

# Speciation in Living Hominoid Primates

## 5

COLIN P. GROVES

### *Introduction*

The most widely discussed review of models of speciation in animals (White, 1978) lists seven possible modes:

1. Gradual divergence of two large populations after their geographic isolation
2. The founder principle
3. De facto differentiation of two races following extinction of the geographic intermediates
4. Local steepening of a cline
5. Selection against hybridization of strongly differentiated local races (area effects)
6. Stasipatric speciation: spread of chromosomal rearrangements aided by high levels of inbreeding
7. Sympatric speciation, in the strict sense, by assortative mating

Discussion of these models by Groves (1989) and examination of the mammalian evidence suggested that strictly allopatric (1-3) and parapatric (4-5) models do not necessarily explain observed patterns better than modes 6 and 7. A common pattern, in which modes 6 and 7 would work very well, is the modified centrifugal speciation pattern of Brown (1957).

It seems worthwhile to examine the applicability of these modes in the Hominoidea. Of the two families to be recognized in a cladistic schema (Groves,

1986, 1989), the Hylobatidae offer more evidence than do the Homiinae, but as we shall see a certain amount of inference is possible with regard to the Homiinae also.

### Speciation in the Hylobatidae

The Hylobatidae have been assigned to a single genus, *Hylobates*, since the revision of Groves (1972). Of the four subgenera, the distribution of one (*Symphalangus*) is entirely contained within that of one of the others (nominotypical *Hylobates*); the other three are allopatric to each other.

The initial divisions within the Hylobatidae are deep, perhaps unexpectedly so: PPED (plasma protein electrophoretic distance) units between the subgenera *Nomascus*, *Symphalangus*, and *Hylobates* average  $1.7 \pm 0.1$ , which is comparable to divisions within the Homiinae and implies a radiation beginning 4–5 million years ago (Cronin *et al.*, 1984). Work in progress by S. Easter and the author will test the amount of differentiation on nuclear and mitochondrial DNA sequences; it may have implications for genus-level taxonomy. By contrast, PPED units within the *H. (H.) lar* group are of the order of  $0.3-0.4$ , implying separation times under half a million years. It is interesting that in Chivers' (1977) model of speciation in the genus, although the initial diversification phase is set much too late according to the PPED criteria (Chivers puts it about 800,000 B.P.), the radiations of the *lar* group are placed, according to sea-level reconstructions, at about the right time period. Indeed, in that the members of the *lar* group are even now rather incompletely separated, a very late diversification is strongly implied.

Two of the four subgenera of *Hylobates* have sufficient diversity at the species/subspecies level to be of interest to the present discussion: *Nomascus* and *Hylobates*. Although species boundaries within these two subgenera appear to be superficially similar to each other, in being parapatric or at most interdigitating, the species-maintaining mechanisms seem on closer examination to be rather different.

### Nomascus

Groves (1972) classified all taxa of this subgenus into a single species, *H. (N.) concolor*, but anticipated its possible dismemberment at some future date when relationships became better known. The described taxa, whether species or subspecies, are mapped in Fig. 1. Since then, Dao (1983) and Ma and Wang (1986) have both proposed to separate *H. leucogenys* as a full species on the grounds of its marginal sympatry with *H. concolor sensu stricto* in Vietnam and Yunnan, respectively. Ma and Wang (1986) also supported their argument with reference to morphological findings, especially the shape of the baculum, which is a simple rod in *H. concolor*, but more complex in shape (probably more derived) in *H. leucogenys*. Groves and Wang (1990) have proposed, in addition, that a southern

