937) or in the axillary glands of humans and the African apes (Brinkmann, 1909; Schiefferdecker, 1922). The sternal gland of gibbons clearly resembles the second type.

No clear differences in the histological structure of the sternal gland were found between the gibbon species examined here. This may be due to the small sample size available for each species. Therefore, until more specimens have been studied, the histological findings presented here give no reliable information on the phylogenetic relationships between gibbon species.

7.2.3 Chemical Analysis

A chemical analysis of the secretion of specialised skin glands has been carried out on only a few primate species (see review in section 4.1.4). Apart from studies on humans, steroids have been found as a major component of glandular secretion only in exudates from the brachial glands of *Nycticebus* (Alterman, 1989). It is possible, however, that steroids have simply not been looked for in previous studies. Certain steroid hormones produced in the axilla are thought to be of major importance in human olfactory communication. The present study shows that steroid hormones are accumulated in the skin glands of some gibbon species.

The samples collected consisted primarily of dried secretion rubbed from the skin with ethanol-soaked compresses. Although the hormone concentrations of these samples can be compared with each other, they give no information on the hormone concentration in the pure secretion. Such information, albeit as a rough approximation, can be derived from one sample (No. 9) of pure sternal exudate collected from the adult male siamang "Bohorok". Hormone concentrations in this exudate are several times higher than the concentrations found in the peripheral plasma of the same animal (see Figure 4.10). This finding is of importance for determining the mechanism of how the hormones are secretioned in the sternal gland of siamangs: The high sternal hormone concentrations cannot be the result of a simple filtration of hormones out of the blood plasma, but must be the result of a more complex accumulation process. This accumulation is by a factor of at least 2.4 and 8.4 in testosterone and DHEA, respectively (conservative estimates), but by a factor of at least 250.5 in androstenedione in the male siamang studied here. In view of this high concentration, it is tempting to assume that androstenedione is of particular importance in olfactory communication of siamangs.

Because skin secretions have been collected in a standardized way, they can be compared with the sternal sample of the adult male "Bohorok", with the latter serving as a standard. All relative hormone concentrations (relative: measured as "ng per *sample*") that are as high or even

higher than those of the standard (i.e. "Bohorok") probably result from an accumulation process as well. In addition, they suggest the presence of actively secreting glandular fields.

Especially high concentrations of all three hormones (all higher than those of "Bohorok") are found in the sternal sample of one adult female siamang ("Floh"), suggesting that the hormonal concentrations in the sternal gland of the siamang are not sex-specific. The sternal concentrations in one male *H. pileatus* are almost as high as those of "Bohorok". Other hormone concentrations surpassing those of "Bohorok" are almost completely restricted to DHEA. Such is the case in other individuals of *H. syndactylus, H. pileatus, Pan* and *Pongo*, and not only for sternal, but also for axillary samples. In these species, DHEA accumulation apparently occurs (in some individuals at least) in the axillary region. This is unexpected, because most of these species (namely *H. syndactylus, H. pileatus* and *Pongo*) are not known to possess axillary glandular fields.

As a consistent finding of the present study, hormone concentrations of *H. leucogenys* were found to be negligible, and significantly lower than those of *H. syndactylus*. This was true not only for the samples of dry secretion collected in various areas of the animals' skin. In a sample of fresh skin secretion from a female *H. leucogenys*, no measurable hormone concentrations were found at all.

7.2.4 Function of Gibbon Skin Glands

The present study has revealed a surprisingly complex system of gibbon skin glands. There are only few observations which may have some bearing on the function of these glands, but the system of gibbon skin glands appears to differ from that so far described for non-hominoid primates. Similarities exist, though, to the axillary glands of humans and the African apes. Although it not yet possible to explain the importance and function of skin glands in gibbon communication, the observations made on secretory activity (Section 4.2.2), and similarities with the aforementioned axillary glands, give some indications which permits some functional interpretations.

Sternal glands are usually thought to play an important role in olfactory communication. In many primates (Table 4.1.1) and other mammals (Table 4.1.2), they are known to be used in elaborate and characteristic ritualised patterns of behaviour. These often very conspicuous motor acts can be comprised within the term "marking behaviour". The present author failed to find any kind of marking behaviour during his extended obserations of all gibbon species in captivity. Likewise, no marking behaviour has been reported from other studies on the behaviour of wild or captive gibbon groups (for a list of references, see reviews by Chivers, 1984; Leighton, 1987; Tuttle, 1986). Interviews with staff members in several zoos revealed only two observations during which gibbon behaviour centred around a skin gland, one in *H. syndactylus* and one in *H. leucogenys* (see Section 4.2.2). Only the latter of these observations could possibly be identified as marking behaviour, and even here the gibbon's ventral area was involved, but apparently not the sternal area. Probably, the function of gibbon sternal glands does not correspond to that of the sternal glands in other primates (see Section 4.2.2).

In addition to sternal glands, fields of coloured glands have been found in various other regions of the skin in gibbons (see Section 4.2.2). Apparently, no equivalent observations have been made with other primates.

The association of marked body odour and high secretory activity suggests that the gland is mainly responsible for the characteristic body odour of the siamang. The odorous qualities of the secretion and the evidently increased – although not quantified – glandular activity on hot days give some hints as to the functional importance of the sternal gland of the siamang, which may apply to sternal glands of other gibbons as well. A primary function can be supposed to lie in olfactory communication, although a more precise interpretation cannot yet be provided. Odour-producing skin glands in mammals are usually thought to provide information on the subject's species, sex, individual identity, the state of its physiological processes, or its propensity to perform a certain behaviour (see reviews by Eisenberg & Kleiman, 1972; Mykytowycz, 1970). Secondly the gland may possibly play a role in thermoregulation through increased "sweating" under high-temperature conditions. In view of the small size of the sternal glandular area, one would not expect this to be more than a minor role.

A similar observation was made on the fields of coloured glands in *H. leucogenys* (see section 4.2.2), during an exceptional situation which resembled an experiment with one control: Of two gibbon females which had to be captured with a net, only one experienced considerable emotional as well as physical stress during capture, under otherwise identical conditions. High secretory activity was observed in this female only, and may have been the result of either stress or elevated body temperature, similar to the observations on the sternal gland in the siamang. Unlike the latter, the fields of coloured glands would be large enough to serve an effective role in thermoregulation.

It is interesting to note that the main secretory activities of the siamang's sternal gland (and apparently the fields of coloured glands in *H. leucogenys*) seem to occur in situations virtually identical to those of the axillary organ of humans: during elevated temperatures and stress (Montagna, 1981, 1982). The logical connection between gibbon skin glands and the axillary organs of humans and the African apes has a more physical equivalent: It has been mentioned that gibbons may exhibit concentrations of coloured pores in various parts of the skin, and the axilla is one of these regions.

In view of the number of histological, physiological and biochemical similarities between sternal glands in gibbons and axillary glands in humans described above, we may suppose that an analogy in function may also exist to some degree. Although the function and importance of the human axillary organ are still not very well understood, it has been suggested that it may play a role in thermoregulation (Keele et al., 1982; Montagna, 1962) and in olfactory communication (Hold & Schleidt, 1977; Labows et al., 1982; Russell, 1976; Schleidt & Hold, 1982a, 1982b; Stoddart, 1990), but evidence for the latter function still seems inconclusive (Doty, 1981; Doty et al., 1978).

It is generally believed that, compared with the situation in strepsirhine primates (Bourlière et al., 1956), specialised skin glands are relatively rare in monkeys and especially in apes, where olfactory communication appears to play a less pre-eminent role (Marler, 1965). In a review article on communication of apes, it has been stated that "apart from genital secretions, there seems to be no evidence of the discrete glands specialised to produce chemical signals that are commonly found in prosimians and are also present in both platyrrhine and catarrhine monkeys" (Marler & Tenaza, 1977). However, such specialised skin glands as the sternal glands and axillary organs have now been reported to occur in every hominoid genus, probably in every species. The use hominoids actually make of olfactory communication may still be underestimated at present. In addition, the discovery of specialised glandular organs in the skin of gibbons suggests that, even in the relatively well-documented apes, external anatomy still remains incompletely described and deserves further attention.

Finally, the observation that glandular activity may change the colouration of female gibbons of the *concolor* group raises the intriguing possibility that skin glands in these gibbons might, in addition to olfactory communication, play a role in visual communication as well.

7.2.5 Summary: Evolution of Gibbon Skin Glands

The results of the present study on gibbon skin glands and the information on skin glands in other primates (reviewed in section 4.1) can be used for a provisional reconstruction of the evolution of skin glands in gibbons and other hominoids. In the following paragraphs, a hypothetical scenario will be presented (summarised in Figure 7.2.1). The numbers indicated on the branches of the phyletic diagram will be referred to in parentheses in the following text. Because few species-specific characteristics of gibbon skin glands have been found, the hypothetical scenario does not show much diversification at the species level.

The possibility that the various sternal glands of primates are homologous characters, as has previously been proposed (Epple & Lorenz, 1967; Schaffer, 1940), has yet to be subjected to critical examination. Hill et al. (1959) suggested that medioventral glandular fields in primates seem to be a "retained primitive feature inherited from tupaioid ancestors."

In view of the large number of primates and other mammals known to both possess a sternal gland and to use it for marking behaviour (see Table 4.1.1 and 4.1.2), it seems reasonable to assume that this combination of characteristics can be regarded as primitive when discussing the evolution of gibbon skin glands (1).

Whereas sternal glands occur in most (probably all) genera of New World monkeys, they have been reported to occur in few species of Old World monkeys. Apparently, the gland has been repeatedly reduced in the latter group (2). But those species which have the sternal gland have been reported to use it for marking behaviour. The alternative interpretation that the sternal gland has been evolved several times independently in anthropoids appears less likely.

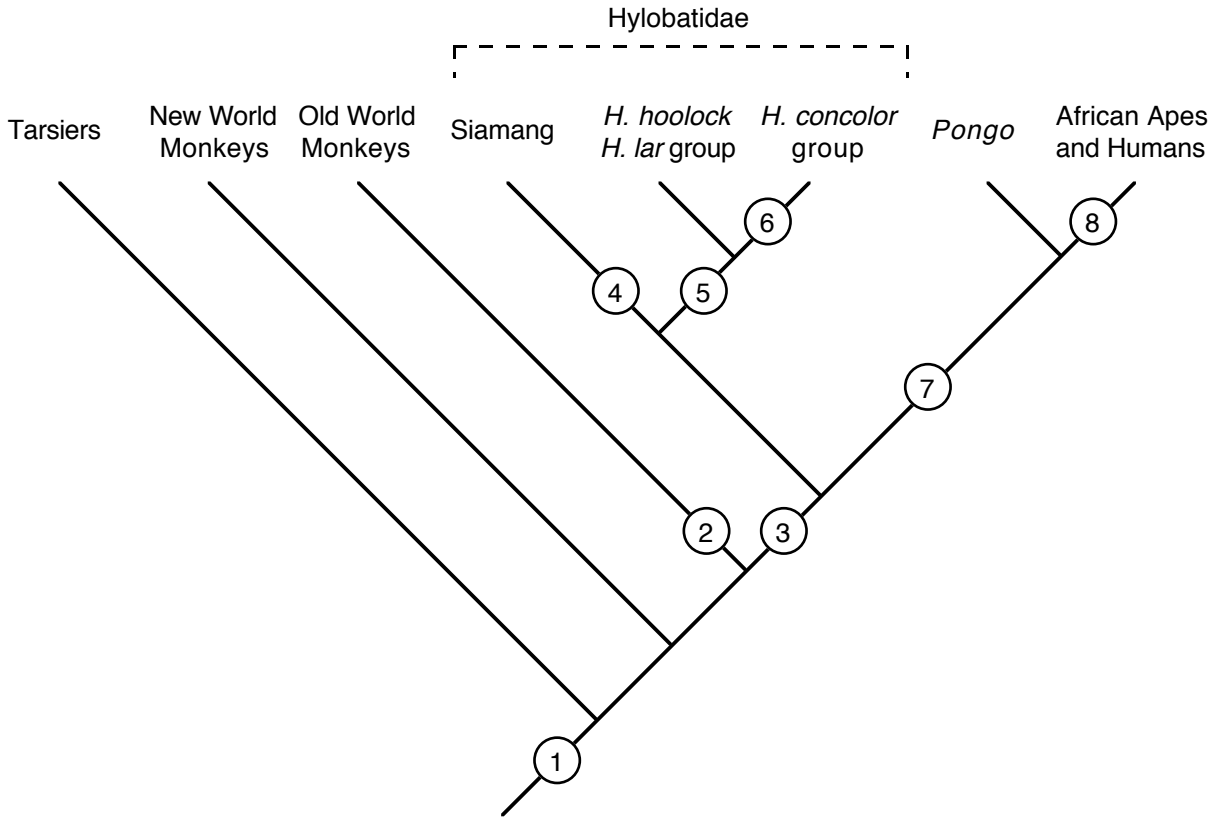


Figure 7.2.1: A phyletic diagram for extant anthropoids showing a hypothetical scenario of the evolution of skin glands. Legend: 1. sternal gland present, used for marking behaviour; 2. sternal gland lacking in many species; 3. sternal gland undergoes functional change, no marking behaviour, secretion of steroid hormones in sternal region; 4. unpigmented sternal skin in neonates and young infants; 5. reduction of body odour; 6. specialisation of fields of coloured pores in various sites of the body, no or reduced secretion of the steroid hormones tested in present study from skin glands; 7. sternal gland variable (reduction); 8. sternal gland absent, axillary gland present. See text for further details.

As the sternal gland occurs among hominoids, but is not known to be involved in marking behaviour, it is reasonable to assume that it only subsequently altered in function (3, see also section 7.2.4). Secretion of steroid hormones from skin glands probably occurred in the hominoid ancestor. Because a characteristic body odour is known for several, only distantly related members of the hominoids (*H. syndactylus*, *Pongo*, *Gorilla*), it is possible that this is a homologous characteristic. It then would be symplesiomorphic within the hominoid group. It is unknown whether the fields of coloured pores which have been described for gibbons occur in

other primates. They can only be observed during careful close examination and could easily have escaped detection in other species. Because the axilla is one of the regions where these fields occur in gibbons, and because most members of their sister group (i.e. the great apes and humans) have an axillary organ which may have evolved from such a field, it is possible that similar fields occurred in the common ancestor of all hominoids (3).

Among the Hylobatidae, only the siamang shows a typical body odour. In addition, it shows a peculiar sternal patch of unpigmented glandular skin in neonates and young infants which has not been found in other species. This may be a specialised characteristic of this species (4). In all other gibbons, the body odour is considerably reduced (5). In the *concolor* group (6), the sternal gland appears to be reduced in some individuals. On the other hand, fields of coloured glands show what is here interpreted as a specialisation of the *concolor* group: Secretions from these fields are able to change the fur colouration of adult females (and possibly of young infants in their natal, light coat, too). This has not been observed in other gibbons, although they, too, show fields of coloured pores. Zero (or reduced) concentrations of the steroid hormones analysed in the present study from skin gland secretions may be a derived characteristic of the *concolor* group, but it is not clear whether it is restricted to this group. Only few members of the *lar* group were available, and these were relatively variable in the steroid concentrations found in the sternal area.

Among the great apes and humans, the sternal gland is only found in the orang-utan, and even there it is found chiefly in juvenile males and has been described as being in a stage of regressive evolution (Weber & Abel, 1928; Wislocki & Schultz, 1925). Probably, this reduction of the sternal gland already occurred in the common ancestor of this group (7). In the African apes and humans, the sternal gland has completely disappeared (8). Instead, a well developed axillary organ is probably a synapomorph characteristic of this group.

Similarities between the axillary glands of humans and the African apes include the macroscopic aspect of the glands, their microscopic structure, chemical properties of their secretions, the external stimuli which lead to increased secretion, and, possibly, the supposed

functions of these glands in olfactory communication and thermoregulation. Moreover, gibbons were discovered to exhibit fields of coloured pores in various areas of the skin, and the axillary region is **one** of these fields.

It seems unlikely that all these similarities between the gibbon skin glands and the axillary organs in humans and the African apes are the result of independent, convergent evolution. It has not previously been possible to explain the phylogenetic origin of the axillary glands. The results presented in this study suggest that axillary glands may have evolved from a **system** of skin glands centred around the **sternal** gland, that is, from a condition **similar** to that seen in modern gibbons.

7.3 Visual Communication

7.3.1 Light Circumfacial Markings and other Light Markings

The observations on the occurrence of a white brow band in the Duisburg siamangs suggests that the genetic substrate for the formation of the face markings typical of gibbons is present in the siamangs, too. However, its phenotypic manifestation seems to be rare and may be genetically suppressed. If this is true, then the facial pattern in gibbons would be a primitive characteristic, and the absence of the pattern in the Kloss gibbon and the siamang would be a derived condition. This finding supports the opinion of Groves (1972), but is in contrast to other more recent studies (Creel & Preuschoft, 1984; Haimoff, 1983a; Haimoff et al., 1982, 1984), which labelled the absence of a facial pattern as a primitive character state in their analyses of gibbon phylogeny and systematics.

There is yet another possible interpretation of the occurrence of the brow band characteristic in siamangs: The occurrence of the trait in the family line in Duisburg could be the result of a *de novo* mutation; its resemblance to the facial markings of other gibbons would then be pure coincidence. However, further evidence is available indicating that the brow band characteristic in the Duisburg siamangs is instead an atavistic trait which corresponds to, and is homologous with, the facial patterns in other gibbons: In one of the females, "Trine", white hair can be found on other parts of her body: This animal has a distinct tuft of long white hair above each ear. In addition, the big toes are covered with purely white fur, and the medial phalanges of hands and feet also carry white hair.

This finding is of interest, because the parts affected by the white colouration are exactly those which show diagnostic white or pale colouration in some other gibbon species: As has been described above (Section 5.1), a bright or white corona can typically be found in pileated gibbons (*H. pileatus*), in Bornean agile gibbons (*H. agilis albibarbis*) (Marshall & Sugardjito,

1986), p. 141), and – at least in certain developmental stages, but rarely in adult males – in male crested gibbons (*H. concolor*, *H. leucogenys*) (for a description of the characteristic in crested gibbons, see Geissmann, 1989). Light hands and feet are characteristic for white-handed and pileated gibbons (*H. lar* and *H. pileatus*, respectively), but also occur in some hoolock females (*H. hoolock*, especially in *H. h. leuconedys*, see Groves, 1972, p. 66) and in about 24% of individuals of *Hylobates muelleri funereus* (Marshall & Sugardjito, 1986, p. 143). It is important to note that no white markings occur in the Duisburg siamangs in those body parts where it would be atypical for other gibbons as well, for instance on the chest, arms, or legs.

The photographs found in the archives of the Duisburg Zoo contain additional evidence supporting the interpretation that the white tufts over the ears in one of the siamang females correspond to a white corona: The same female, at the age of about 8 months, had a fully developed bright corona, which was at least as conspicuous as in those species, where a corona is known to occur normally. When the animal became older, its crown was apparently reduced until only the tufts above the ears remained.

The observations made on the siamangs at the Duisburg Zoo and some additional siamang individuals suggest that their white markings can be interpreted as reappearance of a primitive feature of the fur colouration in ancestral siamangs (and other gibbons), whereas the common monochrome black fur in recent siamangs represents a derived character-state in gibbons. While most authors consider white hands and feet in gibbons as a derived characteristic (Creel & Preuschoft, 1984; Groves, 1984; Haimoff, 1983a; Haimoff et al., 1982, 1984), evidence for the opposite view is presented here for the first time.

7.3.2 Sexual Colour Dimorphism

Some gibbon species show a striking sexual dimorphism in colouration, these species include *H. concolor, H. hoolock, H. leucogenys* and *H. pileatus*. Some sexual colour dimorphism also occurs in *H. agilis*, but is restricted to the facial markings.

Sexual dichromatism in gibbons develops according to three different ontogenetic plans: In *H. concolor, H. hoolock, H. leucogenys*, infants are born with a light natal coat, somewhat similar in colouration to that of the adult female. During the first year of life (Delacour, 1934), at the age of about one year (Groves, 1972), or during the second year of life (Dittrich, 1979), the infants change colouration and assume a dark coat which is virtually identical to that of an adult male. At about the time of sexual maturity (at around 5-8 years of age), females only change colouration a second time and adopt the colouration typical of adult females (Delacour, 1934, 1942; Fischer, 1980, 1981; Groves, 1972; McCann, 1933; Peart, 1935; Pocock, 1905).

As in the colour sequence described above, infants in *H. pileatus* are born with a light natal coat, somewhat similar in colouration to that of the adult female. At the age of about 1.5 -2 years of life (own observation), the infants change colouration and assume a patterned coat (with black cap and black ventral shield) which is even more similar to that of an adult female. About when attaining sexual maturity (at around 5-8 years of age), males change colouration a second time and adopt the black colouration typical of adult males, while females simply reduce the whitish face ring to a thin brow band and become black in the gular region (Dobroruka, 1979; and author's own observations).

In *H. agilis*, young animals show a broad, whitish face ring, which is differentially reduced upon reaching adulthood: Adult males usually keep a distinct white brow band and whitish cheek patches; adult females usually lose the cheek patches and the brow band often becomes thin and divided in two halves.

Sexual dichromatism is uncommon in primates (see below). It seems to be a widely accepted view that this represents a derived characteristic in gibbons (Chivers, 1977; Creel & Preuschoft, 1984; Fooden, 1969; Haimoff, 1983a; Haimoff et al., 1982, 1984). So far, only Groves (1972) has postulated the occurrence of sexual dichromatism in a hypothetical common ancestor of gibbons, though without explaining the basis for this interpretation. To judge from the ontogenetic development described above, gibbons appear to exhibit at least three different, unrelated types of sexual dichromatism. Sexual dichromatism probably evolved independently in several phyletic lines of the gibbon radiation. Groves' view (1972) – which postulates a sexually dichromatic ancestor of gibbons – is less convincing, because this would imply that sexual dichromatism was abandoned in at least two phyletic lines, only to be reinvented later.

The ontogenetic development of sexual dichromatism in the gibbons of the *concolor* group (*H. concolor* and *H. leucogenys*), *H. hoolock* and to lesser degree *H. pileatus* is remarkable because it includes long phases during which young animals resemble adult animals of the opposite sex. This is shown in Table 7.3.1a. A similar phenomenon (Figure 7.3.1b) is also seen in the ontogeny of song development of gibbons of the *concolor* group (as described in section 3.2), where immature animals of either sex produce great call-like phrases only, whereas in adult animals, great calls are uttered only by females. Great call-like phrases by immature male gibbons have not so far been reported for other gibbon species, but the author made one such observation in a young male *H. agilis* (see section 3.2). This may be rare, however, because immature males of the *lar* group seem to be inhibited from singing with their parents (Leighton, 1987).

Table 7.3.1: Development of sexual dimorphism in fur colouration and song in gibbons. Double bars indicate the occurrence of major changes in fur colouration or song repertoire.

	Dimorphic characteristic	Taxon	Sex	Age class		
				Infant	Juvenile	Adult
a.	Fur colouration	*concolor* group	male	light natal coat	like adult male	black adult coat
			female	light natal coat	like adult male	light adult coat
		H. hoolock	male	light natal coat	like adult male	black adult coat
			female	light natal coat	like adult male	light adult coat
		H. pileatus	male	light natal coat	like adult female	black adult coat
			female	light natal coat	like adult female	light adult coat
b.	Song repertoire	*concolor* group	male	similar to adult females	similar to adult females	male song
			female	similar to adult females	similar to adult females	female song (great calls)

Interestingly, a similar observation has been reported for the song development of an East African bird species: Mated pairs of the monomorphic D'Arnauds barbet (*Trachyphonus d'arnaudii*) are known to produce duet songs with sex-specific repertoire (Albrecht & Wickler, 1968; Wickler, 1973; Wickler & Uhrig, 1969). Young *T. d'arnaudii emini* of both sexes that were raised in captivity produced exclusively male calls during their first months of life. Young females were observed to first produce their sex-specific calls when confronted with an unrelated, adult male (Anzenberger, 1974).

The common element in the observations on D'Arnauds barbet and the gibbon species listed in Table 7.3.1 is the fact that sexually dimorphic elements (song or fur colouration) are masked in immature animals. This masking effect is especially prominent in the gibbons of the

concolor group, where young animals adopt a "unisex" pattern both in fur colouration *and* in song repertoire. The sex-specific characteristics are only revealed when the animals become sexually mature. It is possible that the masking effect evolved as a mechanism for incest avoidance, which is of particular importance in "bonding-motivated" animals (Bischof, 1972, 1975): in "animals having the ability to recognise each other *individually*, and the *inclination to affiliate with* acquainted conspecifics … selective preference must generally hit family members, and one could expect that the maturing young would practise sexual activity inside this ready-formed zone of sympathy." It is possible that the masking effect would reduce sexual attractivity of young family members to each other and to their parents.

It is generally believed that there is a correlation between monogamy and monomorphism (i.e. a lack of sexual dimorphism), and many examples in birds and mammals have been cited (Brown, 1975; Helversen, 1980; Kleiman, 1977; Tilson & Tenaza, 1976; Wickler, 1969); but see Farabaugh (1982), and Hrdy and Hartung (1979). "In species exhibiting long-term pair bonding, there is often a reduction in the degree of sexual dimorphism, both behavioural and morphological" (Kleiman, 1977). Gibbons apparently do not follow this rule, either in their song vocalisations or in their fur colouration (as shown above). Although the occurrence of sex-specific loud calls does not appear to be rare among primates (e.g. section 7.1.2), the amount of sexual dichromatism shown by some gibbon species is exceptionally pronounced.

Table 7.3.2 lists all primate species known to show significant sexual dimorphism in fur colouration. As a rule, males are either darker and/or have more contrasting face markings than females (92%). Monogamy is relatively common among sexually dimorphic primates (69%), although this social system occurs only in about 3% of mammals (Kleiman, 1977) and in about 14-18% of primates (Hrdy & Hartung, 1979; Rutberg, 1983). This casts doubt on the general correlation between monorphism and monogamy, at least as far as primates are concerned.

Table 7.3.2: Sexual dimorphism in fur colouration in primate species. [1]

	Species	Males compared to females		Monogamy	Natal coat more similar in colour to adult	
		Male darker	Male face markings more contrasting		male	female
1.	*Lemur coronatus*	–	+	–	n.a.	n.a.
2.	*L. fulvus*	–	+	–	n.a.	n.a.
3.	*L. macaco*	+	–	–	n.a.	n.a.
4.	*L. mongoz*	–	–	+?	n.a.	n.a.
5.	*L. rubriventer*	–	+	+	n.a.	n.a.
6.	*Pithecia aequatorialis*	–	+	+	?	?
7.	*P. pithecia*	+	+	+	n.a.	n.a.
8.	*Alouatta caraya*	+	–	–	–	+
9.	*Hylobates agilis*	–	+	+	+	–
10.	*H. concolor*	+	–	+	–	+
11.	*H. hoolock*	+	+	+	–	+
12.	*H. leucogenys*	+	+	+	–	+
13.	*H. pileatus*	+	+	+	–	+
	% +	54%	69%	69%	17%	83%
		92%				

[1] n.a. = not applicable, refers to species with no distinct natal coat.

In order to further compare various forms of sexual dimorphism among gibbons, a Multidimensional Scaling (MDS) analysis has been carried out. This analysis included not only variables representing dimorphism in fur colouration, song repertoire and body weight, but also several other variables including geographical distribution, isolation and climate. None of the variables accounting for sexual dimorphism was found to be closely associated with any other and these may, therefore, be largely independent characteristics.

Apparently, sexual dimorphism is a composite of several characteristics. This does not mean, however, that a correlation between sexual monomorphism and monogamy does not exist, but such a correlation does not necessarily exclude *all* forms of dimorphism. It may be useful

always to make clear what kind of sexual dimorphism one is referring to. Sexual dimorphism in body weight, for instance, appears to be very low in gibbons. In this case, the correlation between sexual monomorphism and monogamy appears to be confirmed by the gibbon data.

7.3.3 Natal Coat

The infants of many primate species possess distinctly coloured or patterned coats and skin (Alley, 1980; Marchant & Dolhinow, 1990; Tilson, 1976). It has been suggested that these characteristics may elicit caregiving behaviour from older conspecifics (Alley, 1980). Several species of gibbons also have distinct natal coats. Interestingly, this concerns exactly the same species which also show the most pronounced sexual dichromatism (*H. concolor*, *H. hoolock*, *H. leucogenys*, and *H. pileatus*). Table 7.3.2 lists whether natal coats of sexually dichromatic primates are more similar to adult females or adult males. It appears that natal coats of dichromatic species tend to follow more closely the female colour pattern, suggesting that these natal coats may serve a camouflage function when the infants are carried by their mother. This does not exclude other functions, but camouflage is clearly not a function fulfilled by the flamboyant natal coats of some species of leaf monkeys (Alley, 1980).

7.3.4 Body Size

Previous Publications:

Body weights of wild-shot animals are frequently used as a measure of 'total size' (Jungers, 1984). Many previous publications reviewing gibbon body weights have directly or indirectly been using data published by Schultz (1933, 1973). In the case of some gibbon species this may raise serious problems, because Schultz had apparently at various times identified many gibbons in his and other collections as "*H. leuciscus*," as "*H. cinereus*," or as "*H. moloch*", irrespective of whether they came from northern Borneo (*H. muelleri*) or Java (*H.*

moloch). Even more unfortunate was Schultz's continued identification of some grey gibbons from Borneo (mainly *H. muelleri muelleri*, but also *H. m. funereus* and *H. agilis albibarbis*) as "*H. concolor*" (e.g. (Schultz, 1930, 1933, 1944, 1973), even though he must have known that the name was pre-occupied by black gibbons from Indochina (see Groves, 1972, p. 12f for a brief summary of the history of the name "*H. concolor*").

It has previously been demonstrated that Schultz (1972) used neonatal body weights obtained from fixed specimens (Geissmann & Orgeldinger, in prep.). The present author was unable to find out where Schultz obtained the "new" body weights of 5 male and 4 female siamangs published in Schultz (1973), but he suspects that they were taken from the fixed siamangs preserved at the Anthropology Institute of Zürich University. These specimens were obtained from the Institute of Anatomy of Zürich University, but no information on the origin or on the fresh body weight of these specimens is available.

Unfortunately, the body weights of two adult females of *H. pileatus* (Schultz, 1942) had also to be excluded from the present study. In the archive of the late Prof. A.H. Schultz, the present author found hand written notes of Schultz stating that these weights were estimates obtained by comparing skull measurements of *H. pileatus* specimens from the Spaeth collection (Geissmann, 1991b) with *H. lar* specimens of known body weight collected during the APE expedition (Coolidge, 1937a, 1937b, 1938; Schultz, 1938, 1944).

Uncritical citation of Schultz's body weights on species such as "*H. moloch*" or "*H. concolor*" (or of other articles which use his data) continues (Tuttle, 1986), thus further spreading the confusion. For example, Marshall and Sugardjito (1986), p. 138) wrote "We cannot find where Schultz [1933] obtained the weights of 21 concolors, mean 5.7 kg, which seems too slight."

Another problem occurs if the data of Lyon (1908) and Hrdlicka (1925) for *H. agilis* are combined (Jungers, 1984). Because both samples use gibbons collected in Sumatra by W.L. Abbott, both contain at least in part the same data.

The Data Set of the Present Study:

Whenever possible, body weights used for the present study were compiled directly from the original records of the collector or from the specimens' labels (see Appendix 10.9). Some samples are very small and not very reliable (e.g. for *H. moloch* and *H. pileatus*). Especially the weight for *H. moloch* appears to be relatively high, as compared to an earlier estimate derived from a craniometric study (Jungers, 1984). No data are available for *H. leucogenys gabriellae*, the southernmost subspecies of the light-cheeked crested gibbons. To judge from the cranial measurements, this form may be less heavy than other gibbons of the *concolor* group, except possibly *H. concolor hainanus* (Geissmann, 1989).

According to the traditional view, gibbon body weights fall into two size classes, with the siamang (about 11 kg) on one side and the gibbons (about 5 kg) on the other (Kavanagh, 1983; Napier & Napier, 1985). It has for some time been suggested that the hoolock and the crested gibbons (*concolor* group) are of distinctly higher body weight than gibbons of the *lar* group, and that a trichotomy may better describe the weight distribution in gibbons than a dichotomy (Jungers, 1984). Unfortunately, wild-shot body weights for the *concolor* group have been largely unavailable to previous authors (Jungers, 1984; Susman, 1991). The relatively large samples of body weights of wild-shot *H. concolor*, *H. leucogenys* and *H. hoolock* compiled for the present study demonstrate that the traditional dichotomy is inaccurate. In these three species, body weights average around 8 kg, 7 kg and 7 kg, respectively, and are distinctly higher than mean body weights of species of the 44-chromosome gibbons.

Considerable differences in body weight were also found between various populations of *H. lar* (Figure 7.3.1). The Sumatran subspecies (*H. l. vestitus*) and the Malayan form (*H. l. lar*) weigh about 4.9 kg and 5.1 kg on average. The populations of Thailand north of the peninsula are slightly heavier (*H. l. carpenteri*: 5.5 kg, northern *H. l. entelloides*: 5.6 kg). The gibbons from the approximately central part of the peninsula (just north of the isthmus of Kra), however, show considerably higher weights (central peninsular *H. l. entelloides*: 6.3 kg). The reason for the elevated body weights of white-handed gibbons in this area is not clear. It is possible that the

isthmus represents a certain obstacle for gene exchange, but it is not known whether gibbons north and south of the isthmus differ in any of their characteristics.

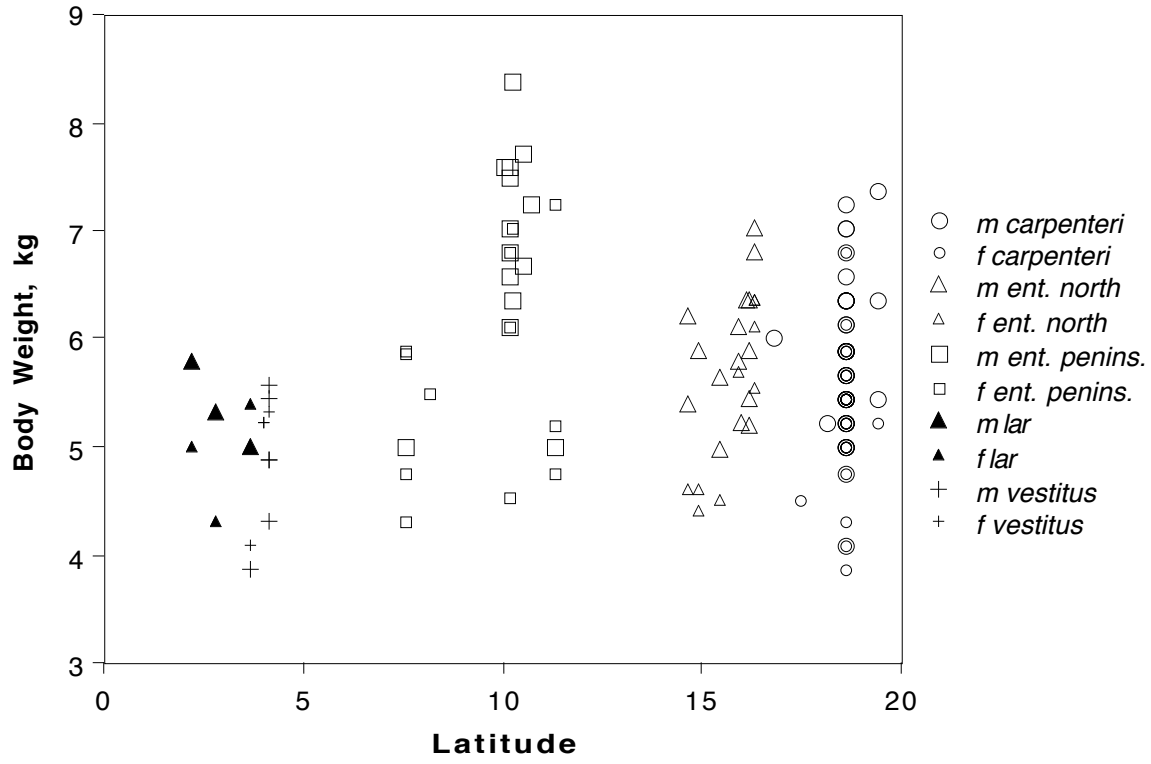


Figure 7.3.1: Variation in body weight with latitude in populations of *Hylobates lar*. Abbreviations: m = male; f = female; ent. north = northern *H. l. entelloides*; ent. penins. = central peninsular *H. l. entelloides*.

Evolution of Gibbon Body Size:

There is some controversy about whether the gibbon ancestor was of larger or smaller body size than modern species, and whether the high body weight in siamangs represents a primitive or a derived character state. According to Schultz "the gibbons have certainly no share in the trend toward a striking increase of in body size, characteristic of the higher primates [great apes]. This trend is at best indicated in the siamang. *Hylobates* (*Brachitanytes*) *klossi* has most likely degenerated to a slight extent in its body size after its isolation on the relatively small Mentawi Islands. Such dwarfing is quite common among insular types" (Schultz, 1933). Apparently, Schultz regarded the larger size of the siamang as a derived feature. A similar view is also presented by Tuttle (1975): "Size increase led to certain modifications in siamang lifeways". In contrast, Groves (1972) regarded the higher body weight of the siamang as a symplesiomorph hominoid characteristic.

Tyler (1991) reported on several morphological characteristics ("large-brachiator traits") among hylobatids which he recognised as being adaptations to support a weight greater than 30 kg, and other biological variables (such as gestation time and longevity) which are characteristic of larger animals. He concluded that modern hylobatids derived from a large-bodied ancestor, possibly a late "sivamorph" clade.

One way to resolve the controversy would be to study the fossil hylobatids. Unfortunately, as discussed in chapter 1.2, fossil material which could reliably attributed to the hylobatid branch is available only since the middle Pleistocene (i.e. younger than 1 myr) and consists chiefly of individual teeth. A comparison of dental measurements of this material with modern gibbons fails to produce a consistent picture:

Pleistocene Material of *H. syndactylus* from Java has been described by Badoux (1959). Only two of 40 teeth are not within the range of their recent homologues (Hooijer, 1960).

Hylobatid teeth from early Holocene cave material from Sumatra and Borneo has been described by Hooijer (1960). In the material from Sumatra, *Hylobates* sp. was reported to be scarce and "either in the upper range of variation for the recent specimens, or even above this

range in dental dimensions", while teeth identified as *H. syndactylus subfossilis* were of statistically significant larger average size. Cave material from Sarawak, Borneo was "indistinguishable from, and either within the limits or slightly above the range of recent *Hylobates moloch abbotti* inhabiting the western parts of Borneo" (Hooijer, 1960). Additional teeth recovered from Niah Great Cave in Sarawak, Borneo, were "indistinguishable from the recent gibbon of Borneo" and "either within, or just above the limits of the recent material" (Hooijer, 1962).

Provided that all the fossil teeth have been properly identified, this leaves us with the inconclusive situation of Pleistocene siamangs of Java apparently being of about the same size as modern siamangs, and early Holocene siamang from Sumatra being significantly larger than their modern equivalents, while smaller gibbons from early Holocene cave material were of about the same size as modern gibbons occurring on the same islands.

7.3.6 Summary: Evolution of Gibbon Fur Characteristics

The occurrence of a white brow band in siamangs is documented for the first time. The trait appears to be inherited (possibly autosomal dominant inheritance). Additional white markings occur in at least one of the study animals on hands, feet, and in a corona above the ears which darkened with age. This finding casts doubt on recent studies identifying the absence of white facial markings in gibbons as a primitive character state. Likewise, the presence or absence of white hands and feet and of a bright corona have to be reconsidered with respect of their evolutionary history. The present study suggests that all these characteristics are primitive gibbon traits.

