Portland State University

1988

Gibbon classification : the issue of species and subspecies

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Recommended Citation

Osterud, Erin Lee, "Gibbon classification : the issue of species and subspecies" (1988). *Dissertations and Theses.* Paper 3925.
https://doi.org/10.15760/etd.5809

AN ABSTRACT OF THE THESIS OF Erin Lee Osterud for the Master of Arts in Anthropology presented July 18, 1988.

Title: Gibbon Classification: The Issue of Species and Subspecies.

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Gibbon classification at the species and subspecies levels has been hotly debated for the last 200 years. This thesis explores the reasons for this debate. Authorities agree that siamang, concolor, kloss and hoolock are species, while there is complete lack of agreement on lar, agile, moloch, Mueller's and pileated. The disagreement results from the use and emphasis of different character traits, and from debate on the occurrence and importance of gene flow.

GIBBON CLASSIFICATION:

THE ISSUE OF SPECIES AND SUBSPECIES

by

ERIN LEE OSTERUD

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF ARTS
in
ANTHROPOLOGY

Portland State University

1989

TO THE OFFICE OF GRADUATE STUDIES:

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ACKNOWLEDGEMENTS

Without the assistance of many people, this thesis would still be a proposal. Marc Feldesman gave me the idea for this thesis, and was incredibly helpful and patient in seeing it to its conclusion. Thank you. I also would like to thank the members of my committee - Ken Ames, Debbie Duffield and Roger Jennings. All of your comments and time are appreciated. Special thank you's are for Mark Wilson, Tom Gordon and Neil Smith. These three provided access to the Emory University Medical Library, the Yerkes Library, and private collections. Finally, I have to thank my husband, David Fleming, who said, "just do it!"

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INTRODUCTION

In the 200 years since Linnaeus classified gibbons, many researchers have created new classifications for them. The early classifications resulted primarily from the discovery of previously unknown gibbon populations. In recent decades, no new gibbon populations have been discovered, yet new classifications are still being proposed. For instance, von Koenigswald (1967) proposed five gibbon species, while Elliot (1913) saw no fewer than 12. The number of subspecies varies directly with the number of proposed species. Why is there so much variation in gibbon classification at the species and subspecies levels?

This thesis explores the reasons why this variation exists. Why is there consensus that *siamang*, *concolor*, *klossii* and *hoolock* gibbons are species, while there is complete lack of agreement on *lar*, *agilis*, *moloch*, *muelleri* and *pileatus*? Are they subspecies of *lar* or are they species? The disagreement is a result of one or a combination of the following: definition of terms, the use of different classificatory methods combined with varying theoretical backgrounds, and/or the taxonomic relevance of certain traits.

HISTORY OF GIBBON CLASSIFICATION

Early gibbon classification (1771 - 1903) consisted of descriptions and the naming and renaming of taxa. The confusion surrounding classification during these years was caused by the small number of gibbons available to researchers. For instance, hoolock undergoes changes in pelage color at one year for both males and females and again for females when they reach sexual maturity. Many researchers only observed animals of a particular age; the result was the renaming of hoolock at least three times (Groves 1972). Another problem was location. Every time gibbons were discovered in a new geographic area, they received a new name. Researchers have repeatedly renamed both concolor and lar for this reason.

After 1903, no new species or 'key' subspecies were described (Groves 1972)(see Table I). The only new information was an extension of the geographic range of the white-handed gibbon (lar) (Carpenter 1939), and the naming and diagnosis of this population (Groves 1968).

MODERN GIBBON CLASSIFICATION

According to Groves (1972), 'modern' gibbon classification began with Pocock's work (1927). Pocock divided gibbons into three 'non-siamang' species (concolor, hoolock and lar); all other gibbon groups became subspecies. Kloss (1929) believed Pocock named too few species. Kloss added

Table I

MAJOR CLASSIFICATORY NAMES FOR GIBBONS
1771 - 1903

Date	Name	Probable Status	Author
1771	*Homo lar*	*H. lar*	Linnaeus
1809	*P. varius*	*H. lar*	Latrielle
	P. variegatus	*H. lar*	Latrielle
1812	*P. lar*	*H. lar*	*E. St. Hilare
1821	*H. agilis*	*H. agilis*	*Cuvier
1826	*Simia concolor*	*H. concolor*	Harlan
1834	*H. hoolock*	*H. hoolock*	Harlan
	H. fuscus	*H. h. leuconedys*	*Lewis
1840	*H. leucogenys*	*H. c. leucogenys*	Ogilby
	H. syndactylus	*S. syndactylus*	*Lesson
1841	*H. muelleri*	*H. muelleri*	Martin
	H. leuciscus	*H. moloch*	Martin
1861	*H. pileatus*	*H. pileatus*	Gray
1876	*H. henrici*	*H. c. leuconedys*	de Pousargues
1884	*H. nasutus*	*H. c. concolor*	*Kunckel
1892	*H. hainanus*	*H. c. hainanus*	Thomas
1903	*S. klossi*	*H. klossi*	Miller

P. = *Pithecus* *H.* = *Hylobates* *S.* = *Symphalangus* *h.* = *hoolock*
c. = *concolor* * From Elliott 1913
See Table VIII for current classificatory names

agilis, klossii and placed syndactylus within Hylobates. He also added several subspecies.

Sody (1949) combined Kloss' cinerus (moloch) with lar, but he kept agilis separate. Delacour (1951) rearranged the supposed races of H. concolor. Simonetta (1957) summarized gibbon classification in 1957, suggesting two new subgenera - Brachitanytes for klossii and Nomascus for concolor. Napier and Napier (1967) updated Simonetta's work with one major difference -- they recognized H. moloch as a full species.

In the 1980s renewed interest in gibbon classification produced new, more complicated classifications, using a wider variety of information.

Groves (1984) proposed one species for Symphalangus, one for Nomascus (with possibly two more) and six for Hylobates. Within Hylobates Groves includes the species klossii, hoolock and lar and believes others may be pulled from the lar group and elevated to the species level. He believes that pileatus, agilis (subspecies - agilis, albibarbis and muelleri) and lar (subspecies - vestitus, lar, entelliodes and carpenteri) are semispecies (a group that has not acquired all of the attributes of species rank, or a borderline case between a species and subspecies [Mayr 1969]) within the superspecies (a monophyletic group made up of almost or completely allopatric species [Mayr 1969]) of lar, and that moloch is a morphospecies (a species recognized solely on the basis of its morphology [Mayr 1969]).

Srikosamatara (1984) elevates *pileatus* to the species level, and Marshall et al. (1984) add *muelleri* to *Hylobates*. Groves (1984) does not concur with species status for *muelleri*. Haimoff et al. (1984) also recognize *pileatus* as a species, but list *moloch* as a subspecies, and *muelleri*, *agilis* and *lar* as races. Creel and Preuschoft (1984) believe there are five species - *syndactylus*, *klossii*, *hoolock*, *concolor* and *lar*. They believe *pileatus*, *agilis*, *moloch*, *lar* and *muelleri* are subspecies of the *lar* species.

AREAS OF POSSIBLE DISAGREEMENT

Species and Subspecies

Clearly, terms such as species and subspecies may be defined differently, and may, in turn, be used to create dissimilar classifications. These certainly are central issues in gibbon classification because hybrid zones exist between wild populations of *lar* and *agilis*, *lar* and *pileatus*, and *muelleri* and *agilis*.

Methods

There are three methods of classification - phenetic, cladistic and evolutionary. In phenetic classification (numerical taxonomy) taxa are grouped in a hierarchical form using clusters. These clusters are based on overall similarity alone, and do not always correlate well with the recency of common ancestry (Gould 1981). Cladistics or phylogenetic systematics generate parsimonious trees (cladograms) that minimize parallel, convergent and reversed evolution of character states (Creel and Preuschoft 1984). Cladistics is based on overall differences alone (Gould 1981). Evolutionary classification looks at the similarities and differences among organisms, and evaluates the similarities and differences after considering the inferred evolutionary history of the organism (Mayr 1981). Inferred histories are often misleading because they often are based on conjecture rather than actual data.

Overall, the three approaches yield congruent classifications except when taxa are closely related, which is especially true of gibbons. Which, then, is best suited for dealing with closely related taxa?

Traits

While definitions and methodological differences may be obstacles to a uniform taxonomy, the problem also may involve the traits used to create classifications. Are gibbons somehow unique? This may be possible; however it is unlikely since the classification of baboons is contested for similar reasons (Szalay and Delson 1979). Again, the problem comes down to closely related taxa. Some authorities, using primarily morphological traits, insist that *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* are subspecies under the species *lar* (Creel and Preuschoft 1984). Other authorities believe they are full species based primarily on pelage and song patterns (Marshall and Sugardito 1986). But Sokal and Sneath (1963) warn that evidence based on too few characters may give an inaccurate picture of overall similarity among taxa.

Researchers weight traits differently. Some researchers weight characters equally, while others weight them unequally. Sokal and Sneath (1963) criticize the unequal weighting of characters because it presumes one trait is more important than another. For example, are pelage traits more important then morphological ones? Unequal weighting leads to the use of certain characters for the species of one genus, while these same characters are ignored in the next genus. The arbitrary assignment of importance may led to artificial taxa. Misclassification also may result because an organism is aberrant in one aspect and similar in others (Sokal and Sneath 1969). Mayr believes some weighting is valuable. Some characters should be given high weight because the characters are consistently reliable "...in permitting predictions as to association with other characters and as to the assignment of previously unknown species" (Mayr 1969:219). Lower weight should be given to characters that are variable because they are poor indicators of relationship.