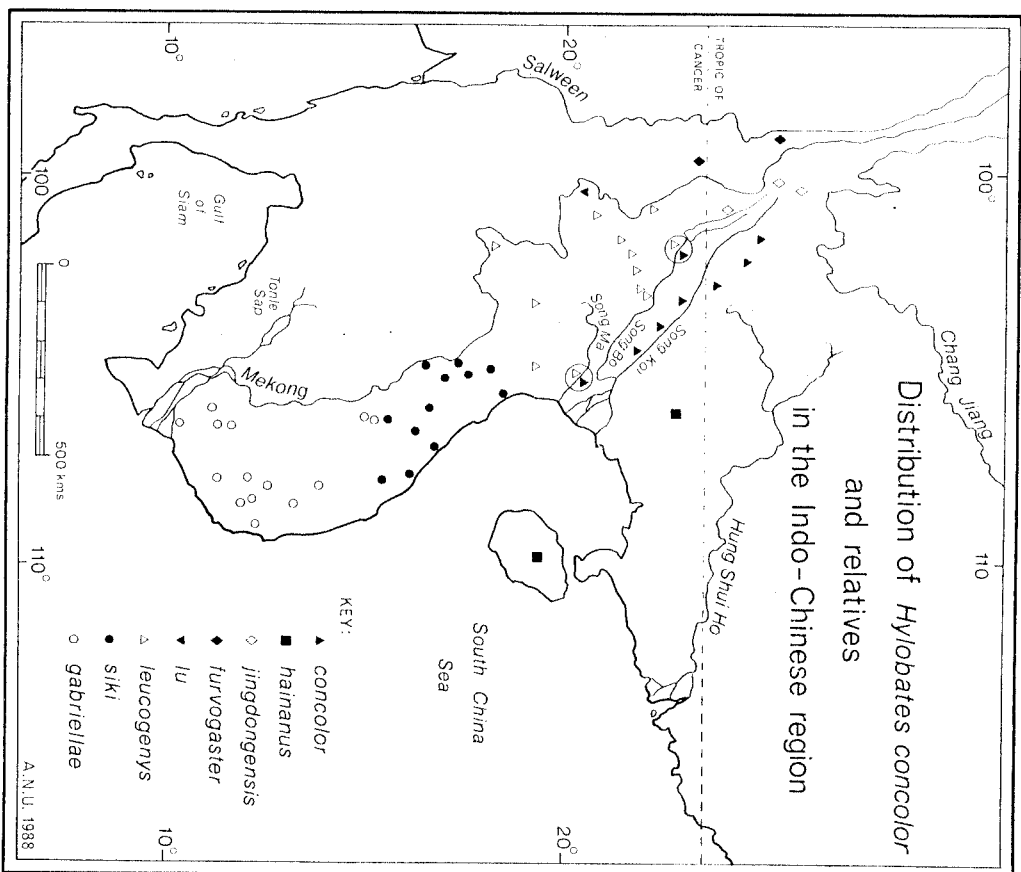


Fig. 1. Distribution of species and subspecies of the subgroup *Nomascus*.

species, *H. gabriellae*, is also distinguishable, appealing again to the morphology of the baculum, which is simple and resembles that of *H. concolor*. Boundary-zone data for *H. gabriellae* and *H. leucogenys* are lacking, but the two subspecies of the latter, *H. g. gabriellae* and *H. g. siki*, are known to interbreed where their ranges meet (Groves, 1972), though at what frequency is unknown.

Coururier and Lermould (1991) have examined karyotypes of four taxa in this taxonomically now rather complex subgenus: listing them north to south, they are *H. concolor hainanus*, *H. leucogenys*, *H. g. siki*, and *H. g. gabriellae* (taxonomy after Groves and Wang, 1990). Compared to *H. leucogenys*, whose karyotype has been well studied, *H. g. siki* differs by a reciprocal translocation

(1:22): *H. g. gabriellae* has the same translocation as *sibi*, as well as a pericentric inversion of chromosome 7, and *H. leucogenys* × *H. concolor* ?*hanianus* hybrids are heterozygous for inversion 7 (implying that it is present in homozygous state in the latter) and lack the 1:22 translocation. This oddly mosaic pattern may imply homoplasmy; alternatively, there have been considerable distributional changes in the past to explain the sharing of an inversion between the northernmost (*H. concolor*) and southernmost (*H. g. gabriellae*) taxa and its absence in the two more centrally distributed taxa.

The subspecies *H. c. lu* is cut off from its conspecifics by a bloc of *H. leucogenys* territory (Fig. 1); this may provide some support for the distributional reshuffling hypothesis; if, as I suspect, most or all of the character states of *H. leucogenys* are derived, then a centrifugal mechanism would explain it best. Again, the bacular similarity between *H. gabriellae* and *H. concolor* may imply past geographic musical chairs, but this similarity too seems likely to be primitive (given the simpler form of the baculum and its resemblance to that in other subgenera), so the same centrifugal mechanism may suffice. The most parsimonious model would seem to be that:

1. A widespread ancestral species resembled *H. concolor* in being all black in the male and juvenile, and with a black venter in the adult female, and possessing the small baculum and pericentric inversion 7
2. The southern populations of this species (proto-*H. gabriellae*) developed light-colored cheeks in the male and juvenile, and lost the ventral blackening of the adult female
3. The northern part (proto-*sibi/leucogenys*) of this southern form lost pericentric inversion 7
4. The northern part (proto-*leucogenys*) of this latter form developed a new style of cheek whiskers and a highly derived bacular morphology, and this morphology began to spread at the expense of preexisting ones
5. The remainder (proto-*gabriellae/sibi*) of the southern populations homogenized for reciprocal translocation 1:22; this and the bacular difference prevented introgression by *leucogenys*. Probably the striking facial differences of the males and ventral pattern differences of the females acted as specific mate-recognition systems protecting *H. concolor* from *leucogenys* introgression, and the bacular difference acted as a *de facto* reinforcement.

In this model speciation does not follow cladistic lines. Groves (1989) has argued that, indeed, there is no reason why it should.