The full face ring appears to be the ancestral form of light face markings in gibbons. It occurs – at least in young animals – in all species of the *lar* group, in females of *H. hoolock* and in females *H. leucogenys* (except *H. l. gabriellae*). Gibbons with light brow bands only, light cheeks only, or without facial markings probably represent derived character states.

It can be shown that several distinct forms of sexual dichromatism exist in gibbons. Sexual dichromatism has probably evolved several times. Although it is not clear whether the ancestral gibbon was sexually dichromatic or not, the latter condition is more probable. With a sexually dichromatic ancestor of all gibbons, sexual dichromatism would have disappeared in at least two phyletic lines only to be reinvented later.

It has repeatedly been suggested that there is a general correlation between monomorphism and monogamy. As far as weight dimorphism is concerned, gibbons appear to correspond to this rule, but not in some other forms of sexual dimorphism, such as fur colouration and song repertoire. In gibbons, these forms of sexual dimorphism appear to be largely independent characteristics and may be under different selective pressures.

Young animals of several species (*H. concolor*, *H. leucogenys*, *H. hoolock* and *H. pileatus*) exhibit a "unisex" fur colouration and – at least in the *concolor* group – a "unisex" song repertoire, thus masking their sexual identity. This condition may have evolved as a mechanism for incest avoidance.

Natal coats in gibbons, and possibly in other sexually dichromatic species, may have evolved as a camouflage device. This does not exclude the possibility that they also serve as elicitors of caretaking behaviour, as has been proposed for natal coats in other primates.

A large data set of body weights of wild-shot adult gibbons was compiled for the present study. The traditional view of a dichotomy between small gibbons of the *lar* group and the larger siamang can be shown to be less clear-cut if the gibbons of the *concolor* group and *H. hoolock* are included in the comparison. Evidence for the body size of the ancestral gibbons is, however, inconclusive.

7.4 Phylogenetic Evaluation

The data matrix of the present study contained not only characters of vocal, olfactory, and visual communication, but also a number of "non-communicatory" features (describing gibbon anatomy, morphology and karyology) which were mainly collected from the literature. Some criticism has been directed at the one study which is most closely related to the present one (Haimoff, 1983b; Haimoff et al., 1982, 1984), because of the choice and the coding of its karyotypic characters (van Tuinen & Ledbetter, 1983) and because of an alleged oversimplification of its vocal and visual characters (Marshall & Sugardjito, 1986). The present study tried to benefit from these criticisms. The data matrix is considerably larger (14 gibbon taxa, 92 characters) as compared to some earlier studies which included characters on gibbon communication for phylogeny reconstruction (e.g. Haimoff et al., 1982: 9 taxa, 55 characters). Most of the new data stem from the present author's own research, as described above.

A phylogenetic analysis using parsimony was carried out both with the whole matrix, and with the subsets on vocal, visual and "non-communicatory" data alone. These subsets were of similar size (29, 33, and 26 characters, respectively). The subset on olfactory communication (4 characters) was too small for an individual analysis.

An evaluation of the characters used in this study revealed that the polarity of the character states (i.e. primitive state vs. derived state) was unknown in 43% of the whole matrix. This contrasts with earlier studies, where polarity estimates were presumed to be available for all characters (Creel & Preuschoft, 1984; Haimoff, 1983b; Haimoff et al., 1982, 1984).

Absence of polarity estimates was more marked in the subsets on vocal and visual communication (48% and 64%, respectively) than in the "non-communicatory" data (19%). The difficulty in obtaining convincing estimates of character polarity in vocal and visual data is largely due to the absence both of singing behaviour and coloured fur patterns in the obvious outgroup to the gibbons, the great apes. A comparison of the gibbons with this outgroup may

have influenced the view that recent gibbons derived from a "large, black ancestor" (Chivers, 1977, p. 557), i.e. "of a *Symphalangus*-like form" (Groves, 1984, p. 556). Results of the present study suggest, however, that light circumfacial markings and a light corona (and possibly light feet) have been secondarily lost in siamangs and probably were present in the last common ancestor of the gibbons. Even the larger body size of the siamang, as compared to other gibbons, does not conclusively represent the ancestral condition, as has been discussed above. It appears that the great apes are a rather problematic outgroup for the analysis of gibbon phylogeny, as far as the vocal and visual characteristics of the present study are concerned.

Although previously published gibbon phylogenies differed from each other in the order of some speciation events, they largely agreed in several respects: The first branch to split off from the main stem of the hylobatids was either *H. syndactylus*, the *concolor* group, or a common ancestor of both (see references in section 1.3), followed by *H. hoolock* and then by *H. klossii*. Both the 44-chromosome gibbons and the *lar* group are usually regarded as monophyletic groups, and *H. klossii* is widely accepted as representing the earliest surviving branch of the former, but not a member of the latter. These "traditional" views were neither convincingly confirmed nor rejected by the analysis of the whole data matrix of the present study. The difference is probably related to the absence of polarity from a large part of the data set used here, as discussed above.

Several cladograms of earlier studies (Chivers, 1977; Creel & Preuschoft, 1984; Garza & Woodruff, 1993; Groves, 1972; Haimoff et al., 1982) have been tested with the data of the present study. All were found to be less parsimonious than those of the present study, but the disagreement with the data matrix used here was least pronounced in the cladogram proposed by Haimoff et al. (1982). Yet, the consistency indices of the cladograms presented here are rather low (range: 0.41-0.66) and imply extensive homoplasy: 34-59% of the evolution of these features requires parallelism or reversal. This corresponds to similar findings in earlier studies (Creel & Preuschoft, 1984, p. 600; Groves, 1984, p. 558). The analysis of individual subsets of the data matrix suggests that characters of vocal communication are better suited for

phylogenetic reconstructions than characters of visual communication, because the former (on average) yield higher bootstrap values and higher consistency indices (compare Figures 6.3.1 and 6.3.3, above).

The phylogenetic analysis of the whole data matrix using parsimony failed to resolve the gibbon radiation in much detail. Bootstrap values were very low for most branches, and the most parsimonious tree showed an almost inverse sequence of branching events than one of two trees only one step less parsimonious. Although the latter tree corresponds in several respects to the traditional view of gibbon phylogeny as described above (showing, for instance, a monophyletic group of 44-chromosome gibbons and a monophyletic *lar* group), the most parsimonious tree shows the members of the *lar* group branching off near the base of the tree and the *concolor* group being the last to differentiate. Interestingly, a purely phenetic analysis (UPGMA cluster analysis) of the whole data matrix more closely corresponds to the traditional view of the phylogenetic tree of gibbons.

As shown by the analysis of the individual subsets, the unexpected branching order mentioned above is determined mainly by the visual characters, whereas the subsets of vocal and "non-communicatory" characters correspond more closely to the "traditional" view of gibbon phylogeny. It should be mentioned again that the subset of visual characters is the one with the lowest proportion of characters with polarity estimates. The resolution obtained in the phylogenetic analysis of the whole data matrix would probably be much improved if the polarity could be estimated in a larger number of characters of gibbon communication, and especially those of visual communication.

In spite of the low resolution of the cladograms obtained from the analysis of the whole data matrix, the monophyly of the several groups is supported by the present study: a) *agilis* and *albibarbis*; b) *abbotti*, *funereus* and *muelleri*; and c) *concolor*, *gabriellae* and *leucogenys*. The finding of monophyly in the first two groups is of particular importance, because there has been some debate about whether *albibarbis* is a subspecies of *H. agilis*, *H. muelleri* or a separate

species (Groves, 1984; Marshall & Sugardjito, 1986). The results of the present study support the first option.

The evidence for monophyly of several groups of taxa, as found in various types of analyses, is summarised in Table 7.4.1. Little support was found for monophyly of either the 44-chromosome gibbons or the *lar* group. It is interesting to note that the most parsimonious cladograms yielded by the vocal and the "non-communicatory" data each showed *H. klossii* as an integral part of the *lar* group. A similar result has recently been reported by Garza and Woodruff (1993) on the basis of DNA sequence data. In contrast, most previous studies have considered *H. klossii* a sister group to the *lar* group (Chivers, 1977; Creel & Preuschoft, 1984; Haimoff, 1983a; Haimoff et al., 1982, 1984).

Table 7.4.1: Evidence for monophyly in selected groups of gibbon taxa, as found in various types of analyses carried out in the present study. [1]

Data set	Type of tree [2]	Groups of taxa				
		agilis and *albibarbis*	*abbotti*, *funereus* & *muelleri*	*concolor* group	44-chromosome gibbons	*lar* group
Whole data matrix	Bootstrap	+	+	+	–	–
	Most pars.	+	–	+	–	–
	Cluster	+	+	+	–	+
Subset: vocal data	Bootstrap	+	+	+	–	–
	Most pars.	+	+	+	+	–
Subset: visual data	Bootstrap	–	–	+	–	–
	Most pars.	(+) [3]	–	+	–	–
Subset: "non-communicatory" data	Most pars.	–	–	+	+	–

1 + evidence for monophyly, – no evidence for monophyly.

2 Most pars. = Most parsimonious tree.

3 evidence for monophyly in 3 out of 4 most parsimonious trees.

Finally, in all analyses using the whole data matrix, as well as in the most parsimonious trees obtained from the analysis of the vocal characters, the hoolock was the earliest taxon to branch off from the main stem of the hylobatids. This contrasts with all previously published cladograms, which usually show either *H. syndactylus*, the *concolor* group, or the common ancestor of both in that position. The significance of this finding from the present study is as yet unclear.

8a. Summary

8.a.1 Aims

In recent years, characteristics of gibbon communication have repeatedly been used to assess systematic relationships among hylobatids and to reconstruct their phylogeny. These interpretations were based on the assumption that homologous characteristics were concerned, and that the polarity of the character states (i.e. primitive state vs. derived state) was known. The reasons for these assumptions were rarely mentioned or convincingly explained.

The aims of the present study included: 1.) tracing the evolution of selected characteristics of gibbon communication and identifying, where possible, homology vs. analogy (i.e. convergent evolution) of characteristics, and primitive vs. derived character states across various gibbon species, and 2.) using these results for a reassessment of the gibbon radiation by reconstructing of a cladogram based on both the characteristics of gibbon communication and more traditional characteristics collected from the relevant literature. Characteristics from each of the following three communication modalities were analysed: Vocal, olfactory and visual communication.

8.a.2 Vocal Communication

The analysis of vocal communication was entirely devoted to gibbon singing behaviour. The present study supports the following conclusions on the evolution of gibbon songs:

1. The last common ancestor of recent hylobatids produced *duet* songs. Gibbon duets probably evolved from a song which was common to both sexes and which only later became separated into male-specific and female-specific parts (song-splitting theory). A process tentatively called "duet-splitting" is suggested to have secondarily led from a duetting species to a non-duetting species, in that the contributions of the pair partners split into temporally segregated solo songs.

2. The analysis of hybrid vocalisations supports the view that gibbon songs are largely genetically determined. A model is presented for females of the *lar* group which allows the prediction of characteristics in hybrid female songs of all species combinations up to at least the second generation.

3. Female great calls of all gibbon species are a homologous song phrase. The fast, bubbling trills of *H. muelleri* and *H. pileatus* are probably homologous features, as are the slower, frequency-modulated great calls common to *H. agilis* and *H. lar*. The acceleration of the rate of note emission during the great call is thought to represent the ancestral condition. The ancestor of modern gibbons probably produced great calls with a rate of note emission similar to that of *H. moloch*.

4. The gradual development of increasingly complex phrases from initially more simple phrases is believed to represent the primitive condition for male songs in gibbons, and the use of bi-phasic notes (alternate production of exhalation and inhalation sounds) during the song probably represents a primitive characteristic for gibbon vocalisations of both sexes.

8.a.3 Olfactory Communication

1. Whereas skin glands specialised for the production of olfactory signals have been described for many primates, such glands in gibbons were virtually unknown at the beginning of this study. The present study revealed that gibbons have a surprisingly complex glandular system which is centred around a sternal glandular organ and which appears to differ in anatomy and functions from what has been described so far in non-hominoid primates.

2. The occurrence of a sternal gland is probably a primitive character state in gibbons. In contrast to non-hominoid primates, no marking behaviour has been observed to occur in gibbons (and other hominoids), probably because of an altered function of the sternal gland in the last common ancestor of all hominoids. In the *concolor* group, the sternal gland appears to be less developed than in other gibbons; this is probably a derived characteristic of the *concolor* group.

3. In some gibbon species, steroid hormones (dehydroepiandrosterone, androstenedione, and testosterone) are accumulated in the sternal gland, and secretory activity of the gland is particularly high under elevated temperatures and under stress. Secretion of steroid hormones from skin glands probably occurred in the hominoid ancestor. The lack of (or reduced concentrations of) steroid hormones analysed in the present study, found in skin gland secretions, may be a derived characteristic of the *concolor* group. A characteristic body odour may be symplesiomorphic within the hominoid group but was secondarily reduced in all gibbons except the siamang.

4. Fields of coloured pores in various areas of the skin probably occur in all gibbon species, but it is unknown whether they occur in other primates. Because the axilla is one of the regions where these fields occur in gibbons, and because most members of the clade combining the great apes and humans have an axillary organ which may have evolved from such a field, it is possible that similar fields occurred in the common ancestor of all hominoids. In the *concolor* group, secretions from the fields of coloured glands can lead to changes in the fur colouration of adult females (and possibly of young infants in their natal, light coat). This has not been observed in other gibbons and may be a specialisation of the *concolor* group.

5. Similarities between the system of skin glands in gibbons and the axillary glands of humans and the African apes include the macroscopic aspect of the glands, their microscopic structure, the chemical properties of their secretions, the external stimuli which lead to increased secretion, and, possibly, the supposed functions of these glands in olfactory communication and thermoregulation. Moreover, gibbons exhibit fields of coloured pores in various areas of the skin, and the axillary region is one of these fields. It is unlikely that all these similarities between the gibbon skin glands and the axillary organs in humans and the African apes evolved independently in the two clades. It has not previously been possible to explain the phylogenetic origin of the axillary glands. The results presented in this study suggest, that axillary glands may have evolved from a system of skin glands centred around the sternal gland that is, from a condition similar to that seen in modern gibbons.

8.a.4 Visual Communication

The analysis of visual communication was mainly confined to characteristics of fur colouration, but a comparison of various forms of sexual dimorphism (including body size) in gibbons was also carried out.

1. The occurrence of a white brow band in siamangs is documented for the first time. The trait appears to be inherited (possibly an autosomal dominant inheritance). Additional white markings occur in at least one of the study animals on hands, feet, and in a corona above the ears. In contrast to other recent studies, the present study suggests that the presence of white facial markings, of white hands and feet and of a bright corona are primitive gibbon traits. The full face ring appears to be the ancestral form of light face markings in gibbons. Gibbons with light brow bands only, light cheeks only, or without facial markings probably represent derived character states.

2. Several distinct forms of sexual dichromatism exist in gibbons. It is most likely that sexual dichromatism has evolved several times. Although it is not clear whether the ancestral gibbon was sexually dichromatic or not, the latter condition is more probable.

3. It has repeatedly been suggested that there is a general correlation between monomorphism and monogamy. As far as weight dimorphism is concerned, gibbons appear to correspond to this rule, but not in some other forms of sexual dimorphism, such as fur colouration and song repertoire. In gibbons, these forms of sexual dimorphism appear to be largely independent characteristics and may be under different selective pressures.

4. Young animals of several species (*H. concolor*, *H. leucogenys*, *H. hoolock* and *H. pileatus*) exhibit a "unisex" fur colouration and – at least in the *concolor* group – a "unisex" song repertoire, thus masking their sexual identity. This condition may have evolved as a mechanism for incest avoidance. In contrast, natal coats in gibbons, and possibly in other sexually dichromatic species, may have evolved as a camouflage device. This does not exclude

the possibility that they also serve as elicitors of caretaking behaviour, as has been proposed for natal coats in other primates.

5. A large data set of body weights of wild-shot adult gibbons was compiled for the present study. The traditional view of a dichotomy between small gibbons of the *lar* group and the larger siamang can be shown to be less clear-cut if the gibbons of the *concolor* group and *H. hoolock* are included in the comparison. The debate on the body size of the ancestral gibbons is, however, not resolved conclusively.

8.a.5 Phylogenetic Evaluation

1. The data matrix of the present study was considerably expanded as compared to some earlier studies which included characters on gibbon communication for phylogeny reconstruction. It contained characters of vocal, olfactory, and visual communication, as well as a number of "non-communicatory" features (i.e. gibbon anatomy, morphology and karyology) which were mainly collected from the literature. A phylogenetic analysis using parsimony was carried out both with the whole matrix, and with the subsets on vocal, visual and "non-communicatory" data alone. The subset on olfactory communication was too small for an individual analysis.

2. An evaluation of the characters used in this study revealed that the polarity of the character states (i.e. primitive state vs. derived state) was unknown in 43% of the whole matrix. This contrasts with earlier studies, where polarity was estimated for all characters.

3. Previously published gibbon phylogenies differed from each other in the order of some speciation events, but largely agreed on a) the first branch to split off from the main stem of the hylobatids (either *syndactylus*, the *concolor* group, or a common ancestor of both), b) the intermediate position of *hoolock* and *klossii*, and c) the monophyly of each of the 44-chromosome gibbons and the *lar* group. These views were neither confirmed (nor rejected) by the analysis of the whole data matrix of the present study. The difference is probably related to the absence of polarity from a large part of the data set used here.

4. All cladograms of earlier studies tested here are less parsimonious than those of the present study. Yet the consistency indices of the cladograms presented here are rather low (range: 0.41-0.66), indicating extensive homoplasy (parallelism or reversal) in the evolution of these features. The analysis of individual subsets of the data matrix suggests that characters of vocal communication are better suited for phylogenetic reconstructions than characters of visual communication, because the former yield higher bootstrap values and higher consistency indices.

5. The significance of one finding of the present study – the early divergence of the hoolock from the main stem of hylobatids – is unclear; this was not found in earlier studies. The monophyly of the following groups is supported by the present study: a) *agilis* and *albibarbis*; b) *abbotti*, *funereus* and *muelleri*; and c) *concolor*, *gabriellae* and *leucogenys*. The finding of the first two groups is of particular importance, because there has been some debate about whether *albibarbis* is a subspecies of *H. agilis*, *H. muelleri* or an own species. The result of the present study supports the first option.

8b. Zusammenfassung

8.b.1 Ziele

In den letzten Jahren wurden zur Ermittlung der verwandtschaftlichen Beziehungen zwischen Gibbonarten und zur Rekonstruktion ihrer Stammesgeschichte wiederholt Merkmale der Gibbonkommunikation herangezogen. Diese Untersuchungen basierten auf der Annahme, dass man es mit homologen Merkmalen zu tun habe, und dass die Polarität der Merkmalszustände (ursprünglich oder abgeleitet) bekannt sei. Die Gründe für solche Annahmen wurden in der Regel weder erwähnt noch schlüssig hergeleitet.

Die vorliegende Untersuchung hatte folgende Ziele: 1.) Die stammesgeschichtliche Entwicklung einzelner Merkmale der Gibbonkommunikation wurde zurückverfolgt, um – wo möglich – homologe oder konvergente Evolution von Merkmalen und ursprüngliche oder abgeleitete Merkmalszustände zu identifizieren. 2.) Es wurde versucht, die stammesgeschichtliche Entfaltung der Gibbons in Form eines Kladogramms zu rekonstruieren. Dazu wurden die unter (1) erhobenen Merkmale der Gibbonkommunikation mit traditionellen Merkmalen aus früheren Untersuchungen kombiniert. Die untersuchten Merkmale stammten aus folgenden drei Kommunikationsformen: stimmliche, geruchliche und visuelle Kommunikation.

8.b.2 Stimmliche Kommunikation

Die Untersuchung der stimmlichen Kommunikation war vollständig dem Gesangsverhalten der Gibbons gewidmet. Die vorliegende Arbeit gelangt zu folgenden Schlussfolgerungen zur stammesgeschichtlichen Entwicklung von Gibbongesängen:

1. Der letzte gemeinsame Vorfahre der heutigen Hylobatiden produzierte bereits Gesänge, die in Form von Duetten vorgetragen wurden. Gibbonduette entwickelten sich vermutlich aus Gesängen, die ursprünglich bei beiden Geschlechtern identisch waren und erst später in

männchen-spezifische und weibchen-spezifische Gesangsanteile aufgespalten wurden ("Song-splitting" Theorie). In einem weiteren Entwicklungsprozess, der hier als "Duett-splitting" bezeichnet wird, gingen erst nachträglich nicht-duettierende Gibbonarten aus duettierenden hervor, indem die Gesangsanteile der beiden Paarpartner sich zu zeitlich getrennten Sologesängen entwickelten.

2. Die Untersuchung von Hybridgesängen zeigt, dass Gibbongesänge weitgehend genetisch festgelegt sind. Es konnte für die Gibbons der *lar*-Gruppe ein Modell erarbeitet werden, das es erlaubt, Gesangsmerkmale weiblicher Hybriden aller Artkombinationen bis mindestens in die zweite Hybridgeneration vorherzusagen.

3. Die sogenannten "Great Calls" der Weibchen aller Gibbonarten sind homologe Gesangs-Strophen. Die schnellen Triller der Great Calls von *Hylobates muelleri* und *H. pileatus* sind wahrscheinlich homologe, gemeinsam abgeleitete Merkmale, ebenso wie die viel langsameren, frequenz-modulierten Great Calls von *H. agilis* und *H. lar*. Das Auftreten einer Beschleunigung im Lauttempo während eines Great Calls stellt wahrscheinlich einen ursprünglichen Merkmalszustand dar. Der gemeinsame Vorfahre der heutigen Gibbons produzierte vermutlich Great Calls mit einem Lauttempo ähnlich demjenigen von *H. moloch*.

4. Die graduelle Entwicklung von anfänglich einfachen Strophen zu zunehmend komplexeren Strophen innerhalb eines Gesangs stellt wahrscheinlich ein primitives Merkmal der Männchengesänge dar. Ebenso dürfte es sich bei der Verwendung von zweiphasigen Lauten (bestehend aus einer beim Ausatmen und einer beim Einatmen erzeugten Komponente) um ein ursprüngliches Merkmal der Gesänge beider Geschlechter handeln.

8.b.3 Geruchliche Kommunikation

1. Während spezialisierte Hautdrüsen zur Erzeugung geruchlicher Signale von vielen Primatenarten beschrieben wurden, waren solche Drüsen bei Gibbons bislang unbekannt. Die vorliegende Untersuchung zeigt aber, dass Gibbons ein sehr komplexes System von Hautdrüsen

aufweisen, welche um ein zentrales Sternaldrüsenorgan angeordnet sind und sich anatomisch und funktionell von dem unterscheiden, was bisher von nicht-hominoiden Primaten bekannt war.

2. Das Auftreten einer Sternaldrüse ist wahrscheinlich ein ursprüngliches Merkmal bei Gibbons. Im Gegensatz zu nicht-hominoiden Primaten wurde bei Gibbons (und anderen Menschenaffen) kein Markierverhalten beobachtet, was darauf hinweist, dass sich die Funktion dieser Drüse bereits beim letzten gemeinsamen Vorfahren aller Menschenaffen verändert hatte. Bei den Gibbons der *concolor*-Gruppe scheint die Drüse weniger stark ausgeprägt zu sein, was wohl einen abgeleiteten Merkmalszustand dieser Gruppe darstellt.

3. Bei einigen Gibbonarten werden Steroidhormone (Dehydroepiandrosteron, Androstendion und Testosteron) in der Sternaldrüse angereichert, und die Ausscheidungsaktivität der Drüse ist bei erhöhter Temperatur und unter Stress angeregt. Die Ausscheidung von Steroidhormonen aus Hautdrüsen stellt vermutlich ein Merkmal dar, das bereits dem gemeinsamen Vorläufer der Menschenaffen zu eigen war. Nicht oder wenig erhöhte Hormonkonzentrationen in den Hautdrüsen scheinen ein abgeleitetes Merkmal der *concolor*-Gruppe darzustellen. Ein stark ausgeprägter, art-typischer Körpergeruch dürfte innerhalb der Menschenaffen ein ursprüngliches Merkmal darstellen, das sekundär bei allen Gibbons reduziert wurde, ausser beim Siamang (*H. syndactylus*).

4. Hautbereiche mit auffällig gefärbten Poren treten vermutlich bei allen Gibbonarten auf, aber es ist unbekannt, ob sie auch bei anderen Primatenarten vorkommen. Weil bei den Gibbons auch die Achselhöhle zu diesen Bereichen zählt, und weil die meisten Arten der Schwestergruppe der Gibbons (d.h. die grossen Menschenaffen und der Mensch) ein Achselhöhlenorgan besitzen, welches wahrscheinlich von einem solchen Porenfeld abgeleitet werden kann, traten diese Porenfelder möglicherweise bereits beim gemeinsamen Vorfahren der Hominoiden auf. Bei den Gibbons der *concolor*-Gruppe können Sekrete aus den genannten Porenfeldern zu reversiblen Veränderungen der Fellfärbung bei Weibchen (und wahrscheinlich bei Jungtieren im hellen Geburtskleid) führen.

5. Es wurden zahlreiche Ähnlichkeiten zwischen dem Hautdrüsensystem der Gibbons und dem Achselhöhlenorgan der afrikanischen Menschenaffen und des Menschen nachgewiesen. Diese Übereinstimmungen erstrecken sich auf das makroskopische Aussehen der Drüsen, ihren mikroskopischen Aufbau, die chemischen Eigenschaften ihrer Sekrete, die äusseren Reize, welche zur erhöhten Sekretion führen, und möglicherweise die vermuteten Funktionen dieser Drüsen im Bereich der geruchlichen Kommunikation und der Thermoregulation. Zudem treten bei den Gibbons Felder mit auffällig gefärbten Poren unter anderem auch in der Achselhöhle auf, so dass auch in der anatomischen Lage eine Übereinstimmung besteht. Es ist unwahrscheinlich, dass sich diese Ähnlichkeiten zwischen den Hautdrüsen der Gibbons und dem Achselhöhlenorgan der afrikanischen Menschenaffen und des Menschen sich unabhängig voneinander in den beiden Schwestergruppen entwickelten. Es war bisher nicht möglich, die stammesgeschichtliche Herkunft des Achselhöhlenorgans zu erklären. Die Resultate der vorliegenden Untersuchung lassen vermuten, dass sich dieses Organ von einem Hautdrüsensystem herleiten lässt, welches um eine Sternaldrüse gruppiert war und demjenigen der modernen Gibbons glich.

8.b.4 Visuelle Kommunikation

Die Untersuchung zur visuellen Kommunikation war hauptsächlich auf Merkmale der Fellfärbung konzentriert, aber zusätzliche Analysen zu verschiedenen Formen des Geschlechtsdimorphismus (einschliesslich des Körpergewichts) wurden ebenfalls durchgeführt.

1. Das Auftreten eines weissen Brauenbandes bei den normalerweise schwarzen Siamangs wurde hier zum ersten Mal dokumentiert. Das Merkmal ist offenbar erblich und weist möglicherweise einen autosomal dominanten Erbgang auf. Zusätzliche weisse Fellmarken treten bei mindestens einem der untersuchten Tiere an Händen und Füssen auf, sowie in einer Corona über den Ohren. Dies lässt darauf schliessen, dass die bei anderen Gibbonarten verbreiteten Fellmerkmale wie weisse Zeichnung um das Gesichtsfeld, hell abgesetzte Hände und Füsse und eine helle Corona ursprüngliche Gibbonmerkmale darstellen. Diese hier vertretene Auffassung

steht im Gegensatz zu früheren Untersuchungen. Ein vollständiger, weisser Gesichtsring stellt wahrscheinlich den ursprünglichen Merkmalszustand heller Gesichtszeichnung bei Gibbons dar. Gibbons mit lediglich weissen Brauen, weissen Wangen oder mit fehlender heller Gesichtszeichnung stellen wahrscheinlich abgeleitete Merkmalszustände dar.

2. Bei Gibbons gibt es mehrere Formen von stark ausgeprägtem Geschlechtsdimorphismus in der Fellfärbung, die sich ontogenetisch stark unterscheiden. Es ist daher wahrscheinlich, dass sich der Geschlechtsdichromatismus bei Gibbons mehrmals unabhängig voneinander entwickelt hat. Obwohl es nicht ganz klar ist, ob der gemeinsame Vorfahre der Gibbons bereits einen Geschlechtsdichromatismus aufgewiesen hat oder nicht, ist letzteres wahrscheinlicher.

3. Es wurde wiederholt vermutet, dass es bei Vögeln und Säugetieren eine generelle Korrelation zwischen Monogamie und Geschlechts-Monomorphismus gebe. Ein Geschlechtsdimorphismus im Körpergewicht ist bei Gibbons nur schwach ausgeprägt; in dieser Hinsicht scheinen die Gibbons dieser Regel zu entsprechen, jedoch nicht in anderen Formen des Geschlechtsdimorphismus, wie zum Beispiel demjenigen in der Fellfärbung oder im Gesangsrepertoir. Bei Gibbons scheinen diese drei Formen von Geschlechtsdimorphismus weitgehend unabhängig voneinander zu sein und unter verschiedenen Selektionsdrücken zu stehen.

4. Junge Tiere mehrerer Arten (*H. concolor*, *H. leucogenys*, *H. hoolock* und *H. pileatus*) zeigen eine in beiden Geschlechtern identische Fellfärbung ("unisex") und – zumindest bei der *concolor* Gruppe – ein identisches Gesangsrepertoire. Auf diese Weise wird das Geschlecht der Jungtiere bis zum Erreichen der Geschlechtsreife maskiert. Diese ontogenetischen Merkmale könnten sich als ein Mechanismus zur Inzestvermeidung entwickelt haben. Im Gegensatz dazu könnten spezielle Natalkleider bei Gibbons, und möglicherweise auch bei anderen geschlechtsdichromatischen Affenarten, eine Tarnfunktion haben. Dies schliesst nicht aus, dass sie auch als Auslöser für Pflegeverhalten dienen könnten, wie dies für die Natalkleider anderer Primatenarten vorgeschlagen wurde.

5. Eine grosse Stichprobe von Körpergewichten von Freilandgibbons wurde für diese Untersuchung zusammengetragen. Traditionellerweise werden die Gibbons nach dem Körpergewicht in zwei Gruppen geteilt, die aus den kleineren Gibbons der *lar*-Gruppe auf der einen und dem grösseren Siamang auf der anderen Seite bestehen. Die vorliegende Arbeit zeigt, dass diese Zweiteilung weniger eindeutig ist, wenn die Gibbons der *concolor*-Gruppe und *H. hoolock* in den Vergleich mit einbezogen werden. Die Kontroverse darüber, welche Körpergrösse der letzte gemeinsame Vorfahre der heutigen Gibbons aufwies, konnte hier jedoch nicht schlüssig aufgelöst werden.

8.b.5 Stammesgeschichtliche Auswertung

1. Die für die vorliegende Studie erarbeitete Datenmatrix von Merkmalen der Gibbonkommunikation ist wesentlich umfangreicher als diejenige, die früheren Arbeiten für stammesgeschichtliche Rekonstruktionen zur Verfügung stand. Sie umfasst Merkmale der stimmlichen, geruchlichen und visuellen Kommunikation, sowie eine Zahl "nicht-kommunikatorischer" Daten (z.B. zur Gibbonanatomie, -morphologie und -karyologie) welche vorwiegend aus der Literatur zusammengetragen wurden. Die ganze Datenmatrix wurde einer kladistischen Analyse unterzogen. Die Teilmengen der stimmlichen und der visuellen Kommunikation, sowie diejenige der "nicht-kommunikatorischen" Merkmale wurden zudem noch einzeln ausgewertet. Die Stichprobe der geruchlichen Merkmale war zu klein für eine getrennte Auswertung.

2. Eine Überprüfung aller Merkmale ergab, dass die Richtung der Merkmalszustände (d.h. ursprünglicher oder abgeleiteter Merkmalszustand) in 43% der Matrix nach Ansicht des Autors nicht schlüssig geschätzt werden kann. Im Gegensatz dazu wurde in bisherigen Studien jeweils bei allen Merkmalen eine Polarität eingesetzt.

3. Auch wenn bisher veröffentlichte Stammbäume der Gibbons sich in der Reihenfolge der Artabspaltungen unterscheiden, so stimmen sie doch in mehreren Punkten überein: a) Der erste Ast, der sich vom Hauptstamm der Gibbons abspaltete, umfasst entweder die Taxa *syndactylus*,

die *concolor*-Gruppe, oder den gemeinsamen Vorfahren beider. b) Zeitlich später, also in etwa intermediärer Position, spalten die Taxa *hoolock* und *klossii* vom Hauptstamm ab. c) Die Gruppe der 44-Chromosomen-Gibbons und die darin enthaltene *lar*-Gruppe sind beide monophyletisch. Dieser Hypothesen konnte in der vorliegenden Arbeit weder bestätigt noch zurückgewiesen werden. Dies hängt damit zusammen, dass hier für eine grosse Zahl der Merkmale keine Polarität eingesetzt wurde.

4. Alle Kladogramme von früheren Untersuchungen sind weniger sparsam und weniger konsistent, als diejenigen, die mit der vorliegenden Datenmatrix konstruiert werden können. Dennoch ist der Konsistenz-Index der hier berechneten Kladogramme relativ niedrig (Variationsbreite: 0.41-0.66). Dies ist ein Hinweis auf hohe Homoplasie (parallele oder reversible Evolution) der Merkmale. Die Auswertung der Teilmengen der Datenmatrix ergab, dass die stimmlichen Merkmale besser für die stammesgeschichtliche Rekonstruktion geeignet sind, als die visuellen, weil erhaltenen Kladogramme im ersteren Fall höhere "bootstrap"-Werte und höhere Konsistenz-Indices liefern.

5. In mehreren der hier erhaltenen Kladogramme spaltet *H. hoolock* als erste Art vom Hauptstamm der Hylobatiden ab. Dieser Befund weicht von bisherigen Untersuchungen ab; seine Bedeutung ist noch unklar ist. Die vorliegende Arbeit lässt annehmen, dass die folgenden Gruppen monophyletisch sind: a) *agilis* und *albibarbis*; b) *abbotti*, *funereus* und *muelleri*; und c) *concolor*, *gabriellae* und *leucogenys*. Besonders der Hinweis auf Monophylie der ersten zwei Gruppen ist von Bedeutung, da sich verschiedene Autoren darüber uneins sind, ob *albibarbis* als eine Unterart von *H. agilis*, von *H. muelleri*, oder als eigene Art zu werten sei. Der Befund der vorliegenden Untersuchung spricht entschieden für die erste Interpretation.

9. References

Adler, H. J. (1991): The crested gibbon, *Hylobates (Nomascus) concolor* Harlan, 1826, in the Nam Cat Tien Reserve, southern Vietnam. *Primate Report* 29: 59-64.

Albignac, R. (1969): Notes éthologiques sur quelques carnivores Malgaches: Le *Galidia elegans* I. Geoffroy. *La Terre et la Vie* 116: 202-215.

Albrecht, H. & Wickler, W. (1968): Freilandbeobachtungen zur "Begrüssungszeremonie" des Schmuckbartvogels *Trachyphonus d'arnaudii*. *Journal für Ornithologie* 109: 255-263.

Allen, G. M. & Coolidge, H. J., Jr. (1940): Mammals. In: Mammal and bird collections of the Asiatic Primate Expedition. *Bulletin of the Museum of Comparative Zoology at Harvard College* 87: 131-166.

Alley, T. R. (1980): Infantile colouration as an elicitor of caretaking behaviour in Old World primates. *Primates* 21: 416-429.

Alterman, L. (1989): Analysis of organic extracts of brachial gland exudate from *Nycticebus coucang*. *American Journal of Primatology* 18: 132 (Abstract only).

Alterman, L. (1990): Isolation of toxins from brachial gland exudate of *Nycticebus coucang*. *American Journal of Physical Anthropology* 81: 187 (Abstract only).

Alterman, L. & Hale, M. E. (1991): Comparison of toxins from brachial gland exudates of *Nycticebus coucang* and *N. pygmaeus*. *American Journal of Physical Anthropology* Suppl. 12: 43 (Abstract only).

Andrews, P. & Groves, C. P. (1976): Gibbons and brachiation. In Rumbaugh, D. M. (Ed.), *Gibbon and siamang, vol. 4* (pp. 167-218). Basel: Karger.

Andrews, P.; Martin, L. & Whybrow, P. (1987): Earliest known member of the great ape and human clade. *American Journal of Physical Anthropology* 72: 174 (Abstract only).

Anzenberger, G. (1974): Über das Auftreten der geschlechtsspezifischen Duettelemente in der Gesangsentwicklung des Schmuckbartvogels *Trachyphonus d'arnaudii*. *Zeitschrift für Tierpsychologie* 34: 395-397.

Arao, T. & Perkins, E. (1969): The skin of primates. XLIII. Further observations on the Philippine tarsier (*Tarsius syrichta*). *American Journal of Physical Anthropology* 31: 93-96.

Aslin, H. J. (1974): Social behaviour of the kowari (*Dasyuroides byrnei*). *Australian Mammalogy* 1: 301-302 (Abstract only).

Aue, D. & Fuchs, E. (1986): Chronic confrontation induces behavioral changes in dominant *Tupaia belangeri*. *Zeitschrift für Säugetierkunde* 51: 121-124.

Badham, M. (1988): *Studbook of gibbons held in the British Isles and Ireland, 1988*. Twycross: Twycross Zoo, East Midland Zoological Society.

Badham, M. & Richards, V. (1991): *Gibbon Regional Studbook: British Isles and Ireland, 13th Edition*. Twycross: Twycross Zoo, East Midland Zoological Society.

Badoux, D. M. (1959): *Fossil mammals from two fissure deposits at Punung (Java)*. Ph.D. diss., Rijksuniversiteit te Utrecht (Kemink en Zoon, Utrecht).

Baldwin, L. A. & Teleki, G. (1976): Patterns of gibbon behavior on Hall's island, Bermuda. In Rumbaugh, D. M. (Ed.), *Gibbon and Siamang, vol. 4* (pp. 21-105). Basel: Karger.

Barry, J. C.; Jacobs, L. L. & Kelley, J. (1986): An Early Middle Miocene catarrhine from Pakistan with comments on the dispersal of catarrhines into Eurasia. *Journal of Human Evolution* 15: 501-508.

Bartecki, U. & Heymann, W. (1990): Field observations on scent-marking behaviour in saddle-back tamarins, *Saguinus fuscicollis* (Callitrichidae, Primates). *Journal of Zoology (London)* 220: 87-99.

Baumgartner, R.; Rübel, A. & Isenbügel, E. (1986): Diarrhoe bei einem Gibbon (*Hylobates agilis*). In *Verhandlungsbericht des 28. Internationalen Symposiums über die Erkrankungen der Zootiere, Rostock 1986* (pp. 209-212). Berlin: Akademie-Verlag.

Bearder, S. K. & Doyle, G. A. (1974): Ecology of bushbabies *Galago senegalensis* and *Galago crassicaudatus*, with some notes on their behaviour in the field. In Martin, R. D.; Doyle, G. A. & Walker, A. C. (Eds.), *Prosimian biology* (pp. 109-130). London: Duckworth.

Belcher, A.; Epple, G.; Greenfield, K. L.; Richards, L. E.; Küderling, I. & Smith, A. B., III (1990): Proteins: Biologically relevant components of the scent marks of a primate (*Saguinus fuscicollis*). *Chemical Senses* 15: 431-446.

Belcher, A.; Epple, G.; Küderling, I. & Smith, A. B., III (1988): The volatile components of scent material from the cotton-top tamarin (*Saguinus o. oedipus*). A chemical and behavioral study. *Primate Report* 20: 13-28.

Bernstein, I. S. (1965): Activity patterns in a cebus monkey group. *Folia Primatologica* 3: 211-224.

