teraural line (*7*)]. The number of silver grains overlying a neuron varied considerably from one cell to another. The silver grains overlying a perikaryon were often not single but clustered in small groups. Only medium-sized (12 to 15 μm) (none of the rarer "giant") neurons were labeled. The majority of labeled perikarya were localized in a more external part of the caudoputamen, close to the unlabeled subcortical white matter. The labeling in fiber bundles in the neuropil and around labeled cell bodies was probably at least partly due to the migration of radioactive material in the axons back to the striatal perikarya. In the globus pallidus, the high density of silver grains over fiber bundles did not permit us to determine whether certain neurons were labeled (*12*). In the [^{3}H]GABA cases we saw no perikaryal labeling in the cortex or in the nucleus raphe dorsalis. In both of these areas, labeling was easily detected after HRP was injected into the nigra. In the HRP cases, the labeling in the caudoputamen extended over a wider rostro-caudal region than it did in the [^{3}H]GABA experiments. The type of neurons labeled was the same in both kinds of experiments. The results obtained with [^{3}H]GABA suggest that striato-nigral neurons containing GABA were selectively labeled, although it was not possible to control for false-positive perikaryal labeling in striatal neurons with neurotransmission mediated by substance P (*13*). Substance P neurons had been localized, however, in more rostral portions of the caudoputamen than the ones in which the labeled perikarya were seen (*14*).

No perikaryal labeling was observed after nigral injection of GABA precursors like glutamate (0.05 μl of L-[G-^{3}H]glutamic acid, 14 μCi; specific activity, 28 Ci/mmole; Radiochemical Centre) or glutamine (0.05 μl of L-[G-^{3}H]glutamine, 15 μCi; specific activity, 21 Ci/mmole; Radiochemical Centre) (*15*). These negative findings might indicate that newly synthetized transmitter did not get into compartments for retrograde axonal migration in amounts high enough to be detected in the perikaryon. The results demonstrated, in addition, a high degree of chemospecificity for the retrograde perikaryal labeling.

The labeling of nigral afferents originating in the cortex, the caudoputamen, and the nucleus raphe dorsalis only with the unspecific tracer HRP confirms earlier studies. A differential pattern was found, however, with radioactive transmitters. After [^{3}H]serotonin injection into the substantia nigra, neurons were retrogradely labeled in the dorsal raphe nucleus but not in the caudoputamen, whereas after [^{3}H]GABA injections the labeling pattern was the opposite. These results support the hypothesis of transmitter-specific retrograde tracing. Certain limitations in the chemospecificity are suggested in the case of serotonin by slight cortical labeling. Although the new method is not yet established, it may prove a useful tool for indicating simultaneously the transmitter and the connectivity of labeled neurons. Whether transmitter-specific retrograde labeling is based on selective uptake and active axonal transport and whether it is biologically meaningful (for example, in signaling the state of the terminal to the neuronal perikaryon) remains to be investigated.

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28 March 1979

Hybrid Ape Offspring of a Mating of Gibbon and Siamang

Abstract. *The serendipitous mating of a male gibbon,* Hylobates moloch, *and a female siamang,* Symphalangus syndactylus, *has produced two female offspring born 1 year apart. The hybrid karyotype of 47 chromosomes comprises the haploid complements of the parental species, 22 for the gibbon and 25 for the siamang. Chromosomal G and C banding comparisons revealed no clear homologies between the parental karyotypes except for the single chromosome in each species containing the nucleolus organizer region. The lack of homology suggests that the structural rearrangement of chromosomes has played a major role in the process of speciation for these lesser apes.*

On 11 August 1975 a siamang, *Symphalangus syndactylus*, gave birth to a female offspring fathered by a silver-gray gibbon, *Hylobates moloch*. Karyotypic analysis of the offspring, locally termed a siabon (*1*), reveals a complement of 47 chromosomes. This is the first reported viable hybrid of apes (*2*). The unexpected mating was made possible when in 1971 two adolescent female siamangs and one adolescent male gibbon were housed together at Atlanta's Grant Park Zoo as an exhibit of lesser apes. The siabon was abandoned by the mother at 3 months of age and was raised at the Primate Behavior Laboratory of Georgia State University apart from other apes. She has been given routine care and maintained in excellent health. A second female offspring, born 30 August 1976 to the same pair, died at 4 1/2 months of age from complications of an infection that

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occurred after a compound fracture of the fibula.

Both hybrid offspring had black natal coats. Now at 3 years of age the surviving siabon has black fur resembling that of her siamang mother. As a very young infant she had a light-colored facial ring, a distinct gibbon feature, which has gradually faded leaving now a white beard, a siamang attribute. She does not have the characteristic throat sac of the siamang, and this may be one reason that her vocalizations lack the variety of the siamang while retaining the lower tonal quality of the maternal species. There is no semblance of a great call in her current vocal repertoire. She has the webbing between the second and third toes characteristic of the siamang, hence the name syndactylus. Body measurements of the siabon at 18 months of age (*3*) reveal some features of each parental species; the length of the leg relative to the trunk is like that of the siamang, whereas the ratio of the arm to leg length is of gibbon proportions. These relationships may, however, change with age.