It is interesting, in conclusion, that the translocation, whose possession differentiates *H. gabriellae* from *H. leucogenys*, may reinforce (or enforce) reproductive isolation, while the pericentric inversion does not (since it differentiates the two subspecies of *H. gabriellae*, known to intergrade in the wild). This, in turn, requires that isolation between *H. leucogenys* and *H. concolor*, separated chromosomally only by the inversion, must depend on some other factor: above I have suggested simple color pattern.

Field work—if sufficient forest survives in Vietnam and Laos—may of course reveal that the picture is quite different from that suggested by the

COLIN P. GROVES

museum data. Recall that to Groves (1972) the picture in the *H. lar* complex appeared quite different from the way we now know it to be.

## Hylobates

The *H. lar* group is a very tight-knit one, with a mosaic distribution of characters, involving mainly color polymorphism and the pattern of face and extremities; their distribution forms a complex of crosscutting north-south and east-west axes. The distributions of the putative species tend to be defined by rivers (Fig. 2), with different levels of interbreeding where their ranges meet across the headwaters. Although deciding how many species there are in this complex has some purely practical importance, one can only agree with Creel and Preuschoft (1984), who stated that "of much greater importance . . . is the opportunity afforded by the lesser apes to study the *process* of systematic differentiation, including speciation, among primates." They are, in reality, semi-species, of which some may have technically (on reproductive criteria) passed the point at which we could award them species status, and others have not.

At the headwaters of the Takhong River in the Khao Yai National Park, Thailand, two members of the group, *H. lar* and *H. pileatus*, meet and occasionally hybridize. Brockelman and Srikosamatara (1984) and Brockelman and Gitins (1984) have described the picture. More than 210 gibbon groups have been mapped in the area, though only 61 have been observed well, and just 18 of these appear to contain hybrids, although second-generation hybrids are not always recognizable. Among them are four "trios," groups of one male with two females of different genotypes, the junior female never having a dependent infant; at the time it appeared that such groups are unique to the hybrid zone, but subsequent fieldwork (Srikosamatara and Brockelman, 1987) has found such a group in pure *H. pileatus* in Khao Soi Dao, though the high frequency of trios in the hybrid zone remains a matter of significance.

In the Khao Yai overlap zone, pure *H. lar* can be found 4 km into the *pileatus* side of the zone, and pure *H. pileatus* go 5 km into the *lar* side; hybrids go further—9–12 km into the *lar* side and 6 km into the *pileatus* side (though the former is better studied). The change of the morphological index from 90% *lar* to 90% *pileatus* occurs over about 9 km (Brockelman and Gitins, 1984).

*Hylobates lar* comes into contact with another species of the group, *H. agilis*, at Ulu Mudah, on the shores of an artificial lake in a logged forest in northern peninsular Malaysia (Gitins, 1984; Brockelman and Gitins, 1984). In general, *H. lar* occurs on the south side of the lake and *H. agilis* on the north, but there are two mixed groups, one on either side (interestingly it is the male, in each case, that has strayed onto the wrong side), as well as a group that may be mixed or may be an *agilis* group on the wrong side.

Marshall *et al.* (1984) and Marshall and Sugardjito (1986) briefly describe a hybrid and backcross zone between what they term *H. mulleri* and *H. agilis albarbis* (two taxa that are difficult to differentiate by pelage characters but easy to distinguish vocally) at the headwaters of the Barito River. Kalimantan: they characterize the hybrid population as "sparse," in contrast to denser populations