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

Bird, S. & Gower, D. B. (1981): The validation and use of a radioimmunoassay for 5a-androst-16-en-3-one in human axillary collections. *Journal of Steroid Biochemistry* 14: 213-219.

Bischof, N. (1972): Inzuchtbarrieren in Säugetiersozietäten. *Homo* 23: 330-351.

Bischof, N. (1975): Comparative ethology of incest avoidance. In Fox, R. (Ed.), *Biosocial Anthropology. ASA Studies vol. 1* (pp. 37-67). London: Malaby Press.

Bourlière, F.; Petter, J.-J. & Petter-Rousseaux, A. (1956): Le dimorphisme sexuel de la glande sous-angulo-maxillaire d'*Avahi laniger* (Gmelin). *Mémoires de l' Institut Scientifique de Madagascar, Sér. A* 10: 29-302, + 2 plates.

Boutan, L. (1913): Le pseudo-langage. Observations effectuées sur un anthropoïde: Le gibbon (*Hylobates leucogenys* Ogilby). *Actes de la Société Linnéenne de Bordeaux* 67: 5-80.

Box, H. O. (1975): Quantitative studies of behaviour within captive groups of marmoset monkeys (*Callithrix jacchus*). *Primates* 16: 155-174.

Box, H. O. (1977): Social interactions in family groups of captive marmosets (*Callithrix jacchus*). In Kleiman, D. G. (Ed.), *The biology and conservation of the Callitrichidae* (pp. 239-249). Washington, D.C.: Smithsonian Institution Press.

Boyd, C. M. & Herzberg, D. L. (1976): Fundamentals of radioimmunoassay. In Moss, A. J.; Dalrymple, G. V. & Boyd, C. M. (Eds.), *Practical radioimmunoassay* (pp. 1-13). Saint Louis: Mosby.

Bradbury, J. W. (1977): Social organization and communication. In Wimsatt, W. A. (Ed.), *Biology of bats, vol. 3* (pp. 1-72). New York: Academic Press.

Brandes, G. (1939): *Buschi. Vom Orang-Säugling zum Backenwülster*. Leipzig: Quelle und Meyer.

Brandes, R. (1931): Über den Kehlkopf des Orang-Utan in verschiedenen Altersstadien mit besonderer Berücksichtigung der Kehlsackfrage. *Morphologisches Jahrbuch* 69: 1-61, + 3 plates.

Brinkmann, A. (1909): Ueber das Vorkommen von Hautdrüsenorganen bei den anthropomorphen Affen. *Anatomischer Anzeiger* 34: 513-520.

Brinkmann, A. (1923-1924): Nachlese zu meinen Hautdrüsenuntersuchungen. *Bergens Museums Aarbok, Naturvidenskabelig Raekke* 1923-24(3): 1-36.

Brinkmann, A. (1926): Ein paar Bemerkungen zu den neuesten Untersuchungen der Hautdrüsen bei den anthropomorphen Affen. *Anatomischer Anzeiger* 62: 236-237.

Brockelman, W. Y. (1978): Preliminary report on relations between the gibbons *Hylobtes lar* and *H. pileatus* in Thailand. In Chivers, D. J. & Joysey, K. A. (Eds.), *Recent Advances in Primatology, vol.3: Evolution* (pp. 315-318). London: Academic Press.

Brockelman, W. Y. & 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. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 498-532). Edinburgh: Edinburgh University Press.

Brockelman, W. Y. & Schilling, D. (1984): Inheritance of stereotyped gibbon calls. *Nature* 312: 634-636.

Brockelman, W. Y. & Srikosamatara, S. (1984): Maintenance and evolution of social structure in gibbons. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 298-323). Edinburgh: Edinburgh University Press.

Brockelman, W. Y. & Treesucon, U. (1986): Observations on social changes and group structure in the gibbon. *Primate Report* 14: 72 (Abstract only).

Brooksbank, B. W. L.; Brown, R. & Gustafsson, J.-A. (1974): The detection of 5a-androst-16-en-3a-ol in human male axillary sweat. *Experientia* 30: 864-865.

Brown, J. L. (1975): *The evolution of behavior*. New York: W.W: Norton & Company, Inc.

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

Burck, H.-C. (1981): *Histologische Technik (4th edition)*. Stuttgart: Georg Thieme Verlag.

Caldecott, J. O. & Haimoff, E. H. (1983): Female solo singing by a wild lar gibbon in peninsular Malaysia. *Malayan Nature Journal* 36: 167-173.

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.

Carroll, J. B. (1985): Pair bonding in Goeldi's monkey *Callimico goeldii* (Thomas, 1904). *Dodo, Journal of the Jersey Wildlife Preservation Trust* 22: 57-71.

Carter, T. D. (1943): The mammals of the Vernay-Hopwood Chindwin Expedition, northern Burma. *Bulletin of the American Museum of Natural History* 82(4): 95-114, + 7 plates.

Chang, Y.; Wang, L.; Dong, X. & Chen, W. (1975): [Discovery of a *Gigantopithecus* tooth from Bama district in Guangxi]. *Vertebrata Palasiatica* 13: 148-153 (Chinese text, English summary).

Chivers, D. J. (1974): *The siamang in Malaya – A field study of a primate in tropical rain forest*. Contributions to Primatology vol. 4. Basel: Karger.

Chivers, D. J. (1976): Communication within and between family groups of siamang (*Symphalangus syndactylus*). *Behaviour* 57: 116-135.

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

Chivers, D. J. (1978): The gibbons of peninsular Malaysia. *Malayan Nature Journal* 30: 565-591.

Chivers, D. J. (1980): Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *Journal of Morphology* 166: 337-386.

Chivers, D. J. (1984a): Feeding and ranging in gibbons: A summary. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 267-281). Edinburgh: Edinburgh University Press.

Chivers, D. J. (1984b): Gibbons. In MacDonald, D. (Ed.), *The Encyclopedia of Mammals, Vol. 1* (pp. 415-419). London: Allen & Unwin.

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

Choudhury, A. (1989): Vocalization in hoolock gibbon (*Hylobates hoolock*). *Primate Report* 25: 53-54.

Christen, A. (1974): *Fortpflanzungsbiologie und Verhalten bei Cebuella pygmaea und Tamarin tamarin (Primates, Platyrrhina, Callithricidae)*. Berlin and Hamburg: Parey.

Ciochon, R. L. (1988): Paleoanthropological research in the Pleistocene karst caves of northern Vietnam. *American Journal of Physical Anthropology* 75: 196 (Abstract only).

Clark, A. B. (1978): Olfactory communication, *Galago crassicaudatus*, and the social life of prosimians. In Chivers, D. J. & Joysey, K. A. (Eds.), *Recent advances in primatology, vol. 3: Evolution* (pp. 109-117). London: Academic Press.

Clark, A. B. (1986): Contrast in communication of *Galago crassicaudatus* and *G. garnettii*. *Primate Report* 14: 216 (Abstract only).

Clark, A. B. (1988): Interspecific differences and discrimination of auditory and olfactory signals of *Galago crassicaudatus* and *Galago garnettii*. *International Journal of Primatology* 9: 557-571.

Claus, R. & Alsing, W. (1976): Occurrence of 5a-androst-16-en-3-one, a boar pheromone, in man and its relationship to testosterone. *Journal of Endocrinology* 68: 483-484.

Claussen, R. (1982): Beobachtungen zur Aufzucht eines männlichen Weissgesichtsakis (*Pithecia pithecia*) im Familienverband. *Der Zoologische Garten (N.F.)* 52: 188-194.

Colbert, E. H. & Hooijer, D. A. (1953): Pleistocene mammals from the limestone fissures of Szechwan, China. *Bulletin of the American Museum of Natural History* 102(1): 1-134, + 40 plates.

Coolidge, H. J., Jr. (1937a): Life of the gibbon in his native home. A scientific expedition in the fastness of Siam records his voice and his customs. *The New York Times Magazine* 1937 (August 8): 6, 7, 20, 23.

Coolidge, H. J., Jr. (1937b): Trailing the gibbon to learn about man. *The New York Times Magazine* 1937 (August 1): 6-7, 21.

Coolidge, H. J., Jr. (1938): The living Asiatic apes. An account of the Asiatic (Harvard) Primate Expedition. *Harvard Alumni Bulletin* 1938 (May 27): 978-988.

Coolidge, H. J., Jr. (1940): Introduction. In: Mammal and bird collections of the Asiatic Primate Expedition. *Bulletin of the Museum of Comparative Zoology at Harvard College* 87(3): 121-130.

Cowlishaw, G. (1992): Song function in gibbons. *Behaviour* 121: 131-153.

Creel, N. & 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). Basel: Karger.

Creel, N. & 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. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 562-613). Edinburgh: Edinburgh University Press.

Crewe, R. M.; Burger, B. V.; Le Roux, M. & Katsir, Z. (1979): Chemical constituents of the chest gland secretion of the thick-tailed Galago (*Galago crassicaudatus*). *Journal of Chemical Ecology* 5: 861-868.

Croft, D. B. (1981a): Behaviour of red kangaroos, *Macropus rufus* (Desmarest, 1822), in northwestern New South Wales, Australia. *Australian Mammalogy* 4: 5-58.

Croft, D. B. (1981b): Social behaviour of the euro, *Macropus robustus* (Gould), in the Australian arid zone. *Australian Wildlife Research* 8: 13-49.

Cronin, J. E.; Sarich, V. M. & Ryder, O. (1984): Molecular evolution and speciation in the lesser apes. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 467-485). Edinburgh: Edinburgh University Press.

Dandelot, P. (1960): Gracieux et merveilleux acrobates: Les gibbons. *Science et Nature* 39(Mai-Juin 1960): 2-12.

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

Dao Van Tien (1985): *Khao sát thú o miên bac Viêt Nam. [Scientific results of some mammals surveys in North Vietnam (1957 – 1971)]*. Ha Noi: Scientific and Technical Publishing House. (In Vietnamese).

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

Darga, L. L.; Goodman, M. & 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). Basel: Karger.

Davis, D. D. (1962): Mammals of the lowland rain-forest of North Borneo. *Bulletin of the National Museum State of Singapore* 31: 1-129, + 23 plates.

de Waal, F. B. M. (1988): The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour* 106: 183-251.

Delacour, J. (1934): Les gibbons Indochinois. *Terre et Vie* 4(1): 1-12.

Delacour, J. (1942): Gibbons – the smallest apes. *Animal Kingdom* 45(2): 34-39.

Delson, E. (1977): Vertebrate paleontology, especially of nonhuman primates, in China. In Howells, W. W. & Tsuchitanis, P. J. (Eds.), *Paleoanthropology in the People's Republic of China* (pp. 40-65). Washington, D.C.: National Academy of Schiences.

Demars, C.; Berthomier, C. & Goustard, M. (1983): The great call of *Hylobates concolor hainanus*: Comparison with the homologous emission of *H. concolor gabriellae* and *H. concolor leucogenys*. In Seth, P. K. (Ed.), *Perspectives in primate biology* (pp. 99-102). New Delhi: Today & Tomorrow's Printers and Publishers.

Demars, C. & Goustard, M. (1972): Structure et règles de deroulement des émissions sonores des *Hylobates* (*Hylobates concolor*). *Bulletin Biologique de la France et de la Belge* 106: 177-191.

Demars, C. & Goustard, M. (1978): Le "grand chant" d'*Hylobates concolor leucogenys*. Comparaison avec les émissions sonores homologues d'*H. concolor gabriellae* et d'*H. klossii* (Îles Mentawei, ouest Sumatra). *Behaviour* 65: 1-26.

Dene, H. T.; Goodman, M. & Prychodko, W. (1976): Immunodiffusion evidence on the phylogeny of the primates. In Goodman, M.; Tashian, R. E. & Tashian, J. H. (Eds.), *Molecular anthropology. Genes and proteins in the evolutionary ascent of the primates* (pp. 171-195). New York: Plenum Press.

Deputte, B. & Goustard, M. (1978): Étude du répertoire vocal du Gibbon à favoris blancs (*Hylobates concolor leucogenys*): Analyse structurale des vocalisations. *Zeitschrift für Tierpsychologie* 48: 225-250.

Deputte, B. L. (1982): Duetting in male and female songs of the white-cheeked gibbon (*Hylobates concolor leucogenys*). In Snowdon, S. T.; Brown, C. H. & Petersen, M. R. (Eds.), *Primate communication* (pp. 67-93). Cambridge: Cambridge University Press.

Deputte, B. L. & Leclerc-Cassan, M. (1981): Sex determination and age estimation in the white-cheeked gibbon *Hylobates concolor leucogenys*. Anatomical and behavioural features. *International Zoo Yearbook* 21: 187-193.

Dittrich, L. (1979): Jugendentwicklung, Geschlechtsreife und Wechsel der Färbung des Haarkleides beim Schopfgibbon (*Hylobates concolor leucogenys*). *Bijdragen tot de Dierkunde (Contr. Zoology), Amsterdam* 49: 247-254.

Dixson, A. F. (1976): Effects of testosterone on the sternal cutaneous glands and genitalia of the male greater galago (*Galago crassicaudatus crassicaudatus*). *Folia Primatologica* 26: 207-213.

Dobroruka, L. (1972): Social communication in the brown capuchin *Cebus apella*. *International Zoo Yearbook* 12: 43-45.

Dobroruka, L. J. (1979): Piebarvování gibona kápového, *Hylobates pileatus* GRAY, 1861 [Colour transformation in the pileated gibbon, *Hylobates pileatus* GRAY, 1861]. *Gazella, Zoo Praha* 2(2): 63-65 (Czech text, English summary).

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

Doty, R. L. (1981): Olfactory communication in humans. *Chemical Senses* 6: 351-376.

Doty, R. L.; Orndorff, M. M.; Leyden, J. & Kligman, A. (1978): Communication of gender from human axillary odors: Relationship to perceived intensity and hedonicity. *Behavioral Biology* 23: 373-380.

Dugmore, S. J. (1986): Behavioural observations on a pair of captive white-faced saki monkeys (*Pithecia pithecia*). *Folia Primatologica* 46: 83-90.

Eisenberg, J. F. (1976): Communication mechanisms and social integration in the black spider monkey, *Ateles fusciceps robustus*, and related species. *Smithsonian Contributions to Zoology (Washington, D.C.)* 213: 1-108.

Eisenberg, J. F. & Kleiman, D. G. (1972): Olfactory communication in mammals. *Annual Review of Ecology and Systematics* 3: 1-32.

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). New York: Holt, Rinehart & Winston.

Ellefson, J. O. (1974): A natural history of white-handed gibbons in the Malayan Peninsula. In Rumbaugh, D. M. (Ed.), *Gibbon and siamang, vol. 3* (pp. 1-136). Basel: Karger.

Elliot, D. G. (1913): *A review of the primates, vol. 3: Anthropoidea, Miopithecus to Pan*. New York: American Museum of Natural History.

Ellis, R. A. & Montagna, W. (1962): The skin of primates. VI. The skin of the gorilla (*Gorilla gorilla*). *American Journal of Physical Anthropology* 20: 79-94.

Epple, G. (1972): Social communication by olfactory signals in marmosets. *International Zoo Yearbook* 12: 36-42.

Epple, G. (1986): Communication by chemical signals. In Mitchell, G. & Erwin, J. (Eds.), *Comparative primate biology, vol. 2, part A: Behavior, conservation, and ecology* (pp. 531-580). New York: Alan R. Liss.

Epple, G.; Belcher, A.; Greenfield, K. L.; Scolnick, L.; Smith, A. B.; Küderling, I. & Zeller, U. (1987a): Making sense out of scents: Species differences in scent glands, scent marking behavior and scent mark composition in the Callitrichidae. *International Journal of Primatology* 8: 434 (Abstract only).

Epple, G.; Belcher, A.; Küderling, I. & Smith, A. B., III (1987b): Olfaction and social communication in callitrichid monkeys. *Chemical Senses* 12: 177 (Abstract only).

Epple, G.; Golob, N. F.; Cebul, M.-S. & Smith, A. B., III (1981): Communication by scent in some Callitrichidae (Primates) – An interdisciplinary approach. *Chemical Senses* 6: 377-390.

Epple, G.; Golob, N. F. & Smith, A. B., III (1979): Odor communication in the tamarin *Saguinus fuscicollis* (Callitrichidae): Behavioral and chemical studies. In Ritter, F. J. (Ed.), *Chemical ecology: Odour communication in animals. Scientific aspects, practical uses and economic prospects* (pp. 117-130). Amsterdam and New York: Elsevier/North-Holland Biomedical Press.

Epple, G. & Lorenz, R. (1967): Vorkommen, Morphologie und Funktion der Sternaldrüse bei den Platyrrhini. *Folia Primatologica* 7: 98-126.

Fadem, B. H. & Cole, E. A. (1985): Scent-marking in the grey short-tailed opossum (*Monodelphis domestica*). *Animal Behaviour* 33: 730-738.

Farabaugh, S. M. (1982): The ecological and social significance of duetting. In Kroodsma, D. E.; Miller, E. H. & Ouellet, H. (Eds.), *Acoustic communication in birds* (pp. 85-124). New York and London: Academic Press.

Feistner, A. T. C. (1991): Scent marking in mandrills, *Mandrillus sphinx*. *Folia Primatologica* 57: 42-47.

Felsenstein, J. (1985): Confidence limits on phylogenies: An approach using bootstrap. *Evolution* 39: 783-791.

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

Fiedler, W. (1957): Beobachtungen zum Markierungsverhalten einiger Säugetiere. *Zeitschrift für Säugetierkunde* 22: 57-76.

Fischer, W. (1980): Einige Ergänzungen zur Haltung und Entwicklung des Schopfgibbons, *Hylobates (Nomascus) concolor* (Harlan). *Milu, Berlin* 5(1/2): 167-193.

Fischer, W. (1981): Forschende Kamera - Farbwechsel beim Schopfgibbon. *Urania, Leipzig* 57(10): 2-5.

Fleagle, J. G. (1984): Are there any fossil gibbons? In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 431-447). Edinburgh: Edinburgh University Press.

Fleagle, J. G. (1988): *Primate adaptation & evolution*. San Diego and New York: Academic Press.

Fooden, J. (1969): Color phase in gibbons. *Evolution* 23: 627-644.

Fooden, J. (1971): Report on primates collected in western Thailand January - April, 1967. *Fieldiana, Zoology* 59: 1-62.

Fooden, J. (1975): Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana, Zoology* 67: 1-169.

Fooden, J. (1976): Primates obtained in peninsular Thailand June-July, 1973, with notes on the distribution of continental Southeast Asian leaf-monkeys (*Presbytis*). *Primates* 17: 95-118.

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

Forbes, H. O. (1894): *A hand-book to the primates, Vol. 2*. London: W.H. Allen & Co.

Ford, D. M. & Perkins, E. M. (1970): The skin of the chimpanzee. In Bourne, G. H. (Ed.), *The chimpanzee, vol. 3* (pp. 82-119). Basel: Karger.

Fossey, D. (1972): Vocalizations of the mountain gorilla (*Gorilla gorilla beringei*). *Animal Behavior* 20: 36-53.

Fossey, D. (1983): *Gorillas in the mist*. Boston: Houghton Mifflin Company.

Fox, G. J. (1977): *Social dynamics in siamang*. Ph.D. diss., University of Wisconsin, Milwaukee.

Frisch, J. E. (1965): *Trends in the evolution of the hominoid dentition*. Bibliotheca Primatologica vol. 3. Basel and New York: S. Karger.

Frisch, J. E. (1973): The hylobatid dentition. In Rumbaugh, D. M. (Ed.), *Gibbon and siamang, vol. 2* (pp. 55-95). Basel: Karger.

Gabriel, C. D. (1983): Tierbestand. *Jahresbericht, Zoo Rostock* 1983: 3-7.

Gabriel, C. D. (1989): Tierbestand. *Jahresbericht, Zoo Rostock* 1989: 2-5.

Galdikas, B. M. F. (1983): The orangutan long call and snag crashing at Tanjung Puting Reserve. *Primates* 24: 371-384.

Gammill, J. (1976): Radioimmunoassay kits. In Moss, A. J.; Dalrymple, G. V. & Boyd, C. M. (Eds.), *Practical radioimmunoassay* (pp. 138-146). Saint Louis: Mosby.

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

Gartlan, J. S. & Brain, C. K. (1968): Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. In Jay, P. C. (Ed.), *Primates. Studies in adaptation and variability* (pp. 253-292). New York: Holt, Rinehart and Winston.

Garza, J. C. & Woodruff, D. S. (1993): A phylogenetic study of the gibbons (*Hylobates*) using DNA obtained non-invasively from hair. *Molecular Phylogeny and Evolution* .

Gautier, J.-P. (1988): Interspecific affinities among guenons as deduced from vocalizations. In Gautier-Hion, A.; Bourlière, F.; Gautier, J.-P. & Kingdon, J. (Eds.), *A primate radiation: Evolutionary biology of the African guenons* (pp. 194-226). Cambridge: Cambridge University Press.

Gautier, J.-P. & Gautier, A. (1977): Communication in Old World monkeys. In Sebeok, T. A. (Ed.), *How animals communicate* (pp. 890-964). Bloomington and London: Indiana University Press.

Geissmann, T. (1983): Female capped gibbon (*Hylobates pileatus* Gray 1891) sings male song. *Journal of Human Evolution* 12: 667-671.

Geissmann, T. (1984a): Inheritance of song parameters in the gibbon song, analyzed in 2 hybrid gibbons (*Hylobates pileatus* x *H. lar*). *Folia Primatologica* 42: 216-235.

Geissmann, T. (1984b): Funktion der gesanglichen Lautäusserungen des Siamangs, *Hylobates syndactylus* (Raffles, 1821). Diploma thesis, Anthropological Institute, Zürich University.

Geissmann, T. (1986a): Mate change enhances duetting activity in the siamang gibbon (*Hylobates syndactylus*). *Behaviour* 96: 17-27.

Geissmann, T. (1986b): Sternal gland in the siamang, *Hylobates syndactylus*. *Primate Report* 14: 22-23 (Abstract only).

Geissmann, T. (1987a): Occurrence of sternal and axillary glands in hominoids. *Chemical Senses* 12: 177-178 (Abstract only).

Geissmann, T. (1987b): A sternal gland in the siamang gibbon (*Hylobates syndactylus*). *International Journal of Primatology* 8: 1-15.

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

Geissmann, T. (1991a): Reassessment of age of sexual maturity in gibbons (*Hylobates* spp.). *American Journal of Primatology* 23: 11-22.

Geissmann, T. (1991b): The Spaeth Gibbon Collection. *Natural History Bulletin of the Siam Society* 39: 53-70.

Geissmann, T. & Orgeldinger, M. (in prep.): Neonatal weight in gibbons (*Hylobates* spp.).

Gittins, S. P. (1978a): Hark! The beautiful song of gibbon. *New Scientist* 80: 832-834.

Gittins, S. P. (1978b): The species range of the gibbon *Hylobates agilis*. In Chivers, D. J. & Joysey, K. A. (Eds.), *Recent Advances in Primatology, vol. 3: Evolution* (pp. 319-321). London: Academic Press.

Gittins, S. P. (1984a): Territorial advertisement and defence in gibbons. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 420-424). Edinburgh: Edinburgh University Press.

Gittins, S. P. (1984b): The vocal repertoire and song of the agile gibbon. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 354-375). Edinburgh: Edinburgh University Press.

Gittins, S. P. & Raemaekers, J. J. (1980): Siamang, lar and agile gibbons. In Chivers, D. J. (Ed.), *Malayan forest primates – Ten years' study in tropical rain forest* (pp. 63-105). New York: Plenum Press.

Gittins, S. P. & Tilson, R. L. (1984): Notes on the ecology and behaviour of the hoolock gibbon. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 258-266). Edinburgh: Edinburgh University Press.

Goldman, D.; Giri, P. R. & 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.

Goustard, M. (1965): Introduction à l'étude des émissions sonores des Hylobatinés. *Annales des Sciences Naturelles, Zoologie et Biologie Animale, Paris, 12e série* 7: 359-396.

Goustard, M. (1969): Étude du "grand chant" du Gibbon (*Hylobates concolor*). *Annales des Sciences Naturelles, Zoologie et Biologie Animale, Paris, 12e série* 11: 505-514.

Goustard, M. (1976): The vocalizations of *Hylobates*. In Rumbaugh, D. M. (Eds.), *Gibbon and siamang* (pp. 135-166). Basel: Karger.

Goustard, M. (1979): Les interactions acoustiques au cours des grandes émissions sonores des Gibbons (*Hylobates concolor leucogenys*). *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences, Paris, série D* 288: 1671-1673.

Goustard, M. (1980): Morphologie acoustique et interactions vocales dans les émissions territoriales des gibbons à favoris blancs (*Hylobates concolor leucogenys*). *G.A.M., Bulletin du Groupe d'Acoustique Musicale, Univ. Paris VI* 104: 1-16.

Goustard, M. (1982): Les vocalisations des singes anthropomorphes. *Journal de Psychologie Normale et Pathologique* 79: 141-166.

Goustard, M. (1984): Patterns and functions of loud calls in the concolor gibbon. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 404-415). Edinburgh: Edinburgh University Press.

Goustard, M. & Demars, C. (1971): Sur les chants à roulades chez le Gibbon *Hylobates concolor*. *Bulletin Biologique de la France et de la Belge* 105: 243-251.

Goustard, M. & Demars, C. (1973): Structure et forme des segments du grand chant du Gibbon (*Hylobates concolor*). *Bulletin Biologique de la France et de la Belge* 107: 171-187.

Goustard, M. & Demars, C. (1974): Sur quelques aspects de la communication vocale chez le Gibbon (*Hylobates concolor*). *Comptes Rendus 2ème Colloqu. Internat. d'Audiophonologie* 1974: 123-144.

Gower, D. B.; Bird, S.; Sharma, P. & House, F. R. (1985): Axillary 5a-androst-16-en-3-one in men and women: relationships with olfactory acuity to odorous 16-androstenes. *Experientia* 41: 1134-1136.

Gower, D. B.; Nixon, A. & Mallet, A. I. (1988): The significance of odorous steroids in axillary odour. In Van Toller, S. & Dodd, G. H. (Eds.), *Perfumery… The psychology and biology of fragrance* (pp. 47-76). London: Chapman and Hall.

Green, L. M. A. (1963): Distribution and comparative histology of cutaneous glands in certain marsupials. *Australian Journal of Zoology* 11: 250-272.

Griswold, J. A., Jr. (1939a): Up Mount Kinabalu. – I. White man and natives begin ascent. *Scientific Monthly (New York)* 48: 401-414.

Griswold, J. A., Jr. (1939b): Up Mount Kinabalu. – II. Camping and collecting in Lumu Lumu and beyond. *Scientific Monthly (New York)* 48: 504-518.

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

Groves, C. P. (1984): A new look at the taxonomy and phylogeny of the gibbons. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 542-561). Edinburgh: Edinburgh University Press.

Groves, C. P. (1989): *A theory of human and primate evolution*. Oxford: Clarendon Press.

Groves, C. P. & 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. (1981): Video analysis of siamang (*Hylobates syndactylus*) songs. *Behaviour* 76: 128-151.

Haimoff, E. H. (1983a): *Gibbon songs: An acoustical, organizational, and behavioural analysis*. PhD. diss., University of Cambridge.

Haimoff, E. H. (1983b): Occurrence of anti-resonance in the song of the siamang (*Hylobates syndactylus*). *American Journal of Primatology* 5: 249-256.

Haimoff, E. H. (1984a): Acoustic and organizational features of gibbon songs. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 333-353). Edinburgh: Edinburgh University Press.

Haimoff, E. H. (1984b): The organization of song in the agile gibbon (*Hylobates agilis*). *Folia Primatologica* 42: 42-61.

Haimoff, E. H. (1984c): The organization of song in the Hainan black gibbon (*Hylobates concolor hainanus*). *Primates* 25: 225-235.

Haimoff, E. H. (1985a): The organization of song in Müller's gibbon (*Hylobates muelleri*). *International Journal of Primatology* 6: 173-192.

Haimoff, E. H. (1985b): Some observations on the singing behaviour of the hoolock gibbon (*Hylobates hoolock*). *Journal of the Bombay Natural History Society* 82: 1-12.

Haimoff, E. H. (1986): Convergence in the duetting of monogamous Old World primates. *Journal of Human Evolution* 15: 51-59.

Haimoff, E. H. (1988): The organization of repair in the songs of gibbons. *Semiotica* 68: 89-120.

Haimoff, E. H.; Chivers, D. J.; Gittins, S. P. & 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. (1985): Individuality in the songs of wild agile gibbons (*Hylobates agilis*) of Peninsular Malaysia. *American Journal of Primatology* 8: 239-247.

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

Haimoff, E. H. & Tilson, R. L. (1985): Individuality in the female songs of wild Kloss' gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Folia Primatologica* 44: 129-137.

Haimoff, E. H.; Yang, X.; He, S. & Chen, N. (1986): Census and survey of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. *Folia Primatologica* 46: 205-214.

Haimoff, E. H.; Yang, X.; He, S. & Chen, N. (1987): Preliminary observations of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. *Primates* 28: 319-335.

Hall, L. S. & Gordon, G. (1982): The throat-pouch of the yellow-bellied bat, *Taphozous flaviventris*. *Mammalia* 46: 247-252.

Han, D. (1982): [Mammalian fossils from Tahsin County, Guangxi]. *Vertebrata Palasiatica* 20: 58-63 (Chinese text, English summary).

Hanson, G. & Montagna, W. (1962): The skin of primates. XII. The skin of the owl monkey (*Aötus trivirgatus*). *American Journal of Physical Anthropology* 20: 421-430.

Hartl, D. L. (1983): *Human genetics*. New York: Harper & Row.

Hasegawa, M.; Kishino, H. & Yano, T. (1985): Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution* 22: 160-174.

Hasegawa, M.; Yano, T. & Kishino, H. (1984): A new molecular clock of mitochondrial DNA and the evolution of hominoids. *Proceedings of the Japan Academy* 60 (Ser. B): 95-98.

Hearn, G. W.; Weikel, E. C. & Schaaf, C. D. (1988): A preliminary ethogram and study of social behavior in captive drills, *Mandrillus leucophaeus*. *Primate Report* 19: 11-17.

Hellekant, G.; DuBois, G.; Geissmann, T.; Glaser, D. & 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). Oslo: GCS A.S.

Helversen, D. (1980): Structure and function of antiphonal duets. In Nöhring, R. (Ed.), *Acta XVII Congr. Int. Orn. Berlin, vol. 1* (pp. 682-688).

Hershkovitz, P. (1983): Two new species of night monkeys, genus *Aotus* (Cebidae, Platyrrhini): A preliminary report on *Aotus* taxonomy. *American Journal of Primatology* 4: 209-243.

Herzog, M. O. & Hohmann, G. M. (1984): Male loud calls in *Macaca silenus* and *Presbytis johnii*. A comparison. *Folia Primatologica* 43: 189-197.

Hess, J. (1988): *Berggorillalaute. Akustische Erinnerungen an die Berggorillas der Familie 5 (audio cassette)*. Fuchsmattstr. 27, CH – 4107 Ettingen: HM Produktion.

Hess-Haeser, J. (1971): Die Siamangs singen Duette. *Zolli, Bulletin des Vereins der Freunde des Zoologischen Gartens Basel* 26: 9-14.

Heymann, W. (1989): Some observations on the scent-marking behaviour of moustached tamarins, *Saguinus mystax* (Platyrrhini: Callitrichidae) in northeastern Peru. *Primate Report* 25: 71 (Abstract only).

Hill, W. C. O. (1944): An undescribed feature in the drill (*Mandrillus leucophaeus*). *Nature* 153: 199.

Hill, W. C. O. (1951): Epigastric gland of *Tarsius*. *Nature* 167: 994.

Hill, W. C. O. (1954): Sternal glands in the genus *Mandrillus*. *Journal of Anantomy* 88: 582.

Hill, W. C. O. (1955): *Primates. Comparative anatomy and taxonomy. II. Haplorhini: Tarsioidea*. Edinburgh: Edinburgh University Press.

Hill, W. C. O. (1960): *Primates. Comparative anatomy and taxonomy. IV. Cebidae, part A*. Edinburgh: Edinburgh University Press.

Hill, W. C. O. (1970): *Primates. Comparative anatomy and taxonomy. 8. Cynopithecinae: Papio, Mandrillus, Theropithecus*. Edinburgh: Edinburgh University Press.

Hill, W. C. O.; Appleyard, H. M. & Auber, L. (1959): The specialized area of skin glands in *Aotes* Humboldt (Simiae, Platyrrhini). *Transactions of the Royal Society of Edinburgh* 63: 535-551.

Hill, W. C. O.; Porter, A. & Southwick, M. D. (1952): The natural history, endoparasites and pseudo-parasites of the tarsiers (*Tarsius carbonarius*) recently living in the Society's menagerie. *Proceedings of the Zoological Society, London* 122: 79-119.

Hinton, M. A. C. & Lindsay, H. M. (1926): Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon: Report No. 41, Assam and Mishmi Hills. *Journal of the Bombay Natural History Society* 31: 383-403.

Hofer, H. (1972): Über den Gesang des Orang-Utan. *Der Zoologische Garten (N.F.)* 41: 299-302.

Hold, B. & Schleidt, M. (1977): The importance of human odour in non-verbal communication. *Zeitschrift für Tierpsychologie* 43: 225-238.

Hood, C. S. & Smith, J. D. (1984): Histology of a sexually dimorphic integumentary gland in *Macroglossus lagochilus* (Chiroptera: Pteropodidae). *Journal of Mammalogy* 65: 1-9.

Hooijer, D. A. (1960): Quaternary gibbons from the Malay archipelago. *Zoologische Verhandelingen, Leiden* 46: 1-42, + 2 plates.

Hooijer, D. A. (1962): Prehistoric bone: The gibbons and monkeys of Niah Great Cave. *The Sarawak Museum Journal* 11: 428-449, + 1 plate.

Hornaday, W. T. (1894): *Two years in the jungle. The experiences of a hunter and naturalist in India, Ceylon, the Malay peninsula and Borneo*. New York: Charles Scribner's Sons. (Fifth Edition).

Horwich, R. H. (1976): The whooping display in Nilgiri langurs: An example of daily fluctuations superimposed on a general trend. *Primates* 17: 419-431.

Hrdlicka, A. (1925): Weight of the brain and of the internal organs in American monkeys. *American Journal of Physical Anthropology* 8: 201-211.

Hrdy, S. B. & Hartung, J. (1979): The evolution of sexual dichromatism among primates. *American Journal of Physical Anthropology* 50: 450 (Abstract only).

Hurley, H. J. & Shelley, W. B. (1960): *The human apocrine sweat gland in health and disease*. Springfield, Ill.: Charles C. Thomas.

Imhof, E. (1965): *Schweizerischer Mittelschulatlas (14th edition)*. Zürich: Lehrmittelverlag des Kantons Zürich.

Istituto Geografico De Agostini S.p.A. (1979): *Der neue Weltatlas (5th edition)*. Novara: Officine Grafiche.

Izawa, K. (1978): A field study of the ecology and behavior of the black-mantle tamarin (*Saguinus nigricollis*). *Primates* 19: 241-274.

Jackman, P. J. H. (1982): Body odor – The role of skin bacteria. *Seminars in Dermatology* 1: 143-148.

Jackman, P. J. H. & Noble, W. C. (1983): Normal axillary skin microflora in various populations. *Clinical and Experimental Dermatology* 8: 259-268.

Jenkins, P. D. (1990): *Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles; part V: The apes, superfamily Hominoidea*. London: British Museum (Natural History).

Jolly, A. (1966): *Lemur behavior. A Madagascar field study*. Chicago: University of Chicago Press.

Jouventin, P. (1975): Observations sur la socio-écologie du Mandrill. *Terre et Vie* 29: 493-532.

Jungers, W. L. (1984): Scaling of the hominoid locomotor sceleton with special reference to lesser apes. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 146-169). Edinburgh: Edinburgh University Press.

Kappeler, M. (1981): *The Javan silvery gibbon (Hylobates lar moloch)*. Doctoral diss., Universität Basel.

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

Katsir, Z. & Crewe, R. M. (1980): Chemical communication in *Galago crassicaudatus*: Investigation of the chest gland secretion. *South African Journal of Zoology* 15: 249-254.

Kaufmann, J. H. (1965): Studies on the behavior of captive tree shrews (*Tupaia glis*). *Folia Primatologica* 3(50-74).

Kavanagh, M. (1983): *A complete guide to monkeys, apes and other primates*. London: Jonathan Cape.

Kay, R. F.; Thewissen, J. G. M. & Yoder, A. D. (1992): Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *American Journal of Physical Anthropology* 89: 477-498.

Keele, C. A.; Neil, E. & Joels, N. (1982): *Samson Wright's applied physiology, 13th ed*. Oxford: Oxford University Press.

Keith, A. (1891): Anatomical notes on Malay apes. *Journal of the Straits Branch of the Royal Asiatic Society* 23: 77-94, + 9 plates.

Keith, A. (1895): The growth of brain in men and monkeys with a short criticism of the usual method of stating brain-ratios. *Journal of Anatomy and Physiology, London* 29: 282-303.

Keith, A. (1896): An introduction to the study of anthropoid apes. *Natural Science (London)* 9: 26-37, 250-265, 316-326, 372-379.

Keith, A. (1940): Fifty years ago. *American Journal of Physical Anthropology* 26: 251-267.

Kinzey, W. G. (1981): The titi monkey, genus *Callicebus*. In Coimbra-Filho, A. F. & Mittermeier, R. A. (Eds.), *Ecology and behavior of Neotropical primates, vol. 1* (pp. 241-276). Rio de Janeiro: Brazilian Academy of Sciences.

Klaar, J. (1924): Ueber die axillaren Knäueldrüsen der Affen. *Zeitschrift für Anatomie und Entwicklungs-Geschichte* 72: 609-627.

Kleiman, D. G. (1977a): Characteristics of reproduction and sociosexual interactions in pairs of lion tamamrins (*Leontopithecus rosalia*) during the reproductive cycle. In Kleiman, D. G. (Ed.), *The biology and conservation of the Callitrichidae* (pp. 181-190). Washington, D.C.: Smithsonian Institution Press.

Kleiman, D. G. (1977b): Monogamy in mammals. *Quarterly Review of Biology* 52: 39-69.

Kleiman, D. G. & Mack, D. S. (1980): Effects of age, sex, and reproductive status on scent marking frequencies in the golden lion tamarin, *Leontopithecus rosalia*. *Folia Primatologica* 33: 1-14.

Klein, L. & Klein, D. (1971): Aspects of social behaviour in a colony of spider monkeys *Ateles geoffroyi* at San Francisco Zoo. *International Zoo Yearbook* 11: 175-181.

Klopfer, F. H. (1977): Communication in prosimians. In Sebeok, T. A. (Ed.), *How animals communicate* (pp. 841-850). Bloomington and London: Indiana University Press.

Kloss, B. C. (1929): Some remarks on the gibbons, with the description of a new subspecies. *Proceedings of the Zoological Society, London* 1929: 113-127.

Kohlbrügge, J. H. F. (1891-92): Versuch einer Anatomie des Genus *Hylobates*: zweiter Teil. In Weber, M. (Ed.), *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien, vol. 2* (pp. 139-206, + 1 plate). Leiden: Brill.

Kortlandt, A. (1981): "Siabon" or "gibbang"? *Laboratory Primate Newsletter* 20(3): 12.

Labhart, A.; Assal, J.-P.; Binswanger, U.; Bürgi, H.; Fischer, J. A.; Froesch, E. R.; Grob, P. J.; Groscurth, P.; Hedinger, C.; Jakob, A.; Kistler, G.; König, M. P.; Landolt, A. M.; Liniger, C.; Martz, G.; Meuli, C.; Müller, J.; Oelz, O.; Prader, A.; Schindler, A. E.; Siebenmann, R.; Studer, H.; Zachmann, M.; Zapf, J.; Ziegler, W. H. & Zuppinger, K. A. (Ed.). (1986): *Clinical endocrinology. – Theory and practice (2nd edition)*. Berlin: Springer-Verlag.