Classification

Does the present system of classification attempt too much? Taxonomists try to classify, to name, to indicate degrees of affinity and to show relationship by descent for organisms. To accomplish this they must demonstrate that 1) taxa have affinity (how much they resemble one another); that 2) characters are homologous; and that 3) taxa share a common line of descent (characteristics that shared in common origin) (Sokal and Sneath 1963).

For gibbons, recent speciation and the absence of a fossil record complicate classification (Creel and Preuschoft 1984). A complete fossil record could help sort out the relationships among lar, agilis, moloch, muelleri and pileatus.

The potential problems stated above need to be addressed before an adequate classification can be completed. Gibbons are one of man's closest relatives, and we need to understand gibbon classification, morphology, behavior, fossil history, ecology and character traits to help us better understand these same things in man. For example, gibbons are an excellent model for interpreting man's social evolution through family structure. Therefore, the purpose of this thesis is to discuss why and where problems exist, and to suggest requirements for an acceptable classification of gibbons.

SUMMARY

All authorities agree that syndactylus, klossii, hoolock and concolor are species. However, there is major disagreement about the status of *lar*, *moloch*, *muelleri*, *agilis* and *pileatus*. Authorities also agree that the three classification methods result in similar classifications except when trying to resolve closely related taxa. Debate about the relevance of taxonomic traits, and especially the weighting of characters is ongoing, and interbreeding in the wild confounds the problem. Therefore, I have chosen to concentrate on the species issue, especially as it relates to the problems of *lar*, *moloch*, *muelleri*, *agilis* and *pileatus*. Problems in classification at this level are far from being resolved.

CHAPTER II

CLASSIFICATION

This chapter contains a discussion of the definition of species, which is an important issue in gibbon classification because of hybridization in the wild, and a synopsis of the major methods of classification.

SPECIES DEFINITIONS

The wording and definitions applied to species do not appear to vary considerably from investigator to investigator. The definition of a biological species is that natural groups that are actually or potentially interbreeding must be reproductively isolated from other such groups (Simpson 1961:150; Mayr 1969:26). The definition of an evolutionary species is that a single lineage of ancestor-descendant populations evolve separately from one another and have their own evolutionary role and historical tendencies (Simpson 1961:153; Wiley 1981:25). Simpson believes the evolutionary definition is just "...a broader theoretical definition that relates the genetical (biological) species directly to the evolutionary processes that produced it" (Simpson 1961:153).

In reviewing the literature, it is clear that the problem is not in the definition, but in how to operationalize the definition in real situations.

definition in real situations.

Species occupy geographic ranges. In many cases, two or more breeding populations occupy the same range without interbreeding. These are sympatric species. Species occupying mutually exclusive but usually adjacent geographic areas are allopatric species (Mayr 1969). Species geographically in contact but not overlapping that may have narrow contact zones are parapatric species (Wiley 1981). Mayr (1964) believes the gaps (meaning genetic or behavioral boundaries as well as actual physical barriers) between sympatric populations must be absolute, otherwise they do not make 'good' species. A good species is one where the genetic and/or behavioral barriers are operating and no interbreeding is occurring (Mayr 1964). Applying the species definition to sympatric species appears straightforward.

Defining allopatric species is less clear-cut. According to Mayr, allopatric species "...lack... clear-cut delimitation of some geographic representatives..., an inevitable consequence of the continued operation of evolution" (1964:153). He believes that we cannot accurately measure the extent to which reproductive isolation has evolved. Inevitably, some groups are in the process of breaking up, making it difficult to define them as a species. Mayr states,

> ...a new species develops if a population which has become geographically isolated from its parental species acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers breakdown (Mayr 1964:155).

zones), or can develop after a period of allopatry (secondary zones). However, if two groups are more closely related to each other than other groups, than the kind of contact zone is impossible to determine. For determining species status, if the contact zone is narrow and 'old', then the groups probably are species because they retained their separate identity despite gene flow. If the contact zone is wide, then the groups have lost their separate identity and probably are geographic variants (Wiley 1980).

Application of these definitions to gibbons is discussed later.

CLASSIFICATION METHODS

How do the major schools of taxonomy deal with the species issue? What methods do they use to create classifications? Do any of them attempt to deal with closely related species, and are any of them effective?

Cladistic Classification

Wiley states that phylogenetic systematics (cladistics)

> ...(1) attempts to recover the phylogenetic (genealogical) relationships among groups of organisms and (2) produces classifications that exactly reflect those genealogical relationships (1981:6).

Phylogenetists or cladists create phylogenetic trees (cladograms) that represent the historic course of speciation. These trees or cladograms are hypotheses about the pattern of each history (Eldredge 1979; Wiley 1981). Each cladogram is constructed and tested on the basis of synapomorphy, which is the sharing of "similarities inherited only from... (an) immediate common ancestor and not shared with more distantly related taxa" (Cracraft 1979:31).

This method of classification splits a parental species into two daughter species. The parental species ceases to exist. The sister groups are given the same rank, and the ancestral species and all of its descendants are included in one holophyletic group (a group with a common ancestor) (Mayr, 1981).

Cladistic reasoning has many opponents. Cladistics approaches classification as a one-step procedure when it is really a sequential set of steps (Mayr 1981). Thus, the major complaints about cladistics are that it is only concerned with branching, ignores the different rates of evolution, and does not use homologous characters. Non-cladists also object to cladist assertions that cladistics is the only method that establishes truly monophyletic taxa (Sokal and Sneath 1963; Mayr 1969; Gould 1981). Cladistics assumes genealogical and genetic distance are the same, and therefore does not take convergence, parallelism or mosiac evolution into consideration. Further, it redefines homologous traits, which are important features for tracing a common ancestor. Homologous traits are used to imply an ancestor-descendant relationship. Lastly, Mayr (1969;1981) denies cladistics is the only method that establishes monophyletic taxa. Monophyly is the "devrivation of a taxon through one or more lineages from one immediately ancestral taxon of the same or lower rank" (Mayr 1969:407). Mayr (1969) insists that monophyly is a postulate of the evolutionary approach. Nonetheless, the cladists definition of monophyly is basically the same; "...two taxa have an ancestor in common not found in common with any other taxon" (Gaffney 1979).

Gould (1981) gives an illustration of a problem with cladistics. According to Gould (1981), there is no such thing as an ape under cladistic methodology. Chimpanzees and gorillas form a sister group because no other species branched off from their common ancestor. Likewise, no common ancestor group branched off from humans. Therefore, humans form another sister group on this cladogram. These three species are more closely related to each other than to any other species. What about orangutans? Traditionally orangs are regarded as apes and as such they also have a place on this cladogram. This is where cladistics falters -- orangs, chimps and gorillas do not form a genealogical unit. Chimps, gorillas and humans form a natural group cladistically, but orangs are included at another level. There is no natural group that includes orangs, chimps and gorillas (the so-called Great Apes) and excludes humans. Either there are no apes, or humans must be apes (Gould 1981). Mayr (1969) illustrates the same problem.

Phenetic Classification

Numerical or phenetic taxonomy is

> ...the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities (Sokal and Sneath 1963:48).

Numerical taxonomists choose as many characters as possible and weight them equally, and then cluster them mathematically by similarity or affinity. Sokal and Sneath (1963) believe phenetic affinity between organisms can provide information on the number of forms descended from an ancestor, may indicate rates of evolution, or solve stratigraphic problems.

Because phenetics is based on overall similarity, Mayr (1969) argues that phenetic classifications are similar to those created by the evolutionary approach. This is only logical because organisms tend to look more alike when they are more closely related (sibling species). Nevertheless, Mayr (1969) believes phenetic classifications are potentially unsound. Weighting all characters equally, according to Mayr (1969), does not allow for mosaic evolution, special adaptation, convergence and parallelism, and developmental and genetic homeostasis.

Evolutionary Classification

Evolutionary classification looks at the similarities and differences of organisms and evaluates them after considering their inferred evolutionary history (Mayr, 1981).

Evolutionary classification attempts to (1) determine the unique properties of every species and higher taxon using comparisons; (2) determine commonality within taxa; (3) determine the biological causes for shared characters and for differences; and (4) to assess the variation within taxa (Simpson 1961). Evolutionary taxonomy requires that all taxa be monophyletic.

Wiley (1981) criticizes evolutionary taxonomists because they name and rank paraphyletic groups (sister groups), and recognize such groups as valid evolutionary entities. Wiley (1981) believes paraphyletic groups are non-natural because these groups consist of a common ancestor and only some of the descendants. Wiley's primary disagreement arises from the placement of sister taxa into different groups; the lower taxon is put in a nonmonophyletic group and the 'higher' taxon is raised in rank because it is distinct. Evolutionary classifiers say that monophyly is required, but Eldredge and Cracraft (1980) believe that the procedures used by evolutionary taxonomists actually create nonmonophyletic taxa, not monophyletic taxa, i.e., they resist historical tendencies. Further, Eldredge and Cracraft believe that the method and theory used in evolutionary taxonomy "lacks logic and conceptual clarity" (1980:210).