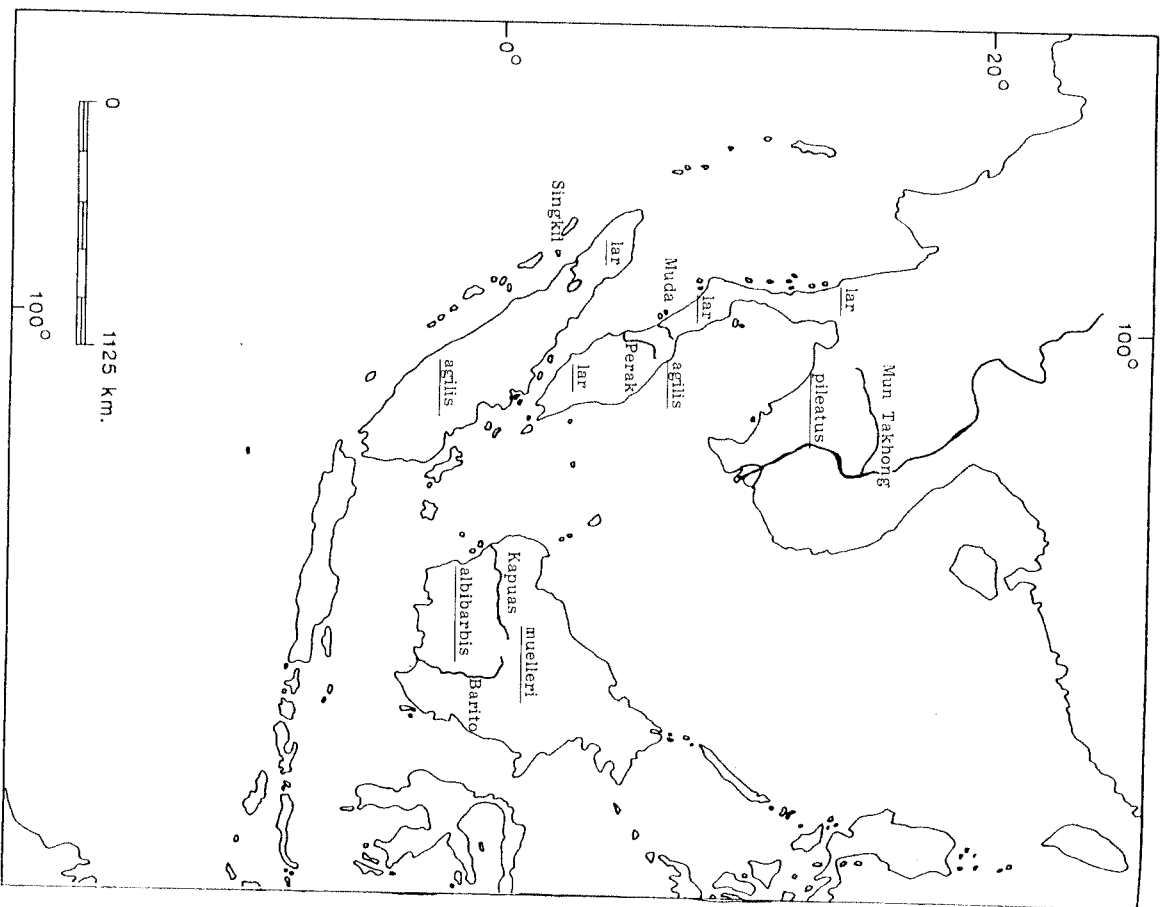


Fig. 2. Distribution of semispecies of the *lar* group, showing river barriers.

of the pure forms on either side. This zone has not yet been fully described, but additional information is given by Bodmer *et al.* (1991). The hybrid zone is between the rivers Busang (to the west) and Muring (to the east), upper feeder streams of the Barito; it covers several thousand square kilometers, with a density of 2.9 groups per square kilometer, which indeed is not high. West of the

Busang, towards the Joloi River, more hybrids occur; these are more *albibarbis*-like in the southern parts and more *muelleri*-like in the north. This doubtless explains Marshall and co-worker's (1984) mention of vocalizations typical of *H. muelleri* heard west of the hybrid zone amid the "dense, pure population of *H. aetilis*." A brief personal communication from R. J. Mather (August, 1990) confirms that the hybrid zone in this case is quite unbroken, with no "pure forms" to be found within it.

Of these three hybrid zones, two (the *lar/pileatus* and *lar/agilis* zones) would appear to produce low frequencies of hybrids only, leaving the parental forms in the majority, though the evidence in the second case is extremely poor due to past disturbance and disruption. On the other hand, the *albibarbis/muelleri* hybrid zone goes much further: only hybrids are encountered within it. The question to be asked is, why should this be? What factors keep them apart in the first and (presumably) second cases, but not in the third?

Members of the *H. lar* group differ from one another essentially only in two parameters: pelage and vocalization.

#### Pelage

*Hylobates lar* has white hands and feet and a full white face ring; either sex (in the Thai subspecies) may be either black or buffy in general body color. *H. pileatus* also has white feet, but the face ring is reduced essentially to a brow band; there is a whitish crown ring, surrounding a black patch, and the crown hair is more flattened and flares out sideways. In *H. pileatus* the mature male is predominantly black; the female is buffy with a black ventral surface.

In *H. agilis* the polymorphism resembles that of Thai *H. lar*, i.e., nonsexually dichromatic, but in Malay *H. lar* there is a wide spectrum of color variation, centered on a medium-brown tone. *H. agilis* lacks the white hands and feet of *H. lar*, and the face ring is reduced to a brow band with whitish cheek whiskers in the male but not usually in the female (Groves, 1984; Marshall *et al.*, 1984).

Between *H. muelleri* and *H. (cf. agilis) albibarbis* there is no such clear-cut color differentiation: Both tend to a gray-brown tone (in the Barito region, *H. muelleri* is the grayer of the two), with a darker crown and ventral region.