Labows, J. N., Jr. (1988): Odor detection, generation, and etiology in the axilla. In Laden, K. & Felger, C. B. (Eds.), *Antiperspirants and deodorants* (pp. 321-343). New York and Basel: Marcel Dekker, Inc.

Labows, J. N.; MacGinley, K. J. & Kligman, A. M. (1982): Perspectives on axillary odor. *Journal of the Society of Cosmetic Chemists* 34: 193-202.

Labows, J. N.; Preti, G.; Hoelzle, E.; Leyden, J. & Kligman, A. (1979): Steroid analysis of human apocrine secretion. *Steroids* 34: 249-258.

Lamprecht, J. (1970): Duettgesang beim Siamang, *Symphalangus syndactylus* (Hominoidea, Hylobatinae). *Zeitschrift für Tierpsychologie* 27: 186-204.

Lang, E. M. (1961): *Goma, das Gorillakind*. Rüschlikon-Zürich: Albert Müller Verlag.

Lang, E. M. (1971): Neue Tiere im Zolli. *Zolli, Bulletin des Vereins der Freunde des Zoologischen Gartens Basel* 26(April 1971): 1-6.

Lang, E. M. (1973): Beobachtungen bei der Eingewöhnung einer Gruppe Zwergsiamangs, *Hylobates klossi* (Miller 1903). *Säugetierkundliche Mitteilungen* 21: 12-17.

Lang, E. M. (1975): Geburt beim Zwergsiamang (*Hylobates klossi*). *Zolli, Bulletin des Vereins der Freunde des Zoologischen Gartens Basel* 35(Okt. 1975): 1-6.

Lang, E. M. (1977): What are endangered species? *International Zoo Yearbook* 17: 2-5.

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

Leighton, D. S. R. & Whitten, A. J. (1984): Management of free-ranging gibbons. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 32-43). Edinburgh: Edinburgh University Press.

Leyden, J. J. (1988): Bacteriology of the human axilla: Relationship to axillary odor. In Laden, K. & Felger, C. B. (Eds.), *Antiperspirants and deodorants* (pp. 311-320). New York and Basel: Marcel Dekker, Inc.

Leyden, J. J.; McGinley, K. J.; Hölzle, E.; Labows, J. N. & Kligman, A. M. (1981): The microbiology of the human axilla and its relationship to axillary odor. *Journal of Investigative Dermatology* 77: 413-416.

Lin, Y.; Gu, Y. & He, N. (1974): [Pleistocene gibbon's upper tooth from Kwansi, China]. *Vertebrata Palasiatica* 12: 231-232 (Chinese text, English summary).

Linke, K. (1988): Beobachtungen zur Entwicklung von 3 Gibbons bei einer Handaufzucht und 2 kombinierten Aufzuchten. *Der Zoologische Garten (N.F.)* 58: 229-250.

Linke, K. (1989): Vergleichende Beobachtungen bei der Aufzucht verschiedener Affen. In Hohmann, H.-D. (Ed.), *Verhandlungsbericht zur Konferenz Haltung und Zucht von Primaten* (pp. 68-77). Jena: VEB Gustav Fischer Verlag.

Liu, R.; Shi, L. & Chen, Y. (1987): [A study on the chromosomes of white-browed gibbon (*Hylobates hoolock leuconedys*)]. *Acta Theriologica Sinica* 7: 1-7 (Chinese text, English summary).

Loireau, J.-N. (1985): *Étude du marquage olfactif chez le Singe de Brazza (Cercopithecus neglectus) et éléments sur la distribution de ce comportement chez les Catarrhiniens Africains*. Unpublished thesis, Université de Rennes I, Station Biologique de Paimpont, DEA d'Écologie-Éthologie.

Loireau, J.-N. & Gautier-Hion, A. (1988): Olfactory marking behaviour in guenons and its implications. In Gautier-Hion, A.; Bourlière, F.; Gautier, J.-P. & Kingdon, J. (Eds.), *A primate radiation: Evolutionary biology of the African guenons* (pp. 246-253). Cambridge: Cambridge University Press.

Lyon, M. W., Jr. (1907): Mammals collected in western Borneo by Dr. W. L. Abbott. *Proceedings of the United States National Museum* 32: 547-572.

Lyon, M. W., Jr. (1908): Mammals collected in eastern Sumatra by Dr. W. L. Abbott during 1903, 1906, and 1907, with descriptions of new species and subspecies. *Proceedings of the United States National Museum* 34: 619-679, + 5 plates.

Lyon, M. W., Jr. (1911): Mammals collected by Dr. W. L. Abbott on Borneo and some of the small adjacent islands. *Proceedings of the United States National Museum* 40: 53-146, + 7 plates.

Ma, S. & 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).

Machida, H.; Perkins, E. & Hu, F. (1967): The skin of primates. XXXV. The skin of the squirrel monkey (*Saimiri sciurea*). *American Journal of Physical Anthropology* 26: 45-54.

Machida, H.; Perkins, E. & Montagna, W. (1964): The skin of primates. XXIII. A comparative study of the skin of the green monkey (*Cercopithecus aethiops*) and the Sykes' monkey (*Cercopithecus mitis*). *American Journal of Physical Anthropology* 22: 453-466.

Mack, D. S. & Kleiman, D. G. (1978): Distribution of scent marks in different contexts in captive lion tamarins *Leontopithecus rosalia* (Primates). In Rothe, H.; Wolkers, H.-J. & Hearn, J. P. (Eds.), *Biology and behaviour of marmosets* (pp. 305-321). Göttingen: Eigenverlag Hartmut Rothe.

MacKinnon, J. (1974): The behaviour and ecology of wild orang-utan (*Pongo pygmaeus*). *Animal Behavior* 22: 3-74.

MacKinnon, J. (1978): Summary of discussion. In Chivers, D. J. & Joysey, K. A. (Eds.), *Recent advances in primatology, vol. 3: Evolution* (pp. 327-329). London: Academic Press.

MacKinnon, J. R. & MacKinnon, K. S. (1984): Territoriality, monogamy and song in gibbons and tarsiers. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 291-297). Edinburgh: Edinburgh University Press.

Maddison, W. P. & Maddison, D. R. (1992): *MacClade: Analysis of phylogeny and character evolution. Version 3.0*. Sunderland, Massachusetts: Sinauer Associates.

Maples, E. G.; Haraway, M. M. & Hutto, C. W. (1989): Development of coordinated singing in a newly formed siamang pair (*Hylobates syndactylus*). *Zoo Biology* 8: 367-378.

Marchant, L. F. & Dolhinow, P. (1990): Infant development in *Presbytis entellus* and its relation to natal coloration. *American Journal of Physical Anthropology* 81: 263 (Abstract only).

Marler, P. (1957): Specific distinctiveness in the communication signals of birds. *Behaviour* 11: 13-39.

Marler, P. (1965): Communication in monkeys and apes. In DeVore, I. (Ed.), *Primate behavior. Field studies of monkeys and apes* (pp. 544-584). New York and London: Holt, Rinehart & Winston.

Marler, P. (1969): Vocalizations of wild chimpanzees. An introduction. In Carpenter, C. R. (Ed.), *Proceedings of the Second International Congress of Primatology, Atlanta, GA 1968. vol. 1: Behavior* (pp. 94-100). Basel and New York: Karger.

Marler, P. & Hobbett, L. (1975): Individuality in a long-range vocalization of wild chimpanzees. *Zeitschrift für Tierpsychologie* 38: 97-109.

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

Marshall, J. T. (1981): The agile gibbon in south Thailand. *Natural History Bulletin of the Siam Society* 29: 129-136.

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

Marshall, J. T. & Marshall, E. R. (1978): *The gibbons (phonograph disc)*. Hardy, J.W. & Hardy, C.K. (Eds.) 1615 NW 14th Ave., Gainesville, FL 32605, USA: ARA-Records.

Marshall, J. T.; Ross, B. A. & Chantharojvong, S. (1972): The species of gibbons in Thailand. *Journal of Mammalogy* 53: 479-486.

Marshall, J. T. & Sugardjito, J. (1986): Gibbon systematics. In Swindler, D. R. & Erwin, J. (Eds.), *Comparative primate biology, vol. 1: Systematics, evolution, and anatomy* (pp. 137-185). New York: Alan R. Liss.

Marshall, J. T.; Sugardjito, J. & Markaya, M. (1984): Gibbons of the lar group: Relationships based on voice. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 533-541). Edinburgh: Edinburgh University Press.

Martin, R. D. (1968): Reproduction and ontogeny in tree-shrews (*Tupaia belangeri*). *Zeitschrift für Tierpsychologie* 25: 409-495, 505-532.

Martin, R. D. (1990): *Primate origins and evolution. A phylogenetic reconstruction*. London: Chapman and Hall.

Martin, R. D.; Willner, L. A. & Dettling, A. (in press.): The evolution of sexual size dimorphism in primates. In Short, R. V. & Balaban, E. (Eds.), The differences between the sexes. Cambridge: Cambridge University Press.

Martin, W. C. L. (1841): *Natural history of man and monkeys. A general introduction to the natural history of mammiferous animals with a particular view of the physical history of man and the more closely allied genera of the order of quadrumana or monkeys*. London: Wright.

Mason, W. A. (1966): Social organization of the South American monkey *Callicebus moloch*: A preliminary report. *Tulane Studies in Zoology* 13: 23-28.

Matschie, P. (1893): Die unterscheidenden Merkmale der Hylobates-Arten. *Sitzungsbericht der Gesellschaft Naturforschender Freunde, Berlin* 1893: 209-212.

Matthew, W. D. & Granger, W. (1923): New fossil mammals from the Pliocene of Sze-chuan, China. *Bulletin of the American Museum of Natural History* 48: 563-598.

McCann, C. (1933): Notes on the colouration and habits of the white-browed gibbon or hoolock (*Hylobates hoolock* Harl.). *Journal of the Bombay Natural History Society* 36: 395-405.

Mellen, J. D.; Littlewood, A. P.; Barrow, B. C. & Stevens, V. J. (1981): Individual and social behavior in a captive troop of mandrills (*Mandrillus sphinx*). *Primates* 22: 206-220.

Mertl-Millhollen, A. S. (1979): Olfactory demarcation of territorial boundaries by a primate – *Propithecus verreauxi*. *Folia Primatologica* 32: 35-42.

Meyer, P. K.-W. (1986): Ein Sternalorgan – Glandulae sternales – bei kleinen Wiederkäuern. *Deutsche Tierärztliche Wochenschrift* 93: 251-253.

Miller, G. S., Jr. (1902): Mammals collected by Dr. W. L. Abbott in the region of the Indragiri River, Sumatra. *Proceedings of the Academy of Natural Sciences of Philadelphia* 54: 143-159.

Miller, G. S., Jr. (1903a): Mammals collected by Dr. W. L. Abbott on the coast and islands of northwest Sumatra. *Proceedings of the United States National Museum* 26: 437-484, + 1 plate.

Miller, G. S., Jr. (1903b): Seventy new Malayan mammals. *Smithsonian Miscellaneous Collections* 45: 1-73, + 19 plates.

Miller, G. S., Jr. (1942): Zoological results of the George Vanderbilt Sumatran Expedition, 1936 - 1939. Part V. – Mammals collected by Frederick A. Ulmer, Jr. on Sumatra and Nias. *Proceedings of the Academy of Natural Sciences of Philadelphia* 94: 107-165, + 2 plates.

Mitani, J. C. (1984): The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). *Behavioral Ecology and Sociobiology* 15: 225-229.

Mitani, J. C. (1985a): Gibbon song duets and intergroup spacing. *Behaviour* 92: 59-96.

Mitani, J. C. (1985b): Location-specific responses of gibbons (*Hylobates muelleri*) to male songs. *Zeitschrift für Tierpsychologie* 70: 219-224.

Mitani, J. C. (1985c): Responses of gibbons (*Hylobates muelleri*) to self, neighbor, and stranger song duets. *International Journal of Primatology* 6: 193-200.

Mitani, J. C. (1985d): Sexual selection and adult male orangutan long calls. *Animal Behavior* 33: 272-283.

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

Mitani, J. C. (1987b): Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behavioral Ecology and Sociobiology* 20: 265-269.

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

Mitani, J. C. (1990): Experimental field studies of Asian ape social systems. *International Journal of Primatology* 11: 103-126.

Mitani, J. C.; Hasegawa, T.; Gros-Louis, J.; Marler, P. & Byrne, R. (1992): Dialects in wild chimpanzees? *American Journal of Primatology* 27: 233-243.

Mitani, J. C. & Marler, P. (1989): A phonological analysis of male gibbon singing behavior. *Behavior* 109: 20-45.

Montagna, W. (1962): *The structure and function of skin*. New York: Academic Press. (2nd ed.).

Montagna, W. (1972): The skin of nonhuman primates. *American Zoologist* 12: 109-124.

Montagna, W. (1976): *The Wesley W. Spink Lectures on comparative medicine, vol. 3: Nonhuman primates in biomedical research*. Minneapolis: University of Minnesota Press.

Montagna, W. (1981): The evolution of human skin. *Giornale Italiano di Dermatologia e Venereologia* 116: 139-143.

Montagna, W. (1982): The evolution of human skin. In Chiarelli, A. B. & Corruccini, R. S. (Eds.), *Advanced Views in Primate Biology* (pp. 35-41). Berlin: Springer.

Montagna, W. (1985): The evolution of human skin (?). *Journal of Human Evolution* 14: 3-22.

Montagna, W. & Ellis, R. A. (1963): New approaches to the study of the skin of primates. In Buettner-Janusch, J. (Ed.), *Evolutionary and genetic biology of primates, vol. 1* (pp. 179-196). New York: Academic Press.

Montagna, W. & Yun, J. S. (1962): The skin of primates. VIII. The skin of the anubis baboon (*Papio doguera*). *American Journal of Physical Anthropology* 20: 131-142.

Montagna, W. & Yun, J. S. (1963): The skin of primates. XV. The skin of the chimpanzee (*Pan satyrus*). *American Journal of Physical Anthropology* 21: 189-204.

Mootnick, A. (1984): Census of gibbons in North America. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 61-73). Edinburgh: Edinburgh University Press.

Moss, A. J.; Dalrymple, G. V. & Boyd, C. M. (Eds.). (1976): *Practical radioimmunoassay*. Saint Louis: Mosby.

Moynihan, M. (1966): Communication in the titi monkey, *Callicebus*. *Journal of Zoology (London)* 150: 77-127.

Müller, S. (1845): Ueber die auf den Sunda-Inseln lebenden ungeschwänzten Affen-Arten. *(Wiegm.) Archiv für Naturgeschichte* 11(1): 72-90.

Myers, R. H. & Shafer, D. A. (1978): Genetic studies of an intergeneric hybrid ape. *Behavioral Genetics* 8: 108 (Abstract only).

Myers, R. H. & Shafer, D. A. (1979): Hybrid ape offspring of a mating of a gibbon and siamang. *Science* 205: 308-310.

Mykytowycz, R. (1970): The role of skin glands in mammalian communication. In Johnson, J. W.; Moulton, D. G. & Turk, A. (Eds.), *Advances in chemoreception, vol. 1: Communication by chemical signals* (pp. 327-360). New York: Appleton-Century-Crofts.

Mykytowycz, R. & Nay, T. (1964): Studies of the cutaneous glands and hair follicles of some species of Macropodidae. *CSIRO Wildl. Res*. 9: 200-217.

Napier, J. R. & Napier, P. H. (1967): *A handbook of living primates*. London and New York: Academic Press.

Napier, J. R. & Napier, P. H. (1985): *The natural history of primates*. London: British Museum (Natural History).

Neville, M. K. (1972): Social relations within troops of red howler monkeys (*Alouatta seniculus*). *Folia Primatologica* 18: 47-77.

Niemitz, C. (1984): An investigation and review of the territorial behaviour and social organisation of the genus *Tarsius*. In Niemitz, C. (Ed.), *Biology of tarsiers* (pp. 117-127). Stuttgart and New York: Gustav Fischer Verlag.

Oates, J. F. & Trocco, T. F. (1983): Taxonomy and phylogeny of black-and-white colobus monkeys. Interactions from an analysis of loud call variation. *Folia Primatologica* 40: 83-113.

Omedes, A. & Carroll, J. B. (1980): A comparative study of pair behaviour of four callitrichid species and the Goeldi's monkey *Callimico goeldii* at Jersey Wildlife Preservation Trust. *Dodo, Journal of the Jersey Wildlife Preservation Trust* 17: 51-62.

Orgeldinger, M. (1989): *Untersuchungen zum Verhalten von Siamangs (Hylobates syndactylus Raffles 1821) in zoologischen Gärten unter besonderer Berücksichtigung des Sozialverhaltens*. Unpubl. Diplomarbeit, Fakultät für Biologie, Ruprecht-Karls-Universität Heidelberg.

Orten, J. M. & Neuhaus, O. W. (1982): *Human biochemistry (Tenth edition)*. St. Louis: Mosby.

Pandey, S. D. & Dominic, C. J. (1987): Gular gland of the Indian sheath-tailed bat. *Acta Theriologica* 32: 83-93.

Parakkal, P.; Montagna, W. & Ellis, R. A. (1962): The skin of primates. XI. The skin of the white-browed gibbon (*Hylobates hoolock*). *Anatomical Records* 143: 169-178.

Peart, J. F. (1935): Notes on the colouration of the white-browed gibbon (*H. hoolock* Harl.). *Journal of the Bombay Natural History Society* 37: 214.

Pellicciari, C.; Formenti, D.; Zuccotti, M.; Stanyon, R. & Manfredi Romanini, M. G. (1988): Genome size and constitutive heterochromatin in *Hylobates muelleri* and *Symphalangus syndactylus* and in their viable hybrid. *Cytogenetics and Cell Genetics* 47: 1-4.

Perkins, E.; Arao, T. & Dolnick, E. H. (1968a): The skin of primates. XXXVII. The skin of the pig-tail macaque (*Macaca nemestrina*). *American Journal of Physical Anthropology* 28: 75-84.

Perkins, E.; Arao, T. & Uno, H. (1968b): The skin of primates. XXXVIII. The skin of the red uacari (*Cacajao rubicundus*). *American Journal of Physical Anthropology* 29: 57-80.

Perkins, E. M. (1966): The skin of primates. XXXI. The skin of the black-collared tamarin (*Tamarinus nigricollis*). *American Journal of Physical Anthropology* 25: 41-70.

Perkins, E. M. (1968): The skin of primates. XXXVI. The skin of the pygmy marmoset – *Callithrix* (=*Cebuella*) pygmaea. *American Journal of Physical Anthropology* 29: 349-364.

Perkins, E. M. (1969a): The skin of primates. XLI. The skin of the silver marmoset – *Callithrix* (=*Mico*) *argentata*. *American Journal of Physical Anthropology* 30: 361-388.

Perkins, E. M. (1969b): The skin of primates. XXIV. The skin of Goeldi's marmoset (*Callimico goeldii*). *American Journal of Physical Anthropology* 30: 231-250.

Perkins, E. M. & Ford, D. M. (1969): The skin of primates. XXXIX. The skin of the white-browed capuchin (*Cebus albifrons*). *American Journal of Physical Anthropology* 30: 1-12.

Petter, J.-J. (1965): The lemurs of Madagascar. In DeVore, I. (Ed.), *Primate behavior. Field studies of monkeys and apes* (pp. 292-319). New York: Holt, Rinehart and Winston.

Petter, J.-J.; Albignac, R. & Rumpler, Y. (1977): Mammifères lémuriens (Primates prosimiens). In *Faune de Madagascar, vol. 44* (pp. 292-319). Paris: Orstom, CNRS.

Pilbeam, D. (1985): Patterns of hominoid evolution. In Delson, E. (Ed.), *Ancestors. The hard evidence* (pp. 51-59). New York: Alan R. Liss, Inc.

Pitts, R. (1988): Classical Heinrothian intimidation displays exhibited by *Galago demidoff demidoff*: A paradigm for pinpointing galagine species diversity. *International Journal of Primatology* 9: 529-556.

Pocock, R. I. (1905): Observations upon a female specimen of the Hainan gibbon (*Hylobates hainanus*), now living in the Society's Gardens. *Proceedings of the Zoological Society, London* 1905(2): 169-180, + 1 plate.

Pocock, R. I. (1925): The external characters of the catarrhine monkeys and apes. *Proceedings of the Zoological Society, London* 1925: 1479-1579.

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

Pocock, R. I. (1939): *The fauna of British India, including Ceylon and Burma. Mammalia. – Vol. I: Primates and Carnivora (in part), families Felidae and Viverridae*. London: Taylor and Francis, Ltd. (Reprint edition: 1985, Today & Tomorrow's Printers & Publishers, New Delhi).

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

Prouty, L. A.; Buchanan, P. D.; Pollitzer, W. S. & Mootnick, A. R. (1983b): A presumptive new hylobatid subgenus with 38 chromosomes. *Cytogenetics and Cell Genetics* 35: 141-142.

Raemaekers, J. J. & Raemaekers, P. M. (1984a): The ooaa duet of the gibbon (*Hylobates lar*). A group call which triggers other groups to respond in kind. *Folia Primatologica* 42: 209-215.

Raemaekers, J. J. & Raemaekers, P. M. (1984b): Vocal interactions between two male gibbons, *Hylobates lar*. *Natural History Bulletin of the Siam Society* 32: 95-106.

Raemaekers, J. J. & Raemaekers, P. M. (1985): Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. *Animal Behavior* 33: 481-493.

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

Raemaekers, P. M. & Raemaekers, J. J. (1985): Long-range vocal interactions between groups of gibbons (*Hylobates lar*). *Behaviour* 95: 26-44.

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

Richard, A. (1974): Patterns of mating in *Propithecus verreauxi verreauxi*. In Martin, R. D.; Doyle, G. A. & Walker, A. C. (Eds.), *Prosimian biology* (pp. 49-74). London: Duckworth.

Rijksen, H. D. (1978): A field study on Sumatran orang utans (*Pongo pygmaeus abelii* Lesson 1827). Ecology, behaviour and conservation. In *Mededelingen Landbouwhogeschool, Wageningen 78 (2)* Wageningen: Veenman & Zonen.

Riley, K. V. & Shortridge, G. C. (1913): Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon: Report No. 14. With field notes by the collector. *Journal of the Bombay Natural History Society* 22: 710-725.

Ritscher, D. (1980): Kaiserschnitt beim Silbergibbon. *Jahresbericht, Zoo Rostock* 1980: 24-28.

Ritscher, D. (1989): Veterinärmedizinische Arbeiten. *Jahresbericht, Zoo Rostock* 1989: 5-7.

Ritscher, D. & Linke, K. (1982): Wiederholter Kaiserschnitt bei einem Silbergibbon (*Hylobates moloch*) und veterinärmedizinische Probleme bei der Aufzucht der beiden Jungtiere. In *Verhandlungsbericht des XXIV. Internationalen Symposiums über die Erkrankungen der Zootiere, Veszprém 1982* (pp. 107-111). Berlin: Akademie Verlag.

Romeis, B. (1968): *Mikroskopische Technik*. München and Wien: Oldenbourg Verlag.

Rühmekorf, E. (1963): Lautäusserungen beim Siamang (*Symphalangus syndactylus*). *Der Zoologische Garten (N.F.)* 28: 17-23.

Rumbaugh, D. M. (1981): "Siabon" or "gibbang"? : A reply. *Laboratory Primate Newsletter* 20(3): 13.

Rumbaugh, D. M.; Wolkin, J.; Wilkerson, B. J. & Myers, R. (1976): Siamang-gibbon hybrid. *Laboratory Primate Newsletter* 15(2): 32.

Rumpler, Y. & Andriamiandra, A. (1971): Étude histologique des glandes de marquage de la face antérieure du cou des Lémuriens malgaches. *Comptes Rendus de la Société de Biologie, Paris* 165: 436-441.

Russell, J. M. (1976): Human olfactory communication. *Nature* 260: 520-522.

Rutberg, A. T. (1983): The evolution of monogamy in primates. *Journal of Theoretical Biology* 104: 93-112.

Rylands, A. B. (1982): *The behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil*. Unpubl. PhD dissertation, University of Cambridge, Cambridge.

Sanderson, I. T. (1949-1950): A brief review of the mammals of Suriname (Dutch Guiana), based upon a collection made in 1938. *Proceedings of the Zoological Society, London* 199: 755-789.

Sarich, V. M. & Cronin, J. E. (1976): Molecular systematics of the primates. In Goodman, M.; E., T. R. & Tashian, J. H. (Eds.), *Molecular anthropology. Genes and proteins in the evolutionary ascent of the primates* (pp. 141-170). New York: Plenum Press.

Sauer, E. G. F. (1974): Zur Biologie der Zwerg- und Riesengalagos. *Zeitschrift des Kölner Zoo* 17: 67-84.

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

Schaffer, J. (1940): *Die Hautdrüsenorgane der Säugetiere mit besonderer Berücksichtigung ihres histologischen Aufbaues und Bemerkungen über die Proktodäaldrüsen*. Berlin and Wien: Urban und Schwarzenberg.

Schaller, G. B. (1963): *The mountain gorilla. Ecology and behavior*. Chicago: University of Chicago Press.

Schiefferdecker, P. (1922): Die Hautdrüsen des Menschen und der Säugetiere, ihre biologische und rassenanatomische Bedeutung, sowie die Muscularis sexualis. *Zoologica (Stuttgart)* 27(72): 1-154.

Schifter, H. (1968): Zucht und Markierungsverhalten von Wollaffen im Zoologischen Garten Zürich. *Der Zoologische Garten (N.F.)* 36: 107-132.

Schilling, A. (1980): The possible role of urine in territoriality of some nocturnal prosimians. *Symposia of the Zoological Society of London* 45: 165-193.

Schilling, D. (1984a): Gibbons in European zoos, with notes on the identification of subspecies of concolor gibbon. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 51-60). Edinburgh: Edinburgh University Press.

Schilling, D. (1984b): Letter to the editor. *Primate Report* 11: 36.

Schilling, D. (1984c): Song bouts and duetting in the concolor gibbon. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 390-403). Edinburgh: Edinburgh University Press.

Schleidt, M. & Hold, B. (1982a): Human axillary odour: Biological and cultural variables. In Steiner, J. E. (Ed.), *Determination of behaviour by chemical stimuli* (pp. 91-104). London: IRL Press.

Schleidt, M. & Hold, B. (1982b): Human odour and identity. In Breipohl, W. (Ed.), *Olfaction and endocrine regulation* (pp. 181-194). London: IRL Press.

Schmidt, C. R. (1992): Zwillinge bei Siamangs (*Symphalangus syndactylus*). *Der Zoologische Garten (N.F.)* 62: 284-286.

Schmidt, R.; Radin, J. & Brodie, J. (1989): *MacRecorder® User's Guide*. Emeryville: Farallon Computing, Inc.

Schmidt-Pfister, A. (1984): Ein seltener Zuchterfolg: Ili, der kleine Kappengibbon. *Irbis, Bulletin Tiergarten-Gesellschaft Zürich* 1984(1): 3.

Schneider, G. (1905): Ergebnisse zoologischer Forschungsreisen auf Sumatra. Erster Teil: Säugetiere (Mammalia). *Zoologisches Jahrbuch* 23: 1-172, + 3 plates + 2 maps.

Schröpel, M. (1977): Die Lautgebung der Gibbons. *Jahresbericht des Zoolog. Gartens Magdeburg* 18: 17-25.

Schultz, A. H. (1921): The occurrence of a sternal gland in orang-utan. *Journal of Mammalogy* 2: 194-196.

Schultz, A. H. (1930): The skeleton of the trunk and limbs of higher primates. *Human Biology* 2: 303-438.

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. (1937): *Harvard Primate Expedition, 1937. Field catalogue*. A.H. Schultz Archives, Anthropology Institute, Zürich University. (Unpublished).

Schultz, A. H. (1938): To Asia after apes. *The Johns Hopkins Alumni Magazine* 26(2): 37-46.

Schultz, A. H. (1941a): *Rel. cranial capacity in H. cinereus, etc.* A.H. Schultz Archives, Anthropology Institute, Zürich University. (Unpublished data sheets).

Schultz, A. H. (1941b): *Rel. cranial capacity in H. lar.* A.H. Schultz Archives, Anthropology Institute, Zürich University. (Unpublished data sheets).

Schultz, A. H. (1942): Conditions for balancing the head in primates. *American Journal of Physical Anthropology* 29: 483-497.

Schultz, A. H. (1944): Age changes and variability in gibbons. A morphological study on a population sample of a man-like ape. *American Journal of Physical Anthropology* 2 (n.s.): 1-129.

Schultz, A. H. (1972): Polydactylism in a siamang. *Folia Primatologica* 17: 241-247.

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). Basel: Karger.

Schultze-Westrum, T. (1965): Innerartliche Verständigung durch Düfte beim Gleitbeutler *Petaurus breviceps papuanus* Thomas (Marsupialia, Phalangeridae). *Zeitschrift für Vergleichende Physiologie* 50: 151-220.

Schwarz, W. (1937): Die Sternaldrüse bei den Klammeraffen, *Ateles*. *Morphologisches Jahrbuch* 79: 600-633.

Sekulic, R. & Eisenberg, J. F. (1983): Throat-rubbing in red howler monkeys (*Alouatta seniculus*). In Müller-Schwarze, D. & Silverstein, R. M. (Eds.), *Chemical signals in vertebrates vol. 3* (pp. 347-350). New York: Plenum Press.

Shafer, D. A. (1986): Evolutionary cytogenetics of the siabon (gibbon-siamang) hybrid apes. In Taub, D. M. & King, F. A. (Eds.), *Current perspectives in primate biology* (pp. 226-239). New York: Van Nostrand Reinhold Company.

Shafer, D. A. & Myers, R. H. (1977): Cytogenetic studies of an intergeneric hybrid gibbon/siamang. *Mammalian Chromosomes Newsletter* 18: 4-8.

Shafer, D. A.; Myers, R. H. & Saltzman, D. (1984): Biogenetics of the siabon (gibbon-siamang hybrids). In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 486-497). Edinburgh: Edinburgh University Press.

Shelley, W. B.; Hurley, H. J. & Nichols, A. C. (1953): Axillary odor. Experimental study of the role of bacteria, apocrine sweat, and deodorants. *British Journal of Dermatology* 68: 430-446.

Shortridge, G. C. (1914): Notes on the weights of animals. *Journal of the Bombay Natural History Society* 22: 793-794.

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

Siegel, S. (1956): *Nonparametric statistics for the behavioral sciences*. New York and London: McGraw-Hill.

Smith, A. B., III; Yarger, R. G. & Epple, G. (1976): The major volatile constituents of the marmoset (*Saguinus fuscicollis*) scent mark. *Tetrahedron Letters* 13: 983-986.

Smith, M. (1980): Behaviour of koala, *Phasolarctos cinereus* (Goldfuss), in captivity. IV. Scent-marking. *Australian Wildlife Research* 7: 35-40.

Snowdon, C. T.; Hodun, A.; Rosenberger, A. L. & Coimbra-Filho, A. F. (1986): Long-call structure and its relation to taxonomy in lion tamarins. *American Journal of Primatology* 11: 253-261.

Soini, P. (1988): The pygmy marmoset, genus *Cebuella*. In Mittermeier, R. A.; Rylands, A. B.; Coimbra-Filho, A. & Fonseca, G. A. B. (Eds.), *Ecology and behavior of neotropical primates, vol. 2* (pp. 79-129). Washington, D.C.: World Wildlife Fund.

Sprankel, H. (1962): Histologie und biologische Bedeutung eines jugulo-sternalen Duftdrüsenfeldes bei *Tupaia glis* Diard 1820. *Verhandlungen der Deutschen Zoologischen Gesellschaft (Saarbrücken)* 1962: 198-206.

Srikosamatara, S. (1982): Imitation of vocal duet by a widow of the pileated gibbon (*Hylobates pileatus*) in Southeast Thailand. *International Journal of Primatology* 3: 336 (Abstract only).

Srikosamatara, S. & Brockelman, W. Y. (1983): Patterns of territorial vocalization in the pileated gibbon (*Hylobates pileatus*). In Seth, P. K. (Ed.), *Perspectives in primate biology* (pp. 19-22). New Delhi: Today & Tomorrow's Printers and Publishers.

Srikosamatara, S. & Brockelman, W. Y. (1987): Polygyny in a group of pileated gibbons via a familial route. *International Journal of Primatology* 8: 389-393.

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

Stoddart, D. M. (1990): *The scented ape – The biology and culture of human odour*. Cambridge: Cambridge University Press.

Stralendorff, v. F. (1982): A behaviorally relevant component of the scent signals of male *Tupaia belangeri*: 2,5-dimethylpyrazine. *Behavioral Ecology and Sociobiology* 11: 101-107.

Stralendorff, v. F. (1987): Partial chemical characterization of urinary signaling pheromone in tree shrews (*Tupaia belangeri*). *Journal of Chemical Ecology* 13: 655-679.

Straus, W. L., Jr. (1950): The microscopic anatomy of the skin of the gorilla. In Gregory, W. K. (Ed.), *The anatomy of the gorilla* (pp. 213-221). New York: Columbia University Press.

Struhsaker, T. T. (1970): Phylogenetic implications of some vocalizations of *Cercopithecus* monkeys. In Napier, J. R. & Napier, P. H. (Eds.), *Old World monkeys. Evolution, systematics, and behavior* (pp. 365-444). New York and London: Academic Press.

Susman, R. L. (1991): Apes of the world (Book review). *Journal of Human Evolution* 20: 185-190.

Sutcliffe, A. G. & Poole, T. B. (1978): Scent marking and associated behaviour in captive common marmosets (*Callithrix jacchus jacchus*) with a description of the histology of scent glands. *Journal of Zoology (London)* 185: 41-56.

Swofford, D. L. (1990): *PAUP: Phylogenetic analysis using parsimony, version 3.0. Computer program.* Champaign, Illinois: Illinois Natural History Survey.

Szalay, F. S. & Delson, E. (1979): *Evolutionary history of the primates*. New York and London: Academic Press.

Talke, L. (1903): Ueber die grossen Drüsen der Achselhöhlenhaut des Menschen. *Archiv für Mikroskopische Anatomie* 61: 537-555.

Tembrock, G. (1970): Bioakustische Untersuchungen an Säugetieren des Berliner Tierparkes. *Milu (Tierpark Berlin)* 3: 78-96.

Tembrock, G. (1974): Sound production of *Hylobates* and *Symphalangus*. In Rumbaugh, D. M. (Ed.), *Gibbon and siamang* (pp. 176-205). Basel: Karger.

Tembrock, G. (1977): *Tierstimmenforschung. Eine Einführung in die Bioakustik*. Wittenberg Lutherstadt: A. Ziemsen Verlag.

Tenaza, R. (1985): Songs of hybrid gibbons (*Hylobates lar* x *H. muelleri*). *American Journal Primatology* 8: 249-253.

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

Thorpe, W. H. (1961): *Bird-song. The biology of vocal communication and expression in birds. Cambridge monographs in experimental biology No. 12*. Cambridge: University Press.

Tilson, R. L. (1976): Infant coloration and taxonomic affinity of the Mentawai Islands leaf monkey, *Presbytis potenziani*. *Journal of Mammalogy* 57: 766-769.

Tilson, R. L. & Tenaza, R. R. (1976): Monogamy and duetting in an Old World monkey. *Nature* 263: 320-321.

Timm, R. M. & Birney, E. C. (1980): Mammals collected by the Menage Scientific Expedition to the Philippine Islands and Borneo, 1890-1893. *Journal of Mammalogy* 61: 566-571.

Träger, L. (1977): *Steroidhormone. Biosynthese, Stoffwechsel, Wirkung*. Berlin and New York: Springer-Verlag.

Tuttle, R. (1975): Parallelism, brachiation, and hominoid phylogeny. In Luckett, W. P. & Szalay, F. S. (Eds.), *Phylogeny of the primates. A multidisciplinary approach* (pp. 447-480). New York and London: Plenum Press.

Tuttle, R. H. (1986): *Apes of the world. Their social behavior, communication, mentality, and ecology*. New Jersey: Noyes Publications.

Tyler, D. E. (1991): The problems of the Pliopithecidae as a hylobatid ancestor. *Human Evolution* 6: 73-80.

U.S. Board on Geographic Names (1952): *Official standard names gazetteer: India (2 vols.).* Washington, D.C.: Defense Mapping Agency.

U.S. Board on Geographic Names (1966a): *Gazetteer: Thailand*. Washington, D.C.: Defense Mapping Agency.

U.S. Board on Geographic Names (1966b): *Official standard names gazetteer: Burma*. Washington, D.C.: Defense Mapping Agency.

U.S. Board on Geographic Names (1970): *Official standard names gazetteer No. 10 (2nd edition): Malaysia, Singapore, and Brunei*. Washington, D.C.: Defense Mapping Agency.

U.S. Board on Geographic Names (1979): *Gazetteer of the People's Republic of China: Pinyin to Wade-Giles, Wade-Giles to Pinyin*. Washington, D.C.: Defense Mapping Agency.

U.S. Board on Geographic Names (1982): *Gazetteer of Indonesia, 2 Vols*. Washington, D.C.: Defense Mapping Agency. (Third Edition).

U.S. Board on Geographic Names (1986): *Gazetteer of Vietnam, 2 Vols*. Washington, D.C.: Defense Mapping Agency.

van Gelderen, J. J. (1962): Einige Mitteilungen über das Achselhöhlenorgan des Chimpanse. *Anatomischer Anzeiger* 61: 407-409.

van Gulik, R. H. (1967): *The gibbon in China. An essay in Chinese animal lore*. Leiden: E.J. Brill.

van Roosmalen, M. G. M. & Klein, L. L. (1988): The spider monkeys, genus *Ateles*. In Mittermeier, R. A.; Rylands, A. B.; Coimbra-Filho, A. & Fonseca, G. A. B. (Eds.), *Ecology and behavior of neotropical primates, vol. 2* (pp. 455-537). Washington, D.C.: World Wildlife Fund.

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

van Tuinen, P. & 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).

Vandenbergh, J. G. (1963): Feeding, activity and social behavior of the tree shrew, *Tupaia glis*, in a large outdoor enclosure. *Folia Primatologica* 1: 199-207.

Vencl, F. (1977): A case of convergence in vocal signals between marmosets and birds. *American Naturalist* 111: 777-782.

Vogel, C. (1973): Acoustical communication among free-ranging common Indian langurs (*Presbytis entellus*) in two different habitats of North India. *American Journal of Anthropology* 38: 469-480.

Volz, W. (1904): Über die Verbreitung einiger anthropoider Affen in Sumatra. *Biologisches Centralblatt* 24(14): 475-476.

von Koenigswald, G. H. R. (1940): Neue Pithecanthropus-Funde 1936-1938. *Wetenschappelijke Mededeelingen van de Dienst van den Mijnbouw in Nederlandsch-Indië* 28: 1-211.

Wang, L.; Lin, Y. & Chang, S. (1982): [Mammalian fossils found in northwest part of Hunan Province and their significance]. *Vertebrata Palasiatica* 20: 350-358 (Chinese text, English summary).

Waser, P. M. (1977): Individual recognition, intragroup cohesion and intergroup spacing: Evidence from sound playback to forest monkeys. *Behaviour* 60: 28-74.

Waser, P. M. (1982): The evolution of male loud calls among mangabeys and baboons. In Snowdon, S. T.; Brown, C. H. & Petersen, M. R. (Eds.), *Primate communication* (pp. 117-143). Cambridge: Cambridge University Press.

Weber, M. (1890-91): Mammalia from the Malay Archipelago. I: Primates, Prosimiae, Galeopithecidae, Carnivora, Artiodactyla, Edentata, Marsupialia. In Weber, M. (Ed.), *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien, vol. 1* (pp. 93-114). Leiden: Brill.