CLOSELY RELATED TAXA

After reviewing the various methods of classification, in different jargon. Boucot states that

> ...after stripping away the jargon of "morphos," "apos," "plesios," "syns," "character states," and whatnot I can only conclude that "phylogenetic systematics," or "cladistics" (call it what you will), is nothing more or less than old-fashioned taxonomic classification so plastered over with jargon as to be unrecognizable to the casual reader" (Boucot 1979:199).

Mayr (1981) points out that each of the methods is beginning to use the other methods to enhance its classifications, which is further proof that the methods are not all that different.

Nevertheless, Mayr (1969) believes that evolutionary classification can deal with closely related taxa better than the other two approaches. Usually, when two species become geographically isolated, they diverge genetically, and may develop isolating mechanisms. From the genetic divergence, morphological differences develop that are useful for diagnosing species. However, some species do not develop conspicuous morphological differences, but instead exhibit changes in chromosomes, behavior and molecularly. This is particularly true of gibbons. Mayr (1969) believes only evolutionary classification uses this information since neither cladistics or phenetics address divergence.

However, with cladistic classification, Wiley (1981) uses the same approach for closely related taxa. He states that careful anatomical studies are essential, and that behavior and the ability to interbreed need assessing.

Phenetics may not solve the problem, according to Sokal and Sneath (1963), but it can create phenetic groupings that reduce error in species designation. Closely related species are treated as phenetic (phenetic means the assessment by phenotype instead of phylogeny) groups if genetic change is insufficient for reproductive isolation. The evidence shows that phenetic groups are usually as distinct as genetic groups. The evidence is assessed similarly to the other methods.

How and which of these methods has been applied to gibbon classification is discussed later.

The following sections discuss gibbon speciation, the characters used to classify gibbons and the classification systems to which these characters are applied.

CHAPTER III

FOSSIL GIBBONS

Evidence on fossil gibbons has the potential to answer important questions about gibbon speciation, and how that speciation has affected the number of gibbon species alive today.

Supposed fossil gibbons come from Oligocene, Miocene, Pliocene and Pleistocene deposits. As of 1988, researchers agree there are no acceptable candidates for fossil gibbons from the Oligocene, Miocene or Pliocene (Fleagle 1988). Fossils such as *Pliopithecus*, *Proconsul africanus*, *Dendropithecus*, *Micropithecus*, *Dionysopithecus* and *Laccopithecus* have been proposed as fossil gibbons (Andrews 1978, Simons et al. 1978, Szalay and Delson 1979). However, most of the features used to identify them, including small size, simple molar teeth and sharp pointed canines, probably are similarities based on primitive retention of these characters or parallel evolution. If the features are primitive retentions, then according to cladistic methodology, there are no fossil gibbons until the Pleistocene. This is because cladistics looks at shared-derived characteristics. The expectation is that the fossils have, at least, a few anatomical features of living gibbons. However, the well-known fossils from these eras lack the characteristics unique to gibbons. Gibbons are the most specialized (e.g. brachiation) of all higher apes, so one would expect that a fossil gibbon would exhibit some features of this specialization. Instead, the proposed fossils have features that are common to all hominoids. The interpretation is that these fossils are too primitive, and probably precede the radiation of modern hominoids (Fleagle 1984). Fleagle (1984) also believes there are not enough similarities between living gibbons and the fossils to justify the extensive parallelisms required for gibbons to have evolved from these fossils.

PLEISTOCENE FOSSILS

Table II lists the scant fossil gibbon remains from the Pleistocene. Except for the partial mandible, all the remains are teeth. Groves (1972) designated the mandible hoolock, but Delson (1977) believes that not enough fossil material is available to sustain such a designation. He calls it Hylobates sp. Most of the fossil teeth are referred to as Hylobates sp. because of the lack of fossil material.

CONCLUSIONS

As the above suggests, aside from the dental remains from the Pleistocene, there are no convincing fossil gibbons or gibbon ancestors.

Even if the fossil record were more complete, the only information the record could supply in the present context is

TABLE II

FOSSIL REMAINS

REMAINS	SPECIES	PERIOD	LOCATION	AUTHOR
Large molars (2)	siamang(?)	Pleistocene	Borneo	Hooijer 1960
Numerous teeth (UNK)	siamang(?)	Pleistocene	Borneo	Hooijer 1960
*Partial mandible	hoolock(?)	Pleistocene	Szechuan	Groves 1972
Upper molar (1)	Hylobates(?)	Pleistocene(?)	Guangxi Prov.	Lin et al. 1974
Teeth (UNK)	Hylobates(?)	Mid-middle Pleistocene	Guangxi Prov.	Chang et al. 1975
Teeth (UNK)	Hylobates(?)	Later Middle Pleistocene	Guangxi Prov.	Wu et al. 1975
*Partial mandible	Hylobates(?)	Early Middle Pleistocene	Szechuan	Delson 1977
Upper molar (1)	concolor(?)	Later Middle Pleistocene	Guangxi Prov.	Delson 1977
Teeth (UNK)	Hylobates(?)	Late Pleistocene	Xizhou, Yunnan	Chen and Qi 1978
Teeth (UNK)	Hylobates(?)	Later Middle Pleistocene	Tongzi, Yunnan	Chin. Acad. Sci. 1980
Teeth (UNK)	concolor(?)	Pleistocene	Guangxi Prov.	Zhao et al. 1981

* same mandible

the timing of the speciation of the last common ancestor of modern or extinct gibbons. From a morphological perspective, finding the closest fossil ancestor would provide very little if any information about diversity among gibbons because they are all morphologically similar.

CHAPTER IV

ECOLOGY AND ETHOLOGY

The following is a brief description of the ecological and ethological variation among gibbons. Because of the lack of fossils, it becomes important to study ecology and ethology. A high degree of variability among taxa in their ecology and ethology is useful for assessing species status. As evidenced in Table III, lar, siamang and agile gibbons have been the most extensively studied and concolor gibbons the least studied. Accessibility of the home ranges of these gibbons varies greatly from region to region.

HOME TERRITORIES AND RANGES

Gibbons occupy ranges from Southeast Asia to Java (see Figure 1 and Appendix). The day territories vary between 1300 and 1700 m (meters) for _klossii_ and are only about 850 m for _pileatus_ and _muelleri_ (Gittins 1984). These differences probably relate to habitat quality rather than species-specific differences (Gittins 1984).

Several gibbon groups occupy territories with documented hybrid zones. As noted by Gittins (1977), _lar_ and _agilis_ live in hybrid groups near the dam and lake in Ulu Mudah, and an overlap occurs between _lar_ and _pileatus_ in Khao Yai National

TABLE III

ECOLOGICAL STUDIES

No. of Animals	Comm. Names	Concentration	Duration	Author
93	lar	Behavior	2000 hrs.	Ellefson 1974
22	agile	Behavior	2000 hrs.	Ellefson 1974
8	siamang	Behavior	2000 hrs.	Ellefson 1974
6	lar	Song	Unknown	Chivers 1978
4	siamang	Song	Unknown	Chivers 1978
9	lar	Song	Unknown	Chivers 1978
3 mixed groups	lar and agile	Song	Unknown	Chivers 1978
2 groups	lar & siamang	Sympatry	12 months	Raemaekers 1979
Populations (?)	lar and siamang	Biomass and altitude	Unknown	Caldecott 1980
*31	agile	Territorial disputes	Unknown	Gittins 1980
*2 groups	lar and agile	Feeding and ranging	12 months	Gittins and Raemaekers 1980
*31	agile	Feeding and ranging	Unknown	Gittins 1982
Unknown	ALL (except concolor)	Ecology	Unknown	Chivers 1984
24 groups	hoolock	Ecology and ethology	21 days	Gittins and Tilson 1984
31 groups	moloch	Ecology	14 months	Kappeler 1984
*2 groups	siamang & lar	Diet and range	12 months	Raemaekers 1984
groups	pileated	Ecology	260 days	Srikosamatara 1984
1 group	kloss	Ecology	2 years	Whitten 1984
Unknown	concolor	Ecology	Unknown	Fleagle 1988