To arrive at some idea of how pelage color might act in mate recognition, the data of Fooden (1969) were reexamined for evidence of assortative mating. Fooden listed the color phase composition of gibbon pairs observed by him and Carpenter (1940), noting that there seemed to be positive assortative mating, i.e., dark × dark and pale × pale pairings predominated over dark × pale. He performed no statistical tests, however, so to test his claim I calculated  $\chi^2$  on the basis of his tables. From Fooden's own data ( $5 \text{ d} \times \text{d}$ ,  $10 \text{ p} \times \text{p}$ ,  $1 \text{ d} \times \text{p}$ ), we get  $\chi^2 = 12.12$  at  $1 \text{ df}$ ,  $p < 0.001$ ; from the data of Carpenter (1940)— $11 \text{ d} \times \text{d}$ ,  $5 \text{ p} \times \text{p}$ ,  $3 \text{ d} \times \text{p}$ ,  $2 \text{ p} \times \text{d}$ —we get  $\chi^2 = 4.95$  at  $1 \text{ df}$ ,  $p < 0.05$ . In both cases, therefore, the claim of positive assortative mating is substantiated: in *H. lar entelloides* and *H. l. carpenteri*, like tends to mate with like, and this differentiates both these subspecies of *H. lar* from *H. pileatus*, in which (there being sexual dichromatism) the pair are always unlike in color.

Turning to the data of Brockelman and Srikamatara (1984), we find that matings within mixed groups are as follows (irrespective of species or hybrid

status):  $6d \times d, 3p \times p, 1d \times p, 2p \times d$ . This gives  $\chi^2 = 5.53$  at  $1df, p < 0.05$ . In the overlap zone, therefore, gibbons tend to behave more like *H. lar*, i.e., like males with like. This is even the case for the two *H. pileatus*  $\times$  hybrid matings: in both cases the male *H. pileatus* had paired with a black hybrid (TO2 and SY3, respectively, in Brockelman and Gittins' Table 41.2), implying that pelage color may not be the most crucial factor in this species' mate preference, although it does seem to be so for *H. lar*.

The two mixed *H. lar/agilis* groups (Brockelman and Gittins, 1984) were one  $d \times p$ , one  $p \times p$ ; there is no basis for determining assortative mating tendencies here.

The two protagonists in the Borneo hybrid zone do not differ strongly in pelage characters. It may or may not be significant that here alone hybridization is more than merely occasional, but first the data from vocalizations must be examined.

### Vocalizations

Taxa of the *H. lar* group differ most strikingly in the vocalizations of both sexes: not only in the form of the vocalizations themselves, but also in the structure of the male/female duet and in the daily timing of the calls. The male's solo is typically given around dawn in *H. agilis* and *H. muelleri* (in which it is very frequent) and in *H. moloch* (in which it is rarer), but later (8–9 AM) in *H. lar* and *H. pileatus*, in both of which it is rarely given; whereas the duet (great call) is usually somewhat after dawn in the first three species and in *H. lar* (where it follows on from the male solos), but later in the morning in *H. pileatus* (Haimoff *et al.*, 1984). All these differences are potentially significant as Specific Mate-Recognition Systems (see below).

Mitani (1987a,b) studied the significance of vocalizations and of the difference between *H. muelleri* and *H. (cf. agilis) albibarbis* by playback experiments. When a group call or a solitary female call was played back, a nearby pair would approach and duet; but when a male solo was played, only mated males approached (Mitani, 1987a). This seems to imply a greater tolerance by females of males' vocalizations than vice versa. When male songs of *H. muelleri* were played to these same *albibarbis* groups (Mitani, 1987b), males did not invariably approach and females usually gave an alarm call. He concludes that the male song is strictly a spacing call, so that in this sense they are less inclined to recognize *H. muelleri* as competitors; but females are alarmed by *H. muelleri* males rather than regarding them as potential mates.

These findings now have to be placed in the context of the finding that the two taxa concerned interbreed and form a complete hybrid swarm. It may be that the differences in frequency of the various response behaviors are inadequate to prevent interbreeding, given the slowness of the visual (pelage) differences and/or the identity in timing and frequency of the male solos between the two.

*H. agilis* and *H. lar* differ in both these respects much more substantially than do the two Bornean taxa; while *H. lar* and *H. pileatus* differ in visual appearance, but neither makes a high frequency of male solos. To test which factor is more important, it would be necessary to determine whether the hybrid-

ization rates in the two cases are similar (which would suggest that the visual factor is crucial) or lower in *H. agilis* (implying that timing and frequency of male solos are crucial). The very limited evidence suggests the latter, but as the contact zones between *H. lar* and *H. agilis* seem to be completely disrupted now, the evidence may never be fully satisfactory. It must be noted, finally, that duet and female solitary playback experiments also need to be conducted, and all such experiments need to be repeated on different pairs of species.

### Perspective

It is certainly the case that taxonomic differentiation within species groups of *Hylobates* runs through an exceptionally wide gantlet, from 70-km wide intergrade zones (as between *H. lar entelloides* and *H. l. carpenteri*; Groves, 1972) to the very narrow ones, as surveyed above. It is tempting to suggest that the presence or absence of vocal differences may be a crucial factor; on the other hand, the two subspecies of *H. hoodlock*, which are not known to differ vocally, also hybridize over a very restricted area (Groves, 1972). Again, it is tempting to see the deciding factor as the presence of rivers as barriers, as rivers intervene between all the pairs of taxa in the *lar* group described above; yet the *Nomascus* taxa are not separated by rivers (it may be, of course, that in this case the differentiation between these taxa is so ancient that the rivers have long since altered their courses).

