

Taxonomy and Evolution of Gibbons

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Three different data sets of approximately equal size were collected in order to assess their relevance for a reconstruction of gibbon phylogeny with cladistic methods. Set 1 uses characteristics of fur coloration, set 2 consists mainly of morphological and anatomical data, and set 3 consists of vocal data.

Because the fossil history of gibbons is virtually unknown,^{1,2} gibbon evolution can only be reconstructed from a comparative analysis of evolutionarily informative characteristics of modern gibbons and, to some degree, of related primate taxa that can be used as outgroups.

Several studies have tried to reconstruct gibbon phylogeny, using fur coloration, morphological, vocal, or molecular data.^{3–10} Each study produced a different result. As a consequence, the relationships among the various hylobatids are under debate, and even the evolutionary relationships among the major groups of gibbons remain unresolved.¹¹

For the present study, three different data sets of approximately equal size were collected in order to assess their relevance for a reconstruction of gibbon phylogeny with cladistic methods. Set 1 uses characteristics of fur coloration, set 2 consists mainly of morphological and anatomical data, and set 3 consists of vocal data.

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MATERIALS AND METHODS

Most recent studies agree that there are four distinct groups of gibbons, which are here referred to as genera. Table 1 presents the classification used for the present study.^{12,13}

The three large data sets that were analyzed are listed in Table 2. They were analyzed separately and compared with one another using partition-homogeneity tests.¹⁴

Phylogenetic analyses were conducted with unweighted characters using the PAUP program, version 4.0b3a.¹⁴ Two types of maximum-parsimony trees were generated: a branch-and-bound search of the same data set in PAUP yielded the shortest tree, i.e., a single most parsimonious cladogram, and the bootstrap option of PAUP was used to examine the robustness of internal nodes.

A hypothetical “ancestor” was used as an outgroup. This “ancestor” was assembled using primitive character states wherever they could be reconstructed or plausibly assumed.

The following standard measures were calculated in order to assess the “quality” of trees: consistency index (CI), retention index (RI), and the rescaled consistency index (RC),^{15,16} as well as the number of bootstrap values larger than 50. The indices basically range from 0–1, with higher RC values indicating that characters in the data set are more congruent with each other and the tree.

Mean pairwise distances between taxa (i.e., the sum of their character state differences, divided by the number of characters¹⁴) were calculated

with each data set. Three types of distances were compared: 1) distances among subspecies of the same species ($n = 4$), 2) distances among species of the same genus ($n = 38$), and 3) distances among members belonging to different genera ($n = 63$). In order to increase the sample of subspecies distances, *H. muelleri* was separated into its subspecies (*H. m. muelleri*, *H. m. funereus*, and *H. m. abbotti*) for this part of the analysis.

RESULTS

Because the three data sets are statistically different ($P = 0.01$) when compared with the partition-homogeneity test, they are not combined in this study.

The trees based on fur coloration (Fig. 1a) strongly contradict all previously published gibbon phylogenies.^{3–10} For instance, members of the *lar* group appear in the most basal positions of the two shortest trees (not shown). The *lar* group is not identified as a monophyletic group: *Hylobates klossii* is shown as the sister taxon of the siamang (*Symphalangus syndactylus*), obviously because both gibbons are completely black. In contrast, most previously published phylogenies identify *H. klossii* as a member of the genus *Hylobates*, whereas the siamang is placed in the genus *Symphalangus*.

The trees based on “noncommunicatory” data (Fig. 1b) resemble the trees of earlier studies far more closely. The data set has a relatively low resolution because of the many missing values in the data matrix. Many of the anatomical data were collected during very early studies, when several gibbon taxa were simply not known. As a result of the empty cells in the matrix, there is not one single most parsimonious tree, but an ensemble of 117 shortest trees.

TABLE 1. Main Divisions of Genus *Hylobates*^a

| Genus | Diploid Number of Chromosomes | Other Division Names | Species | English-Language Name |
|---------------------|-------------------------------|--|-----------------------------------|-------------------------------|
| <i>Hylobates</i> | 44 | <i>lar</i> group | <i>H. agilis</i> ^b | Agile gibbon |
| | | | <i>H. klossii</i> | Kloss's gibbon |
| | | | <i>H. lar</i> | White-handed gibbon |
| | | | <i>H. moloch</i> | Silvery gibbon |
| | | | <i>H. muelleri</i> ^c | Müller's gibbon |
| | | | <i>H. pileatus</i> | Pileated gibbon |
| <i>Bunopithecus</i> | 38 | | <i>B. hoolock</i> | Hoolock |
| <i>Nomascus</i> | 52 | <i>concolor</i> group, crested gibbons | <i>N. concolor</i> | Western black crested gibbon |
| | | | <i>N. sp. cf. nasutus</i> | Eastern black crested gibbon |
| | | | <i>N. gabriellae</i> | Yellow-cheeked crested gibbon |
| <i>Symphalangus</i> | 50 | | <i>N. leucogenys</i> ^d | White-cheeked crested gibbon |
| | | | <i>S. syndactylus</i> | Siamang |

^a Raising the four main groups of gibbons to genus rank follows the consensus reached at the workshop "Primate Taxonomy for the New Millennium" (February 25–29, 2000, Orlando, Florida), to be presented in a future publication, and reference 20.