Weber, M. & Abel, O. (1928): *Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. Band 2: Systematischer Teil (2nd ed.)*. Jena: Fischer.

Weitzel, V.; Yang, C. M. & Groves, C. P. (1988): A catalogue of primates in the Singapore Zoological Reference Collection. *The Raffles Bulletin of Zoology* 36: 1-166.

West, K. L. (1982): *The ecology and behavior of the siamang (Hylobates syndactylus) in Sumatera*. MSc. dissertation, University of California, Davis.

Wheeler, J. W.; Blum, M. S. & Clark, A. (1977): □-(p-hydroxyphenyl) ethanol in the chest gland secretion of a galago (*Galago crassicaudatus*). *Experientia* 33: 988-989.

White, B.; Dew, S.; Prather, J.; Schneider, E.; Taylor, S. & Stearns, M. (1989): Chest-rubbing ritual in captive wooly monkeys (*Lagothrix lagotricha*): Gender differences in environmental marking. *American Journal of Primatology* 18: 169.

Whitten, A. J. (1984): The trilling handicap in Kloss gibbons. In Preuschoft, H.; Chivers, D. J.; Brockelman, W. Y. & Creel, N. (Eds.), *The lesser apes. Evolutionary and behavioural biology* (pp. 416-419). Edinburgh: Edinburgh University Press.

Whitten, T. (1982): The ecology of singing in Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *International Journal of Primatology* 3: 33-51.

Wickler, W. (1969): *Sind wir Sünder? Naturgesetze der Ehe*. München & Zürich: Droemer Knaur. (English translation: The sexual code, Doubleday, Garden City, 1972)).

Wickler, W. (1973): Artunterschiede im Duettgesang zwischen *Trachyphonus d'arnaudii usambiro* und den anderen Unterarten von *T. d'arnaudii*. *Journal für Ornithologie* 114: 123-128.

Wickler, W. (1974): Duette und Paarbindung bei Tieren. *Mitteilungen der Max-Planck-Gesellschaft* 1974: 237-252.

Wickler, W. & Seibt, U. (1982): Song splitting in the evolution of dueting. *Zeitschrift für Tierpsychologie* 59: 127-140.

Wickler, W. & Uhrig, D. (1969): Bettelrufe, Antwortszeit und Rassenunterschiede im Befrüssungsduett des Schmuckbartvogels *Trachyphonus d'arnaudii*. *Zeitschrift für Tierpsychologie* 26: 651-661.

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

Wilkinson, L. (1989): *SYSTAT: The system for statistics*. Evanston, IL: SYSTAT, Inc.

Wilson, W. L. & Wilson, C. C. (1975): Species-specific vocalizations and the determination of phylogenetic affinities of the *Presbytis aygula-melalophos* group in Sumatra. In Kondo, S.; Kawai, M. & Ehara, A. (Eds.), *Contemporary primatology. Proceedings of the Fifth International Congress of Primatology, Nagoya* (pp. 459-463). Basel: Karger.

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.

Wislocki, G. B. & Schultz, A. H. (1925): On the nature of modifications of the skin in the sternal region of certain primates. *Journal of Mammalogy* 6: 236-244.

Wolkin, J. R. (1977): *Structural and behavioral characteristics of a young hybrid ape (Hylobates lar moloch x Symphalangus syndactylus)*. M.A. thesis, Georgia State University, Atlanta.

Wolkin, J. R. & Myers, R. H. (1980): Characteristics of a gibbon-siamang hybrid ape. *International Journal of Primatology* 1: 203-221.

Wroughton, R. C. (1915): Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon: Report No. 17. *Journal of the Bombay Natural History Society* 23: 795-720.

Wroughton, R. C. (1916): Bombay Natural History Society's Mammal Survey of India, Burma and Ceylon: Report No. 20. *Journal of the Bombay Natural History Society* 24: 291-309.

Xu, L.; Liu, Z. & Yu, S. (1983): [Mammalia]. In Xu, L.; Liu, Z. & Yi, X. (Eds.), *[Birds and mammals of Hainan Island]* (pp. 278-401, Chinese text). Beijing: Scientific Publishing Agency.

Yarger, R. G.; Smith, A. B., III; Preti, G. & Epple, G. (1977): The major volatile constituents of the scent mark of a South American primate, *Saguinus fuscicollis*, Callithricidae. *Journal of Chemical Ecology* 3: 45-56.

Young, O. P. (1982): Tree-rubbing behavior of a solitary male howler monkey. *Primates* 23: 303-306.

Zeller, U. (1984): Die funktionelle Anatomie der Gulardrüse von *Propithecus verreauxi coquereli* (Indriidae, Primates). In *Deutsche Gesellschaft für Säutetierkunde, 58. Hauptversammlung, Kurzfassungen der Vorträge und Posterdemonstrationen* (pp. 61, Abstract only). Hamburg: Parey.

Zeller, U. (1986): Die Gulardrüse von *Propithecus* (Indriidae, Primates). *Zeitschrift für Säugetierkunde* 51: 1-15.

Zeller, U.; Richter, J.; Clavien, H.-J. & Kuhn, H.-J. (1989): The monoptychic jugulo-sternal scent glands of *Tupaia*: A TEM and SEM study. *Primate Report* 25: 91 (Abstract only).

Zhao, Z.; Lix, X. & Wang, L. (1981): [Human fossils and associated fauna of Jiulengshan hill, Guangxi]. Vertebrata Palasiatica 19: 45-54 (Chinese text, English summary).

10. Appendices

Appendix 10.1: Tape-Recorded Songs of Hybrid Gibbons

Hybrids are arranged first by paternal species, second by maternal species.
Abbreviations: ad. = adult; sad. = subadult; juv. = juvenile; M = male; F = female.

H. agilis x *H. muelleri*

1 M "Männlein" ad. Born in 1978 at Dortmund Zoo. Together with ad. female *H. muelleri x H. lar* no. 2. Brother of animal no. 1. Together with *H. muelleri* x *H. lar* female no. 2. Tape-recorded at Duisburg Zoo on 24-27 June 1987, and 1-2 March 1988.

2 F "Bertha" ad. Born on 12 May 1979 at San Antonio Zoo. Together with mother. Tape-recorded by Mr. S. Kingswood at San Antonio Zoo in July and Aug. 1987 (fragments of great calls).
Same female, but ad., together with animal 3 and a juvenile third female; all 3 are full sisters. Recorded at Lion Country Safari Park, West Palm Beach, on 1-3 Aug. 1988.

3 F "Bernice" sad. Born on 13 March 1983 at San Antonio Zoo. Together with mother.Tape-recorded by Mr. S. Kingswood at San Antonio Zoo in July and Aug. 1987 (fragments of great calls).
Same female, but sad., together with animals 2 and a juvenile third female; all 3 are full sisters: Tape-recorded at Lion Country Safari Park, West Palm Beach, on 1-3 Aug. 1988.

H. lar x *H. agilis*

1 F no name sad. Born at 24 Sept. 1983 at Asson Zoo. Together with sad. male *H. lar*. Great-calls of low intensity, possibly not fully developed. Tape-recorded at Zoo Asson on 1-2 June 1988.

H. lar x *H. moloch*

1 F "Frieda" ad. Born on 21 March 1981 at Berlin Zoo. Half-sister of *H. pileatus* x *H. moloch* no. 1: same mother. Tape-recorded at Safari Park Hodenhagen on 9-11 July 1987.

2 F "Gipsy" ad. Born on 2 April 1979 at Rheine Zoo. Together with *H. lar* mate and their offspring. Tape-recorded at Rheine Zoo on 4-5 July 1987.

H. lar x (*H. lar* x *H. moloch*)

1 F "Alice" sad. Born on 5 Dec. 1983 at Rheine Zoo. Offspring of *H. lar* x *H. moloch* no. 2. Kept together with several juv. and ad. *H. lar* by Mr. & Mrs. P. & R. Manzke, Hasenmoor. Tape-recorded by Mr. and Mrs. P. and R. Manzke on 8 Nov. 1989.

Appendix 10.1: Continued.

H. lar x *H. muelleri*

1 M no name ad. Born on 13 Aug. 1965 at Micke Grove Zoo, Lodi, CA. Together with, and full sibbling of, animal no. 2. Tape-recorded by Dr. R. Tenaza at Micke Grove Zoo on 10 Feb. 1976, and 18-19 Oct. 1977.

2 F no name ad. Born on 25 Dec. 1968 at Micke Grove Zoo, Lodi, CA. Together with, and full sibbling of, animal no. 1. Tape-recorded by Dr. R. Tenaza at Micke Grove Zoo on 10 Feb. 1976.

H. muelleri x *H. agilis*

1 F no name, age unknown. Born at Louisiana Zoo, Monroe. Older sister of animal no. 2. Tape-recorded at Louisiana Zoo, Monroe on 5 July 1979 by members of the Psychology Department of Northeast Louisiana University; in Sept. 1979 by Mr. C. Welch, and on 4-5 July 1980 by Dr. J.T. Marshall (all tapes made available to the present author by Dr. J.T. Marshall).

2 F no name, age unknown. Born at Louisiana Zoo, Monroe. Younger sister of animal no. 1. Tape-recorded at Louisiana Zoo, Monroe on 10 Feb. 1987 by Dr. M.M. Haraway.

H. muelleri x *H. lar*

1 M "Barney" ad. Born on 24 Jan. 1978 at Banham Zoo. Brother of animal no. 5. Together with *H. lar* mate and their offspring. Tape-recorded at Banham Zoo on 15 Oct. 1988.

2 M "Frodo" sad. Born on 13 May 1983 at Twycross Zoo. Together with father *H. muelleri*. Tape-recorded at Twycross Zoo on 2-9 Oct. 1988.

3 F "Micky" ad. Born on 6 Sept. 1979 at Duisburg Zoo. Together with *H. agilis* x *H. muelleri* male no. 1. Tape-recorded at Duisburg Zoo on 24-27 June 1987, and on 1-2 March 1988.

4 F no name ad. Born on 31 July 1979 in Mazé; privately kept by Mr Jack Bauné, Mazé. Together with 1 male *H. pileatus* and 1 female *H. lar*. Tape-recorded in Mr Jack Bauné's garden on 30 May 1988.

5 F "Tina" ad. Born on 24 Oct. 1978. Sister of animal no. 1. Solitary. Tape-recorded at Ravensden Farm, Rushden on 12 Oct. 1988.

Appendix 10.1: Continued.

H. muelleri x *H. moloch*

1 M "Adolf" ad. Born on 25 July 1968 at Bristol Zoo. Together with animal 3. Brother of animals 2 and 3. Tape-recorded at Bristol Zoo on 18-19 Oct. 1988.

2 M "Mooli" ad. Born on 8 April 1979 at Bristol Zoo. Together with ad. female *H. moloch*. Brother of animals 1 and 3. Tape-recorded at Paignton Zoo on 20-23 Oct. 1988.

3 F "Juvi" ad. Born on 14 Nov. 1975 at Bristol Zoo. Together with animal 1. Sister of animals 1 and 2. Tape-recorded at Bristol Zoo on 18-19 Oct. 1988.

4 F "Maria" ad. Born on 13 Oct. 1967 at Münster Zoo. Together with *H. muelleri* mate and their offspring. Tape-recorded at Münster Zoo on 1-3 July 1987.

H. muelleri x (*H. muelleri* x *H. moloch*)

1 M "Fritzke" = "Tarzan" ad. Born on 5 May 1980 at Münster Zoo; brother of animal no. 2; offspring of *H. muelleri* x *H. moloch* no. 3. Solitary. Tape-recorded at Eberswalde Zoo on 11 July 1988.

2 F "Bo" juv. Born on 23 July 1984 at Münster Zoo; sister of animal no. 1; offspring of *H. muelleri* x *H. moloch* no. 3. Still with parental group. Tape-recorded at Münster Zoo on 1-3 July 1987. Tape-recorded again by Ms. B. Uphoff in July 1990. Female then sad./ad., but still with parental group.

H. muelleri x *H. syndactylus*

1 F "Shawn-Shawn" sad. Born on 11 Aug. 1975 at Atlanta Zoo. Recorded by Dr. D. Saltzman at the Georgia State University Primate Behavior Laboratory on 6 Jan. 1981 (tape made available to the present author by Dr. J.T. Marshall). Solitary female tape-recorded again at the Yerkes Regional Primate Research Center, Atlanta in 4-7 Aug. 1988.

H. pileatus x *H. agilis*

1 F "Barbara" ad. Born on 20 Oct. 1944 at the U.S. National Zoological Park, Washington, D.C. Tape-recorded there on 16 March -ca.8 April 1979 by Mr. D. Kessler and Mr. M. Roberts (tape made available to the present author by Dr. J.T. Marshall).

H. pileatus x *H. lar*

1 M "Charly" ad. Born in Feb. 1980 at Saarbrücken Zoo (Germany). Together with *H. lar* mate and their offspring. Tape-recorded at Zoo Nordhorn on 6-8 July 1978 and 9 Sept. 1988.

2 M "Wombel" ad. Born on 3 March 1978 at Opel Zoo. Brother of animals 3 and 4. Together with animal no. 3. Tape-recorded at Opel Zoo, Kronberg, on 17-18 June 1987.

Appendix 10.1: Continued.

3	F	"Toni" ad. Born in Nov./Dec. 1969 at Opel Zoo. Sister of animals 2 and 4. All 3 siblings together with mother when tape-recorded at Opel Zoo, Kronberg on 21 Sept. 1981. Tape-recorded again on 17-18 June 1987 then together with animal no. 2.
4	F	"Johnny" ad. Born on 5 Nov. 1975 at Opel Zoo. Sister of animals 2 and 3. All 3 siblings together with mother. Sings short phrases, no great calls. Tape-recorded at Opel Zoo, Kronberg, on 21 Sept. 1981. Tape-recorded again on 17-18 June 1987, then together with a male *H. pileatus* and singing great calls.
5	F	"Miss" = "Petronella" ad. Born on 17 Sept. 1969 at Skansen Zoo (Sweden). Tape-recorded at Asson Zoo on 1-2 June 1988.
6	F	"Sapuloh" = "Suse" ad. Born on 17 May 1970 at Zürich Zoo. Tape-recorded at Ruhr Zoo, Gelsenkirchen on 28-30 June 1987.
7	F	"Yoko" ad. Born in 1975 at Southport Zoo. Together with *H. lar* mate, their offspring, her *H. lar* mother, and her *H. lar* half-sister. Tape-recorded at Southport Zoo on 10 Oct. 1988.
H. pileatus x *H. moloch*		
1	M	"Peter" ad. Born on 2 Sept. 1972 at Berlin Zoo. Half-brother of *H. lar* x *H. moloch* no. 1 (same mother). Tape-recorded at Ruhr Zoo, Gelsenkirchen, on 28.-30 June 1987.
2	M	"Franz" ad. Born on 9 March 1965 at Berlin Zoo. Together with male *H. lar* x *H. moloch* no. 1. Tape-recorded at Safari Park Hodenhagen on 9-11 July 1987.
Undetermined, probably *H. agilis* x *H. lar* or *H. lar* x *H. agilis* [1]		
1	F	"Pauline" ad. Born on 25 April 1977, Jaderberg Zoo (Germany). Together with *H. lar* mate and their offspring. Tape-recorded at Berlin Zoo on 29 June -1 July 1988.

[1] Tentative identification based on vocalizations only. Parents of animals in question are unknown.

Appendix 10.2: Vocal Characteristics of Gibbons

Abbreviations: agi.= *H. agilis agilis* (& *H. a. unko*); alb.= *H. a. albibarbis*; lar= *H. lar*; mol.= *H. moloch*, abb.= *H. muelleri abbotti*; fun.= *H. m. funereus*; mu.= *H. m. muelleri*; pil.= *H. pileatus*; klo.= *H. klossii*, hoo.= *H. hoolock*; con.= *H. concolor*; leu.= *H. leucogenys leucogenys* (& *H. l. siki*); gab.= *H. l. gabriellae*; syn.= *H. syndactylus*; anc.= hypothetical ancestor; ?= missing data.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
1	Duetting in pairs: absent=0, facultative=1, always=2.														
	1	1	1	0	1	1	1	1	0	2	2	2	2	2	2
2	Introductory sequence: absent=0, present=1.														
	1	1	1	1	1	1	1	1	1	1	0	0	0	1	?
3	Introductory sequence: male-female duet=0, female solo=1.														
	1	1	2	1	1	1	1	2	1	2	?	?	?	2	?
4	Interlude sequence: male only=0, male-female duet=1, female mostly=2.														
	1	1	1	2	1	1	1	1	2	1	0	0	0	1	?
5	Boom notes (during throat sac infaltion): absent=0, males only=1, males and females=2.														
	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2
6	Staccato notes in male phrases: absent=0, present=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?
7	Quaver notes in male phrases: absent=0, weak=1, pronounced=2.														
	0	0	2	0	1	1	1	0	0	0	0	0	0	0	0
8	Trills in male phrases: absent=0, rare=1, present=2.														
	0	0	0	1	2	2	2	2	2	0	0	0	2	2	2
9	Inspiration notes in males: absent=0, rare=1, present=2.														
	2	2	0	1	0	0	0	2	0	2	0	0	0	0	2
10	Inspiration notes in female great call: absent=0, climax only=1, extensive=2.														
	1	1	1	0	0	0	0	0	0	2	0	0	0	0	2
11	Introductory notes to female great call: absent=0, present=1.														
	1	1	1	1	1	1	1	1	1	0	0	0	0	0	?

Appendix 10.2: Continued.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
12	Twitter-notes after female great call: absent=0, present=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?
13	Climaxes per female great call: one climax=0, two climaxes=1.														
	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
14	Climax type in female great call: acceleration=0, modulation=1.														
	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
15	Note rhythm in female climax: slow=0, moderate=1, fast=2.														
	0	0	0	1	2	2	2	2	2	1	1	1	1	1	1
16	Slow-down of female note rhythm after climax: absent=0, present=1.														
	0	0	0	1	0	0	0	0	1	1	0	0	0	1	?
17	Codas per great call: none=0, one=1, two=2.														
	1	1	1	0	1	1	1	1	0	1	1	1	1	2	1
18	Coda timing: during great call=0, end of great call=1.														
	1	1	1	?	1	1	1	0	?	0	1	1	1	0	1
19	Great call duration: short, <20s=0, long, >20=1.														
	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
20	Frequency range of song: <2kHz=0, >2.5kHz=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
21	Peak fundamental frequency of song: <1.2kHz=0, 1.2-2kHz=1, >2.5kHz=2.														
	1	1	1	1	1	1	1	1	1	1	2	2	2	0	0
22	Peak frequency of female notes towards climax: increasing=0, stable=1, decreasing=2.														
	0	0	0	2	2	2	2	1	2	1	0	0	0	1	0
23	Onset time of female song and duet: mid-morning=0, near dawn=1.														
	1	1	1	1	1	1	1	0	0	0	0	0	0	0	?
24	Inter-group relations of female songs and duets: sequential=0, chorus=1.														
	1	1	1	1	1	1	1	0	0	0	0	0	0	0	?
25	Frequency of female song and duet per day: <1=0, >1=1.														
	1	1	1	1	1	1	1	0	0	0	0	0	0	0	?
26	Frequency of male solo: absent=0, rare=1, infrequent=2, frequent=3.														
	3	3	2	1	3	3	3	2	3	0	0	0	0	0	?
27	Pre-dawn male solo: no male soli at all=0, pre-dawn soli absent=1, frequent=2, typical=3.														
	2	2	1	1	2	2	2	1	3	0	0	0	0	0	?

Appendix 10.2: Continued.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
28	Sexual dimorphism in song repertoire: absent=0, moderate=1, strong=2.														
	1	1	1	1	1	1	1	1	1	0	2	2	2	1	?
29	Song switch from female to male repertoire in subadult males: absent=0, present=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?

Appendix 10.3: Study Animals for Olfactory Communication

Appendix 10.3.1: Description of study animals for macroscopic study (Section 4.2), arranged by species, age class, and sex. [1]

Appendix 10.3.2: Description of study animals for microscopic study (Section 4.3), and number of skin samples collected from each. Animals are arranged by species and age class, and sex. [1]

Appendix 10.3.3: Description of study animals for chemical analysis (Section 4.4), and number of secretion samples collected from each. Animals are arranged by species, age class, and sex. [1]

[1] Abbreviations: ad. = adult; sad. = subadult; juv. = juvenile; inf. = infant; neo. = neonate; M = male; F = female.

Appendix 10.3.1: Study Animals for Macroscopic Study.

Hylobates agilis unko

ad. F "Blacky", about 6 years old when examined, probably wild-born, weight 4.1 kg, owned by Ms. H. Bron-Brüllmann, Zoo Rothaus, Thielle (Switzerland). Dark-brown fur colouration. Died about in 1990 (from cancer). Anaesthetised animal examined at the Tierspital of Zürich University, on 25 Sept., 1985 (Baumgartner et al., 1986).

Hylobates lar

ad. M "Buddy" (Yerkes #729I), probably wild-born, about in 1973. Father of juvenile male (Yerkes #H861, see below). Buff fur colouration. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 10 August, 1988.

ad. M "Pumi", probably wild-born. Arrived at the Zoo Seeteufel in Studen (Switzerland) in about 1971, probably adult on arrival. Buff fur colouration. Nearly tame animal inspected at the Zoo Seeteufel, on 20 July, 1981.

ad. F "Ilse", arrived at Duisburg Zoo on 22 Jan., 1986, probably adult on arrival. Buff fur colouration. Nearly tame animal examined at Duisburg Zoo, on 24 June, 1987.

ad. F "Mimi", wild-born about in 1963, hand-reared, arrived at the Knie's Kinderzoo in Rapperswil (Switzerland) on 12 June, 1981. Dark-brown fur colouration. One offspring. Died on 15 Nov., 1983. Body weight 4.65 kg. Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 9784), on 17 Nov., 1983.

ad. F "Susie", wild-born, hand-reared, imported from Thailand in 1969, arrived at the Al Maglio Zoo in Magliaso (Switzerland) in Oct., 1987. Black fur colouration. Tame animal examined at the Al Maglio Zoo, on 23 Nov., 1987.

ad. F "Virgo" (LEMSIP #48), captive born on 19 Jan., 1974, at the University of California, Davis. Arrived at LEMSIP Primate Center, New York, on 10 Sept., 1981. Brown fur colouration. Anaesthetised animal examined at the LEMSIP Primate Center on 15 August, 1988.

juv. M 3.97 years old. Born on 27 Nov., 1987, at the Ostrava Zoo (CSFR). Buff fur colouration. Arrived at the Knie's Kinderzoo in Rapperswil on 31 Oct., 1989. Died on 15 Nov., 1991. Body weight about 5 kg. Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 10524), on 28 Nov., 1991.

Appendix 10.3.1: Continued.

juv. M (Yerkes #H861), 2.35 years old. Captive-born on 8 April 1986, son of "Buddy" (see above). Buff fur colouration. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 10 August, 1988.

juv. F "Chastity" (Yerkes #H851), 3.09 years old. Captive-born on 7 July, 1985. Buff fur colouration. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 10 August, 1988.

Hylobates leucogenys leucogenys

ad. M "Claude", wild-born. Previously kept in La Palmyre Zoo. Arrived at the Mulhouse Zoo (France) on 27 June, 1985. Anaesthetised animal examined at the Mulhouse Zoo, on 9 Dec., 1986.

ad. M "Jack", wild-born. Previously kept by private owner. Arrived at the Mulhouse Zoo on 25 March, 1983. Several offspring. Anaesthetised animal examined at the Mulhouse Zoo, on 9 Dec., 1986.

ad. F "Püppi", wild-born. Arrived at Duisburg Zoo on 6 Jan., 1977. Anaesthetised animal examined at the Duisburg Zoo, on 1 March, 1988.

ad. F "Sophie", wild-born. Arrived in Duisburg Zoo on 23 Jan., 1976. One offspring in 1983. Anaesthetised animal examined at the Duisburg Zoo, on 1 March, 1988.

inf. F 1.27 years old. Born on 4 April, 1985 at the Mulhouse Zoo. Offspring of male "Jack" (see above). Died on 12 July, 1986. Freshly dead animal examined at the Mulhouse Zoo, on 16 July., 1986.

Hylobates leucogenys siki

ad. M "Charly", wild-born. Previously at Hanoi Zoo (at least since 1961), then in Leipzig Zoo (since 1964), where the gibbon's name had been "Ming-Dam" (Fischer, 1980). Arrived at Munich Zoo on 14 Nov., 1975. Sent to Mulhouse Zoo on 17 Jan., 1991. Several offspring. Anaesthetised animal examined at the Zoo Hellabrunn, Munich, on 17 Jan., 1991.

ad. F "Charlotte", wild-born in Laos in about September 1969. Previously at Clères Zoo (France), since 1 April, 1970. Arrived at the Zoo Hellabrunn in Munich, on 1 June, 1989. Carrying infant when samples were collected. Sent to Mulhouse Zoo on 17 Jan., 1991. Anaesthetised animal examined at the Zoo Hellabrunn, on 17 Jan., 1991.

ad. F "Mimi", wild-born in Laos. Previously at Mulhouse Zoo (since 5 Aug., 1969). On loan to the Zoo Hellabrunn in Munich from 6 Oct., 1986 to 17 Jan., 1991. Several offspring. Carrying infant when samples were collected. Anaesthetised animal examined at the Zoo Hellabrunn, on 17 Jan., 1991.

Appendix 10.3.1: Continued.

Hylobates leucogenys gabriellae x H. l. siki

ad. M "Charlot 1". Captive-born at Clères Zoo (France) on 10 Dec., 1980. Son of female *H. l. siki* "Mimi" (see above), and brother of following animal. Only temporarily in Paris (for medical treatment). Anaesthetised animal examined at the Ménagerie du Jardin des Plantes, Paris, on 26 May, 1988.

sad. M "Charlot 2", 5.44 years old. Captive-born at Clères Zoo on 18 Dec., 1982. Son of female *H. l. siki* "Mimi" (see above), and brother of preceding animal. Only temporarily in Paris (for medical treatment). Anaesthetised animal examined at the Ménagerie du Jardin des Plantes, Paris, on 26 May, 1988.

Hylobates moloch

ad. M "Omar". Wild-born about in 1983. Arrived at Howletts Zoo in Bekesbourne (England) from Jakarta on 7 Jan., 1987. Nearly tame animal examined at Howletts Zoo, on 16 Oct., 1988.

Hylobates muelleri

ad. M "Banju" (="Silver"), *H. m. abbotti* (this male has previously been identified as *H. moloch*, but see (Geissmann, 1991). Probably wild-born, about in 1976. Arrived at the Rostock Zoo (Germany, former GDR) on 24 Oct., 1979. Several offspring (Gabriel, 1983; Gabriel, 1989; Linke, 1988; Linke, 1989, Ritscher, 1980 #476; Ritscher, 1989; Ritscher & Linke, 1982). Tame animal examined at Rostock Zoo, on 6 July, 1988.

ad. M "Fridolin", *H. m. muelleri*. Arrived at the Münster Zoo (Germany) on 15 Aug., 1973, about 3 years old on arrival. Several offspring. Tame animal examined at Münster Zoo, on 1 July, 1987.

sad. F "Joka", *H. m. abbotti* x *H. m.* cf. *funereus*, 5.25 years old. Born at Rostock Zoo on 7 April, 1983 (Gabriel, 1983; Linke, 1988). Daughter of male "Banju" (see above). Mother-reared. Arrived at the Schwerin Zoo (Germany, former GDR) on 11 June, 1986. Tame animal examined at Schwerin Zoo on 8 July, 1988.

Hylobates pileatus

ad. M "Blacky". Previously at the Opel Zoo (Kronberg, Germany). Arrived at Zürich Zoo on 9 March, 1981 (see also (Geissmann, 1983). Several offspring. Anaesthetised animal examined at the Zürich Zoo, on 18 May, 1987.

Appendix 10.3.1: Continued.

ad. M "Pipin Fabian", 8.44 years old (same animal as juvenile male listed below). Captive-born on 6 Jan., 1984, at Twycross Zoo (England). Arrived at Zürich Zoo on 6 April, 1987. Died on 14 June, 1992. Body weight 9.56 kg. Freshly dead animal examined at the Tierspital of Zürich University (AIMUZ No. 10531), on 14 June, 1992.

ad. F "Gray". Previously at the Tierpark Berlin (Germany, former GDR). Arrived at Zürich Zoo on 10 March, 1981 (see also (Geissmann, 1983). Several offspring. Anaesthetised animal examined at the Zürich Zoo, on 18 May, 1987, and freshly dead animal examined at the Tierspital of Zürich University, on 28 July, 1992.

ad. F "Iok". Arrived at Zürich Zoo on 29 Oct., 1982 from Bangkok, probably adult on arrival. Anaesthetised animal examined at the Zürich Zoo, on 7 Oct., 1987.

juv. M "Pipin Fabian", 3.36 years old (same animal as adult male listed above). Anaesthetised animal examined at the Zürich Zoo, on 18 May, 1987.

inf. F "Mioche", 0.90 years old. Born on 23 June, 1986 at Zürich Zoo. Parents: "Blacky" and "Gray" (see above). Hand-reared. Anaesthetised animal examined at the Zürich Zoo, on 18 May, 1987.

neo. F Born and died on 4 Nov., 1983 at Zürich Zoo. Parents: "Blacky" and "Gray" (see above). Body weight: 393g. Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 9977), on 6 Nov., 1983.

neo. M Stillborn on 8 July, 1984 at Zürich Zoo. Parents: "Blacky" and "Gray" (see above). Body weight: 332 g. Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 9794), on 10 July, 1984.

neo. M Born and died on 23 Feb., 1985 at Zürich Zoo. Parents: "Blacky" and "Gray" (see above). Body weight: 429 g (inclusive placenta). Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 9986), on 25 Feb., 1985.

Various inter-species hybrids of the *lar* group:

Hylobates muelleri x *(H. muelleri* x *H. moloch)*

ad. M "Tarzan" (="Fritzke"). Born on 5 May, 1980 at the Münster Zoo (Germany). Arrived at the Eberswalde Zoo (Germany, former GDR) in April 1984. Tame animal examined at the Eberswalde Zoo, on 11 July, 1988.

Hylobates muelleri x *H. lar*

ad. M "Micky", born at the Duisburg Zoo (Germany) on 6 Sept., 1979. Nearly tame animal examined at the Duisburg Zoo, on 24 June, 1987.

Appendix 10.3.1: Continued.

Hylobates pileatus x H. lar

ad. F "Johnny", born at the Opel Zoo in Kronberg (Germany) on 5 Nov., 1975 (Geissmann, 1984). Daughter of male *H. pileatus* "Blacky" (see above). Nearly tame animal examined at the Opel Zoo in Kronberg, on 16 June, 1987.

Hylobates syndactylus

ad. M "Narong". Wild-born in about 1967 (estimate). Arrived at Zürich Zoo on 5 Oct., 1973, from Oklahoma City Zoo. Several offspring (see also Geissmann, 1984b, 1986a). Sent to the Zoo Seeteufel in Studen on 14 July, 1981. Died on 19 May, 1982 (from kidney failure). Nearly tame animal examined at the Zoo Seeteufel on 22 July, 1981, and freshly dead animal at the Naturhistorisches Museum Bern on 27 Oct., 1982 (Geissmann, 1987b).

ad. M "Bohorok". Born on 23 June, 1975, at the Zürich Zoo. Offspring of "Narong" (see above) and "Ratana" (see below). Hand-reared. Several offspring (see also (Geissmann, 1984b, 1986a). Sent to Thrigby Hall Wildlife Gardens (Norfolk, England) on 30 August, 1989. Anaesthetised animal examined at the Zürich Zoo, on 30 Aug., 1989.

ad. M "Bobby". Wild-born, arrived at Frankfurt Zoo on 12 Dec., 1961 (Lamprecht, 1970; Orgeldinger, 1989). Believed to be infertile. Transferred to Basle Zoo on 14 Apr., 1969, later to the Seeteufel Zoo in Studen 19 May, 1972 (see also (Geissmann, 1984b, 1986a). Died on 8 Oct., 1981 (from Klebsiella infection). Freshly dead animal examined at the Naturhistorisches Museum Bern (NHMBe 4521981), on 10 Oct., 1981.

ad. F "Gaspa". Wild-born in about 1963 (estimate). Previously at the Seeteufel Zoo in Studen (Switzerland). Arrived at Zürich Zoo on 21 July, 1980. Several offspring (see also (Geissmann, 1984b, 1986a). Sent to Thrigby Hall Wildlife Gardens (Norfolk, England) on 30 August, 1989. Anaesthetised animal examined at the Zürich Zoo, on 22 January, 1987, and 30 August, 1989.

ad. F "Ratana". Wild-born in about 1963 (estimate). Arrived at Zürich Zoo on 19 Oct., 1965. Several offspring (see also (Geissmann, 1984b, 1986a). Sent to the Seeteufel Zoo in Studen on 21 July, 1980. Nearly tame animal examined at the Seeteufel Zoo, on 22 July, 1981.

Appendix 10.3.1: Continued.

ad. F "Vreneli". Wild-born in about 1963 (estimate). Arrived at the Seeteufel Zoo in Studen in about 1967. Several offspring (see also (Geissmann, 1984b, 1986a). Nearly tame animal examined at the Seeteufel Zoo, on 21 July, 1981.

ad. F "Mücke" (="Inga"). Born on 3 April, 1974, at the Zoo Hellabrunn in Munich (Germany). Sister of "Floh" (see below). Pregnant with first offspring when examined. Anaesthetised animal examined at the Zoo Hellabrunn, on 11 February, 1988.

ad. M "Trine" (="Griseldis"). Born on 29 Sept., 1974, at the Duisburg Zoo (Germany). Hand-reared. Several Offspring. Nearly tame animal examined at the Duisburg Zoo, on 23 June, 1987.

sad. M "Floh", 4.52 years old. Born on 5 Aug., 1983, at the Zoo Hellabrunn in Munich (Germany). Brother of "Mücke" (see above). No offspring when examined. Anaesthetised animal examined at the Zoo Hellabrunn, on 11 February, 1988.

juv. M "Luang", 2.27 and 2.32 years old. Born on 23 July 1985, at the Zürich Zoo. Mother of this animal is sister of "Bohorok" (father of previous animal). Anaesthetised animal examined at the Zürich Zoo, on 28 October, 1987 and on 17 Nov., 1987.

juv. M "Bobby II", 2.17 years old. Born on 28 Dec., 1981, at the Seeteufel Zoo in Studen. Died on 26 Feb., 1984 (amebic dysentery). Freshly dead animal examined at the Naturhistorisches Museum Bern (NHMBe 511984) on 29 Feb., 1984 (Geissmann, 1987b).

inf. M "Fadoro", 1.52 years old. Born on 2 June, 1979, at the Zürich Zoo. Offspring of "Narong" (see above) and "Ratana" (see below); brother of "Bohorok" (see above). Hand-reared. Transferred to the Dortmund Zoo (Germany) late in 1984. Tame animal examined at the Zürich Zoo, on 8 Dec., 1980.

inf. M "Elliott", 1.07 years old. Born on 28 May, 1986, at the Duisburg Zoo (Germany). Hand-reared. Nearly tame animal examined at the Duisburg Zoo, on 23 June, 1987.

inf. M "Khao", 0.67 years old. Born on 28 Sept., 1984, at the Zürich Zoo. First-born of a set of twins (Geissmann, 1991a; Schmidt, 1992). Mother-reared, died on 30 May, 1985 (from cachexia). Body weight 660g. Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 9936), on 31 May, 1985.

Appendix 10.3.1: Continued.

inf. M "Layang", 0.64 years and 1.51 years old. Born on 12 Nov., 1985, at the Zürich Zoo. Parents: "Bohorok" and "Gaspa" (see above). Hand-reared, nearly tame animal examined in Effretikon, on 3 July, 1986; anaesthetised animal examined at the Zürich Zoo, on 18 May, 1987.

neo. M Born alive and died on 21 Jan., 1985, at the Zürich Zoo. Parents: "Bohorok" and "Gaspa" (see above). Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 9795), on 23 Jan., 1985.

neo. M Stillborn on 28 Sept., 1984, at the Zürich Zoo. Second-born of a set of twins (Geissmann, 1991a; Schmidt, 1992). Body weight 411.5g. Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 9825) on 29 Sept., 1984.

Pan troglodytes

ad. M "Mortimer" (# C423). Captive-born on 20 Dec., 1976. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 5 Aug., 1988.

ad. F "Lulu" (# C076).Wild-born in about 1957. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, 8 Aug., on 1988.

Pongo pygmaeus pygmaeus

ad. M "Adam", about 36 years old. Died at Zürich Zoo on 27 Nov., 1989. Freshly dead animal examined at the Anthropology Institute of Zürich University (AIMUZ No. 10314), on 30 Nov., 1989.

ad. M "Teriang" (# 059). Captive-born on 13 Nov., 1972. At least one offspring. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 9 Aug., 1988.

ad. F "Datu" (# 020). Wild-born in about 1960. Several offspring (see also below). Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 9 Aug., 1988.

inf. M "Tiram" (# 107). 1.47 years old. Captive-born on 18 Feb., 1986, offspring of "Teriang" & "Datu" (see above). Tame animal examined at the Yerkes Primate Center, Atlanta, on 9 Aug., 1988.

Pongo pygmaeus abelii

ad. M "Pongo". Born about in 1961. Several offspring. Anaesthetised animal examined at the Zürich Zoo, on 23 Jan., 1987.

ad. M "Jolo". About 15 years old. Nearly tame animal examined at the Duisburg Zoo (Germany), on 24 June, 1987.

Appendix 10.3.1: Continued.

ad. F "Surawa". About 18 years old. Nearly tame animal examined at the Duisburg Zoo (Germany), on 24 June, 1987.

inf. M "Kertawa". 0.66 years old. Born on 9 Feb., 1988, at Twycross Zoo (England). Nearly tame animal examined at Twycross Zoo, on 8 Oct., 1988.

inf. M "Mentubar" (# 113). 0.46 years old. Captive-born on 23 Feb., 1988. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 8 Aug., 1988.

Pongo-Hybrids:

Pongo pygmaeus abelii x F1-Hybrid?

inf. F "Zoe". 1.83 years old. Born on 10 Dec., 1985, at Rome Zoo. Tame animal examined at Rome Zoo, on 8 Oct., 1987.

Pongo pygmaeus pygmaeus x *P. p. abelii*

ad. M "Loklok" (# 041). Captive-born on 17 March, 1969. Son of female "Datu" (see above). Half-brother of "Chantek" (see below). Several offspring. Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 8 Aug., 1988.

ad. F "Chantek" (# 085). Captive-born on 17 Dec., 1977. Son of female "Datu" (see above). Half-sister of "Loklok" (see above). Anaesthetised animal examined at the Yerkes Primate Center, Atlanta, on 9 Aug., 1988.

Appendix 10.3.2: Study Animals for Microscopic Study.

Hylobates klossii

ad. F "Buschi". Wild-born. Arrived in Basle Zoo on 13 July, 1970, from Siberut; body weight upon arrival 950g (Lang, 1971; 1973; 1975; 1977). Died on 16 Oct., 1975. Cadaver deep-frozen at the Naturhistorisches Museum Basel, NHMBa Z10674.
Samples 3a: sternal skin; 3b: axillary skin; 3c: skin from lateral abdomen; 3d: inguinal skin; 3e: dorsal skin (interscapular).

Hylobates hoolock

ad. M Wild-shot specimen of Vernay-Hopwood expedition to northern Burma (Carter, 1943). American Museum of Natural History, New York, AMNH 201741, field No. VH 345. Embalmed specimen, but almost dried out.
Samples 14a: sternal skin; 14b: axillary skin.

ad. F Wild-shot specimen of Vernay-Hopwood expedition to northern Burma (Carter, 1943). American Museum of Natural History, New York, AMNH 201740, field No. VH 245. Embalmed specimen, but almost dried out.
Samples 15a: sternal skin; 15b: inguinal skin.