If vocalizations and perhaps pelage or facial patterns are such good Specific Mate-Recognition Systems (SMRS), how did they originate? Marshall *et al.* (1984) make the point that, starting from Javanese *H. moloch* as the putatively primitive taxon, we can distinguish an eastern and a western lineage of increasingly northward differentiation: soaring great calls and white face rings to the west (*lar* and *agilis*), and bubbling calls and fancy hair-dos to the east (*muelleri* and *pileatus*). At the same time there are crosscutting strands: black morphs, white hands and feet, and also three-rooted P<sub>3</sub>s (see Groves, 1972) in the north (*pileatus* and the northern races of *lar*), dorsoventral contrasts in the south (*muelleri* and light-phase *agilis*) (see also Groves, 1984). It looks like the result of an original clinal pattern being disturbed by the development of barriers, followed by homogenization on either side of them, an imprinting mechanism being implied.

Geissman (1984) has made interesting observations of two captive *H. lar*  $\times$  *H. pileatus* hybrids. The male's vocalization was almost identical to that of *H. agilis*, and the female's to that of *H. moloch*. Geissman reports that he consulted those familiar with the natural hybrid zones (Brockelman and Marshall) and discovered that this was noticeable in some wild hybrids also. The implication of a predominantly northward differentiation (see above) seems to be confirmed.

Brockelman and Gittins (1984) discuss the gibbon data, with comments on speciation, which they note is poorly or not at all correlated with ecological boundaries. The specific mate-recognition system concept is but a "starting point in defining a broader concept that includes any social communication character that affects reproductive success. . . . [it] is under strong stabilising selection": the demonstrative communication paradigm (Brockelman, 1984: p. 289), consisting of displays and other signals affecting potential mate recogni-

tion, resource defense, intrasexual interaction, and social bonding. Such a paradigm, they argue, would have to arise at the point of speciation itself: when the founder population was very small, given that new forms of such conservative characters would have no chance of spreading by natural selection in a large population: only in small isolated populations, with no near neighbors, would there be any chance of new variants becoming widespread and finally fixed.

This is fair enough, but given the observations and analyses of Groves (1972), Geissman (1984), and Marshall *et al.* (1984), that pelage character states and vocalizations are progressively more derived (from south to north), we can view each of them, to a degree, as elaborations on the one before: if a more southerly (= more primitive) state is a sign stimulus, then its more northerly (= more derived) version is the supernormal stimulus and so would spread. The stimuli form constellations (the total demonstrative communication paradigms, henceforth, DCPs), and their new, supernormal versions would spread in concert, their progress braked only by barriers such as seaways or river systems. Such a model opens up the possibilities that the recorded hybrid zones could be moving frontiers, shifting in time but temporarily held up by the river barriers. This would imply that the upper Barito feeder streams are, in effect, a genetic bottlenecking system, acting as a temporary brake on the spread of the *H. muelleri* DCP. The case of the *H. lar/pileatus* boundary is more complex, because *H. pileatus* is a combination of both eastern and western evolutionary streams, not merely a "supernormalization" of *H. lar*, so that the latter retains its own DCP validity and is not subject to invasion by that of *H. pileatus*.

### Speciation in the Hominidae

In contrast to the Hylobatidae, the Homnidae offer no discernable evidence of the mechanics of speciation. Instead, we have a group whose phylogeny is probably the most intensively researched of all living organisms, offering a wealth of inferential clues.

As summarized by Groves (1986), the evidence to the mid-1980s suggested a scenario approximated by follows. The earliest split in the hominoid line was between the orangutan lineage (Ponginae) and the others (Homninae). In the Homninae, the gorilla would be the sister group of the human/chimpanzee clade, a still controversial view, supported by some analyses (Diamond, 1988; Ruvoilo *et al.*, 1991) but challenged by others (Andrews, 1987). The view that sees evolutionary change as concentrated around speciation events—hence fast-evolving lines are more speciose than slower-evolving ones—was supported, and in particular there seemed to be much greater time depth within any one of the three great ape genera (*Pongo*, *Gorilla*, *Pan*) than within *Homo*. More recent findings have, however, indicated that in many respects, such as a chromosome morphology, humans have actually changed less from the common ancestor than have chimpanzees (Stanyon *et al.*, 1986).

The divergence between the two recognized orangutan subspecies is unexpectedly great, certainly way above the 10,000 years since the terminal Pleistocene sea-level rise separated Borneo from Sumatra. The possibility of

cranio-metric differences between intra-Bornean populations as great as those between any of these and the Sumatran population (Courtenay *et al.*, 1988; Groves *et al.*, 1992) is a reason for being cautious about recommending species separation for Bornean and Sumatran subspecies. For the moment, it may be noted that the genetic distance between catchall Bornean and Sumatran subspecies is considerably greater than between subspecies of other mammals, such as big cats (Janczewski *et al.*, 1990) and infers a separation date of some 1.13 ma (based on a 13-ma Ponginae/Homninae separation date).