* same animals

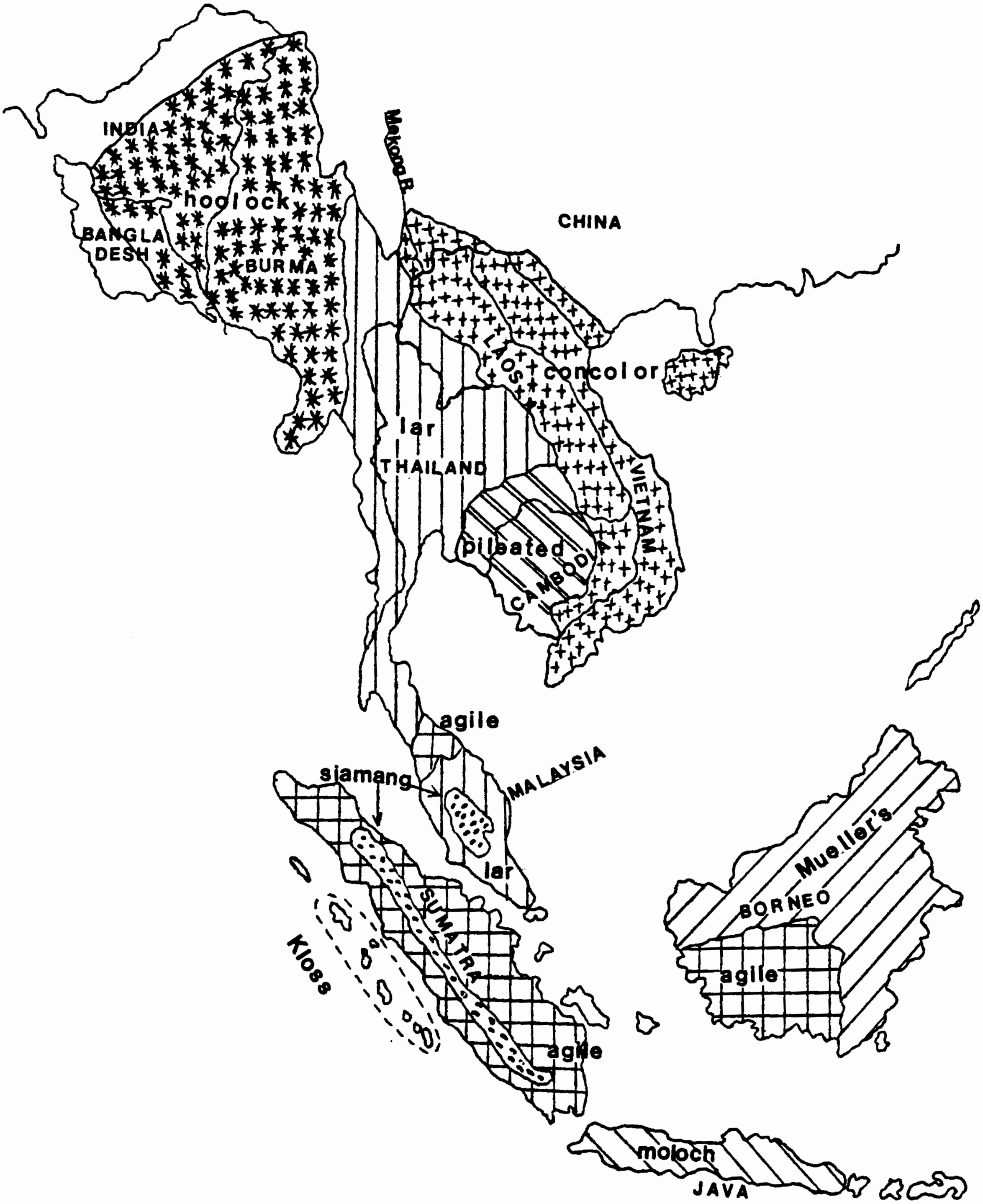

Figure 1: Gibbon Distribution Map. Although these borders appear absolute, there is overlap between 'species'.

Park (Marshall and Sugardito 1986). A third hybrid zone occurs between agilis and muelleri on Borneo.
Other hybrid zones may exist, as boundary surveys are incomplete (see the discussion on hybrid zones).

GROUP COMPOSITION

Field work done by Carpenter (1940) and many others has shown that most gibbons are monogamous and live in family groups that average four members: an adult male and an adult female, and up to four young (an infant, a juvenile and/or a subadult) (Ellefson 1974; Chivers 1974, 1977, 1984; Raemaekers 1979, 1984; Gittins 1979; Tilson 1981; Gittins and Tilson 1984; Kappeler 1984; Srikosamatara 1984; Whitten 1984; Fleagle 1988). However, observations on concolor gibbons show these animals sometimes live in polygynous groups (Fleagle 1988). In the wild, gibbons live between 20 and 30 years, and apparently, they mate for life. The young are born at 2 to 3 year intervals. Sexual activity is restricted to a few months during these intervals. Gibbons are considered juvenile until about six years of age. From 6 to 8 or 10 years, the animals are designated subadults. After this time, they should mate (Gittins and Raemaekers 1980). Parents drive the young from their territory when they become adults (Fleagle 1988).

Gibbons show almost no variation in group composition.

DAILY ACTIVITIES

The only real variant in gibbon activity is the timing of singing and song patterns. For instance, agilis song time peaks at dawn, while lar peaks between 0800 and 0900 (Brockelman and Gittins 1984). This subject is discussed in detail under nonmetric characters.

FEEDING

Gibbons are primarily frugivores. However, some gibbons appear to eat more leaves and arthropods than fruits. These differences are thought to relate to the availability of a particular food source rather than species-specific differences (Gittins and Tilson 1984, Raemaekers 1984, Whitten 1984, Fleagle 1988).

CONCLUSIONS

Gibbons are similar in their ecology and ethology; any 'real' differences probably relate to the absence of adequate data and to observer error. Except for song patterns, ecology and ethology are not useful indicators of species differences and have little value for classifying gibbons.

CHAPTER V

HYBRID ZONES

As discussed in the previous chapter, hybrid zones occur between several groups (see Table IV). One of these hybrid zones is between lar and pileatus in the Khao Yai National Park in Thailand. The zone is about 100 kilometers square. The gibbons in this hybrid zone have intermediate call patterns and pelage coloration compared with purebred lar and pileatus (Brockelman and Gittins 1984; Marshall and Sugardito 1986). This information is based purely on observation. The genetics of song and coat color are unknown. Nevertheless. Marshall and Sugardito (1986) have implied song and coat color are controlled by a single gene.

The hybrid zone between pileatus and lar is the best documented. Many juveniles live in these mixed groups with hybrid adults, which shows the hybrids and backcrosses are fertile and capable of reproducing (Brockelman and Gittins 1984). However, since the hybrid zone is small, the contact probably is secondary. Creel and Preuschoft (1984) agree that the hybrid zones are secondary (because the zones are narrow), a result of isolation. However, the isolating mechanisms appear to have broken down because the supposed separate

TABLE IV

KNOWN HYBRIDS

No. of Animals	Comm. names	Location	Author
2	♀ siamang ♂ Mueller's or moloch	Atlanta, GA	Shafer and Myers 1977, 1979
4	♂ lar ♀ agile juvenile & infant	Northern West Malaysia	Brockelman and Gittins 1984
4	♂ agile ♀ lar 2 juveniles	Northern West Malaysia	Brockelman and Gittins 1984
?	possible mixed group or group of agiles	Northern West Malaysia	Brockelman and Gittins 1984
? 18 groups	lar and pileated	Khao National Park	Brockelman and Gittins 1984
2	♂ pileated ♀ pileated-backcross (lar)+	Khao National Park	Marshall and Sugardito 1986

TABLE IV

KNOWN HYBRIDS
(continued)

No. of Animals	Comm. Names	Location	Author
2	♀ lar backcross (pileated) ♂ hybrid (lar/ pileated)	Khao National Park	Marshall and Sugardito 1986
2	♂ lar backcross (pileated) ♀ lar backcross (pileated)	Khao National Park	Marshall and Sugardito 1986
2	♀ hybrid (lar/ (pileated) ♂ pileated	Khao National Park	Marshall and Sugardito 1986
3	♀ pileated ♂ pileated backcross (lar) female briefly consorted with a mated pair of lars	Khao National Park	Marshall and Sugardito 1986

TABLE IV

KNOWN HYBRIDS
(continued)

No. of Animals	Comm. Names	Location	Author
1+	♂ hybrid (lar/ pileated) Associated with different female lars at different times.	Khao National Park	Marshall and Sugardito 1986
3	♀ lar ♀ pileated ♂ hybrid (lar/ pileated) Eventually replaced by lar	Khao National Park	Marshall and Sugardito 1986
2	* agile backcross (Mueller's) * agile backcross (Mueller's)	Barito River	Marshall and Sugardito 1986
2	* agile backcross (Mueller's) * hybrid (Mueller's/ agile)	Barito River	Marshall and Sugardito 1986

TABLE IV

KNOWN HYBRIDS
(continued)

No. of Animals	Comm. Names	Location	Author
3	* agile backcross (Mueller's) * Mueller's backcross (agile) hybrid daughter(?)	Barito River	Marshall and Sugardito 1986

+ Backcross designations established using song.
* No visual contact. Observations based on song.

'species' are interbreeding in the wild. Further, from all evidence, pileatus are the most distinct of the 'lar-group' gibbons in pelage coloration and cranial morphology. Yet, pileatus are interbreeding in the wild. Still, Haimoff et al. (1984) argue that the interbreeding is inconsequential because little or no gene flow is occurring. However, there are, at present, no measurements of gene flow. On the other hand, Creel and Preuschoft (1984) point out that any exchange of genes, especially under natural conditions, means the animals are members of the same species. Interestingly, syndactylus overlap with lar in one territory and with agilis in another, and no interbreeding occurs in the wild, even though a documented case has occurred in captivity (Shafer and Myers 1977). This possibly shows that behavioral and morphological mechanisms are guaranteeing reproductive isolation in the absence of geographical barriers.

Marshall et al. (1984) argue that because contact in the wild occurs only in small hybrid zones, and few cases of documented fertile hybrids exist, that gene flow is restricted between populations. Only if unrestricted gene flow is occurring are forms considered conspecific.

Others argue that gene flow can vary between complete and totally absent, but is still real. Only the absolute inability to pass genes is acceptable evidence of speciation (Creel et al. 1984).