Hylobates lar cf. *entelloides*

ad. M Buff fur colouration. Embalmed at the Anthropological Institute (Zürich University), AIMUZ 9822.
Samples 16a: sternal skin; 16b: axillary skin; 16c: inguinal skin.

ad. F "Mimi", wild-born about in 1963, hand-reared, arrived at the Knie's Kinderzoo in Rapperswil (Switzerland) on 12 June, 1981. Dark-brown fur colouration. One offspring. Died on 15 Nov., 1983. Body weight 4.65 kg. Embalmed at the Anthropological Institute (Zürich University), AIMUZ 9784.
Samples 17a: sternal skin; 17b: axillary skin; 17c: inguinal skin.

ad. F "Khajal", buff fur colouration, reported to be about 7-8 years old, upper canines only partially developed, but animal of about adult body size (6.9 kg). Arrived at Zürich Zoo on 26 June, 1984, from Bangkok (confiscated animal). Later given to Knie's Kinderzoo Rapperswil. Died of cancer on 3 Nov., 1988. Cadaver embalmed at the Anthropological Institute (Zürich University), AIMUZ 10211.
Samples 9a and 18a: sternal skin; 9b and 18b: axillary skin; 9c and 18c: inguinal skin; 9d: dorsal skin (inter scapular).

Appendix 10.3.2: Continued.

juv. M 3.97 years old. Born on 27 Nov., 1987, at the Ostrava Zoo (CSFR). Buff fur colouration. Arrived at the Knie's Kinderzoo in Rapperswil on 31 Oct., 1989. Died on 15 Nov., 1991. Body weight about 5 kg. Embalmed at the Anthropological Institute (Zürich University), AIMUZ 10524.
Samples 24a: sternal skin; 24b: axillary skin; 24c: lateral abdomen; 24d: dorsal skin (inter scapular).

Hylobates leucogenys leucogenys

ad. F "Püppi", wild-born. Arrived at Duisburg Zoo on 6 Jan., 1977. Biopsy taken on 1 March, 1988, when animal was anaesthetised for medical check.
Sample 7: inguinal skin from biopsy.

inf. F (no name), 1.27 years old. Born on 4 April, 1985, at the Mulhouse Zoo (France); died on 12 July, 1986 (probably due to fall). Skin samples collected from the relatively fresh specimen which was not fixed post-mortem.
Sample 5a: sternal skin; 5b: skin from lateral abdomen.

Hylobates moloch

ad. M Wild-shot in Java. Embalmed specimen received at Johns Hopkins University in October 1926 from Government Medical School, Java (old inventory number JH 152). Today housed at the Anthropological Institute (Zürich University), AS 152.
Samples 19a: sternal skin; 19b: axillary skin; 19c: inguinal skin.

ad. F "Paula" (="Wauwau"), at least 19 years old. Wild born. Arrived in Rheine Zoo (Germany) in 1970 or before that time. Several offspring. Sent to Hellabrunn Zoo (Munich, Germany) on 11 Nov., 1982. Died on 13 June, 1989. Skin samples collected from the relatively fresh specimen which was not fixed post-mortem.
Samples 10a: sternal skin; 10b: axillary skin; 10c: inguinal skin.

Hylobates muelleri cf. *funereus*

ad. F "Java", f Estimated birth date about 1963, arrived at the Rostock Zoo (Germany, former GDR) from San Diego Zoo (U.S.A.) on 3 Feb., 1969. Several offspring (Gabriel, 1983; Gabriel, 1989; Ritscher, 1980; Ritscher, 1989; Ritscher & Linke, 1982). Has previously been identified as *H. moloch* by these authors, but actually is *H. muelleri*, as shown by Geissmann (1991a, p.14). Died on 5 June, 1988 (uterus inflammation). Skin samples collected from the relatively fresh specimen which was not fixed post-mortem.
Samples 8a: sternal skin; 8b: axillary skin.

Appendix 10.3.2: Continued.

Hylobates muelleri muelleri

juv. M Embalmed specimen at the Anthropological Institute (Zürich University), AIMUZ 9933; unknown provenience.
Samples 20a: sternal skin; 20b: axillary skin; 20c: inguinal skin.

Hylobates pileatus

juv. M "Ili", 3.85 years old. Born on 25 Nov., 1982, at Zürich Zoo, hand-reared (Schmidt-Pfister, 1984). Died on 3 Oct., 1986 (leukemia virus). Body weight 4700g. Skin samples collected from the relatively fresh specimen which was not fixed post-mortem. Cadaver deep-frozen at the Anthropological Institute (Zürich University), AIMUZ No. 10116.
Samples 6: sternal skin; 6b: axillary skin; 6c: inguinal skin; 6d: dorsal skin (inter scapular); 6e: skin from lateral abdomen.

Hylobates syndactylus

ad. M "Narong". Wild-born in about 1967 (estimate). Arrived at Zürich Zoo on 5 Oct., 1973, from Oklahoma City Zoo. Several offspring (see also (Geissmann, 1984b, 1986a). Sent to the Zoo Seeteufel in Studen on 14 July, 1981. Died on 19 May, 1982 (from kidney failure). Skin samples collected at the Naturhistorisches Museum Bern (NHMBe) from the relatively fresh specimen which was not fixed post-mortem. Sample quality slightly deteriorated because it has been kept in concentrated salt solution for some time before histological analysis was carried out.
Sample 1: sternal skin.

ad. M Wild-shot. Embalmed specimen at the Anthropological Institute (Zürich University), AIMUZ 7298.
Samples 21a: sternal skin; 21b: axillary skin.

ad. F Wild-shot. Embalmed specimen at the Anthropological Institute (Zürich University), AIMUZ 7297.
Sample 22: sternal skin.

juv. M "Bobby II", 2.17 years old. Born on 28 Dec., 1981, at the Seeteufel Zoo in Studen. Died on 26 Feb., 1984 (amebic dysentery). Skin samples collected from the relatively fresh specimen which was not fixed post-mortem. Skeleton at the Naturhistorisches Museum Bern (NHMBe #511984).
Samples 2a: sternal skin; 2b: skin of lateral chest.

Appendix 10.3.2: Continued.

	juv. F	"Mareille", 3.38 years old. Born on 23 March, 1986, at Hellabrunn Zoo (Munich). Died on 9 Aug., 1989 (lung emphysema following viral infection). Skin samples collected from the relatively fresh specimen which was not fixed post-mortem. Samples 11a: sternal skin; 11b: axillary skin; 11c: inguinal skin.
inf.	M	"Khao", 0.67 years old. Born on 28 Sept., 1984, at the Zürich Zoo. First-born of a set of twins (Geissmann, 1991a; Schmidt, 1992). Mother-reared, died on 30 May, 1985 (from cachexia). Body weight 660g. Skin samples collected from the relatively fresh specimen which was not fixed post-mortem. Cadaver embalmed at the Anthropological Institute (Zürich University), AIMUZ 9936. Sample 4: sternal skin.
	neo. M	Stillborn on 28 Sept., 1984, at the Zürich Zoo. Second-born of a set of twins (Geissmann, 1991a; Schmidt, 1992). Body weight 411.5g. Embalmed at the Anthropological Institute (Zürich University), AIMUZ 9825. Sample 23: sternal skin.
Gorilla gorilla gorilla		
	ad. M	"Stephi", wild-born. Arrived at Basle Zoo on 16 Sept., 1954, at the age of about 4.5 years (Lang, 1961). Several offspring. Died of meningitis on 6 September 1981. Embalmed at the Anthropological Institute (Zürich University), AIMUZ 9348. Samples 12a: sternal skin; 12b: axillary skin; 12c: skin from lateral abdomen.
Pongo pygmaeus pygmaeus		
	ad. M	"Adam", wild-born. Lived at Zürich Zoo, died on 27 Nov., 1989, at the age of about 36 years. Embalmed at the Anthropological Institute (Zürich University), AIMUZ 10314. Samples 13a: sternal skin; 13b: axillary skin; 13c: skin from lateral abdomen.

Appendix 10.3.3: Study Animals for Chemical Analysis.

Hylobates lar

ad. M "Buddy" (Yerkes #729I)
Samples 96 and 97: Yerkes Primate Center, Atlanta, 10 August, 1988.

ad. F "Virgo" (LEMSIP #48)
Samples 108 and 109: LEMSIP Primate Center, New York, 15 August, 1988.

juv. M (Yerkes #H861), 2.35 years old.
Samples 104 and 105: Yerkes Primate Center, Atlanta, 10 August, 1988.

juv. F "Chastity" (Yerkes #H851), 3.09 years old.
Samples 100 and 101: Yerkes Primate Center, Atlanta, 10 August, 1988.

Hylobates leucogenys leucogenys

ad. M "Claude".
Sample 5: Zoo Mulhouse, 9 Dec., 1986.

ad. M "Jack".
Sample 7: Zoo Mulhouse, 9 Dec., 1986.

ad. F "Püppi".
Samples 53-60: Zoo Duisburg, 1 March, 1988.

ad. F "Sophie".
Samples 48-52: Zoo Duisburg, 1 March, 1988.

Hylobates leucogenys siki

ad. M "Charly".
Samples 122-126: Zoo Hellabrunn, Munich, 17 Jan., 1991.

ad. F "Charlotte".
Samples 127-130: Zoo Hellabrunn, Munich, 17 Jan., 1991.

ad. F "Mimi".
Samples 131-135: Zoo Hellabrunn, Munich, 17 Jan., 1991.

Hylobates leucogenys gabriellae x H. l. siki

ad. M "Charlot 1".
Samples 62-64: Ménagerie du Jardin des Plantes, Paris, 26 May, 1988.

sad. M "Charlot 2", 5.44 years old.
Samples 65-67: Ménagerie du Jardin des Plantes, Paris, 26 May, 1988.

Appendix 10.3.3: Continued.

Hylobates pileatus

ad. M "Blacky".
Samples 18 and 19: Zürich Zoo, 18 May, 1987.

ad. F "Gray".
Samples 20 and 21: Zürich Zoo, 18 May, 1987.

juv. M "Pipin Fabian", 3.36 years old.
Samples 24 and 25: Zürich Zoo, 18 May, 1987.

inf. F "Mioche", 0.90 years old.
Samples 22 and 23: Zürich Zoo, 18 May, 1987.

Hylobates syndactylus

ad. M "Bohorok".
Sample 9: Zürich Zoo, 14 October, 1986.
Samples 112-116: Zürich Zoo, 30 August, 1989.

ad. F "Gaspa".
Samples 11, 12 and 15: Zürich Zoo, 22 January, 1987.
Samples 117-121: Zürich Zoo, 30 August, 1989.

ad. F "Mücke" (="Inga").
Samples 43-46: Zoo Hellabrunn, Munich, 11 February, 1988.

sad. M "Floh", 4.52 years old.
Samples 38-42: Zoo Hellabrunn, Munich, 11 February, 1988.

juv. M "Luang". 2.27 years old.
Samples 29-33: Zürich Zoo, 28 October, 1987.

inf. M "Layang". 0.64 years (sample 1) and 1.51 years old (samples 16 and 17).
Sample 1: Effretikon, 3 July, 1986.
Samples 16 and 17: Zürich Zoo, 18 May, 1987.

Pan troglodytes

ad. M "Mortimer" (# C423).
Samples 73 and 74: Yerkes Primate Center, Atlanta, 5 August, 1988.

ad. F "Lulu" (# C076).
Samples 77 and 78: Yerkes Primate Center, Atlanta, 8 August, 1988.

Pongo pygmaeus pygmaeus

ad. M "Teriang" (# 059).
Samples 87 and 88: Yerkes Primate Center, Atlanta, 9 August, 1988.

ad. F "Datu" (# 020).
Samples 90 and 91: Yerkes Primate Center, Atlanta, 9 August, 1988.

Appendix 10.3.3: Continued.

Pongo pygmaeus abelii

ad. M "Pongo".
Samples 13-14: Zürich Zoo, 23 January, 1987.

inf. M "Mentubar" (# 113). 0.46 years old.
Samples 85 and 86: Yerkes Primate Center, Atlanta, 8 August, 1988.

Pongo pygmaeus pygmaeus x *P. p. abelii*

ad. M "Loklok" (# 041).
Samples 81 and 82: Yerkes Primate Center, Atlanta, 8 August, 1988.

ad. F "Chantek" (# 085).
Samples 93 and 94: Yerkes Primate Center, Atlanta, 9 August, 1988.

Appendix 10.4: Skin Secretions

Sample numbers, short descriptions of the secretion samples collected from each study animal, and hormone concentrations determined in each sample. Animals are arranged by species, age class, and sex. All of these hormone concentrations have been corrected with controls. See section 2.4.3 for a description of the controls and the method of correction used in the various samples.

Appendix 10.4

Taxon	Name, Age, and Sex [2]	Sample No.	Sample Type	Steroid Concentrations [1]		
				DHEA	Androstene-dione	Testosterone
Hylobates lar						
	"Buddy", ad. M					
		96	sternal	3.14	1.59	0.57
		97	axillary	2.72	1.49	1.32
	"Virgo", ad. F					
		108	sternal	2.79	1.78	0.37
		109	axillary	3.11	2.18	0.44
	"Chastity", juv. F (3.09 years)					
		100	sternal	3.46	2.84	1.80
		101	axillary	2.28	2.28	1.95
	"H 861", juv. M (2.35 years)					
		104	sternal	2.20	3.48	1.89
		105	axillary	4.38	2.31	1.16
H. leucogenys leucogenys						
	"Claude", ad. M					
		5	sternal	5.36	0	0
	"Jack", ad. M					
		7	sternal	7.62	0	0.69
	"Püppi", ad. F					
		53	sternal	1.46	3.00	0.49
		54	lat. neck	2.74	2.12	0.50
		55	axillary	2.00	4.13	0.91
		56	lat. abdomen	1.52	0.59	0.52
		57	inguinal	2.50	2.85	0
		58	dorsal	3.42	2.19	0.90
		59	pure exudate	0	0	0
	"Sophie", ad. F					
		48	sternal	2.68	3.48	0
		49	claviculary	1.90	0.52	0.53
		50	axillary	2.26	2.93	0.82
		51	lat. abdomen	1.70	0.18	0
		52	inguinal	1.96	0.08	0

Appendix 10.4: Continued.

H. leucogenys siki					
"Charly", ad. M					
	122	sternal	11.48	5.82	0.97
	123	axillary	1.58	0.94	0.36
	124	inguinal	4.66	4.46	0.76
	125	dorsal	1.74	1.48	0.42
	126	lat. abdomen	5.13	0.64	1.19
"Charlotte", ad. F					
	127	sternal	2.66	0.55	1.12
	128	axillary	2.84	0.40	0.70
	129	dorsal	2.68	0.70	0.27
	130	lat. abdomen	2.13	2.09	2.18
"Mimi", ad. F					
	131	sternal	3.38	0.63	1.50
	132	axillary	2.72	1.65	2.04
	133	inguinal	3.24	1.75	1.24
	134	dorsal	2.88	0.94	2.14
	135	lat. abdomen	3.18	2.22	2.23
H. leucogenys gabriellae x *H. l. siki*					
"Charlot 1", ad. M					
	62	sternal	7.54	0.89	0
	64	axillary	0.12	0	0.24
"Charlot 2", sad. M (5.44 years)					
	65	sternal	1.62	0.81	0.30
	67	axillary	1.60	0.57	0
H. pileatus					
"Blacky", ad. M					
	18	sternal	34.83	207.17	8.04
	19	axillary	29.21	0	0.42
"Gray", ad. F					
	20	sternal	24.18	0	1.78
	21	axillary	24.63	0	0
"Pipin Fabian", juv. M (3.36 years)					
	24	sternal	11.60	0	1.75
	25	axillary	15.35	0	0.77
"Mioche", inf. F (0.9 years)					
	22	sternal	12.76	0	0.10
	23	axillary	8.53	0	0.31

Appendix 10.4: Continued.

H. syndactylus					
"Bohorok", ad. M					
	9	pure exudate	5.22	143.18	2.15
	112	sternal	20.08	255.18	14.97
	113	axillary	7.08	14.88	2.16
	114	inguinal	3.78	23.83	6.59
	115	dorsal	4.27	7.58	1.43
	116	plasma	(694)	(635)	(992)
"Gaspa", ad. F					
	11	sternal	31.78	0	2.67
	12	axillary	28.23	0	0.38
	15	plasma	(280)	(238)	(82)
	117	sternal	23.81	205.18	12.67
	118	axillary	6.17	11.79	2.61
	119	inguinal	2.98	7.78	3.17
	120	dorsal	3.73	5.03	1.98
	121	plasma	(481)	(288)	(144)
"Mücke", ad. F					
	43	sternal	22.21	327.68	10.48
	44	axillary	8.06	11.39	0.64
	45	inguinal	13.38	19.35	7.28
	46	lat. abdomen	9.23	12.82	4.77
"Floh", sad. M					
	38	sternal	22.63	67.58	10.48
	39	claviculary	10.28	6.56	4.07
	40	axillary	8.02	10.16	0.69
	41	circumgenital	11.78	7.99	4.36
	42	lat. abdomen	10.98	5.54	4.02
"Layang", inf. M (sample 1: 0.64 years; samples 16 and 17: 1.51 years)					
	1	sternal	11.25	0	0.82
	16	sternal	34.63	1.34	0.61
	17	claviculary	29.68	0	0.36
"Luang", juv. M					
	29	sternal	9.28	12.59	1.09
	30	axillary	13.84	19.18	0.49
	31	inguinal	12.78	8.58	5.07
	32	dorsal	11.63	8.37	4.15
	33	dorsal [3]	10.77	16.70	1.18

Appendix 10.4: Continued.

Pan troglodytes				
"Mortimer", ad. M				
73	sternal	18.59	10.05	3.36
74	axillary	28.52	85.35	7.64
"Lulu", ad. F				
77	sternal	90.30	15.81	7.00
78	axillary	130.48	116.28	44.00
Pongo pygmaeus pygmaeus				
"Terian", ad. M				
87	sternal	8.44	33.25	4.17
88	axillary	22.71	116.68	7.05
"Datu", ad. F				
90	sternal	24.21	11.65	1.84
91	axillary	39.99	9.95	2.24
Pongo pygmaeus abelii				
"Pongo", ad. M				
13	sternal	12.26	0	0.47
14	axillary	16.25	0	0.81
"Mentubar", inf. M (0.46 years)				
85	sternal	2.48	2.56	1.77
86	lat. abdomen	1.93	2.86	1.89
Pongo pygmaeus pygmaeus x *Pongo p. abelii*				
"Loklok", ad. M				
81	sternal	7.37	20.24	2.67
82	axillary	19.35	37.61	8.54
"Chantek", ad. F				
93	sternal	4.76	3.70	1.25
94	axillary	4.56	3.21	1.18

1 ad.=adult; sad.=subadult; juv.=juvenile; inf.=infant; M=male; F=female; lat.=lateral.

2 Hormone concentrations are measured in ng/sample, except plasma samples (values in brackets) which are given as ng/dl.

3 Sample No. 33 collected without gloves, for comparison with sample 32.

Appendix 10.5: Olfactory Characteristics of Gibbons

Abbreviations: agi.= *H. agilis agilis* (& *H. a. unko*); alb.= *H. a. albibarbis*; lar= *H. lar*; mol.= *H. moloch*, abb.= *H. muelleri abbotti*; fun.= *H. m. funereus*; mu.= *H. m. muelleri*; pil.= *H. pileatus*; klo.= *H. klossii*, hoo.= *H. hoolock*; con.= *H. concolor*; leu.= *H. leucogenys leucogenys* (& *H. l. siki*); gab.= *H. l. gabriellae*; syn.= *H. syndactylus*; anc.= hypothetical ancestor; ?= missing data.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
30	Sternal gland: present=0, reduced=1.														
	0	0	0	0	0	0	0	0	?	0	1	1	1	0	0
31	Body odour: inconspicuous=0, strong=1.														
	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
32	Sternal steroid concentrations: low=0, high=1.														
	?	?	?	?	?	?	?	1	?	?	?	0	?	1	1
33	Fields of coloured pores: unspecialised=0, specialised=1. Specialized: secretion influences coat colouration.														
	0	0	0	0	0	0	0	0	?	0	1	1	1	0	0

Appendix 10.6: Visual Characteristics of Gibbons

Abbreviations: agi.= *H. agilis agilis* (& *H. a. unko*); alb.= *H. a. albibarbis*; lar= *H. lar*; mol.= *H. moloch*, abb.= *H. muelleri abbotti*; fun.= *H. m. funereus*; mu.= *H. m. muelleri*; pil.= *H. pileatus*; klo.= *H. klossii*, hoo.= *H. hoolock*; con.= *H. concolor*; leu.= *H. leucogenys leucogenys* (& *H. l. siki*); gab.= *H. l. gabriellae*; syn.= *H. syndactylus*; anc.= hypothetical ancestor; ?= missing data.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
34	Male light brow band: absent=0, sometimes present=1, present=2.														
	2	2	2	2	2	2	2	2	0	2	0	0	0	1	2
35	Female light brow band: absent=0, sometimes present=1, present=2.														
	1	2	2	2	2	2	2	1	0	2	0	2	1	1	2
36	Male light cheeks: absent=0, sometimes present=1, present=2.														
	2	2	2	1	1	1	1	2	0	0	0	2	2	0	2
37	Female light cheeks: absent=0, sometimes present=1, present=2.														
	0	1	2	1	1	1	1	0	0	2	0	2	1	0	2
38	Male light chin: absent=0, optional=1, present=2.														
	1	1	2	2	1	1	1	2	0	0	0	2	2	0	2
39	Female light chin: absent=0, sometimes present=1, present=2.														
	1	1	2	2	1	1	1	0	0	2	0	2	1	0	2
40	Male face ring: absent=0, sometimes present=1, present=2.														
	1	1	2	1	1	1	1	2	0	0	0	0	0	0	2
41	Female face ring: absent=0, sometimes present=1 present=2.														
	0	0	2	1	1	1	1	0	0	2	0	2	1	0	2
42	Juvenile face ring: absent=0, sometimes present=1, present=2.														
	1	1	2	1	1	1	1	2	0	0	0	0	0	0	2
43	Female light intra-facial hair: absent=0, sometimes present=1, present=2.														
	0	0	0	0	0	0	0	0	0	2	1	2	1	0	0
44	Male light corona: absent=0, sometimes present=1, present=2.														
	1	1	0	1	0	0	0	2	0	0	1	1	1	0	?
45	Female light corona: absent=0, sometimes present=1, present=2.														
	1	1	0	1	0	0	0	2	0	0	0	0	0	0	?

Appendix 10.6: Continued.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
46	Male dark crown: absent=0, sometimes present=1, present=2.														
	1	2	1	1	1	2	2	2	2	2	2	2	2	2	2
47	Female dark crown: absent=0, sometimes present=1, present=2.														
	1	2	1	1	1	2	2	2	2	0	2	2	2	2	2
48	Male occipital hair: flat=0, erect=1, crest=2, big crest=3.														
	0	0	1	0	0	0	0	0	0	0	2	3	2	0	?
49	Female occipital hair: flat=0, erect=1.														
	0	0	1	0	0	0	0	0	0	0	1	1	1	0	?
50	Male dark chest: absent=0, sometimes present=1, present=2.														
	1	2	1	1	1	2	2	2	2	2	2	2	0	2	?
51	Female dark chest: absent=0, sometimes present=1, present=2.														
	1	2	1	1	1	2	2	2	2	1	1	0	0	2	?
52	Male light back: absent=0, sometimes present=1, present=2.														
	1	2	1	2	2	2	2	0	0	0	0	0	0	0	?
53	Female light back: absent=0, sometimes present=1, present=2.														
	1	2	1	2	2	2	2	2	0	2	2	2	2	0	?
54	Male light hands & feet: absent=0, light feet sometimes present=1, white, small=2, white, big=3.														
	0	0	3	0	0	1	0	2	0	0	0	0	0	0	?
55	Female light hands & feet: absent=0, light, sometimes present=1, white, small=2, white, big=3.														
	0	0	3	0	0	1	0	2	0	1	0	0	0	0	?
56	Male dark hands & feet: absent=0, sometimes present=1, present=2.														
	1	2	0	0	0	1	2	0	2	2	2	2	2	2	?
57	Female dark digits: absent=0, sometimes present=1, present=2.														
	1	2	0	0	0	1	2	0	2	0	1	1	2	2	?
58	Male dark genital hair: absent=0, sometimes present=1, present=2.														
	1	0	1	1	2	2	2	0	2	1	2	2	2	2	?
59	Female dark genital hair: absent=0, sometimes present=1, present=2.														
	1	0	1	1	2	2	2	0	2	0	1	1	2	2	?
60	Male light genital hair: absent=0, sometimes present=1, present=2.														
	1	2	0	0	0	0	0	2	0	1	0	0	0	0	?

Appendix 10.6: Continued.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
61	Male genital tuft: absent=0, moderate=1, big=2.														
	1	1	0	0	0	0	0	0	0	2	0	0	0	2	?
62	Sexual dichromatic face: absent=0, moderate=1, pronounced=2.														
	1	1	0	0	0	0	2	0	0	2	2	2	2	0	?
63	Sexual dichromatic body: absent=0, present type1=1, present type2=2. (type 1: all juveniles like ad. female; type 2: all juveniles like ad. female).														
	0	0	0	0	0	0	0	1	0	2	2	2	2	0	?
64	Polymorphous body colouration: absent=0, present=1.														
	1	0	1	0	0	0	0	0	0	0	0	0	0	0	?
65	Natal coat: absent=0, present=1.														
	0	0	0	0	0	0	0	1	0	1	1	1	1	0	?
66	Body weight: 5-6kg=0, 6-8kg=1, 10-12kg=2.														
	0	0	0	0	0	0	0	0	0	1	1	1	1	2	?

Appendix 10.7: Key to Abbreviations for Museum Collections

Collections visited during the present study are indicated with an asterisk.

*	AIMUZ	Anthropologisches Institut und Museum der Universität Zürich
*	AMNH	American Museum of Natural History, New York
	ANSP	Academy of Natural Sciences, Philadelphia
*	A.S.	A.H. Schultz Collection, today housed at the Anthropological Institute of Zürich University (see AIMUZ)
	B	Museum Zoologicum Bogoriense
*	BM(NH)	British Museum (Natural History)
*	FMNH	Field Museum Museum of Natural History, Chicago
	IBH	Institute of Biology, Hanoi
*	KIZ	Kunming Institute of Zoology, Kunming, China
	MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
	MMNH	James Ford Bell Museum of Natural History, Minneapolis
*	MNHN	Museum National d'Histoire Naturelle, Paris
*	NHMBa	Naturhistorisches Museum Basel
*	NHMBe	Naturhistorisches Museum Bern
*	NMS	Natur-Museum Senckenberg, Frankfurt
*	PAL	Physical Anthropological Laboratory Collection at the Johns Hopkins Medical School in Baltimore, later incorporated into the A.H. Schultz Collection, today housed at the Anthropological Institute of Zürich University (see AIMUZ)
	USNM	United States National Museum of Natural History, Wahington, D.C.
*	SCIEA	South China Institute of Endangered Animals, Guangzhou, China
*	ZMB	Zoologisches Museum der Humboldt-Universität, Berlin
*	ZMUZ	Zoologisches Museum der Universität Zürich
	ZRCS	Zoological Reference Collection, University of Singapore
*	ZSBS	Zoologische Sammlung des Bayerischen Staates

Appendix 10.8: Key to Abbreviations for Collectors

WLA	Abbott, W.L.
CWB	Beebe, C.W.
FSB	Bourns, F.S.
CRC	Carpenter, C.R.
DJC	Chivers, D.J.
CSW	Coolidge, H.J., Schultz, A.H. & Washburn, S.L.
DDD	Davis, D.D.
JF	Fooden, J.
JAG	Griswold, J.A., Jr.
WTH	Hornaday, W.T.
RFI	Inger, R.F.
SAM	Macmillan, S.A.
WAM	Mijsberg, W.A.
SM	Müller, S.
HCR	Raven, H.C.
GS	Schneider, G.
AHS	Schultz, A.H.
GCS	Shortridge, G.C.
FAU	Ulmer, F.A., Jr.
ASV	Vernay, A.S.
SLW	Washburn, S.L.
MW	Weber, M.
HWW	Wells, H.W.

Appendix 10.9: Individual Data on Body Weights

The following appendix presents tabulated lists those gibbon specimens of known body weight used in chapter 5. Only adult or reportedly adult specimens are included. Criteria for determination of adult specimens are also discussed in chapter 2. Species and subspecies appear in alphabetical order. Information for each subspecies appears in a separate table. Within each table, specimens are sorted by locality. All specimens are wild-caught and assumed to be adult (although not all specimens could be personally examined by the present author). Detailed information on specimens localities (spelling of localities, geographical position of localites, coordinates, references for localities, and additional comments on localities) are presented in the gazetteer (see below: Appendix 10.10). Keys to abbreviations for museum collections and to abbreviations for authors and collectors are listed in Appendices 10.7 and 10.8, respectively (see above).

The sequence of information presented in each column is as follows:

1. body weight in kg (original records for many specimens are in lbs and have been converted)
2. sex of individual; m = male, f = female
3. name of locality (for more information see below: Appendix 10.7)
4. altitude in m
5. date of collection or observation
6. abbreviated name of author or collector
7. field number and other early collection numbers of specimen
8. present collection number
9. reference to body weight

Hylobates agilis

Hylobates agilis agilis:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a)]
6.65	m	probably Padang, Sumatera		ca. 1836	SM			1
6.237	m	Tapanuli Bay, Sumatera		14 Feb. 1902	WLA	1530	USNM 114499	2
4.536	f	Tapanuli Bay, Sumatera		22 Feb. 1902	WLA	1564	USNM 114501	2

a) Code to references:

1 Müller (1845, p. 87)

2 Ms. H. Kafka, USNM (in litt. 8 Jul. 1989)

Hylobates agilis albibarbis:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
4.876	m	Batu Jurong, Kalimantan		19 Jun. 1908	WLA	5981, USNM 153796	BM(NH) 33.6.6.2.	1, 2
6.8	f	Batu Jurong, Kalimantan			WLA		USNM 153797	1
6.0	m	Batu Jurong, Kalimantan			WLA		USNM 153798	1
6.5	f	Batu Jurong, Sumatera			WLA		USNM 153799	1
6.5	m	Kendawangan R., Kalimantan			WLA		USNM 153800	1
6.2	f	Kendawangan R., Kalimantan			WLA		USNM 153801	1
5.783	m	Matan River, Kalimantan		16 Aug. 1907	WLA	5501	USNM 145327 [b]	1, 3
6.1	f	Matan River, Kalimantan			WLA		USNM 145328	1
5.4	m	Matan River, Kalimantan			WLA		USNM 145329	1
5.9	f	Sukadana, Kalimantan	305-610		WLA		USNM 145326	1

a) Code to references:
   1 Lyon (1911, p. 144)
   2 personal examination of specimen tags or inventory cards
   3 Dr. R. Thorington, USNM (in litt., undated, 1988)

b) Type specimen

Hylobates agilis unko:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight a)
6.25	m	Batu ridial, Sumatera		10 Feb. 1899	GS			1
5.75	f	Batu ridial ?, Sumatera			GS			1
4.99	f	Indragiri River, Sumatera		22 Sept. 1901	WLA	1324	USNM 113176	2
5.443	m	Indragiri River, Sumatera		23 Sept. 1901	WLA	1328	USNM 113178	2
4.423	m	Indragiri River, Sumatera		26 Sept. 1901	WLA	1334	USNM 113179	2
5.897	m	Kateman River, Sumatera			WLA		USNM 123151	3
7.371	m	Kateman River, Sumatera			WLA		USNM 123152	3
5.67	f	Kateman River, Sumatera			WLA		USNM 123154	3
7.031	m	Kateman River, Sumatera			WLA		USNM 123155	3
5.443	m	Little Siak River, Sumatera			WLA		USNM 144089	3
5.67	m	Little Siak River, Sumatera			WLA		USNM 144091	3
5.783	f	Little Siak River, Sumatera			WLA		USNM 144092	3
4.99	m	Salat Rupat, Sumatera			WLA		USNM 143572	3
5.897	m	Salat Rupat, Sumatera			WLA		USNM 143573	3

6.35	m	Salat Rupat, Sumatera			WLA		USNM 143574	3
5.443	m	Salat Rupat, Sumatera			WLA		USNM 143575	3

a) Code to references:

1 Schneider (1905, p. 63)

2 Ms. H. Kafka, USNM (in litt. 8 Jul. 1989)

3 Lyon (1908, p. 675)

Hylobates concolor

Hylobates concolor concolor:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a)]
10	f	Ailao Mountains					Without No.	1
7.5	f	Môc Châu: Lóng Sâp, Son La		16 Nov. 1963			IBH? 365	2
6.2	m	Môc Châu: Lóng Sâp, Son La		16 Nov. 1963			IBH? 564	2
9	m	Thuong Bang La, Van Chan, Nghia Lo		4 Oct. 1963			IBH? 185	3
10	f	Thuong Bang La, Van Chan, Nghia Lo		4 Oct. 1963			IBH? 193	3
7.7	f	Xinshuigoutou, Lüchun	1800	30.4. or 1.5.1972		72119	KIZ 009643	4

a) Code to references:

1 Dr. Ma Shilai, KIZ (in litt., 17 May 1988)

2 Dao Van Tien (1985, p. 178f)

3 Dao Van Tien (1985, p. 192)

4 original data on specimen (own examination at KIZ)

Hylobates concolor furvogaster:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
5.75	f	Baoshan: Wayao		Oct. 1960			BIZ 17929	1
5.5	m	Cangyuan: Menglai Banlie	2400	19 Dec. 1983	Wei N.	830038	KIZ 009642	2
8	f	Cangyuan: Menglai	2000	25 Dec. 1983	Li J.	830071	KIZ 009641	3

[a] Code to references:

1 Groves (pers. comm. 15.9.1989)

2 original data on specimen (own examination at KIZ)

3 original data on specimen (own examination at KIZ), except body weight: Dr. Ma Shilai, KIZ (in litt., 17 May 1988)

Hylobates concolor hainanus:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
5.75	f	Bawangling, Hainan	ca. 1000	14 May 1964			SCIEA 0502	1
6.509	m	Bawangling, Hainan	ca. 1000	14 May 1964			SCIEA 0503	1
10	m	Jianfengling, Hainan	ca. 1000	4 Dec. 1962			SCIEA 0087	1
7.5	f	Jianfengling, Hainan	ca. 1000	4 Dec. 1962			SCIEA 0088	1

a) Code to references:
1 original data on specimen (own examination at SCIEA), and Xu et al. (1983, p. 315)

Hylobates concolor cf. *hainanus*, sensu Dao Van Tien (1983):

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
7	f	Trùng Khánh: Khâm Thành; Cao Bang		11 June, 1965			IBH? 50	1
8.5	m	Trùng Khánh: Khâm Thành; Cao Bang		11 June, 1965			IBH? 51	1

a) Code to references:
1 Dao Van Tien (1985, p. 40f)

Hylobates concolor jingdongensis:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collec-tor	Other numbers	Museum number	Reference for body weight [a]
8.7	m	Modaohe, Jingdong Co.	2100	9 Aug. 1964		640289	KIZ 003150	1
7.2	f	Modaohe, Jingdong Co.	2100	9 Aug. 1964		640290	KIZ 003152	1
7.3	f	Wenpu, Jingdong Co.	1800	7 or 17 Oct. 1957		012	KIZ 000168	1
7.5	f	Wenpu, Jingdong Co.	1800	28 Oct. 1957		050	KIZ 000170	1
7.8	f	(probably Wenpu), Jingdong Co.	1840	18 Nov. 1957		106	KIZ 000167	1

[a] Code to references:

1 original data on specimen (own examination at KIZ); and Ma & Wang (1986, p. 401)

Hylobates hoolock

Hylobates hoolock ssp:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
6.577	m	[c]						1
6.01 [b]	f	[c]						1
6.01	m	Hkamti, upper Chindwin						2
6.577	f	Hkamti, upper Chindwin						2
6.123	m	Hkamti, upper Chindwin						3

a) Code to references:
1 Shortridge (1914, p. 793)
2 Pocock (1927, p. 733)
3 Pocock (1939, p. 21)

b) This weight is a mean value of two animals; it was entered as *one* individual body weight into the calculations in Section 5.3 (see above)

c) No locality reported, but the publication is on "Indian mammals" (Shortridge, 1914, p. 793)

Hylobates hoolock hoolock:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
7.938	m	Hatikhali, Cachar Hills	488	1 Oct. 1920	HWW	1017	BM(NH) 21.7.9.1.	1, 2
7.326	m	Hkamti, west bank upper Chindwin	152	26 Jul. 1914	GCS &SAM	5840	BM(NH) 1937.3.24 .1.	1
6.69	m	Hkamti, west bank upper Chindwin	152	6 Aug. 1914	GCS &SAM	5949	BM(NH) 15.5.5.1.	1
6.35	f	Margharita, Naga Hills	366	29 Oct. 1919	HWW	20	BM(NH) 1937.3.24 .6.	1, 2

a) Code to references:

1 original data on specimen (own examination at BM(NH), London)

2 Pocock (1927, p. 733)

3 Pocock (1939, p. 21)

Hylobates hoolock leuconedys:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
6.577	m	Gokteik, N. Shan States	650		GCS ?			1, 2
6.804	m	Hkamti, east bank upper Chindwin	152	28 Jul. 1914	GCS &SAM	5858	BM(NH) 1937.3. 24.2	1, 3
7.257	m	Homalin, east bank upper Chindwin	122	16 Jul. 1914	GCS &SAM	5704	BM(NH) 15.5.5.2.	1, 2, 3
7.484	f	Nanyaseik	137	8 Jan. 1935	HCR	12	AMNH 112667	4
7.257	m	Nanyaseik	137	8 Jan. 1935	HCR	13	AMNH 112668	4
7	m	Tengchong County					KIZ 553	5
8.5	m	Tengchong County					KIZ 569	5
5.3	m	Tengchong County					KIZ 585	5
8	f	Tengchong County					KIZ 586	5

[a] Code to references:

1 Pocock (1927, p. 733)

2 Pocock (1939, p. 21)

3 original data on specimen (own examination at BM(NH), London)

4 original data on specimen (own examination at AMNH, New York)

5 Dr. Ma Shilai, KIZ (in litt., 17 May 1988)

Hylobates klossii

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
6.123	m	South Pagi Island		13 Nov. 1902	WLA	2032	USNM 121678 [b]	1, 2
5.21	m	South Pagi Island		1902	WLA			1
5.21	f	South Pagi Island		1902	WLA			1
5.783	f	South Pagi Island		16 Nov. 1902	WLA	2050, USNM 121685	BM(NH) 4.5.4.1.	1, 3
6.12	f	South Pagi Island		1902	WLA			1 [c]
6.464	f	South Pagi Island		15 Dec. 1902	WLA		MCZ 38641	1, 4

a) Code to references:
   1 Miller (1903b, p. 71)
   2 Dr. R.Thorington, USNM (in litt., undated, 1988)
   3 original data on specimen (own examination at BM(NH), London)
   4 Ms. M.E. Rutzmoser, MCZ (in litt., 29 April 1988)

b) Type specimen

c) This specimen is probably identical with specimen FMNH 43333, Field No. 2099, collected by W.L. Abbott on 2 Dec. 1902, old USMNH No. 121687: original data on specimen (own examination at FMNH, Chicago), but no body weight recorded on tag