Similarly, the indicated time depth between eastern and western lowland gorillas, and the implied time depth between eastern lowland and mountain gorillas (Groves, 1986) is startling. There is now a need to examine the genetic differences between population isolates within each subspecies of great apes.

According to the data cited in Groves (1986), the genetic distance between *Pan paniscus* and *P. troglodytes* is somewhat less than that between the two subspecies of *Pongo pygmaeus*, although this is not confirmed by the most recent study (Janczewski *et al.*, 1990). There are also indications of considerable differences among the populations of *P. troglodytes* traditionally given subspecific status, even though these are very poorly defined cranio-metrically (Groves *et al.*, 1992). Favoring a 4-million-year split between human and chimpanzee lines, Hasegawa and Horai (1991) calculate a separation time of between 1.70 and 2.45 ma between pygmy and common chimpanzees based on three data sets from noncoding portions of mtDNA (the standard errors of the three estimates overlap). These would be somewhat increased were a 5-million-year human/chimpanzee separation accepted instead, a probable maximum according to Hasegawa and Horai (1991).

These data all suggest that, morphologically at least, evolution in the non-human Homnidae (the so-called great apes) has been very slow. When their fossil records become better known, they will furnish excellent tests for the view that slowly evolving lineages have low speciation rates. Again, we must qualify this as "morphologically" (i.e., not in molecular factors; see above).

The only speciation mode indicated is geographical. Water barriers have traditionally been implicated in quasi-speciation among the great apes, and there seems no question of interbreeding in the wild between any two taxa (except perhaps the mysterious "subspecies" of *Pan troglodytes*). There is a rather striking contrast to gibbons: over the vast period of time since their separation, reproductive isolation has not evolved between Bornean and Sumatran orangutans (which interbreed confusingly in captivity), whereas to different degrees this has occurred between pairs of the far less well-differentiated taxa of lar-group gibbons.

### Conclusions

This brief survey of the nonhuman Homnidae serves to remind us of the diversity of possible pathways for speciation. In *Nomascus*, speciation has been accompanied by chromosome change; in nonmonotypical *Hylobates*, it has not, and it may be significant that these two different patterns define separate supra-

specific groups (see also Groves, 1989, 47–8). Specific mate-recognition systems take several forms, and the hybrid zones of *lar*-group gibbons offer opportunities for elucidating their relative importance. In general, the differences among the quasi-specific taxa of the Hylobatidae are considerably less than among the subspecies of *Gorilla gorilla* or *Pongo pygmaeus*, and far less than, say, among the semispecies of the genus *Papio*. It seems very doubtful whether such taxa could be differentiated if they were found as fossils, reinforcing the conclusions of several contributors to this symposium that species-level diversity in the fossil record is likely to be underestimated. The sorts of characters that differentiate the *lar*-group species are in no way different from those that differentiate subspecies, or even morphs. As discussed above, the most likely mode of origin for species in this group is precisely as derived polymorphic variants that spread as supernormal stimuli and, indeed, may still be "predatory" upon their plesiomorphic parents. On the other hand, the great ape data show us the other end of the spectrum: gibbon (at least *lar*-group) speciation is young and still active; great ape speciation and even subspeciation is ancient and stable.