According to Mayr (1969), if secondary intergradation occurs in narrow zones, species are still species. Yet if they are true allopatric species and they intergrade in a secondary contact zone, then they were never reproductively isolated. These should be considered subspecies. If human interference is occurring, and two species are distinct over most of their range but have complete hybrid zones in a few areas, they should be considered full species.

Obviously, one first has to decide if something is really an allopatric species before deciding the issue of hybrid zones. Wiley (1981) believes 'allopatric' species with narrow hybrid zones are really incomplete cases of allo-parapatric speciation. Allo-parapatric speciation occurs when two populations differentiate, but not enough to call them independent populations. However, these groups then develop into independent populations during a period of parapatry. How these definitions have been applied to gibbons is discussed later.

CHAPTER VI

CHARACTER TRAITS

The following chapter discusses the character traits used to distinguish gibbon species. The metric characters include morphology (dentition, cranial and postcranial), karyology and molecular data, and the nonmetric characters include pelage and song patterns.

METRIC CHARACTERS

Table V lists the numbers and kinds of metric studies involving gibbons.

General Morphology

Morphologically, all gibbons are very similar. Gibbons (and siamangs) weigh between 4 and 11 kg. Unlike other apes, they always have ischial callosities. Their forelimbs are the longest, relative to body size, of any primate, and their legs are longer as well. The digits on both their hands and feet are long and slender, with a very muscular thumb and a large big toe. Gibbon braincases are globular and have no nuchal crest. Rarely is a sagittal crest present. Their snouts are short and their faces shallow. The orbits are large and have protruding rims. Overall, the interorbital range is wide. The face and mandible are shallow, and the ramus is broad. Gibbons have a catarrhine dental formula (2:1:2:3). The

TABLE V

METRIC STUDIES

No. of Animals	Comm. Names	Concentration	Author
23	siamang, kloss and lar	Morphology	Miller 1933
3	hoolock, lar and moloch	Chromosome number	Hamerton 1963
72	Bornean gibbon	Skull morphopology	Groves 1971
Unknown	concolor, siamang kloss, hoolock, pileated and lar	Chromosomes (autosomal arms, acrocentrics and satellites)	Groves 1972
468 (Teeth)	agile, concolor, hoolock, moloch, siamang, lar and pileated	Molar size	Kitahara-Frisch 1973
4	concolor and lar	Banding patterns	Dutrillaux et al. 1975
2	moloch and lar	Karotypes and banding patterns	Tantravahi et al. 1975
Unknown	concolor, lar and pileated	Chromosome number and type	Tanticharoenyos and Markvong 1975
Unknown	lar	Unbanded karyotype	Warburton et al. 1975
Unknown	lar	Chromosome number and type	Miller 1977
Unknown	ALL	Chromosome number	deGrouchy 1978
7	lar, concolor and siamang	Genetic distances and allelic variation	Bruce and Ayala 1979
3	moloch, siamang and hybrid	Chromosome number	Myers and Shafer 1979

TABLE V

METRIC STUDIES
(continued)

No. of Animals	Comm. Names	Concentration	Author
6	siamang, concolor and agile	Banding patterns and structural differences	VanTuinen and Ledbetter 1983
50 from each group (except for Western Sumatran pileated and lar)	ALL	Cranial and dental measurements	Creel and Preuschoft 1984
Unknown	lar, agile, concolor, moloch, pileated and siamang	Molecular evolution	Cronin et al. 1984
Unknown	lar, agile concolor and siamang	Molecular evolution	Darga et al. 1984

molars are simple and broad with low-rounded cusps. The canines are long and sharp in both sexes. The blade-like sectorial P3, typical of catarrhines, sharpens the canines. The incisors are relatively short (Fleagle 1988).

Dentition

The size of all the molars (M1, M2, M3) in the gibbons is different enough to distinguish between species. However, there is considerable overlap between groups occupying contiguous geographic ranges. There is an actual increase in the size of molars as the distance from the equator increases. The only exception appears to be in the third molar. Pileatus and moloch have unreduced third molars, while in agilis and vestitus reduction is great.

The lingual cingulum shows no reduction in concolor, very little reduction in moloch (Java) and pileatus, moderate reduction in lar and moloch (Borneo), and extreme reduction in agilis and hoolock.

The frequency of triangular anterior lower premolars is high in carpenteri, drops as it reaches pileatus, and is virtually absent in entelloides.

The position of the hypoconulid varies widely between and within groups, making it a poor indicator of similiarities or differences between species (Frisch 1965; Kitahara-Frisch 1973; Groves 1984).

Overall, there are no real taxonomic differences in the dentition of gibbons and siamangs. However, there is a geographic distribution of dentition traits.

Cranial and Postcranial Studies

Marshall and Sugardito (1986) were able to identify five distinct groups: *syndactylus*, *concolor*, *klossii*, *hoolock* and all other gibbons combined from transmitted light superimposed on skulls that were reconstructed from mean coordinates taken by Creel and Preuschoft (1984). *Concolor* have the most unique features. For example, the skull is lower, the face is long and the orbits flat. All other gibbons have thick orbits. *Syndactylus* followed by *hoolock* have the largest cranium. *Lar*, *agilis*, *moloch*, *muelleri* and *pileatus* are indistinguishable as a group, and have smaller crania than *hoolock*. *Klossii* have the smallest cranium.

Creel and Preuschoft (1984) performed an analysis on 10 groups of the *lar*-group (Malayan *lar*, *entelliodes*, *carpenteri*, *vestitus*, Malayan *agilis*, *albibarbis*, *muelleri*, *moloch* and *pileatus*), using 90 cranial and postcranial variables. The univariate results showed a significant difference in cranial shape among the 10 groups, but not in cranial size. Gender differences were very minor.

Multivariate analysis revealed that all 10 groups overlap considerably in their cranial morphology. The principal clusters showed that animals from the same geographic area tend to clump together. This parallels Kitahara-Frisch's (1973) results. When individual specimens were clustered, *vestitus* showed affinities with female Malayan *lar* (but not male Malayan *lar*) and also with *entelliodes* and Sumatran *agilis*. Malayan *agilis* showed no affinity to any group in particular, i.e., they are not any more similar to Sumatran *agilis* than to Malayan *lar* or *entelliodes*. In addition, Malayan *lar* males resemble Malayan *agilis* females more than they do Malayan *lar* females. *Pileatus* exhibited the most difference from the other gibbons. *Pileatus* have a larger face, a receding orbital region, and larger teeth. Nevertheless, Creel and Preuschoft (1984) believe the differences are not great enough to separate them from the other 10 groups.

The geographic groupings do not correspond well with the supposed boundaries between species. Since groups in geographical proximity resemble each other more than geographically separated groups, the groups sharing boundaries may still be exchanging genes (Creel and Preuschoft 1984; Groves 1984). Furthermore, the cranial differences between the groups are less than found between other primate species (Fleagle 1988). There is so much overlap among all ten '*lar*' groups that Creel and Preuschoft (1984) believe they are nothing more than subspecies. Even Marshall and Sugardito (1986) believe if extant lar-group gibbons were fossil gibbons, they would be conspecific. However, they believe the use of cranial data buries "the interesting biological and distributional facts" (Marshall and Sugardito 1986:148).

Karyological and Molecular Studies

Karyotypes readily distinguish *syndactylus*, *concolor* and *hoolock*, but not *lar*, *agilis*, *moloch*, *muelleri* and *pileatus*. *Syndactylus* have a diploid number of 50, *concolor* 52, *hoolock* 38, and all other gibbons have 44 (Marshall and Sugardito 1986). The karyotypes of the gibbons studied, exhibit amazing diversity.

Forty percent of the banding patterns between *syndactylus* and *concolor* are similar. Unlike *lar*, *agilis*, *moloch*, *muelleri* and *pileatus*, both have large terminal C-bands (VanTuinen and Ledbetter 1983; Shafer et al. 1984). *Syndactylus* has one pair of acrocentric chromosomes (Warburton et al. 1975).

Hoolock have no acrocentric chromosomes, but they do have large submetacentrics. Interestingly, *hoolock* show very little homology with *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* (Prouty et al. 1983) in banded and unbanded patterns.

Lar, *agilis*, *moloch*, *muelleri* and *pileatus* all have metacentric or submetacentric chromosomes; no acrocentric chromosomes occur. No differences in the unbanded karyotypes of *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* have been found (Warburton 1975). The banded and unbanded karyotypes of *lar* and *moloch* are indistinguishable (Tantravahi et al. 1975;

deGrouchy et al. 1978). This indicates these two groups are not separate species. There is no genetic barrier between them. All of the chromosomes, except the Y, have some C-banding positive material at the centromere. The autosomes and X are biarmed, and the Y appears to resemble a dot (Tantravahi et al. 1975). The C-bands in agilis and muelleri occur at the centromeres of chromosomes as well (VanTuinen and Ledbetter 1983).

A comparison of lar and concolor karyotypes showed that only seven pairs of chromosomes have similar c-banding and g-banding (Dutrillaux et al. 1975). A similar study showed that pileatus and concolor also only share similar banding patterns for seven pairs of chromosomes. Further, syndactylus and muelleri probably share only one pair of chromosomes (VanTuinen and Ledbetter 1983).