^b Including *H. agilis albibarbis*.

^c Including *H. muelleri abbotti* and *H. muelleri funereus*.

^d Including *N. leucogenys siki*.

The trees based on vocal characteristics (Fig. 1c) are similar to those of data set 2. *Bunopithecus hoolock* appears in an unusually basal position in the tree, however, because of its many apparently primitive vocal characteristics. *Hylobates klossii* is identified as the sister taxon of *H. moloch*.

The various standard measures calculated in order to assess the "quality" of trees are shown in Table 2 (bootstrap values, CI, RI, and RC). Data set 1 scores distinctly worse in all variables than the other two data sets. The difference between data sets 2 and 3 is less distinct in these variables. Nevertheless, data set 3 has higher values in all of these variables (especially in bootstrap values) than set 2, indicat-

ing that particularly "good" trees are generated with vocal data.

The mean pairwise distances between gibbon taxa are shown in Figure 2. Fur coloration data are able to differentiate not only between species and genera, but also between subspecies. Both the range and standard deviation of the distances are extremely large, however, and show a broad overlap among different systematic levels. This means that differences in fur coloration provide little information on the genetic distance between any two taxa. Two subspecies may be more different in fur coloration than members of two different genera.

"Noncommunicatory" data, on the other hand, do not differentiate well

between subspecies, and the standard deviations for subspecies and species overlap. These data differentiate between some, but not all, species. The pairwise differences between members of different genera are distinctly greater than those between species, and standard deviations for species and genera do not overlap.

The vocal data produce similar results to the "noncommunicatory" data. This data set does not differentiate between subspecies at all, but differentiates well between species and genera. Standard deviations of subspecies, species, or genera do not overlap.

The three data sets also differ in the species groups they support (Table 2).

TABLE 2. Various Parameters of Trees in Figure 1, and Topologies of Gibbon Taxa Supported by These Trees^a

| Data Set Number of Characters Type of Tree | Set 1 37 | | Set 2 34 | | Set 3 34 | |
|---|-------------|------|-------------|------|-------------|------|
| | S | B | S | B | S | B |
| Tree length | 158 | 191 | 73 | 78 | 88 | 90 |
| Number of bootstrap values above 50 | | 5 | | 5 | | 10 |
| Number of shortest trees | 2 | | 117 | | 1 | |
| Consistency index (CI) | 0.49 | 0.41 | 0.66 | 0.62 | 0.67 | 0.66 |
| Retention index (RI) | 0.63 | 0.47 | 0.80 | 0.77 | 0.81 | 0.80 |
| Rescaled consistency index (RC) | 0.31 | 0.19 | 0.53 | 0.47 | 0.54 | 0.52 |
| Monophyly of <i>agilis</i> and <i>albibarbis</i> | – | – | – | – | + | + |
| Monophyly of <i>concolor</i> group | + | + | + | + | + | + |
| Monophyly of <i>lar</i> group (44-chromosome gibbons) | – | – | + | + | + | + |
| <i>H. hoolock</i> as sister group of <i>lar</i> group | – | – | + | + | – | – |
| <i>H. klossii</i> sister of all other members of <i>lar</i> group | – | – | – | – | – | – |

^a et 1, fur coloration data; Set 2, "noncommunicatory" data; Set 3, vocal data. S, shortest tree; B, Bootstrap 50% majority-rule consensus tree; +, supported; –, not supported.