### References

- Andrews, P. 1987. Aspects of hominoid phylogeny, in: C. Paterson (ed.), *Malesius and Monophyly in Evolution: Conflict or Compromise?*, pp. 21–53. Cambridge University Press, Cambridge, England.
- Bothner, R. E., Mather, R. J. and Chivers, D. J. 1991. Rain forests of central Borneo—threatened by modern development. *Oryx* 29:21–26.
- Broekelman, W. Y. 1984. Social behavior of gibbons: Introduction, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman and N. Creel (eds.), *The Lesser Apes*, pp. 285–290. Edinburgh University Press, Edinburgh.
- Broekelman, W. Y. and Gitlins, S. P. 1984. Natural hybridization in the Hylobates *lar* species group: implications for speciation in gibbons, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, pp. 498–532. Edinburgh University Press, Edinburgh.
- Broekelman, W. Y., and Sirkosamatra, S. 1984. Maintenance and evolution of social structure in gibbons, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, pp. 298–323. Edinburgh University Press, Edinburgh.
- Brown, W. L. 1957. Centrifugal speciation. *Q. Rev. Biol.* 32:247–277.
- Carpenter, C. R. 1940. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Monogr.* 16:1–212.
- Chivers, D. J. 1977. The lesser apes, in: HRH Kanter and G. A. Bourne (eds.), *Primate Conservation*, pp. 539–98. Academic Press, London.
- Coumter, J., and Lennoult, J. M. 1991. Karyotypic study of four gibbon forms previously considered as subspecies of *Hylobates (Nomascus) concolor* (Primates: Pongidae, Hylobatidae). *Folia Primatol.* 56:95–104.
- Courney, J., Groves, C., and Andrews, P. 1988. Inter- and intra-land variation? An assessment of the differences between Bornean and Sumatran Orang-utans, in: J. H. Schwartz (ed.), *Orangutan Biology*, pp. 19–29. Oxford University Press, New York.
- Creel, N., and Preuschoft, H. 1984. Pathways of speciation: an introduction, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, University Press, Edinburgh.
- Cronin, J. E., Saich, V. M., and Ryder, O. 1984. Molecular evolution and speciation in the lesser apes, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, pp. 467–483. Edinburgh University Press, Edinburgh.
- Dao, V. T. 1983. On the north Indochinese gibbons (*Hylobates concolor*) Primates: Hylobatidae) in North Vietnam. *J. Hum. Evol.* 12:367–72.
- Diamond, J. M. 1988. DNA-based phylogenies of the three chimpanzees. *Nature* 332:6856.
- Fooden, J. 1969. Color phase in gibbons. *Evolution* 23:627–644.
- Geissmann, T. 1984. Inheritance of song parameters in the gibbon song, analysed in 2 hybrid gibbons (*Hylobates pilosus* × *H. lar*). *Folia Primatol.* 42:216–235.
- Gitlins, S. P. 1984. Territorial advertisement and defence in gibbons, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, pp. 420–424. Edinburgh University Press, Edinburgh.
- Groves, C. P. 1972. Systematics and phylogeny of gibbons, in: D. M. Rumbaugh (ed.), *Gibbon and Siamang*, Vol. 1, pp. 1–89. S. Karger, Basel.
- Groves, C. P. 1984. A new look at the taxonomy and phylogeny of the gibbons, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, pp. 542–561. Edinburgh University Press, Edinburgh.
- Groves, C. P. 1986. Systematics of the Great Apes, in: D. R. Swindler and J. Erwin (eds.), *Comparative Primate Biology. I. Systematics, Evolution and Anatomy*, pp. 187–217. Alan R. Liss, New York.
- Groves, C. P. 1989. *A Theory of Human and Primate Evolution*. Oxford University Press, Oxford.
- Groves, C. P., and Wang Y. 1990. The gibbons of the subgenus *Nomascus* (Primates, Mammalia). *Zool. Rev.* 11:147–154.
- Groves, C. P., Westwood, C., and Shea, B. T. 1992. Unfinished business: Mahalanobis and a clock-work orang. *J. Hum. Evol.* 22:327–340.
- Hannoff, E. H., Gitlins, S. P., Whitem, A. J., and Chivers, D. J. 1984. A phylogeny and classification of gibbons based on morphology and ethology, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, pp. 614–632. Edinburgh University Press, Edinburgh.
- Hasegawa, M., and Horai S. 1991. Time of the deepest root for polymorphism in human mitochondrial DNA. *J. Mol. Evol.* 32:37–42.
- Janczewski, D. N., Goldman, D., and O'Brien, S. J. 1990. Molecular genetic divergence of Orang Utan (*Pongo pygmaeus*) subspecies based on isozyme and two-dimensional gel electrophoresis. *J. Hered.* 81:375–387.
- Ma S., and Wang Y. 1986. The taxonomy and distribution of the gibbons in southern China and its adjacent region, with description of three new subspecies. *Zool. Res.* 7:393–410.
- Marshall, J., and Sugardjito, J. 1986. Gibbon systematics, in: J. Erwin and D. R. Swindler (eds.), *Comparative Primate Biology. I: Systematics, Evolution and Anatomy*, pp. 137–185. Alan R. Liss, New York.
- Marshall, J. T., Sugardjito, J., and Markaya, M. 1984. Gibbons of the Lar Group: relationship based on voice, in: H. Preuschoft, D. J. Chivers, W. Y. Broekelman, and N. Creel (eds.), *The Lesser Apes*, pp. 535–541. Edinburgh University Press, Edinburgh.
- Mianni, J. C. 1987a. Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behav. Ecol. Sociobiol.* 20:265–269.
- Mianni, J. C. 1987b. Species discrimination of male song in gibbons. *Am. J. Primatol.* 13:413–423.
- Ruvolo, M., Disotell, T. R., Allard, M. W., Brown, W. M., and Honeycutt, R. L. 1991. Resolution of the African hominoid trichotomy by use of mitochondrial gene sequence. *Proc. Natl. Acad. Sci. USA* 88:1370–1374.
- Sirkosamatra, S., and Broekelman, W. Y. 1987. Polypyny in a group of pileated gibbons via a familial route. *Int. J. Primatol.* 8:389–393.
- Sanjayan, R., Chiarulli, B., Gonthier, K., and Patton, W. H. 1986. The phylogenetic and taxonomic status of *Pan paniscus*: a chromosomal perspective. *Am. J. Phys. Anthropol.* 69:489–498.
- White, M. J. D. 1978. *Models of Speciation*. W. H. Freeman, San Francisco.