The karyological data show syndactylus, concolor and hoolock have different numbers of chromosomes from each other and from lar, agilis, moloch, muelleri and pileatus, while each of the latter five share the same number of chromosomes. These five also are identical for unbanded chromosomes, while syndactylus, concolor and hoolock show diversity among themselves and compared with lar, agilis, moloch, muelleri and pileatus. The banding patterns probably are identical (indicating these groups are not separate species) between lar, agilis, moloch, muelleri and pileatus, yet lar and pileatus share only seven pairs of chromosomes with concolor, and muelleri shares only one with syndactylus. Considering the diversity (heterozygosity of chromosomes is only 2.3%, according to Bruce and Ayala 1979) between species that are so similar in every other way, this is strong evidence that the lar, agilis, moloch, muelleri and pileatus are not separate species. Marshall and Sugardito (1986) object to the use of chromosome number as an indicator of species status because klossii has the same chromosome number as lar, agilis, moloch, muelleri and pileatus. However, no studies other than chromosome number exist for klossii.

Molecular studies on the gibbons are incomplete. No data exist for klossii and hoolock specimens (Creel and Preuschoft 1984). Unfortunately, most of the molecular studies have concentrated on the divergence of hominoid lineages. The divergence studies usually use information from one siamang, one concolor and a probable lar; the actual species of the gibbon chosen is often questionable. Nevertheless, the data show that even though all gibbon groups (including the syndactylus) exhibit few chromosomal differences, syndactylus and concolor are distinct and lar, agilis, moloch, muelleri and pileatus are very similar (Darga et al. 1984).

1Nei's distance measures the accumulated allele difference between two populations. Amino acid sequences in proteins can be used to estimate the distances. The equation is useable for populations under sexual isolation or for populations separated by geographic distance (Nei 1972).

Ayala (1979), Nei's distance is 0.274. *H*. *concolor* also differ

Studies comparing 23 proteins from *syndactylus* and *lar* show the plasma protein electrophoretic distance (PPED) to be 1.6 to 1.8 between the two groups. According to Cronin et al. (1984), Nei's distancel is 0.337. According to Bruce and by 1.6 PPED units from *lar* and *syndactylus* (Cronin et al. 1984).

Nei's distance between *lar* and *concolor* is 0.130 (Bruce and Ayala 1979). Cronin et al. (1984) found that the PPED is between 0.3 to 0.4 for *lar*, *agilis*, *moloch*, *muelleri* and *pileatus*. Cronin et al. (1984) believe since the PPED range is so close that little time has elapsed since divergence. Further, they believe that these genetic data does not show that *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* are anything but sub- or semispecies (Cronin et al. 1984).

NON-METRIC CHARACTERS

Pelage

Brockelman and Gittins (1984) argue that characters independent of coat color such as face rings, brow patches and cheek patches are useful indicators of species. Creel and Preuschoft (1984) disagree because some of these characters are present in more than one species, i.e., white hands and feet.

Marshall and Sugardito (1986) state that the range of coat color is a useful indicator of subspecies. However, Brockelman and Gittins (1984) found that the range of coat colors overlaps all gibbon groups. For instance, *syndactylus* and *klossii* (everyone recognizes these as different species) are the same color. Further, Wilson and Wilson (1976) found that *lar* and *agilis* exhibit the same range of colors.

Because coat colors cross all gibbon groups, this character probably is a poor indicator of species or subspecies status. Assessment of coat color has been based purely on observation of live animals and museum pelt collections (see Table VI). The genetics of coat color is currently unknown.

Song

Table VII lists the numbers and kinds of studies on song. The following is a brief synopsis of song for *lar*, *agilis*, *moloch*, *muelleri* and *pileatus*.

Both male and female *lar* produce 'wa' notes. The males produce a set of simple quaver or quiver notes (that supposedly are species-specific) during the solo, as a part of the coda and during the organizing sequence (Haimoff 1984). At Kuala Lumpur, the great calls are protracted with long notes and have a high degree of complexity. However, at Ulu Mudah, the great calls are far simpler and resemble the great calls of *agilis* gibbons (Chivers 1973).

Male and female *agilis* produce 'whoops', which sound more like 'was', and a 'whoo-aa' sound (Haimoff 1984). All *lar*-

TABLE VI

PELAGE

No. of Pelts & Sex	Age	Species	Author
103?	Adult	*hoolock*	Groves 1967
19?	Adult	*hoolock*	Groves 1967
3?	Adult	*hoolock*	Groves 1967
81?	Adult	*hoolock*	Groves 1967
27?	Unknown	*lar*	Fooden 1967
154?	Unknown	*lar carpenteri*	Groves 1970
43?	Unknown	*lar entelliodes*	Groves 1970
100?	Unknown	*lar*	Groves 1970
58?	Unknown	*agilis*	Groves 1970
125?	Unknown	Bornean	Groves 1971
1/2	Adult	*concolor*	Groves 1972
2/2	Juvenile	*concolor*	Groves 1972
3/0	Infant	*concolor*	Groves 1972
1/0	Adult	*concolor lu*	Groves 1972
0/1	Juvenile	*concolor lu*	Groves 1972
1/1	Infant	*concolor lu*	Groves 1972
2/1	Adult	*concolor hainan*	Groves 1972
3/1	Adult	*concolor siki*	Groves 1972
1/0	Juvenile	*concolor siki*	Groves 1972
1/1	Infant	*concolor siki*	Groves 1972
14/8	Adult	*concolor gabriellae*	Groves 1972
7?	Unknown	*syndactylus continentis*	Groves 1972
18?	Unknown	*klossii*	Groves 1972
45?	Unknown	*hoolock*	Groves 1972
37?	Unknown	*hoolock leuconedys*	Groves 1972
24?	Unknown	*pileatus*	Groves 1972
26?	Unknown	*lar* (Java)	Groves 1972
63?	Unknown	*agilis*	Groves 1972
12?	Unknown	*lar lar*	Groves 1972
26?	Unknown	*lar*	Groves 1972

TABLE VI

PELAGE
(continued)

No. of Pelts	Age	Species	Author
44?	Unknown	lar entelliodes	Groves 1972
168?	Unknown	lar carpenteri	Groves 1972
2?	Adult	concolor	Marshall and Sugardito 1986
7?	Adult	concolor leucogenys	Marshall and Sugardito 1986
2?	Adult	concolor siki	Marshall and Sugardito 1986
23?	Adult	concolor gabrillae	Marshall and Sugardito 1986
45?	Adult	syndactylus syndactylus	Marshall and Sugardito 1986
6?	Adult	syndactylus continentis	Marshall and Sugardito 1986
29?	Adult	hoolock	Marshall and Sugardito 1986
32?	Adult	hoolock leuconedys	Marshall and Sugardito 1986
15?	Adult	moloch	Marshall and Sugardito 1986
32?	Adult	agilis unko	Marshall and Sugardito 1986
40?	Adult	agilis	Marshall and Sugardito 1986
31?	Adult	agilis alibibarbis	Marshall and Sugardito 1986
148?	Adult	lar entelliodes	Marshall and Sugardito 1986
17?	Adult	lar vestitus	Marshall and Sugardito 1986
18?	Adult	lar	Marshall and Sugardito 1986
14?	Adult	muelleri	Marshall and Sugardito 1986
69?	Adult	muelleri funerus	Marshall and Sugardito 1986
23?	Adult	muelleri abbotti	Marshall and Sugardito 1986
13?	Adult	pileatus	Marshall and Sugardito 1986
28?	Adult	klossii	Marshall and Sugardito 1986

TABLE VII

SONG

No. of Animals	Species	Emphasis	Duration	Author
Unknown	*lar*, *pileatus*, *concolor*	General	?	Marshall et al. 1972
Unknown	*lar*	General	?	Chivers 1974
14 populations	ALL	General	?	Marshall and Marshall 1976
15 groups	*klossii*	General	3 years	Tenaza 1977
2 groups with 3 individuals & 1 group with 4 individuals	*lar* *syndactylus*	General	2 years	Chivers 1978
Two groups - one with 4 and one with 5	*agilis*	General	2 years	Chivers 1978
3 mixed groups 2 hybrid infants	*lar* and *agilis*	General	2 years	Chivers 1978
Unknown	ALL	Calls of male and female	?	Chivers and Gittins 1978
Unknown	*concolor leucogenys* and *gabriellae*	Sunrise and morning differences	?	Demars and Goustard 1978
Unknown	*concolor leucogenys* and *klossi*	Sunrise and morning differences	?	Demars and Goustard 1978
2 males	*concolor gabriellae*	Great calls	?	Demars et al. 1978
31	*lar*	Function	?	Gittins 1978
1 group with 3 individuals	*klossii*	General	2 years	Whitten 1980

TABLE VII

SONG
(continued)

No. of Animals	Species	Emphasis	Duration	Author
Mated pair	*syndactylus*	General	?	Haimoff 1981
40 groups with 14 infants (mean group size 3.7)	*lar*	General	?	Brockelman and Srikosamatara 1984
1 main group - 30 total	*lar* and *agilis*	General	2 years	Gittins 1984
Unknown	*hoolock*	General	16 days	Gittins and Tilson 1984
2 groups	*concolor*	General	?	Goustard 1984
Unknown	ALL	Song bouts	150 hours	Haimoff 1984
Unknown	ALL	Characters	?	Haimoff et al. 1984
Unknown	*moloch*, *agilis* *lar*, *muelleri*, *pileatus*	General	?	Marshall et al. 1984
5 pairs and 1 male individual	*concolor*	General	?	Schilling 1984
3	*klossii*	General	6 months	Whitten 1984
1 captive group 1 wild group	*muelleri*	Comparison	?	Haimoff 1985
Unknown	Bornean	Territorial Response	?	Mitani 1985
Unknown	ALL	General analysis	?	Marshall and Sugardito 1986

group gibbons produce the 'wa' note. Male and female and female *agilis* vary their songs to avoid confusion with adjacent *agilis* (Gittins 1984; Marshall and Sugardito 1986). However, Gittins (1984) states that the overall structure is the same, and that no geographic variation exists in the structure.