Hylobates lar

Hylobates lar carpenteri:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers a)	Museum number	Reference for body weight b)
6	m	Ban Mae Lamao	350	March 1967	JF			1
7.371	m	Chieng Dao	427	18 May 1937	CRC &SLW	APE 608, C10-1	MCZ 41529	2
5.216	f	Chieng Dao	427	18 May 1937	CRC &SLW	APE 606, C10-2	MCZ 41530	2
6.35	m	Chieng Dao	427	19 May 1937	CRC &SLW	APE 605, C10-3	MCZ 41531	2
5.443	m	Chieng Dao	427	20 May 1937	CRC &SLW	APE 603, C10-4	MCZ 41533	2
4.5	f	Huai Kwang Pah	300	29 March 1967	JF		FMNH 99757	1
5.443	F	Angka Camp 1	1311	28 Feb. 1937	CSW	APE 1, S 2	MCZ 41547	3
5.443	F	Angka Camp 1	1311	28 Feb. 1937	CSW	APE 2, S 3	MCZ 41416	3
5.67	m	Angka Camp 1	1311	1 March 1937	CSW	APE 6, S 4	MCZ 41417	3
4.763	F	Angka Camp 1	1311	1 March 1937	CSW	APE 7, S 5	MCZ 41418	3
6.804	F	Angka Camp 1	1311	2 March 1937	CSW	APE 9, S 6	MCZ 41419	3
6.35	m	Angka Camp 1	1311	2 March 1937	CSW	APE 10, S 7	MCZ 41420	3

3.856	F	Angka Camp 1	1311	2 March 1937	CSW	APE 13, S 8	MCZ 41421	3
5.897	m	Angka Camp 1	1311	10 March 1937	CSW	APE 18, S 12	MCZ 41423	3
5.897	F	Angka Camp 1	1311	11 March 1937	CSW	APE 24, S 16	MCZ 41426	3
5.443	m	Angka Camp 1	1311	12 March 1937	CSW	APE 26, S 17	MCZ 41427	3
5.897	m	Angka Camp 1	1311	12 March 1937	CSW	APE 27, S 18	MCZ 41428	3
4.99	m	Angka Camp 1	1311	14 March 1937	CSW	APE 32, S 21	MCZ 41430	3
5.897	m	Angka Camp 1	1311	15 March 1937	CSW	APE 33, S 23	MCZ 41431	3
5.443	F	Angka Camp 1	1311	19 March 1937	CSW	APE 42, S 29	MCZ 41436	3
5.217	m	Angka Camp 1	1311	21 March 1937	CSW	APE 46, S 32	MCZ 41413	3
5.67	F	Angka Camp 1	1311	21 March 1937	CSW	APE 49, S 34	MCZ 35945	3
5.67	m	Angka Camp 1	1311	23 March 1937	CSW	APE 51, S 38	MCZ 41439	3
4.99	f	Angka Camp 1	1311	24 March 1937	CSW	APE 55, S 39	MCZ 41440	3
5.897	m	Angka Camp 1	1311	24 March 1937	CSW	APE 57, S 40	MCZ 41441	3
5.897	f	Angka Camp 1	1311	25 March 1937	CSW	APE 58, S 42	MCZ 41442	3
4.99	m	Angka Camp 1	1311	25 March 1937	CSW	APE 63, S 45	MCZ 41445	3
5.217	m	Angka Camp 1	1311	27 March 1937	CSW	APE 64, S 46	MCZ 41446	3
6.124	m	Angka Camp 1	1311	29 March 1937	CSW	APE 65, S 47	MCZ 41447	3

5.67	m	Angka Camp 1	1311	29 March 1937	CSW	APE 67, S 48	MCZ 41448	3
5.443	f	Angka Camp 1	1311	30 March 1937	CSW	APE 69, S 50	MCZ 41449	3
4.763	m	Angka Camp 1	1311	30 March 1937	CSW	APE 71, S 51	MCZ 41450	3
7.031	m	Angka Camp 1	1311	31 March 1937	CSW	APE 72, S 52	MCZ 41451	3
5.217	f	Angka Camp 1	1311	31 March 1937	CSW	APE 76, S 55	MCZ 35943	3
5.443	m	Angka Camp 1	1311	31 March 1937	CSW	APE 81, S 58	MCZ 41453	3
4.309	f	Angka Camp 1	1311	2 April 1937	CSW	APE 83, S 59	MCZ 41454	3
5.443	f	Angka Camp 1	1311	2 April 1937	CSW	APE 85, S 61	MCZ 41455	3
6.35	m	Angka Camp 1	1311	2 April 1937	CSW	APE 88, S 62	MCZ 35951	3
6.35	m	Angka Camp 1	1311	5 April 1937	CSW	APE 90, S 66	MCZ 41456	3
4.99	f	Angka Camp 1	1311	6 April 1937	CSW	APE 93, S 71	MCZ 41458	3
5.443	f	Angka Camp 1	1311	7 April 1937	CSW	APE 96, S 73	MCZ 41460	3
5.897	m	Angka Camp 1	1311	7 April 1937	CSW	APE 98, S 72	MCZ 41459	3
6.35	m	Angka Camp 1	1311	9 April 1937	CSW	APE 109, S 80	MCZ 41464	3
5.443	m	Angka Camp 1	1311	9 April 1937	CSW	APE 110, S 81	MCZ 41465	3
6.124	m	Angka Camp 1	1311	11 April 1937	CSW	APE 118, S 88	MCZ 41471	3

7.258	m	Angka Camp 1	1311	11 April 1937	CSW	APE 119, S 89	MCZ 41472	3
5.897	f	Angka Camp 1	1311	13 April 1937	CSW	APE 123, S 92	MCZ 41474	3
4.082	f	Angka Camp 1	1311	13 April 1937	CSW	APE 125, S 93	MCZ 41475	3
6.804	m	Angka Camp 1	1311	13 April 1937	CSW	APE 128, S 94	MCZ 41476	3
5.67	f	Angka Camp 1	1311	13 April 1937	CSW	APE 130, S 97	MCZ 41478	3
5.443	f	Angka Camp 1	1311	13 April 1937	CSW	APE 132, S 96	MCZ 41477	3
5.443	m	Angka Camp 1	1311	14 April 1937	CSW	APE 134, S 98	MCZ 41479	3
4.99	f	Angka Camp 1	1311	14 April 1937	CSW	APE 135, S 99	MCZ 41480	3
4.99	m	Angka Camp 1	1311	14 April 1937	CSW	APE 138, S 100	MCZ 41481	3
6.577	m	Angka Camp 1	1311	15 April 1937	CSW	APE 140, S 103	MCZ 41485	3
5.217	m	Angka Camp 1	1311	16 April 1937	CSW	APE 142, S 107	MCZ 41483	3

7.031	m	Angka Camp 1	1311	16 April 1937	CSW	APE 143, S 108	MCZ 41484	3
5.217	f	Angka Camp 1	1311	16 April 1937	CSW	APE 145, S 109	MCZ 41485	3
4.082	m	Angka Camp 1	1311	17 April 1937	CSW	APE 148, S 111	MCZ 41486	3
5.897	m	Angka Camp 1	1311	17 April 1937	CSW	APE 152, S 114	MCZ 41489	3
4.99	m	Angka Camp 1	1311	17 April 1937	CSW	APE 154, S 115	MCZ 41490	3
5.897	m	Angka Camp 1	1311	17 April 1937	CSW	APE 157, S 117	MCZ 41492	3
5.67	f	Angka Camp 1	1311	18 April 1937	CSW	APE 158, S 118	MCZ 41493	3
5.443	f	Angka Camp 1	1311	19 April 1937	CSW	APE 162, S 119	MCZ 41494	3
5.67	m	Angka Camp 1	1311	19 April 1937	CSW	APE 164, S 120	MCZ 41495	3
5.897	m	Angka Camp 1	1311	19 April 1937	CSW	APE 165, S 121	MCZ 35946	3
5.443	m	Angka Camp 1	1311	20 April 1937	CSW	APE 174, S 128	MCZ 41501	3

5.443	f	Angka Camp 1	1311	21 April 1937	CSW	APE 176, S 131	MCZ 41503	3
5.217	f	Angka Camp 1	1311	22 April 1937	CSW	APE 178, S 132	MCZ 41414	3
5.443	m	Angka Camp 1	1311	22 April 1937	CSW	APE 180, S 133	MCZ 41504	3
5.443	f	Angka Camp 2	1524	23 March 1937	CSW	APE 53, S 37	MCZ 35950	3
4.99	f	Angka Ridge	1905	8 April 1937	CSW	APE 105, S 78	MCZ 41463	3
5.443	f	Angka Ridge	1905	8 April 1937	CSW	APE 107, S 79	MCZ 41412	3
6.35	m	Angka Camp 3	1829	10 April 1937	CSW	APE 112, S 84	MCZ 41468	3
5.443	f	Angka Camp 3	1829	10 April 1937	CSW	APE 113, S 85	MCZ 41469	3
5.217	f	Angka Camp 3	1829	17 April 1937	CSW	APE 149, S 112	MCZ 41487	3
5.217	f	Angka Camp 3	1829	19 April 1937	CSW	APE 166, S 123	MCZ 41496	3
4.99	f	Angka Camp 3	1829	10 March 1937	CSW	APE 20, S 13	MCZ 41411	3
5.67	f	Angka Camp 3	1829	10 March 1937	CSW	APE 21, S 14	MCZ 41424	3
5.443	m	Angka Camp 3	1829	16 March 1937	CSW	APE 38, S 26	MCZ 41433	3

6.124	f	Angka Camp 3	1829	6 April 1937	CSW	APE 91, S 69	MCZ 35949	3
5.217	m	Angka Camp 3	1829	6 April 1937	CSW	APE 95, S 70	MCZ 41457	3
5.217	m	Kun Wang (village beyond Angka Camp 3)	1219	16 March 1937	CSW	APE 40, S 27	MCZ 41434	3

a) Gibbon specimens collected during the Asian Primate Expedition (APE) in 1937 were given several numbers by A.H. Schultz: One number was given to the skeleton of each specimen after it had been prepared at the camp. This first number is here termed the APE-number. Additional APE-numbers were also given to preserved parts of a specimen other than the skeleton (e.g. reproductive tracts, single hands and feet). Accordingly, a single specimen could have several APE-numbers. In these cases, only the first number (usually for the skeleton) is listed here. An additional, but independent, numbering system was used for each specimen's skin, here labelled S-numbers. Finally, Carpenter also used an independent set of numbers for the gibbons he observed, some of which were then collected towards the end of the APE expedition (Carpenter, 1940, 105); these numbers are here termed C-numbers. All field numbers were recorded in an unpublished Field Catalogue (Schultz, 1937). The individual body weights have never been published. A list of body weights for each APE specimen (Schultz, 1941b) was found among other handwritten documents in the A.H. Schultz Archives, housed at the Anthropological Institute of Zürich University. A link between Schultz's data and the actual specimens at MCZ was made with the aid of a list showing the S-numbers and the corresponding Museum numbers. This list was kindly made available by Ms. M.E. Rutzmoser, MCZ (in litt., 19 Jan. 1989).

b) Code to references:

1 Fooden (1971, p. 44)

2 Carpenter (1940, p. 104)

3 Schultz (1941b)

Hylobates lar entelloides, northern localities:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collec-tor	Other numbers	Museum number	Reference for body weight [a)]
4.4	f	Ban Muang Baw Ngam	1100	15 Jan. 1967	JF		FMNH 99736	1
5.2	m	Ban Nam Lai Tai	300	April 1967	JF			1
5.55	f	Ban Pong Nam Ron	200 - 300	10 April 1967	JF		FMNH 99760	1
5.88	m	Ban Tamrong Phato	100	Feb. 1967	JF			1
4.6	f	Ban Tamrong Phato	100	10 Feb. 1967	JF		FMNH 99745	1
5.4	m	Chongkrong	600 - 900	Jan. 1967	JF			1
4.6	f	Chongkrong	600 - 900	27 Jan. 1967	JF		FMNH 99741	1
6.2	m	Chongkrong	600 - 900	Jan. 1967	JF			1
4.97	m	Kata Taek	200	Feb.-Mar. 1967	JF			1
4.5	f	Kata Taek	200	28 Feb. 1967	JF		FMNH 99747	1
5.65	m	Kata Taek	200	Feb.-Mar. 1967	JF			1
5.7	f	Ko Keow	200	7 March 1967	JF		FMNH 99751	1
6.1	m	Ko Keow	200	March 1967	JF			1
5.8	m	Ko Keow	200	March 1967	JF			1
6.35	m	Lakya	351	19 Jan. 1924	ASV	70	AMNH 54670	3

5.443	m	17 mi East of Lakya	396	20 Jan. 1924	ASV	73	BM(NH) 24.9.2.2.	2
5.897	m	17 mi East of Lakya	396	22 Jan. 1924	ASV	75	BM(NH) 24.9.2.3.	2
6.35	f	Lampha	305	30 Dec. 1923	ASV	23	AMNH 54659	3
6.804	m	Taok Plateau	930	1 Jan. 1924	ASV	44	AMNH 54663	3
6.35	f	Taok Plateau	945	8 Jan. 1924	ASV	48	BM(NH) 24.9.2.6.	2
7.031	m	Taok Plateau	975	12 Jan. 1924	ASV	59	AMNH 54669	3
6.123	f	Taok Plateau	975	13 Jan. 1924	ASV	63	BM(NH) 24.9.2.7.	2
6.35	m	28 mi East of UmPang	533	28 Jan. 1924	ASV	87	BM(NH) 24.9.2.1.	2
5.216	m	28 mi East of UmPang	533	31 Jan. 1924	ASV	97	AMNH 54671	3

a) Code to references:

1 Fooden (1971, p. 44)

2 original data on specimen (own examination at BM(NH), London)

3 original data on specimen (own examination at AMNH, New York)

Hylobates lar entelloides, central peninsular localities:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a)]
6.69	m	Sungei Balik, Singapore		27 Nov. 1900	WLA	744	USNM 111988	1
7.711	m	Sungei Balik, Singapore		28 Nov. 1900	WLA	745	USNM 111989	1
5.5	f	Ban Thap Blik	75	3 June 1973	JF			2
7.25	f	Bangtaphan Province						3
5	m	Bangtaphan Province						3
4.76	f	Bangtaphan Province						3
5.2	f	Bangtaphan Province						3
6.804	m	Bankachon		16 Dec. 1913	GCS	4525	BM(NH) 14.12.8.1	4
7.598	m	Bankachon		21 Dec. 1913	GCS	4596	BM(NH) 14.12.8.2	4
6.804	f	Bankachon		21 Dec. 1913	GCS	4606	BM(NH) 14.12.8.8	4
7.031	m	Bankachon		21 Dec. 1913	GCS	4607	BM(NH) 14.12.8.3	4
7.484	m	Bankachon		28 Dec. 1913	GCS	4643	BM(NH) 51.607	4
6.577	m	Bankachon		5 Jan. 1913	GCS	4705	BM(NH) 14.12.8.6	4
6.123	f	Bankachon		5 Jan. 1913	GCS	4708	ZRC 4.606	5
6.123	m	Bankachon			GCS ?			6
4.536	f	Bankachon			GCS ?			6

6.35	m	Champong, Tenasserim		19 Dec. 1903	WLA	2924	USNM 124024	1
8.391	m	Meliwini, Victoria Point		6 Feb. 1913	GCS	4767	ZRC 4.617	5
7.031	f	Meliwini, Victoria Point		6 Feb. 1913	GCS	4768	ZRC 4.607	5
7.257	m	Red Point, Singapore		18 Feb. 1904	WLA	3125	USNM 124232	1
7.598	m	Tanjong Badak, Tenasserim		28 Dec. 1900	WLA	805	USNM 111970	1

a) Code to references:

1 Ms. H. Kafka, USNM (in litt. 8 Jul. 1989)

2 Fooden (1976, p. 106)

3 Keith (1895, p. 296); for the first three specimens see also Keith (1891, p. 86)

4 original data on specimen (own examination at BM(NH), London)

5 Mrs. Yang Chang Man, ZRC, (in litt. 29 April 1988)

6 Pocock (1939, p. 28) reported maximum and minimum body weights of both male and female specimens from "the long series of skins from Bankachon." Specimens with the same maximum weights were also found in this study among Bankachon skins at BM(NH), London; these were probably the same specimens referred to by Pocock (1939). On the other hand, no specimens were found with body weights corresponding to the minimum weights reported by Pocock (1939, 28). Because the other specimens mentioned by Pocock were apparently already included in the present sample, only his minimum male and minimum female weights have been added here.

Hylobates lar entelloides, southern peninsular localities:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
4.309	f	Trong, Lower Siam		5 March 1896	WLA		USNM 83264	1
5.874	f	Trong, Lower Siam		1 April 1896	WLA	116	USNM 83262	1
4.763	f	Trong, Lower Siam		9 Apr. 1896	WLA	118	USNM 83265	1
5.897	f	Trong, Lower Siam		23 Aug. 1896	WLA		USNM 83515	1
4.99	m	Trong, Lower Siam		31 Aug 1896	WLA		USNM 83514	1

[a] Code to references:

1 Ms. H. Kafka, USNM (in litt. 8 Jul. 1989)

Hylobates lar lar:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collec-tor	Other numbers	Museum number	Reference for body weight [a)]
5.783	m	Jambu Luang, Johore		31 July 1901	WLA	1197	USNM 112710	1
4.99	f	Jambu Luang, Johore		1 Aug. 1901	WLA	1198	USNM 112711	1
4.309	f	Rumpin River, Pahang		1 July 1901	WLA	1803	USNM 115502	1
5.33	m	Rumpin River, Pahang		8 June 1901	WLA	1764	USNM 115501	1
5	m	nr. Tanjung Malim	<50		DJC		P 05	2
5.4	f	nr. Tanjung Malim	<50		DJC		P 06	2

a) Code to references:

1 Ms. H. Kafka, USNM (in litt. 8 Jul. 1989)

2 Dr. D.J. Chivers, Cambridge (in litt. 21 Dec.1989) and (1980, p. 364)

Hylobates lar vestitus:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a)]
4.876	m	Aru Bay			WLA		USNM 143564	1
5.443	m	Aru Bay			WLA		USNM 143565	1
4.309	m	Aru Bay			WLA		USNM 143566	1
4.876	m	Aru Bay			WLA		USNM 143567	1
5.557	m	Aru Bay			WLA		USNM 143569	1
5.33	f	Aru Bay			WLA		USNM 143570	1
5.216	f	Blangnanga	1097	March - Apr. 1939	FAU		ANSP 20208	2
5.216	f	Blangnanga	1097	March - Apr. 1939	FAU		ANSP 20209	2
3.856	m	Meluwak	500	March - Apr. 1939	FAU		ANSP 20205	2
4.082	f	Meluwak	500	March - Apr. 1939	FAU		ANSP 20210	2

a) Code to references:

1 Lyon (1908, p. 675)

2 Miller (1942, p. 131)

Hylobates lar yunnanensis:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
5	f	Menglian Co., probably Lafu	2000	May 1964		640219	KIZ 031476	1

[a] Code to references:

1 original data on specimen (own examination at KIZ, Kunming), and Ma & Wang (1986, p. 403)

Hylobates leucogenys

Hylobates leucogenys leucogenys:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collec-tor	Other numbers	Museum number	Reference for body weight [a)]
7.5	f	Hoi Xuân, Thanh Hoa		18 March 1964			IBH? 541	1
7.5	m	Hoi Xuân, Thanh Hoa		18 March 1964			IBH? 542	1
7.8	f	Longlin, Mengla County		22 Dec. 1959		592010	KIZ 000175	2
8	m	Longlin, Mengla County		22 or 24 Dec. 1959		592011	KIZ 000171	2
6.9	m	Mengla County (prob. Longlin)		22 Dec. 1959		592012	KIZ ?	3
7.2	m	Mengla County		10 Feb. 1958		008	KIZ 003144	2
6.8	m	Mengla County		8 May 1959		80848	KIZ ?	2
7.2 [b)]	m	Quì Châu, Nghê An		29 - 30 Nov. 1964		110	IBH? 670	1

a) Code to references:
1 Dao Van Tien (1985, pp. 210f and 228)
2 original data on specimen (own examination at KIZ, Kunming)
3 original data on specimen (own examination at KIZ), except body weight: Dr. Ma Shilai, KIZ (in litt., 17 May 1988)

b) Dao Van Tien (1985, pp. 228) listed a further male (No. 679) from the same locality. The specimen had a body weight of only 4.7 kg and was of diminutive body dimensions, as compared to other *leucogenys* in this study. It was probably not adult (although Dao Van Tien did not mention this) and was not used in this study.

Hylobates leucogenys siki:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
6.5	f	Tân Ky, Nghê An		5 -10 Dec. 1964		143	IBH? 703	1
10	m	Tân Ky, Nghê An		5 -10 Dec. 1964		178	IBH? 736	1
7.5	f	Tân Ky, Nghê An		5 -10 Dec. 1964		179	IBH? 737	1
5.7	m	Tân Ky, Nghê An		5 -10 Dec. 1964		180	IBH? 738	1

a) Code to references:
1 Dao Van Tien (1985, p. 228)

b) This weight is a mean value of two animals.

Hylobates moloch

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
6.25	f	nr. Buitenzorg (Bogor)			MW	263		1
6.577	m	Java			WAM	JH 189	PAL 166	2

a) Code to references:
1 Weber (1890-91, p. 99), see also Kohlbrügge (1891-92, p. 196)
2 A.H. Schultz, unpublished hand-written notes and (without body weight) P.A.L.-Catalogue, both kept at the A.H. Schultz Archives at the Anthropological Institute of Zürich University

Hylobates muelleri

Hylobates muelleri abbotti:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
6.35	m	Kapuas River below Tyan		7 Sep. 1905	WLA	USNM 142174	BM(NH) 33.6.6.1	1, 2
5.896	m	Kapuas River below Tyan		Sep. 1905	WLA		USNM 142175	1
6.01	f	Kapuas River below Tyan		Sep. 1905	WLA		USNM 142177	1
5.557	f	Kapuas River below Tyan		Sep. 1905	WLA		USNM 142178	1
6.35	m	10 miles South of Kuching		26 June 1910	CWB	Bo.39	AMNH 32636	3
6.464	m	Landak River: Sungei Nya		29 June 1905	WLA		USNM 14172	1, 4
6.35	m	Landak River: Sungei Nya		1905	WLA		USNM 14173	1
5.897	f	Region of Sebangan R. [b]		6 April 1893	FSB		MMNH 4742	5
4.649	m	Sibuyau River, Sarawak		3 Nov. 1878	WTH			6

a) Code to references:
1 Lyon (1907, p. 570)
2 original data on specimen (own examination at BM(NH), London)
3 original data on specimen (own examination at AMNH, New York)
4 Dr. R. Thorington, USNM (in litt., undated, 1988)
5 Ms. G.E. Nordquist, MMNH (in litt. 25 April 1988, and 17 Feb. 1989)
6 Hornaday, (1894)

b) See Gazetteer 4, below, for more details on this locality.

Hylobates muelleri funereus:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers a)	Museum number	Reference for body weight b)
6.35	m	Abai	0	14 June 1937	SLW &AHS	APE241, S 337	MCZ 37385	1, 2
5.897	m	Abai	0	20 June 1937	SLW &AHS	APE276, S 360	MCZ 37382	1, 2
4.99	m	Abai	0	5 July 1937	SLW &AHS	APE379, S 437	MCZ 37374	1
5.443	f	Abai	0	15 July 1937	SLW &AHS	APE430, S 476	MCZ 37379	1
6.123	m	Abai	0	15 July 1937	SLW &AHS	APE432, S 477	MCZ 37381	1
6.123	f	Abai	0	21 July 1937	SLW	APE448, S 489	MCZ 37378	1, 2
4.99	m	Abai	0	26 July 1937	SLW	APE474, S 506	MCZ 37380	1, 2
4.536	f	Abai	0	26 July 1937	SLW	APE475, S 507	MCZ 37383	1, 2, 3
5.443	m	Abai	0	July 1937	SLW	APE476	A.S. 1542	1, 4
4.5	f	Kalabakan, Sungei Tibas		19 June 1956	RFI	3102	FMNH 85925	5, 6
6.577 c)	f	Kinabalu, Mount	1372	8 July 1937	Labuan or JAG?	165	MCZ 37373	1, 3
4.11	f	Little Kretam River		11 May 1950	DDD	225	FMNH 68674	5, 6, 7
5.095	m	Little Kretam River		19 May 1950	DDD	243	FMNH 68675	5, 6, 7
5.285	f	Little Kretam River		19 May 1950	DDD	244	FMNH 68676	5, 6, 7
6.4	m	Little Kretam River		28 May 1950	DDD	274	FMNH 68678	5, 6, 7

5.6 [d]	f	Little Kretam River		28 May 1950	DDD	275	FMNH 68679	5, 6, 7
5.025	f	Little Kretam River		6 June 1950	DDD	294	FMNH 68680	5, 6, 7
5.557	m	Seliman, Sungai, 13th mile [e]		21 Jan. 1926			MCZ 35881	3

a) For a comment on the various numbering schemes used for gibbon specimens collected during the Asian Primate Expedition (APE) in 1937 see above (Footnote "a" after list of body weights for *H. lar carpenteri*).

b) Code to references:
1 Schultz (1941a)
2 Schultz (1937, p. 85)
3 Ms. M.E. Rutzmoser, MCZ (in litt., 19 Jan. 1989)
4 original data on specimen (own examination at AIMUZ, Zürich)
5 original data on specimen (own examination at FMNH, Chicago)
6 Dr. J. Fooden, FMNH (in litt., 25 April 1988)
7 Davis (1962, p. 68)

c) The body weight of this specimen is recorded as 17 1/2 lbs (7.94 kg) in Griswold's field journal and in the MCZ inventory cards, but the label that is with the skeleton has written 14 1/2 (6.58kg) over top of 17 1/2 (Ms. M.E. Rutzmoser, MCZ, in litt., 19 Jan. 1989). Schultz, who certainly had access to the original data, records a weight of 14 1/2 for this specimen (Schultz, 1937, p. 85). Because the weight of 7.94 kg is much higher than all other known body weights for *H. muelleri*, the weight recorded by Schultz appears to be more realistic and is used in this study.

d) Davis' (1962, p. 68) published body weights for *H. muelleri funereus* collected by himself differ in one specimen from those recorded in his field notes (Dr. J. Fooden, FMNH, in litt., 25 April 1988): 4.5kg vs. 5.6 kg. In this study, the weight as recorded in Davis' field notes is used.

e) See Gazetteer (Appendix 10.10), below, for more details on this locality.

Hylobates muelleri muelleri:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
5.2	m	Balik Papan Bay		1908	WLA		USNM 154370	1
5.4	f	Balik Papan Bay		1908	WLA		USNM 154371	1
5.4	f	Balik Papan Bay		1908	WLA		USNM 154372	1
5.6	f	Balik Papan Bay		1908	WLA		USNM 154373	1
5	m	Klumpang Bay		1908	WLA		USNM 151832	1
5.8	f	Klumpang Bay		1908	WLA		USNM 151833	1
6.8	m	Klumpang Bay		1908	WLA		USNM 151834	1
5	m	Klumpang Bay		1908	WLA		USNM 151835	1
4.6	f	Klumpang Bay		1908	WLA		USNM 151836	1
5.2	m	Pangkallahan River		1908	WLA		USNM 151837	1
5.897 [b]	f	Pangkallahan River		10 Feb. 1908	WLA	5783, USNM 151838	FMNH 41514	1, 2
4.196 [b]	f	Pasir River		1908	WLA		USNM 154369	1, 3

[a] Code to references:

1 Lyon (1911, p. 144)

2 Dr. J. Fooden, FMNH (in litt., 25 April 1988)

3 Ms. H. Kafka, USNM (in litt. 23 Jan. 1989)

b) Lyon (1911, p. 144) published body weights of eight female *H. muelleri muelleri*. Three of these specimens were reportedly "young adult". One of these (USNM 151839 from Pankallahan River) has an extremely low body weight of 7 1/4 lbs (3.29 kg), suggesting an immature animal. Apparently, the skull of this animal is not in the collections of the USNM (Ms. H. Kafka, USNM, in litt. 23 Jan. 1989). The specimen was not used in this study. The skull of the second-smallest, young adult animal (USNM 154369) is available. According to Ms. H. Kafka (USNM, in litt. 23 Jan. 1989), who kindly inspected the specimen for me, the sutures are well-fused and all teeth (of the full dental set) show considerable wear. Consequently, this animal was considered adult, as was the third and largest of the three young adult animals (USNM 151838).

Hylobates pileatus

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight a)
5.5	m	Probably Thailand		1889-1892				1
5.44	f	Probably Thailand		1889-1892				1

a) Code to references:

1 Keith (1895, p. 296)

Hylobates syndactylus

Hylobates syndactylus syndactylus:

Body weight [kg]	Sex	Locality	Alt. [m]	Collecting date	Collector	Other numbers	Museum number	Reference for body weight [a]
10.546	m	Aru Bay, Sumatra		18 Nov. 1905	WLA	4475	USNM 143577	1, 2
11	m	Aru Bay, Sumatra		19 Nov. 1905	WLA	4476	USNM 143578	1, 2
9.299	f	Aru Bay, Sumatra		19 Nov. 1905	WLA	4477	USNM 143579	1, 2
11.34	f	Aru Bay, Sumatra		3 Dec. 1905	WLA	4531	USNM 143580	1, 2
9.072	f	Aru Bay, Sumatra		23 Dec. 1905	WLA	4578	USNM 143581	1, 2
12.474	f	Kungke, Atjeh, Sumatra	975	March 1939	FAU		ANSP 20202	3
15.12	m	Padang (?), W.Sumatra [b]		ca. 1836	SM			4
11.49	f	Padang (?), W.Sumatra [b]		ca. 1836	SM			4
8.4	f	Padang, Sumatra		12 Jan. 1937	SM ?		B 6459	5
9.5	m	Paninggahan [b] (=?Paninjawan)			MW	121		6
9.752	f	Tapanuli Bay, Sumatra [c]		23 March 1902	WLA	1683, USNM 114494	ZRC 4.711	7, 8
11.793	m	Tapanuli Bay, Sumatra		23 March 1902	WLA	1684	USNM 114495	1, 7
12.701	m	Tapanuli Bay, Sumatra		28 March 1902	WLA	1696	USNM 114496	1, 7

10.773	f	Tapanuli Bay, Sumatra [d)]		28 March 1902	WLA	1697	USNM 114497	1, 7
12.474	m	Tarussan Bay, Sumatra		30 Dec. 1904	WLA	3860	USNM 141160	2
11.793	f	Tarussan Bay, Sumatra		30 Dec. 1904	WLA	3861	USNM 141161	2
12.701	f	Tarussan Bay, Sumatra		3 Jan. 1905	WLA	3877	USNM 141162	2

a) Code to references:
   1 Lyon (1908, p. 675)
   2 Dr. R. Thorington, USNM (in litt., undated, 1988)
   3 Miller (1942, p. 132)
   4 Müller (1845, p. 82)
   5 Dr. J. Sugardjito, Museum Zoologicum Bogoriense (in litt., undated, 1988)
   6 Weber (1890-91, p. 100), see also Kohlbrügge (1891-92, p. 196)
   7 Miller (1903b, p. 71)
   8 Mrs. Yang Chang Man, ZRC, (in litt. 29 April 1988)

b) See Gazetteer 4, below, for more details on this locality.

c) The weight recorded on the specimen at ZRC is 21 1/2 lbs (9.75 kg) (Ms. Yang, in litt. 29 April 1988), and thus differs very slightly from the weight published by Miller (1903b, p. 71: 9.71 kg). In this study, the weight recorded at the collection housing the specimen is used.

d) The weight recorded on the specimen at USNM is 23 3/4 lbs (10.77 kg) (Dr. R. Thorington, in litt., undated, 1988), and thus differs from the weight published by Miller (1903b, p. 71: 11.56 kg). In this study, the weight recorded at the collection housing the specimen is used.

Appendix 10.10: Gazetteer

The following Gazetteer lists the localities for those gibbon specimens of known adult body weight used in chapter 5 and Appendix 10.9. The localities are sorted by species and subspecies; both appear in alphabetical order. The form and spelling of primary entries in this gazetteer follow, where possible, those in the U.S. Board on Geographic Names (USBGN) gazetteers for Burma (1966b), China (1979), India (1952), Indonesia (1982), Malaysia (1970), Thailand (1966a), Vietnam (1986). Primary entries for gibbon localities that are not included in the USBGN gazetteers consulted are spelled here as in the original source or as in an indicated reference. Secondary entries, with cross references to corresponding primary entries, give variant spellings or alternate locality names that appear on specimen tags or in published literature on gibbons. Where possible, coordinates of localities were extracted from the U.S. Board on Geographic Names (USBGN) gazetteers mentioned above.

The sequence of information presented in each primary entry is as follows:

1. locality name
2. altitude, if reported by collector or observer
3. name of province, state or first-order administrative unit, and name of country (capital letters)
4. coordinates of locality
5. name of collector followed by parenthetical reference to published locality notes, if any
6. date of collection or observation
7. additional notes by this author, where necessary

A key to the abbreviations for museum collections is presented in Appendix 10.4 (see above).

Hylobates agilis

Hylobates agilis agilis:

Padang; Sumatera; INDONESIA; 0°57'S, 100°21'E; collected by S. Müller (1845, p. 86-89), 1836.

Müller (1845) published a body weight for one old lamp-black ("russschwarzes") male *agilis*, and, in the same report, also mentioned his observations of wild *agilis* near Padang: "In dem Urwalde der östlich hinter Padang gelegenen Gebirgskette, sah ich den Ungko oft die reifen Früchte einer *Bassia* verzehren, welche Baumart daselbst häufig sich findet…" (Müller, 1845, p. 89), but he did not explicitely state that the old male specimen was collected at the same locality. Hooijer (1960) published a detailed list of *agilis* specimens he examined, 16 of which were collected by S. Müller. Fifteen of these 16 specimens were collected at Padang; only one adult male was reported to originate from Batang Singalang (central Sumatera). Therefore, the old male specimen with known body weight was probably collected near Padang. A similar situation can also be observed with the siamang specimens collected by Müller (see below).

Tapanuli Bay. See Tapanuli, Teluk.

Tapanuli, Teluk; Sumatera; INDONESIA; 1°38'N, 98°45'E; collected by W.L. Abbott (Miller, 1903a, p. 438 and 482), 14-22 Feb., 1902.

Hylobates agilis albibarbis:

Batujurang, Tanjung; Kalimantan; INDONESIA; 2°37'S, 110°09'E; collected by W.L. Abbott (Lyon, 1911, p. 56 and 144), 17 June - 29 Sept., 1908.

Batu Jurong. See Batujurang, Tanjung

Kendawangan River. See Kendawangan, Sungai

Kendawangan, Sungai; Kalimantan; INDONESIA; 2°32'S, 110°12'E; collected by W.L. Abbott (Lyon, 1911, p. 54ff and 144), 17 June - 29 Sept., 1908.

Matan River. See Matan, Sungai

Matan, Sungai; Kalimantan; INDONESIA; 1°03'S, 110°06'E; collected by W.L. Abbott, (Lyon, 1911, p. 54 and 144), 6 June - 16 Sept., 1907.

Sukadana, altitude about 1000 - 2000 ft [305-610 m]; Kalimantan; INDONESIA; 1°15'S, 109°57'E; collected by W.L. Abbott (Lyon, 1911, p. 54 and 144), 6 June-16 Sept., 1907.

Hylobates agilis unko:

Batu ridial. See Baturijal.

Baturijal; Sumatera; INDONESIA; 0°31'S, 101°56'E; collected by G. Schneider (1905, p. 28, 55 and 63), Nov., 1898 - Feb., 1899.

Schneider (1905, p. 63) reported body weights of two specimens, but explicitly reported the exact locality of proveniance for only one of them. All his *H. agilis*-specimens were collected in the Indragiri area. In this study, both specimens of known body weight are assumed to originate from the same locality (i.e. Baturijal).

Indragiri River. See Indragiri, Sungai.

Indragiri, Sungai; Sumatera; INDONESIA; 0°22'S, 103°26'E; collected by W.L. Abbott (Miller, 1902, p. 159, erroneously identified as Hylobates hoolock), 21-26 Sept., 1901.

Kateman River. See Kateman, Sungai.

Kateman, Sungai; Sumatera; INDONESIA; 0°14'N, 103°37'E; collected by W.L. Abbott (Lyon, 1908, p. 625f and 675), Aug.-Sept., 1903.

Little Siak River; Sumatera; INDONESIA; 1°00'N, 102°08'E; collected by W.L. Abbott (Lyon, 1908, p. 625 and 675), Oct., 1906 - Feb., 1907. Coordinates from Groves (1972).

Salat Rupat; Sumatera; INDONESIA; 1°42'N, 101°30'E; collected by W.L. Abbott (Lyon, 1908, p. 622 and 675), 24 Feb. - 3 April, 1906. Coordinates from Groves (1972, p. 72).

Hylobates concolor

Hylobates concolor concolor:

Ailao Mountains. See Ailao Shan.

Ailao Shan; Yunnan Sheng; CHINA; ca. 23°15'N, 102°20'E; collector unknown (Dr. Ma Shilai, KIZ, in litt., 17 May, 1988).

Huanglian Mountain. See Lüchun.

Môc Châu: Lóng Sâp; Son La; VIETNAM; 20°51'N, 104°37'E (Môc Châu); collector unknown (Dao Van Tien, 1985, p. 167), 16 Nov., 1963.

Lóng Sâp. See Môc Châu.

Thuong Bang La; Van Chan; Hoàng Liên Son; VIETNAM; 21°25'N, 104°47'E; collector unknown (Dao Van Tien, 1985, p. 184), 4 Oct., 1963.

Lüchun [Xian]: Xinshuigoutou; altitude 1800 m; Yunnan Sheng; CHINA; ca. 23°02'N, 102°20'E (Lüchun Xian); collector unknown, 30 April or 1 May, 1972.

The collecting date recorded on the label attached to the skin differs from the date on the skull-box for the same specimen (KIZ 009643).

Xinshuigoutou. See Lüchun.

Hylobates concolor furvogaster:

Baoshan: Wayao (Gaoshan Production Brigade); Yunnan Sheng; CHINA; 25°28'N, 99°11'E; collector unknown (Fooden et al., 1987, p. 162), Oct., 1960.

Cangyuan [Vazu Zizhixian]: Menglai; altitude 2000-2400 m. Yunnan Sheng; CHINA; ca. 23°09'N, 99°15'E; collected by Wei Niluo, 19 Dec., 1960, and Li Jiaqiang, 25 Dec., 1983.

Hylobates concolor hainanus:

Bawanglin, altitude about 1000m; Hainan Dao; Guangdong Sheng; CHINA; 19°06'N, 109°04'E; collector unknown, 14 May, 1964. Altitude estimated by Prof. Liu Zhenhe, SCIEA (personal communication, 6 Sept. 1990).

Jiangfenlin, altitude about 1000m; Hainan Dao; Guangdong Sheng; CHINA; 18°42'N, 108°48'E (Jianfeng); collector unknown, 4 Dec., 1962. Altitude estimated by Prof. Liu Zhenhe, SCIEA (personal communication, 6 Sept. 1990).

Hylobates concolor cf. *hainanus*, sensu Dao Van Tien (1983):

Trùng Khánh: Khâm Thành; Cao Bang; VIETNAM; 22°50'N, 106°31'E (Trùng Khánh); collector unknown (Dao Van Tien, 1985, p. 38), 11 June., 1965.

Hylobates concolor jingdongensis:

Jingdong [Xian];, altitude 1840 m; Yunnan Sheng; CHINA; ca. 24°28'N, 100°54'E; collector unknown, 18 Nov., 1957.

Modaohe, altitude 2100 m; Jingdong [Xian]; Yunnan Sheng; CHINA; ca. 24°28'N, 100°54'E (Jingdong Xian); collector unknown, 9 Aug., 1964.

Wenbu. See Wenpu.

Wenpo. See Wenpu.