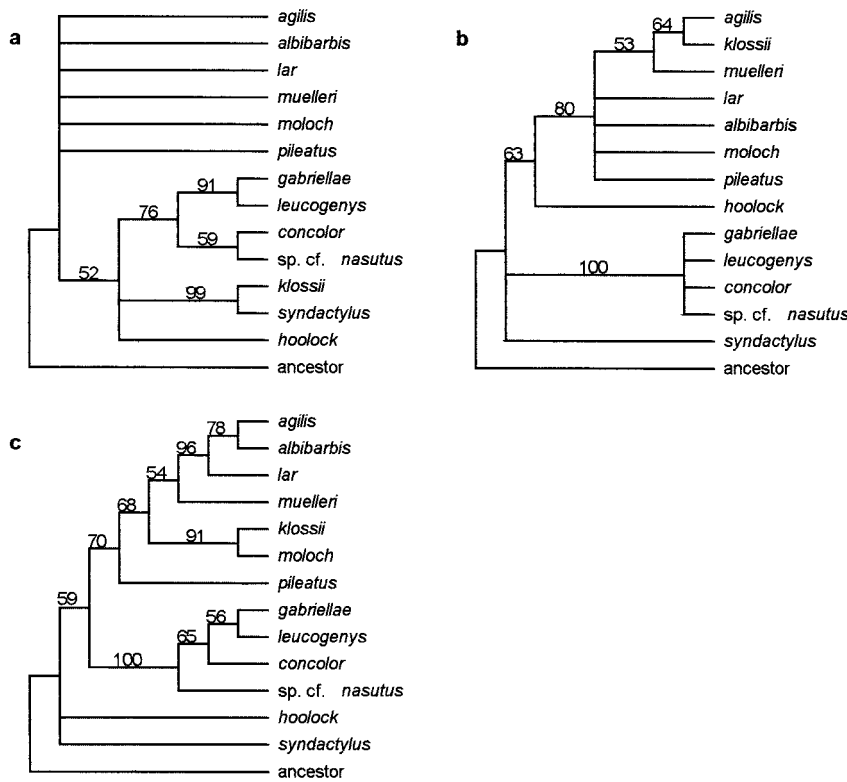


Figure 1. Maximum parsimony trees (bootstrap 50% majority-rule consensus) of three different data sets. **a:** Fur coloration data. **b:** "Noncommunicatory" data. **c:** Vocal data.

The sets do agree, however, in supporting monophyly of the *concolor* group at least to some degree, and in not supporting *H. klossii* as the sister taxon to the other members of the *lar* group.

DISCUSSION

A cladistic analysis suggests that the tempo of evolutionary change differs among the data sets under study, similar to DNA sequences derived from different parts of the genome. Fur coloration characters appear to change considerably faster than either "noncommunicatory" or vocal characters.

The three data sets produce different results, and each set appears to be suited to the analysis of different levels of resolution within the hylobatid radiation. Fur coloration characteristics appear to provide little information for a gibbon phylogeny, but may be valuable tools for subspecies identification, in contrast to most characters of the other two data sets. In addition, many fur coloration characters

differ among individuals of the same taxon (polymorphisms).

"Noncommunicatory" data would seem to be much better suited for reconstructing the gibbon phylogeny,

but of the data sets under study, the vocal data produce the most reliable phylogeny. The trees generated using vocal data suggest that:

Gibbons of the genus *Hylobates* (*lar* group) and the genus *Nomascus* (crested gibbons or *concolor* group) are each monophyletic groups. There is weak support for a sister-group relationship between the *concolor* and *lar* groups.

Hylobates klossii is neither the sister taxon of the siamang (*Symphalangus syndactylus*), as suggested by some early studies,^{17,18} nor the sister taxon or the most basal group of the *lar* group, in contrast to many previous studies.^{4-6,9,19} This species is a fully integrated member of the *lar* group,⁷ and apparently the sister taxon of *H. moloch*.

The same conclusion was independently reached by a study using a much smaller set of vocal characteristics (including degree of sex-specificity of the vocal repertoire, occurrence of solo songs, and preference for a specific time of day for song production).¹⁰

Bunopithecus hoolock may be more basal than previously believed. Most earlier studies recognized this species as the sister

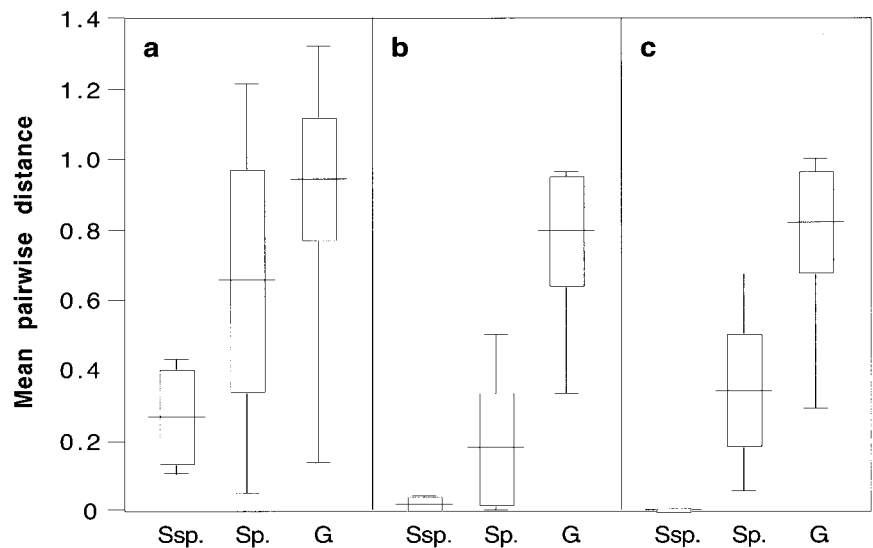


Figure 2. Pairwise character differences between (left to right) different subspecies (Ssp.) of the same species, species (Sp.) of the same genus, and genera (G.) of the same genus. **a:** Fur coloration data. **b:** "Noncommunicatory" data. **c:** Vocal data. Each boxplot shows mean value (horizontal line through box), standard deviation (box), and range ("whiskers").

taxon to the *lar* group,^{4,5,9} whereas a more basal position has only rarely been suggested.^{6,10,21}

The radiation of the four genera and of the species within the genera is not reliably resolved with these preliminary results. In future studies, the reliability of the trees may be improved by integrating data from several data sets, by weighting the characters, and by supplementing the missing variables in data set 2.

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