Moloch produce 'oo' notes, but not as often as 'wa' notes. A 'species-specific' sound produced by moloch is a 'wa-oo-wa' (Haimoff 1984). The female produces a solo, the only other female that does this is *klossii* (Gittins 1984; Marshall and Sugardito 1986). Both the female and male *muelleri* produce 'wa' and 'oo-wa' notes during the organizing sequence. The female produces a great call very similar to *pileatus*, but shorter (Chivers and Gittins 1978). According to Haimoff (1984), *muelleri* produces a quaver note that is much different from *lar*. Apparently, the solo of the males is unique because of its staccato notes and simply inflected tones.

Pileatus males and females produce a bubble sound during the introductory sequence. The male produces a diphasic trill after the female call that is faster than any other gibbon (Chivers and Gittins 1978). The females' great call begins with long introductory notes, according to Marshall and Marshall (1976) and Haimoff (1984), but with short rising notes, according to Chivers and Gittins (1978). All of them agree that the call ends in a long bubble (Marshall and

Marshall 1976; Haimoff 1984; Marshall and Sugardito 1986). The end of the female great call is similar to *moloch* and *klossii*.

Usefulness of Song

Song is of questionable value for assessing gibbon species. The song differences among *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* are not great enough, causing some investigators to feel the need to correlate song with pelage characteristics to justify labeling a particular gibbon group a species.

Groves (1984) contends that calls are unuseable for identifying a species (as Marshall et al. 1984 have done). Groves believes Marshall et al. have misidentified *agilis* and *muelleri* on Borneo. Marshall et al. (1984) believe the animals that Groves (1984) identifies as *muelleri* are really *agilis*, based on their calls. Groves (1984) states that the *agilis albibarbis* resembles *muelleri* morphologically, and is very different from *agilis*. However, the call of *agilis albibarbis* is very similar to *agilis* and quite different from *muelleri*.

These same investigators have used song and pelage to suggest that hybrid zone gibbons do not affect the species designation they gave to *lar*, *agilis*, *moloch*, *muelleri* and *pileatus*. Brockelman and Gittins (1984) state that when an animal has odd pelage (a hybrid), then the call patterns are intermediate. Four females with lar coloration apparently give great calls that have more loud notes than other lar females. They believe these females are lar-pileatus backcrosses, but are not positive because all second generation backcrosses may or may not be recognizable by pelage color. At the same time, however, they state that if the pelage resembles either lar or pileatus nothing about the hybrid calls is intermediate. This is inconsistent.

Marshall et al. (1984) reiterate the above. They found absolutely no intergradation in songs in hybrid zones, "anymore than there is in facial pattern" (Marshall et al. 1984:539). Yet, they acknowledge that backcrosses and hybrids produce different calls. Songs may not vary in structure within the non-hybrid zones, which makes sense since the different populations are not exchanging genes in these areas, but intermediate calls within the hybrid zones indicate intergradation.

The above information is an indication, as Creel and Preuschoft (1984) state, that boundary surveys may be inadequate. The varying descriptions of songs and the absence of agreement on song terms makes song a difficult trait to use for classifying gibbon species. A further complication is the lack of genetic evidence. I find it difficult to believe that one can identify a hybrid or a backcross on the basis of coat color and/or song alone.

CHAPTER VII

CURRENT CLASSIFICATIONS

Haimoff et al. (1984) used phylogenetic reconstruction to determine classification. Phylogenetic reconstruction establishes genealogical relationships using characters. Haimoff et al. (1984) used 55 morphological and behavioral characters to develop phylogenetic trees. The characters were tested using character compatibility analysis, which assesses the evolutionary changes in anatomical and behavioral characters, and whether or not the characters are compatible. The characters used included 40 morphological characters, consisting of pelage color and markings, cranial and postcranial measures, dentition, the number and kinds of chromosomes, and external features. The behavioral characters included behavior, the acoustics and organization of songs, and the timing of singing. Character-state trees were directed because of the absence of fossil data. In other words, Haimoff et al. (1984) assumed ancestral gibbons were generalized primates with suspensory behavior, sexual monomorphism, monogamy, territoriality, frugivory and simple vocal patterns.

The results show a direct phyletic connection among lar, agilis, moloch, muelleri and pileatus. Haimoff et al. (1984) believe pileatus is a species, moloch is a subspecies, and that *lar*, *agilis* and *muelleri* are races (see Table VIII). The data also show that *syndactylus* and *concolor* constitute the earliest distinct taxa because *syndactylus* and *concolor* retain the most primitive characters of ancestral gibbons, and *lar*, *agilis*, *moloch* and *muelleri* speciated latest because these gibbons have the most derived characters. *H. klossii* and *hoolock* are intermediate.

Creel and Preuschoft (1984) used a combination of phenetics and cladistics. Based on a computer simulation of constant and varying rates of evolution, they believe each approach works equally well, except that cladistics is slightly better if rates of evolution of individual traits are variable (this conflicts with Sokal and Sneath's (1963) assertion that cladistics ignores rates of evolution), and phenetics is marginally better if the rates are constant. Whether or not differential rates are common is unanswerable because the fossil record is incomplete, and whether phenetics or cladistics is superior is impossible to answer since 'true' phylogenies are unknowable.

Nevertheless, Creel and Preuschoft (1984) believe the approaches provide an assessment of the reliability of constructed phylogenies when used together. Using 90 cranial and dental variables, they found *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* exhibit considerable overlap in their morphology. Further, no pattern developed that would indicate bifurcation of parent species to create new ones. *Pileatus* shows the most difference, but not enough in Creel and Preuschoft's (1984) opinion to elevate them to species status (see Table VIII).

Creel and Preuschoft (1984) did not use song or pelage features because of too few characters and because these characters vary significantly within populations. In addition, some of the diagnostic features occur in more than one 'species'.

Groves (1984) used the evolutionary approach. He looked at most of the traits listed in this paper. From geographic isolation, color phases, morphology and vocal patterns, he believes *lar*, *agilis*, *moloch* and *pileatus* are semispecies within a superspecies. He excludes *muelleri*, placing them with *agilis* (see Table VIII).

The methodologies of other authorities are primarily evolutionary classification with some cladistic reasoning. Marshall et al. (1984) and Marshall and Sugardito (1986) rely heavily on pelage and song features because they believe the other traits are too similar among gibbon populations to establish species differences. They and Brockelman and Gittins (1984) believe the structure of vocal patterns are absolutely distinct and correlate well with pelage features. They believe *syndactylus*, *concolor*, *klossii*, *hoolock*, *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* are all species (see Table VIII).

TABLE VIII

CURRENT CLASSIFICATIONS

Genus	Subgenus	Species	Subspecies	Race	Author
Hylobates		*syndactylus*			Creel and Preuschoft 1984
		hoolock			
		concolor			
		klossii			
		lar			
Nomascus		*concolor*			Haimoff et al. 1984
Hylobates	*Symphalangus*	*syndactylus*			
	Hylobates	*hoolock*			
		klossii			
		pileatus			
			moloch		
				muelleri	
				agilis	
				lar	
Hylobates	*Symphalangus*	*syndactylus*			Groves 1984
	Nomascus	*concolor*			
	Hylobates	*hoolock*			
		klossii			
		pileatus			
		moloch			
		agilis	*muelleri*		
		lar			

TABLE VIII

CURRENT CLASSIFICATIONS
(continued)

Genus	Subgenus	Species	Subspecies	Race	Author
Hylobates		*syndactylus* *concolor* *hoolock* *moloch* *agilis* *lar* *muelleri* *pileatus* *klossii*			Brockelman and Gittins 1984 Marshall et al. 1984 Marshall and Sugardito 1986

CHAPTER VIII

SUMMARY AND CONCLUSIONS

ABSOLUTE GIBBON SPECIES

All authorities agree *syndactylus*, *concolor*, *hoolock* and *klossii* are each species. Users of each of the three classification methods place each of these groups into separate species. Further, there is total agreement that *syndactylus* is sympatric with *lar* and *agilis* and interbreeds with neither in the wild, and that *concolor*, *hoolock* and *klossii* are true allopatric species. The traits separating these gibbons into species is agreed upon as well. *Syndactylus*, *concolor* and *hoolock* have different diploid chromosome numbers: 50, 52 and 38, respectively. These three species also have unique banding patterns and are biomolecularly distinct. All four of these species are morphologically distinct. *Syndactylus* is the largest with the largest cranium followed by *hoolock*, *concolor* and *klossii*. *Klossii* is the smallest of all gibbons with the smallest cranium. An interesting note is that these four are and would be considered species without using song, pelage or coat color characters.