Wenpu, altitude 1800 m; Jingdong [Xian]; Yunnan Sheng; CHINA; 24°30'N, 100°45'E; collector unknown (Ma & Wang, 1986, p. 409), Oct., 1957. Coordinates from Haimoff (1986, p. 207; 1987, p. 321).

Hylobates hoolock

Hylobates hoolock hoolock:

Hatikhali, Cachar Hills; altitude 1600 ft [488 m]; ASSAM; 25°39'N, 93°06'E; collected by H.W. Wells; (Pocock, 1927, p. 733; 1939, p. 21), 1 Oct., 1920.

Hati Khali. See Hatikhali.

Hatikholi. See Hatikhali.

H'kamti. See Hkamti.

Hkamti; [westbank of] upper Chindwin River; altitude 500 ft [152 m]; Kachin State; BURMA; 25°21'N, 96°54'E; collected by G.C. Shortridge and S.A. Macmillan (Pocock, 1927, p. 733; 1939, p. 21; Wroughton, 1916), 26 July - 6 Aug., 1914.

Margharita. See Margherita.

Margherita; Naga Hills; altitude 1200 ft [366 m]; ASSAM; 27°17'N, 95°41'E; collected by H.W. Wells; (Hinton & Lindsay, 1926; Pocock, 1927, p. 733; 1939, p. 21), 29 Oct., 1919.

Nargharita. See Margherita.

Hylobates hoolock leuconedys:

Gokteik, altitude 2133 ft. (650 m); Shan State; BURMA; 22°21'N, 96°55'E; probably collected by G.C. Shortridge (Pocock, 1927, p. 733; 1939, p. 21). Altitude from Riley and Shortridge (1913, p. 711).

Goktiek. See Gokteik.

H'kamti. See Hkamti.

Hkamti; eastbank of upper Chindwin River; altitude 500 ft [152 m]; Kachin State; BURMA; 25°21'N, 96°54'E; collected by G.C. Shortridge and S.A. Macmillan (Pocock, 1927, p. 733; 1939, p. 21; Wroughton, 1916), 28 July, 1914.

Homalin; eastbank of upper Chindwin; altitude 400 ft [122 m]; Sagaing Division; BURMA; 24°52'N, 94°55'E; collected by G.C. Shortridge and S.A. Macmillan (Pocock, 1927, p. 733; 1939, p. 21; Wroughton, 1916), 16 July, 1914.

Nanyaseik; altitude 450 ft [137 m]; Kachin State; BURMA; 25°37'N, 96°36'E; collected by H.C. Raven, 8 Jan., 1935.

Tengchong Xian; CHINA; ca. 25°02'N, 98°28'E; collector unknown (Dr. Ma Shilai, KIZ, in lit., 17 May 1988).

Hylobates klossii

South Pagi Island. See Pagai Selatan, Pulau.

Pagai Selatan, Pulau; Sumatera; INDONESIA; ca. 3°00'S, 100°20'E; collected by W.L. Abbott (Miller, 1903b, p. 71), 13 Nov. - 15 Dec., 1902.

Hylobates lar

Hylobates lar carpenteri:

Angka. See Inthanon, Doi.

Ban Mae Lamao, altitude ca. 350 m; Changwat Tak; THAILAND; 16°48.5'N, 98°45'E; collected by J. Fooden (Fooden, 1971, p. 18 and 43f), 17-26 March, 1967. Coordinates from Fooden (1971, p. 18).

Chiang Dao, altitude 1400 ft [427 m]; Changwat Chiang Mai; THAILAND; 19°22'N, 98°58'E; collected by C.R. Carpenter and S.L. Washburn (Carpenter, 1940; Coolidge, 1937a; 1938; 1940; Schultz, 1937; 1944), 20 April - 24 May, 1937.

Chieng Dao. See Chiang Dao.

Doi Angka. See Inthanon, Doi.

Huai Kwang Pah, altitude ca. 300 m; Changwat Tak; THAILAND; 17°28'N, 98°50'E; collected by J. Fooden (1971, p. 18 and 43f), 28-30 March, 1967. Coordinates from Fooden (1971, p. 18).

Inthanon, Doi, altitude 4300-6500 ft [1311-1981 m]; Changwat Chiang Mai; THAILAND; 18°35'N, 98°29'E; collected by H.J. Coolidge, A.H. Schultz; S.L. Washburn (1937a; Coolidge, 1937b; 1938; 1940; Schultz, 1937; 1938; 1944), Feb.-April, 1937.

Altitudes: Several camps were used for collecting primates at Doi Angka (Doi Inthanon) and each camp was situated at a different altitude. Schultz (1937) recorded the collecting camp for each gibbon. Most gibbons were collected in the vicinity of Angka Camp 1, which was situated at 4300 ft [1311 m] (Schultz, 1937). Gibbons were also collected at Angka Camp 2 at 5000 ft (1524 m) and at Angka Camp 3, situated at about 6000 ft [1829 m] (Coolidge, 1937a, p. 6). Camp 4 was at 7000 feet on the top of the mountain, but "gibbons, macaques and langurs did not range this high; we saw the last at 6500 feet [1981 m]" (Schultz, 1938, p. 42). Several gibbons were collected at a locality called

"Angka ridge." This ridge is probably identical to the trail leading to Camp 4, described by Coolidge (1937a, p. 6) as "steep climb up a long wooded ridge". The gibbons from "Angka ridge" probably were collected at an altitude lying somewhere between that of Camp 3 (6000 ft) and the highest altitude for gibbons (6500 ft). In this study, the average of 6250 ft (1905 m) is used.

Hylobates lar entelloides, northern localities:

These localities possibly comprise a vast *entelloides/carpenteri* intergradation zone (see (Groves, 1972, p. 75f).

Ban Muang Baw Ngam, altitude ca. 1100 m; Changwat Kanchanaburi; THAILAND; 14°55'N, 98°55'E; collected by J. Fooden (1971, p. 14 and 43f), 11-23 Jan., 1967. Coordinates from Fooden (1971, p. 14).

Ban Nam Lai Tai, altitude ca. 300 m; Changwat Kamphaeng Phet; THAILAND; 16°10'N, 98°20'E; collected by J. Fooden (1971, p. 19 and 43f), 8-15 April, 1967. Coordinates from Fooden (1971, p. 19).

Ban Pong Nam Ron, altitude ca. 200-300 m; Changwat Kamphaeng Phet; THAILAND; 16°20'N, 98°18'E; collected by J. Fooden (1971, p. 19 and 43f), 8-15 April, 1967. Coordinates from Fooden (1971, p. 19).

Ban Tamrong Phato (= Ban Wang Phato), altitude ca. 100 m; Changwat Kanchanaburi; THAILAND; 14°54'N, 98°31'E; collected by J. Fooden (1971, p. 15 and 43f), 9-13 Feb., 1967. Coordinates from Fooden (1971, p. 15).

Chongkrong, altitude ca. 600-900 m; Changwat Kanchanaburi; THAILAND; 14°41'N, 98°52'E; collected by J. Fooden (1971, p. 14 and 43f), 26-29 Jan., 1967. Coordinates from Fooden (1971, p. 14).

Kata Taek, altitude ca. 200 m; Changwat Uthai Thani; THAILAND; 15°28'N, 99°23'E; collected by J. Fooden (1971, p. 17 and 43f), 27 Feb. - 10 March, 1967. Coordinates from Fooden (1971, p. 17).

Ko Keow, altitude ca. 200 m; Changwat Kamphaeng Phet; THAILAND; 15°57'N, 99°26'E; collected by J. Fooden (1971, p. 17 and 43f), 5-10 March, 1967. Coordinates from Fooden (1971, p. 17).

Lakya, altitude 1150 ft. [351 m]; and Lakya, 17 miles east of, altitude 1300 ft. (396 m); Tenasserim; THAILAND; ca. 16°10'N, 98°40.5'E; collected by A.S. Vernay, 19-22 Jan., 1924.

Locality not found; its coordinates are assumed here to be situated between those of Ta-ok Plateau and Umphang, because collections at all three localities were carried out within one

month, and because the date of collection for Lakya is intermediate between the dates for Ta-ok Plateau and Umphang. Jenkins (1990, p. 16) reports the coordinates of "c.12°N, 99'E" for the locality "Lakya, 17 miles E. of." If these coordinates were correct, Vernay, after having collected at Ta-ok Plateau until at least 13 Jan. 1924, would have had to travel more than 400km to the South in only 6 days in order to collect at Lakya on 19-22 Jan., only to travel back the same distance to the North in 6 days again in order to collect at Umphang on 28-31 Jan. 1924. Such a travel route is implausible and it appears unlikely that Vernay could have travelled that fast for such long distances in the forested areas of Thailand in 1924.

Lampha, altitude 1000 ft. (305 m); Kawthule State; BURMA; 16°18'N, 98°19'E; collected by A.S. Vernay, 30 Dec., 1923.

Ta-ok Plateau, altitude 3050-3200 ft. [930-975 m]; Kawthule State; BURMA; 16°19'N, 98°29'E; collected by A.S. Vernay, 1-13 Jan., 1924.

Toak Plateau. See Ta-ok Plateau.

UmPang. See Umphang.

Umphang, 28 miles east of, altitude 1750 ft. [533 m]; Changwat Tak; THAILAND; 16°01'N, 98°52'E (Umphang); collected by A.S. Vernay, 28-31 Jan., 1924.

Hylobates lar entelloides, central peninsular localities:

Baleih, Sungei; Tenasserim Division; BURMA; 10°28'N, 98°30'E; collected by W.L. Abbott (Ms. H. Kafka, USNM, in litt. 8 July 1989), 27-28 Nov., 1900.

Balik, Sungei. See Baleih, Sungei.

Bangtaphan [=Bang-taban]; THAILAND: "Siamese Province… at the eastern basis of the peninsula" (Keith, 1891, p. 77); not found; ca. 11°20'N, 99°20'E. Coordinates from Prof. A. Leemann, Geograph. Institute, Zürich University (pers. communication, 22 Aug. 1989). Keith (1891, p. 86) reports an average body weight of 12.5 lbs [5.67 kg] for three lar gibbons from Bangtaphan Province. In a later publication, Keith (1895, p. 296) presents individual body weights of four lar gibbons "obtained and examined in the jungle" (Keith, 1895, p. 284). Although he does not explicitly state that these gibbons were caught in Bangtaphan, this is probably the case, because the average body weight for the first three of the four specimens is exactly 12.5 lbs, suggesting that these specimens are identical to those of the former publication.

Bankachon; Tenasserim Division; BURMA; 10°09'N, 98°36'E; collected by G.C. Shortridge (Weitzel et al., 1988, p. 22; Wroughton, 1915, p. 696 and 699), 16 Dec., 1913 - 5 Jan., 1914.

Ban Thap Plik, altitude 75 m; Changwat Krabi; THAILAND; 8°11'N, 98°53'E; collected by J. Fooden (1976, p. 98 and 106), 3 June, 1973.

Champang; Tenasserim Division; BURMA; 10°13'N, 98°31'E; collected by W.L. Abbott (Ms. H. Kafka, USNM, in litt. 8 July 1989), 19 Dec., 1903. Coordinates from Fooden (1975, p. 140).

Champong. See Champang.

Maliwun, Victoria Point; Tenasserim Division; BURMA; 10°14'N, 98°37'E; collected by G.C. Shortridge (Weitzel et al., 1988, p. 22; Wroughton, 1915, p. 696), 6 Feb., 1914.

Meliwini. See Maliwun.

Red Point; Tenasserim Division; BURMA; 10°40'N, 98°30'E; collected by W.L. Abbott (Ms. H. Kafka, USNM, in litt. 8 July 1989), 18 Feb., 1904. Coordinates from Fooden (1975, p. 140).

Sungei Balik. See Baleih, Sungei.

Tanjong Badak; Tenasserim Division; BURMA; 10°00'N, 98°34'E; collected by W.L. Abbott (Ms. H. Kafka, USNM, in litt. 8 July 1989), 28 Dec., 1900. Coordinates from Groves (1972, p. 75).

Hylobates lar entelloides, southern peninsular localities:

Specimens from southern peninsular Thailand are considered belonging to *H. lar lar* by some authors (Groves, 1972; Groves, 1984, p. 74f; Weitzel et al., 1988, p. 13f), to *H. lar entelloides* by others (e.g., (Chivers, 1974, p. 330; Marshall & Sugardjito, 1986, p. 143f).

Trang; Changwat Trang; THAILAND; 7°33'N, 99°36'E; collected by W.L. Abbott (Ms. H. Kafka, USNM, in litt. 8 July 1989), 5 March - 31 Aug., 1896.

Trong. See Trang.

Hylobates lar lar:

Jambu Luang; Johor; WEST MALAYSIA; 2°14'N, 103°45'E; collected by W.L. Abbott (Ms.H. Kafka, USNM, in litt. 8 July 1989), 31 July - 1 Aug., 1901. Coordinates from Groves (1972, p. 74).

Rumpin River; Pahang; WEST MALAYSIA; 2°48'N, 103°17'E; collected by W.L. Abbott (Ms. H. Kafka, USNM, in litt. 8 July 1989), 8 June - 1 July, 1902. Coordinates from Groves (1972, p. 74).

Tanjong Malim, near, Altitude less than 50m; border of Perak and Selangor; WEST MALAYSIA, peninsular; ca. 3°41'N, 101°31'E; collected by D.J. Chivers (Chivers, in litt. 21 Dec., 1989, and personal communication, 5 April, 1991).

Tanjung Malim. See Tanjong Malim.

Hylobates lar vestitus:

Aru, Teluk; Sumatera; INDONESIA; 4°09'N, 98°12'E; collected by W.L. Abbott (Lyon, 1908, p. 620f and 673ff), 15 Nov., 1905 - 12 Feb., 1906.

Aru Bay. See Aru, Teluk.

Blangnanga, altitude 3600 ft [1097 m]; Sumatera; INDONESIA; 4°00'N, 97°00'E; collected by F.A. Ulmer, Jr. (Miller, 1942, p. 108 and 131), 29 March - 6 April, 1939. Coordinates from Groves (1972, p. 73).

Meluwak, altitude 1640 ft [500 m]; Sumatera; INDONESIA; 3°40'N, 97°45'E; collected by F.A. Ulmer, Jr. (Miller, 1942, p. 108 and 131), March, 1939. Coordinates from Groves (1972, p. 73).

Hylobates lar yunnanensis:

Menglian Co. [possibly near Lafu], altitude 2000 m; Yunnan Sheng; CHINA; 22°08'N, 99°25'E (Lafu); collector unknown (Ma & Wang, 1986, p. 410), 19 May, 1964. Coordinates from Fooden (1987, p. 162).

Although the locality "Lafu" is not recorded on the label of the adult specimen of known body weight (KIZ 03146), such is the case for a juvenile female (KIZ 03147) which was also collected in May 1964.

Hylobates leucogenys

Hylobates leucogenys leucogenys:

Hoi Xuân; Quan Hóa; Thanh Hoa; VIETNAM; 20°22'N, 105°07'E; collector unknown (Dao Van Tien, 1985, p. 197), 18 March, 1964.

Taxonomic identification of gibbons from Hoi Xuân has been somewhat controversial. For a brief review, see review in Geissmann (1989, p. 457).

Longlin; Mengla Xian; Yunnan Sheng; CHINA; ca. 21°33'N, 101°28'E; collector unknown (Ma & Wang, 1986, p. 405), 22(-24?) Dec., 1959. Coordinates from Ma and Wang (1986, p. 405)

Mengla [Xian]; Yunnan Sheng; CHINA; ca. 21°28'N, 101°35'E; collector unknown (Ma & Wang, 1986, p. 405), 10 Feb., 1958, and 8, May, 1959.

Quì Châu: Châu Bình; Nghê An; Nghê Tinh; VIETNAM; 19°33'N, 105°06'E (Quì Châu); collector unknown (Dao Van Tien, 1985, p. 228), 29-30 Nov., 1964.

Specimens from Quì Châu have variously been identified as *H. leucogenys siki* by (Dao Van Tien, 1983, p. 370), and as *H. l. leucogenys* in another publication by the same author (Dao Van Tien, 1985, p. 217). Because these specimens could not be examined for the present study, the latter of the two publications mentioned above will provisionally be followed here.

Hylobates leucogenys siki:

Tàn Ky: Nghia Dung; Nghê An; Nghê Tinh; VIETNAM; 19°03'N, 105°16'E (Tàn Ky); collector unknown (Dao Van Tien, 1985, p. 217f), 5-10 Dec., 1964.

Hylobates moloch

Bogor, near; Jawa, Pulau; INDONESIA; ca. 6°35'S, 106°47'E; collected by M. Weber (1890-91, p. 99).

Buitenzorg. See Bogor.

Java. See Jawa, Pulau.

Jawa, Pulau; INDONESIA; (no exact locality known; plotted together with specimen from previous entry); collected by "Prof. [W.A.] Mijsberg, Weltevreden, Batavia" (A.H. Schultz, unpublished notes housed in the Schultz Archives, Anthropological Institue of Zürich University); specimen sent to A. H. Schultz on 27 Jan., 1928.

Hylobates muelleri

Hylobates muelleri abbotti:

Kapuas River. See Kapuas, Sungai.

Kapuas, Sungai; below Tyan; Kalimantan; INDONESIA; 0°25'S, 109°40'E; collected by W.L. Abbott (Lyon, 1907, p. 547ff and 570), Sept., 1905.

Kuching, 10 miles south of; Sarawak; EAST MALAYSIA; 1°33'N, 110°20'E; collected by C.W. Beebe, 26 June, 1910.

Landak River. See Naya, Sungai.

Landak, Sungai. See Naya, Sungai.

Naya, Sungai; Landak, Sungai; Kalimantan; INDONESIA; 0°13'N, 109°52'E; collected by W.L. Abbott (Lyon, 1907, p. 547ff and 570), June-Aug., 1905.

Nya, Sungei. See Naya, Sungai.

Sarawak. See Kuching.

Sebangan River, Sibuyan (=Sebuyau) River, and near mouth of Sadeng River, Sarawak; EAST MALAYSIA; 1°15'-1°35'N, 110°45'-111°E; collected by F.S.Bourns (Ms. G.E. Nordquist, MMNH, in litt. 25 April 1988, and 17 Feb. 1989; (Timm & Birney, 1980, p. 568), 6 April, 1893. Coordinates from Timm (1980, p. 568).

Sibuyau River. See Sebuyau, Sungai.

Sebuyau, Sungai, Sarawak; EAST MALAYSIA; ca. 1°3'N, 111°14'E; collected by W.T. Hornaday (Hornaday, 1894, p. 419), 3 Nov., 1878. Coordinates estimated with map in Hornaday (1894).

Hylobates muelleri funereus:

Abai; Sabah; EAST MALAYSIA; 5°42'N, 118°23'E; collected by S.L. Washburn and A.H. Schultz (Coolidge, 1940, p. 124 and 129), 14 June - 26 July, 1937. Coordinates from Fooden (1975, p. 125).

Kalabakan. See Tibas, Sungai.

Kinabalu, Mount. See Lumu Lumu.

Kretam Kechil, Sungai; Sabah; EAST MALAYSIA; 5°30'N, 118°33'E; collected by D.D. Davis (1962, p. 126), 11 May - 6 June, 1950.

Little Kretam River. See Kretam Kechil, Sungai.

Lumu Lumu, altitude ca. 4500 ft [1372 m]; Sabah; EAST MALAYSIA; 6°02'N, 116°34'E; collected by Labuan or by J.A. Griswold, Jr. (Allen & Coolidge, 1940, p. 148; Coolidge, 1940, p. 123 and 129; Griswold, 1939a; Griswold, 1939b), 8 July, 1937. Coordinates from Fooden (1975, p. 131).

According to inventory cards at MCZ, the only gibbon specimen from this locality was collected by Labuan, Griswold's guide (Griswold, 1939a, p. 411), whereas only Griswold is mentioned by Allen and Coolidge (1940, p. 148), and Coolidge (1940, p. 123 and 129).

Seliman, Sungai, 13th mile; Sabah; EAST MALAYSIA; ca. 4°25'N, 116°26'E (Allen & Coolidge, 1940, p. 148).

The locality record on the inventory card for specimen (MCZ 35881) at the MCZ says "B.N. Borneo, 13th mile (?); Sliman " (Ms. M.E. Rutzmoser, MCZ, in litt. 29 April 1988), but Allen and Coolidge (1940, p. 148) report "S.E. Borneo" as the locality for the same specimen. The specimen was bought from the Sarawak Museum on 21 Jan., 1926 (Ms. M.E. Rutzmoser, MCZ, in litt. 29 April 1988), and it's coloration resembles that of *H. muelleri abbotti* according to Marshall and Sugardjito (1986, p. 145, their locality No. 21). The latter authors identify the locality as Sungai Seliman; their opinion is followed here.

Sliman. See Seliman, Sungai.

Tibas, Sungai; Tawau Resid.; Sabah; EAST MALAYSIA; 4°26'N, 117°29'E; collected by R.F. Inger (Davis, 1962, p. 127), 19 June, 1956. Coordinates from Davis (1962, p. 127).

Hylobates muelleri muelleri:

Balik Papan Bay. See Balikpapan, Teluk.

Balikpapan, Teluk; Kalimantan; INDONESIA; 1°15'S, 116°43'E; collected by W.L. Abbott, (Lyon, 1911, p. 59 and 144), 1 Feb. - 24 Feb., 1909.

Klumpang Bay. See Klumpang, Teluk.

Klumpang, Teluk; Kalimantan; INDONESIA; 3°00'S, 116°12'E; collected by W.L. Abbott, (Lyon, 1911, p. 144), 8 Jan. - 13 March, 1908; and 18-19 April, 1909.

Pangkallahan River; Kalimantan; INDONESIA; 2°50'S, 116°10'E; collected by W.L. Abbott (Lyon, 1911, p. 57f and 144), 6 June-16 Sept., 1908. Coordinates estimated from map in Lyon (1911, p. 57).

Pasir River. See Pasir, Sungai.

Pasir, Sungai, altitude about 1000 - 2000 ft [305-610 m]; Kalimantan; INDONESIA; 1°53'S, 116°21'E; collected by W.L. Abbott (Lyon, 1911, p. 58 and 144), 31 Dec., 1908 - 22 Jan., 1909.

Hylobates pileatus

No locality has been provided for the gibbon specimens (including four adult *H. lar* and two adult *H. pileatus*) reported upon by Keith (1895, p. 296), but his observations on brain [and body] weights were "made on animals obtained and examined in the jungle" (Keith,

1895, p. 284), probably in Thailand, as were his observations reported in an earlier publication (Keith, 1891, p. 77). From 1889-1892, Keith was in the Bangtaphan Province (not found in the Gazetteer of Thailand (U.S. Board on Geographic Names, 1966a), during which time he dissected, among others, 9 gibbons (Keith, 1940).

Hylobates syndactylus

Hylobates syndactylus syndactylus:

Body weights of wild-caught siamangs are known for the Sumatran subspecies only; no body weights were found for *H. syndactylus continentis* from West Malaysia.

Aru Bay. See Aru, Teluk.

Aru, Teluk; Sumatera; INDONESIA; 4°09'N, 98°12'E; collected by W.L. Abbott (Lyon, 1908, p. 620f and 675); Dr. R. Thorington, USNM, in litt., undated, 1988), 18 Nov. - 23 Dec., 1905.

Kungke, altitude 3200 ft [975 m]; Atjeh; Sumatera; INDONESIA; 3°45'N, 97°40'E; collected by F.A. Ulmer, Jr. (Miller, 1942, p. 108 and 132), March, 1939. Coordinates from Groves (1972, p. 73).

Padang; Sumatera; INDONESIA; 0°57'S, 100°21'E; collected by S. Müller (1845, p. 86-89), ca 1836.

Müller (1845, p. 82) published body weights for two siamangs (*H. syndactylus*), and, in the same report, also mentioned his observations of wild siamangs near Padang: "Zu Anfang des Monats April 1836 traf ich, in den Küstenbergen südlich Padang, einige Mal mehrere Weibchen dieses Affen beieinander an, wovon jedes ein Junges am Vorderleibe hängen hatte, die ungefähr einen Monat alt gewesen sein mochten." (Müller, 1845, p. 83), but he did not explicitly state that two specimens of known body weight were collected at the same locality. Hooijer (1960, p. 3ff) published a detailed list of siamang specimens he examined, nine of which were collected by S. Müller. Eight of these nine specimens were collected at Padang; only one adult male was reported to originate from Batang Singalang (central Sumatera). Therefore, the two specimens with known body weight were probably collected near Padang. A similar situation can also be observed with the *H. agilis* specimens collected by Müller (see above).

Padang; Sumatera; INDONESIA; 0°57'S, 100°21'E; collector unknown (Dr. J. Sugardjito, in litt., undated, 1988), 12 Jan., 1837.

Probably collected by S. Müller, who collected in Padang during several years, also in 1937 (see list of Müller's siamang (*H. syndactylus*) specimens in Hooijer (1960, p. 3ff)).

Paninggahan. See Paninjawan.

Paninjawan; Sumatera; INDONESIA; ca. 0°41'S, 100°39'E; collected by M. Weber (1890-91, p. 100).

Locality "Paninggahan" not found, but probably identical with Paninjawan (0°41'S, 100°39'E). Coordinates of other collecting localities of M. Weber on Sumatera are clustered around 0°18'S-0°48'S and 100°14'E and 100°58'E (Weber, 1890-91,: e.g. Kaju Tanam, Manindjau, Sidjungdjung, Singkarah, Solok). Therefore, it appears reasonable to assume that Paninggahan is situated in the same region. The median coordinates of Weber's other collecting localities mentioned above (0°41'S, 100°36'E) are virtually identical with the coordinates of Paninjawan.

Tapanuli Bay. See Tapanuli, Teluk.

Tapanuli, Teluk; Sumatera; INDONESIA; 1°38'N, 98°45'E; collected by W.L. Abbott (Miller, 1903a, p. 438 and 482f,, 1903 #23, p. 71; Weitzel et al., 1988, p. 36), 23-28 Feb., 1902.

Tarussan Bay. See Tarusan, Teluk.

Tarusan, Teluk; Sumatera; INDONESIA; 1°13'S, 100°25'E; collected by W.L. Abbott (Dr. R. Thorington, USNM, in litt., undated, 1988), 30 Dec., 1904 - 3 Jan., 1905.

Appendix 10.11: "Non-communicatory" Characteristics of Gibbons

Abbreviations: agi.= *H. agilis agilis* (& *H. a. unko*); alb.= *H. a. albibarbis*; lar= *H. lar*; mol.= *H. moloch*, abb.= *H. muelleri abbotti*; fun.= *H. m. funereus*; mu.= *H. m. muelleri*; pil.= *H. pileatus*; klo.= *H. klossii*, hoo.= *H. hoolock*; con.= *H. concolor*; leu.= *H. leucogenys leucogenys* (& *H. l. siki*); gab.= *H. l. gabriellae*; syn.= *H. syndactylus*; anc.= hypothetical ancestor; ?= missing data.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
Skull morphology (data from (Groves, 1972; Marshall & Sugardjito, 1986):															
67	Cranial vault: low=0, high=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
68	Facial profile: sinuous=0, straight=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
69	Orbital rim: thick=0, flat=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
70	Cranio-pharyngeal canal, persistence of: >10%=0, <10%=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Dentition (data from (Frisch, 1965; Frisch, 1973):															
71	Cingulum reduction: not pronounced=0, moderate=1, strong=2.														
	2	?	1	0	1	1	1	0	1	2	0	0	0	1	0
72	Lower M3 Reduction: not pronounced=0, moderate=1, strong=2.														
	2	?	0	0	2	2	2	0	2	0	1	1	1	0	0
73	Upper M3 Reduction: not pronounced=0, moderate=1, strong=2.														
	2	?	0	0	?	2	1	0	2	1	1	1	1	0	0
74	Metaconid shift: not pronounced=0, moderate=1, strong=2.														
	2	?	2	1	2	2	2	1	1	0	0	0	0	1	0
75	Hypoconid shift: not pronounced=0, moderate=1, strong=2.														
	2	?	1	1	2	2	2	0	2	0	1	1	1	1	0
76	Dryopithecus pattern: present=0, modified=1.														
	1	?	1	0	1	1	1	1	0	1	0	0	0	0	0

Appendix 10.11: Continued.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
Postcranial and soft parts anatomy (data from (Groves, 1972; Schultz, 1933) and own unpublished observations):															
77	Thoracical vertebrae: <14=0, 14=1.														
	0	0	0	0	0	0	0	?	0	0	1	1	1	0	0
78	Cocygeal vertebrae: >3=0, 3=1.														
	1	1	1	1	1	1	1	?	0	0	1	1	1	1	0
79	Brachial index: <110=0, >110=1.														
	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0
80	Intermembral index: >135=0, <135=1.														
	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
81	Relative length of first digit: relatively long=0, relatively short=1.														
	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0
82	Throat sac: absent=0, small/sometimes present=1, large=2.														
	0	0	0	0	0	0	0	0	0	1	1	1	?	2	2
83	Nasal septum: long-narrow=0, long-broad=1, short-broad=2.														
	2	2	2	2	2	2	2	2	1	1	0	0	0	1	?
84	Ear form: Lower border free=0, fused=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
85	Os clitoridis: absent=0, present=1.														
	?	?	0	?	?	?	?	0	?	1	?	1	?	1	1
86	Scrotum: semi-pendulous scrotum=0, postpenial pouches=1, pre/parapenial pouches=2.														
	2	2	2	2	2	2	2	2	2	2	0	0	0	1	?
87	Interdigital webbing: rare, <20%=0, frequent, >50%=1.														
	0	0	0	0	0	0	0	0	1	0	0	0	0	1	?
88	Hair density: sparse=0, dense=1.														
	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Karyology (data from (Liu et al., 1987; Prouty et al., 1983b; Stanyon et al., 1987; van Tuinen & Ledbetter, 1983):															
89	2n: 38=0, 44=1, 50=2, 52=3.														
	1	1	1	1	1	1	1	1	1	0	3	3	3	2	?
90	Accrocentrics: 0=0, 2=1, 6=2.														
	0	0	0	0	0	0	0	0	0	0	2	2	2	1	?

Appendix 10.11: Continued.

Char. no.	agi.	alb.	lar	mol.	abb.	fun.	mu.	pil.	klo.	hoo.	con.	leu.	gab.	syn.	anc.
91	NOR on Y chromosome: absent=0, present=1.														
	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
92	Long arm of HAG1: absent=0, present=1.														
	1	?	?	?	?	?	?	?	?	?	?	0	?	0	1

Appendix 10.12: Data Matrix for Phylogenetic Evaluation

This data matrix combines the data presented in Appendices 10.2, 10.5, 10.6, and 10.11. The matrix has 15 taxa and 92 characters. The hypothetical taxon "ancestor" is used as outgroup.

Missing data are identified by "?"

All characters are ordered, except 63, 89, and 90, which are unordered.

The data can be divided into the following subsets of characters: 1-29: Vocal communication; 30-33: olfactory communication; 34-66: visual communication; 67-70: skull morphology; 71-76: dentition; 77-88: postcranial skeleton and soft parts anatomy; 89-92: karyology.

Data matrix:

Taxon	Character No.																														
										1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
agilis	1	1	1	1	0	0	0	0	2	1	1	0	1	1	0	0	1	1	0	0	1	0	1	1	1	3	2	1	0	0	0	?
albibarbis	1	1	1	1	0	0	0	0	2	1	1	0	1	1	0	0	1	1	0	0	1	0	1	1	1	3	2	1	0	0	0	?
lar	1	1	2	1	0	0	2	0	0	1	1	0	1	1	0	0	1	1	0	0	1	0	1	1	1	2	1	1	0	0	0	?
moloch	0	1	1	2	0	0	0	1	1	0	1	0	0	0	1	1	0	?	0	0	1	2	1	1	1	1	1	1	0	0	0	?
abbotti	1	1	1	1	0	0	1	2	0	0	1	0	0	0	2	0	1	1	0	0	1	2	1	1	1	3	2	1	0	0	0	?
funereus	1	1	1	1	0	0	1	2	0	0	1	0	0	0	2	0	1	1	0	0	1	2	1	1	1	3	2	1	0	0	0	?
muelleri	1	1	1	1	0	0	1	2	0	0	1	0	0	0	2	0	1	1	0	0	1	2	1	1	1	3	2	1	0	0	0	?
pileatus	1	1	2	1	0	0	0	2	2	0	1	0	0	0	2	0	1	0	0	0	1	1	0	0	0	2	1	1	0	0	0	1
klossii	0	1	1	2	0	0	0	2	0	0	1	0	0	0	2	1	0	?	1	0	1	2	0	0	0	3	3	1	0	?	0	?
hoolock	2	1	2	1	0	0	0	0	2	2	0	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	?
concolor	2	0	?	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	1	2	0	0	0	0	0	0	2	1	1	0	?
leucogenys	2	0	?	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	1	2	0	0	0	0	0	0	2	1	1	0	0
gabriellae	2	0	?	0	0	1	0	2	0	0	0	1	0	0	1	0	1	1	0	1	2	0	0	0	0	0	0	2	1	1	0	?
syndactylus	2	1	2	1	2	0	0	2	0	0	0	0	1	0	1	1	2	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1
ancestor	2	?	?	?	2	?	0	2	2	2	?	?	0	0	1	?	1	1	0	0	0	0	?	?	?	?	?	?	?	0	1	1

Appendix 10.12: Continued.

Taxon	Character No.																														
	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	6	6	6	6	6
	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
agilis	0	2	1	2	0	1	1	1	0	1	0	1	1	1	1	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1
albibarbis	0	2	2	2	1	1	1	1	0	1	0	1	1	2	2	0	0	2	2	2	2	0	0	2	2	0	0	2	1	1	0	0
lar	0	2	2	2	2	2	2	2	2	2	0	0	0	1	1	1	1	1	1	1	1	3	3	0	0	1	1	0	0	0	0	1
moloch	0	2	2	1	1	2	2	1	1	1	0	1	1	1	1	0	0	1	1	2	2	0	0	0	0	1	1	0	0	0	0	0
abbotti	0	2	2	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	1	2	2	0	0	0	0	2	2	0	0	0	0	0
funereus	0	2	2	1	1	1	1	1	1	1	0	0	0	2	2	0	0	2	2	2	2	1	1	1	1	2	2	0	0	0	0	0
muelleri	0	2	2	1	1	1	1	1	1	1	0	0	0	2	2	0	0	2	2	2	2	0	0	2	2	2	2	0	0	2	0	0
pileatus	0	2	1	2	0	2	0	2	0	2	0	2	2	2	2	0	0	2	2	0	2	2	2	0	0	0	0	2	0	0	1	0
klossii	?	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	2	2	0	0	0	0	2	2	2	2	0	0	0	0	0
hoolock	0	2	2	0	2	0	2	0	2	0	2	0	0	2	0	0	0	2	1	0	2	0	1	2	0	1	0	1	2	2	2	0
concolor	1	0	0	0	0	0	0	0	0	0	1	1	0	2	2	2	1	2	1	0	2	0	0	2	1	2	1	0	0	2	2	0
leucogenys	1	0	2	2	2	2	2	0	2	0	2	1	0	2	2	3	1	2	0	0	2	0	0	2	1	2	1	0	0	2	2	0
gabriellae	1	0	1	2	1	2	1	0	1	0	1	1	0	2	2	2	1	0	0	0	2	0	0	2	2	2	2	0	0	2	2	0
syndactylus	0	1	1	0	0	0	0	0	0	0	0	0	0	2	2	0	0	2	2	0	0	0	0	2	2	2	2	0	2	0	0	0
ancestor	0	2	2	2	2	2	2	2	2	2	0	?	?	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 10.12: Continued.

Taxon	Character No.																										
	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9
	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
agilis	0	0	0	0	0	0	2	2	2	2	2	1	0	1	1	1	1	0	2	0	?	2	0	1	1	0	0	1
albibarbis	0	0	0	0	0	0	?	?	?	?	?	?	0	1	1	1	1	0	2	0	?	2	0	1	1	0	0	?
lar	0	0	0	0	0	0	1	0	0	2	1	1	0	1	1	1	1	0	2	0	0	2	0	1	1	0	0	?
moloch	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0	2	0	?	2	0	1	1	0	0	?
abbotti	0	0	0	0	0	0	1	2	?	2	2	1	0	1	1	1	1	0	2	0	?	2	0	1	1	0	0	?
funereus	0	0	0	0	0	0	1	2	2	2	2	1	0	1	1	1	1	0	2	0	?	2	0	1	1	0	0	?
muelleri	0	0	0	0	0	0	1	2	1	2	2	1	0	1	1	1	1	0	2	0	?	2	0	1	1	0	0	?
pileatus	1	0	0	0	0	0	0	0	0	1	0	1	?	?	1	1	1	0	2	0	0	2	0	1	1	0	0	?
klossii	0	0	0	0	0	0	1	2	2	1	2	0	0	0	1	1	0	0	1	0	?	2	1	0	1	0	0	?
hoolock	1	1	0	0	0	0	2	0	1	0	0	1	0	0	0	1	1	1	1	0	1	2	0	0	0	0	0	?
concolor	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	0	1	1	0	1	?	0	0	0	3	2	1	?
leucogenys	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	0	1	1	0	1	1	0	0	0	3	2	1	0
gabriellae	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	0	1	?	0	1	?	0	0	0	3	2	1	?
syndactylus	0	2	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	2	1	0	1	1	1	0	2	1	1	0
ancestor	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	?	0	1	?	?	0	?	?	0	1

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12. Curriculum Vitae

Am 28. Oktober 1957 wurde ich, Thomas Geissmann, Bürger von Hägglingen, in Aarau geboren. Dort besuchte ich von 1964 bis 1968 die Primarschule, von 1968 bis 1973 die Bezirksschule, und 1973 bis 1977 die Kantonsschule Aarau, die ich mit der Matura (Typ B) abschloss.

Im Herbst 1977 immatrikulierte ich mich an der Philosophischen Fakultät II der Universität Zürich. Von 1982 bis 1983 verbrachte ich einen einjährigen Forschungsaufenthalt als Gast am Max-Planck-lnstitut für Verhaltensphysiologie in Seewiesen, Deutschland. Das Diplom als Naturwissenschafter erwarb ich 1984 mit dem Hauptfach Anthropologie und den Nebenfächern Ethologie und Zoologie.

Während meines Studiums besuchte ich Vorlesungen und Kurse bei folgenden Dozenten: K. Akert, A. Anzenberger, G. Bächli, R. Bachofen, E. Batschelet, J. Biegert, M. Birnstiel, E. Brun, H. Burla, E. Butenandt, P.S. Chen, P. Christen, C.D.K. Cook, M. Cuénod, A. Dübendorfer, C.H. Eugster, H. Fischer, D. Glaser, P. Groscurth, R. Hantke, H.S. Herzka, H.R. Hohl, H. Hotz, J.R. Huber, R. Humbel, K.A. Hünermann, R. Hunsperger, J. Kägi, R.F. Keller, E.A. Koller, S. Kubik, H. Kummer, R.D. Martin, M. Müntener, B. Nievergelt, H.R. Oswald, M. Primas, D. Rast, J. Rickenbacher, H. Rieber, O. Rieppel, M. Roy, W. Scheffrahn, H. Scheier, P. Schmid, W. Schmid, G. Schmidtchen, K. Schneider, E. Stammbach, A. Steiner, P. Tardent, K. Theiler, D.C. Turner, G. Wagniere, H. Wanner, R. Wehner, C. Weissmann, J. Wellauer, O. Woodtli, W. Zenker, V. Ziswiler.

Seit 1986 arbeitete ich am Anthropologischen Institut der Universität Zürich an der vorliegenden Dissertation unter der Leitung von Prof. Dr. R.D. Martin. Von 1986 bis 1987 war ich Stipendiat der A. H. Schultz-Stiftung. Zur Zeit bin ich immatrikulierter Student der Universität Zürich und bereite eine Postdoktoratsstudie über die Erhaltungsbiologie der Schopfgibbons vor.