CHARACTER TRAITS

There is disagreement among authorities regarding appropriate character traits for determining the species status of *lar*, *agilis*, *moloch*, *muelleri* and *pileatus*. Creel and Preuschoft (1984) believe many overlapping pelage and song characteristics are present in more than one species, and thus, are poor characters for determining species status. Haimoff et al. (1984) believe pelage and song are useful, but do not heavily weight these characters. According to Groves (1984), calls are a weak character trait, but pelage is a relatively good indicator of species status. At the opposite end, Marshall and Sugardito (1986) find song and pelage characters the best indicators of species status. They believe gibbons are similar enough in all other character traits as to make them useless for determining species status.

The data, presently, show that *lar*, *agilis*, *moloch*, *muelleri* and *pileatus* are quantitatively identical genetically and biomolecularly. Morphologically, these gibbons overlap considerably, and there is a geographical trend to the morphological characters rather than taxonomic differences between species. The possible exception is *pileatus*. *Pileatus* has a larger face, a receding orbital region and larger teeth. Haimoff et al. (1984) believe the difference is enough to elevate *pileatus* to the species level, but Creel and Preuschoft (1984) do not believe the difference is enough to call pileatus a species.

The data on pelage and song are controversial. Groves (1984), and Marshall and Sugardito (1986) believe the pelage characters are absolute, i.e., each of these groups evidences unique pelage. However, Groves (1984), and Marshall and Sugardito (1986) vehemently disagree on the pelage of muelleri. Groves (1984) believes muelleri is a subspecies of agilis, while Marshall and Sugardito (1986) insist muelleri is a full species.

Marshall and Sugardito (1986) believe all gibbon songs are species-specific. Gittins (1984) and Haimoff (1984) agree. Nevertheless, there is disagreement about the songs. For example, Marshall and Marshall (1976) and Haimoff (1984) believe the song of pileatus ends one way, and Chivers and Gittins (1978) believe the song ends differently.

Only Marshall and Sugardito (1986) dismiss the metric characters as taxonomically relevant, while only Creel and Preuschoft do so for nonmetric character traits. Creel and Preuschoft's (1984) arguments against song and pelage are stronger than Marshall and Sugardito's (1986) arguments for the nonmetric traits.

To date I have found that pelage and song traits are not quantified; if they were quantifiable, perhaps these traits could be useful in the future. Breeding experiments could determine if there is a genetic component to song and pelage traits. Further, standard definitions and procedures must be developed for both metric and nonmetric characters. Users of metric characters are further advanced in this regard as Creel and Preuschoft's (1984) work was duplicated by Marshall and Sugardito (1986).

CLASSIFICATION METHODS

As stated earlier, the classification methods yielded the same results for syndactylus, concolor, hoolock and klossii. However, for the rest of the gibbons the results of each method were different. This difference is attributable to the use of different character traits and dissimilar treatment of these characters. Weighing cranial data heavier than other data, Haimoff et al. (1984) labeled pileatus a species and moloch a subspecies. Using just cranial and postcranial data, Creel and Preuschoft (1984) concluded there are no subspecies, just the species lar. Concentrating on pelage, Groves (1984) designated muelleri a subspecies and the rest species. Using primarily song, Marshall and Sugardito (1986) gave species status to lar, agilis, moloch, muelleri and pileatus. Therefore, the methods per se are not the problem in the case of the gibbons; the character traits used are the problem.

GIBBON HYBRID ZONES AND SPECIATION

Whether gibbons are allopatric with secondary zones of overlap, or are parapatric, or allo-parapatric is not the issue for researchers working on gibbon classification. The issue really is gene flow. All authorities on gibbons recognize the existence of hybrid zones. The arguments center on whether or not gene flow is unrestricted between 'species', or restricted to narrow areas, leaving the rest of the 'species' genetically pure. Another argument expressed is that if any gene flow is occurring these gibbon 'populations' are not species. According to Wiley (1981), if the zones are narrow and 'old' then the populations in these areas are species, but Creel and Preuschoft (1984) insist that any gene flow under natural conditions means the animals are from the same species. Most authorities assume the gibbon hybrid zones are narrow, but the boundaries of these zones have not been accurately surveyed. Further survey is needed. However, this entire issue may be moot if the classifications of Creel and Preuschoft (1984) and Haimoff et al. (1984) are correct.

CONCLUSIONS

The primary disagreement in the creation of classification for gibbons arises from the use and emphasis of different character traits. For instance, Marshall and Sugardito (1986) created their classification using just coat color and song, while Creel and Preuschoft (1984) primarily used cranial and postcranial characters. A secondary problem is the hybrid zones and whether or not gene flow is occurring between 'populations'. Before an acceptable classification is possible, authorities must agree on which traits to use and how much weight to place on each trait, and they must agree on whether or not gene flow is occurring, and how that influences the question of species and subspecies.

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APPENDIX

GIBBONS OF THE LAR GROUP

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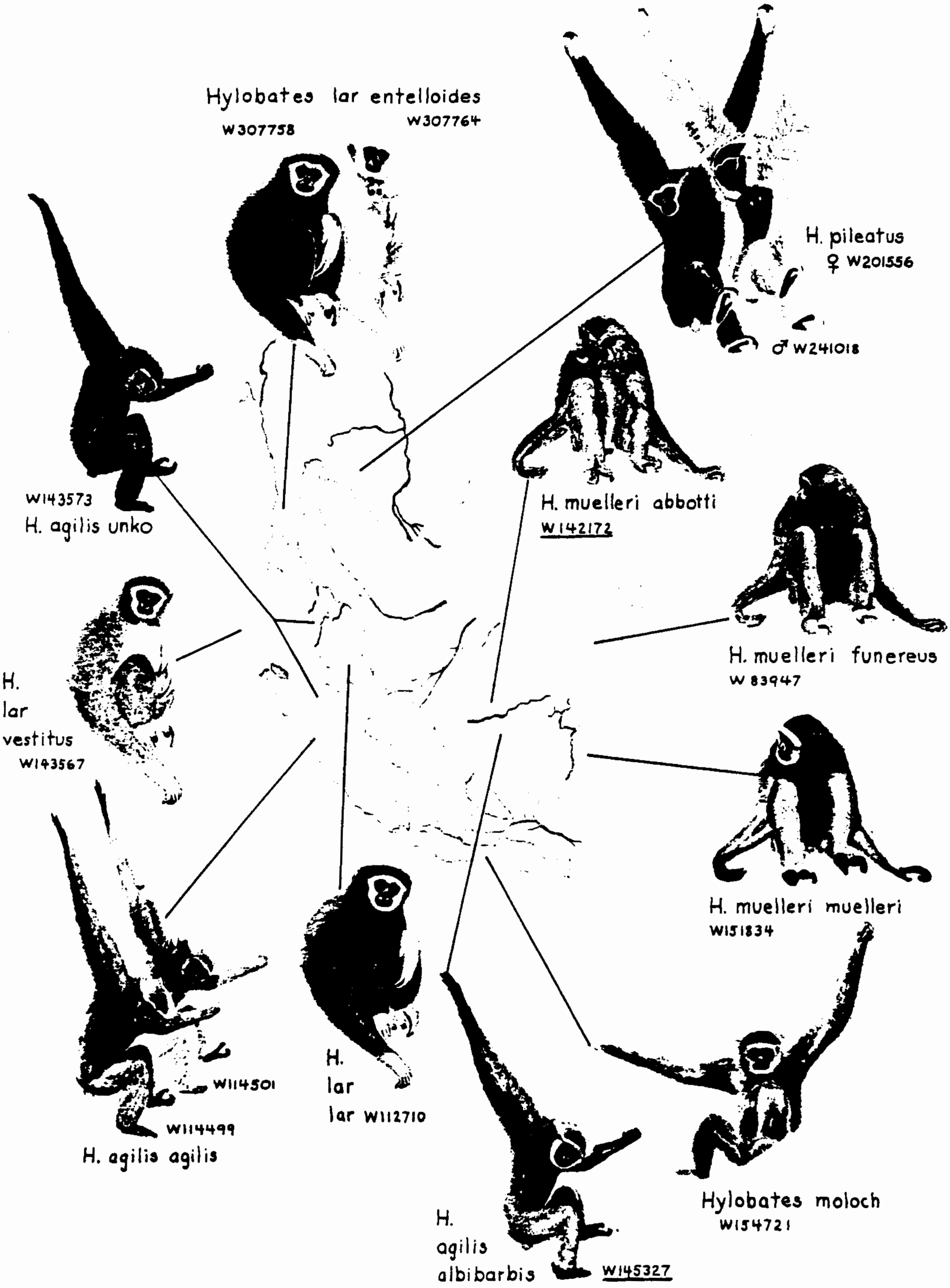
Hylobates lar entelloides
W307758
W307764
H. pileatus
♀ W201556
♂ W241018
W143573
H. agilis unko
H. muelleri abbotti
W142172
H. lar vestitus
W143567
H. muelleri funereus
W 83947
H. muelleri muelleri
W151834
W114501
W114499
H. agilis agilis
H. lar lar W112710
H. agilis albibarbis
W145327
Hylobates moloch
W154721