This gibbon-siamang cross is genetically noteworthy because it involves animals of marked chromosomal disparity. The gibbon has 44 chromosomes (22 pairs) while the siamang has 50 (25 pairs). The siabon has the combined haploid complements (22 + 25), producing a total of 47 chromosomes (*4*). The G band chromosome patterns for the parental species with the matching hybrid karyotype are presented in Fig. 1. The G bands of the *Hylobates moloch* presented here match those of *Hylobates lar* (*5*). In addition to the difference in the absolute number of chromosomes, only one G band homology between the parental karyotypes can be positively identified. It was found that the metacentric chromosome 15 of the gibbon and the acrocentric chromosome 20 of the siamang each contained the achromatic nucleolus organizer region. With this clue to homology, the patterns of these two chromosomes can be matched with one another by a pericentric inversion; the dark-staining segment above the light-staining nucleolus organizer region on the upper arm of gibbon chromosome 15 has either shifted to or shifted from the dark terminal segment of the lower arm of siamang chromosome 20. The absence of any other obvious homologies indicates that many other chromosomal rearrangements have occurred since the divergence of these two species.

Chromosomal C band patterns (Fig. 2) also reveal restructuring. The gibbon has centromeric C bands while the siamang has predominantly telomeric C band patterns (*4*). The function of the C band region remains the subject of much debate (*6*). Studies indicate that, as this heterochromatic material is increased in size and in its proximity to adjacent euchromatic gene regions, the frequency of recombination in these regions is reduced (*7*). Thus the formation of large telomeric C bands may be responsible for the reduction in species diversification, which is indicated by there being only two subspecies of siamang while there are 15 subspecies of gibbon (*8*).

Ecologically, the gibbon and siamang are sympatric inhabitants of Southeast Asia. They consume essentially the same vegetation, but a greater portion of the gibbon diet consists of fruits and berries, while the siamang relies more on leaves and shoots (*9, 10*). Siamangs are nearly twice the weight of gibbons of the corresponding sex (*10*), with the males of each species being slightly larger (the gibbon father weighed 7.3 kg while the siamang mother has maintained a weight of 9.5 kg since the birth of the first hybrid). The family group of the gibbon and the siamang is characterized by a monogamous pair bond (*9, 11*). The vocalizations of each species differ distinctly from each other and by sex (*12*). The most striking aspect of the sympatric nature of these two species is that one has not displaced

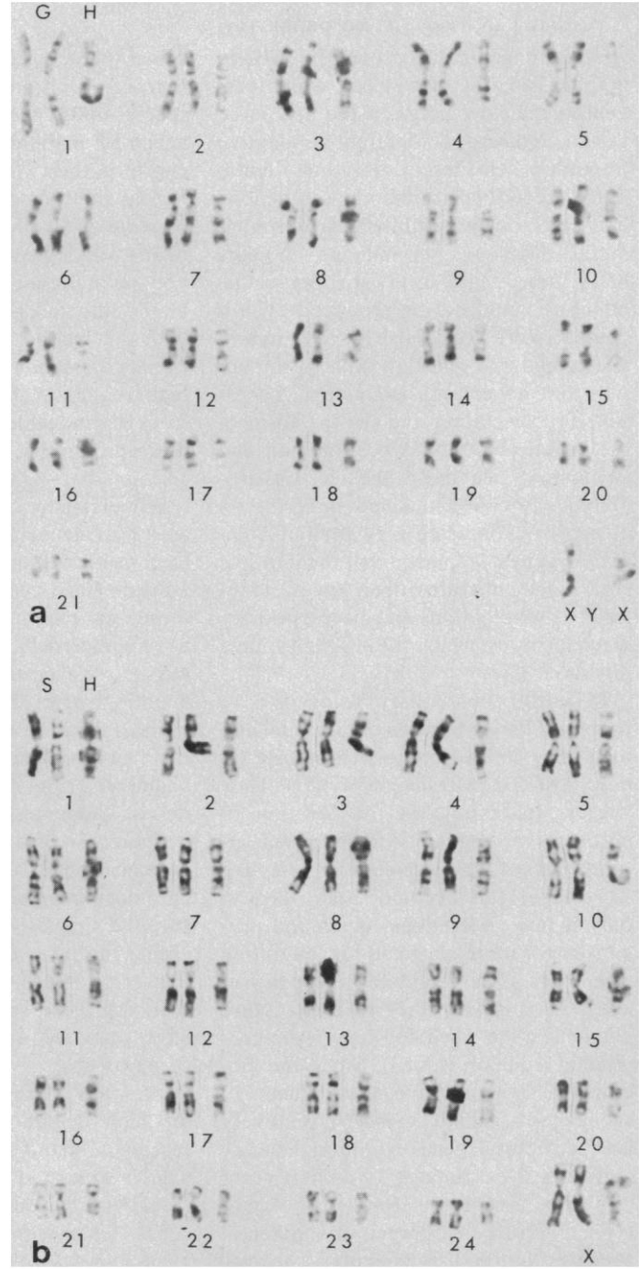

Fig. 1. G-banded karyotypes of the gibbon and siamang parents with the matching siabon chromosomes. The chromosomes are presented in groups of three. (a) The two chromosomes on the left are the gibbon (*G*) pair and the one on the right is the corresponding hybrid (*H*) chromosome. (b) The siamang (*S*) pair is displayed to the left of the hybrid (*H*) chromosome. The 47 siabon chromosomes shown are from a single leukocyte. The gibbon chromosome 15 and the siamang chromosome 20 contain the very light nucleolus organizer region just above the centromere. The dark-staining upper end of gibbon chromosome 15 appears to have either shifted to or shifted from the lower end of siamang chromosome 20. The small number of banding homologies indicates that many structural rearrangements must have occurred with the divergence of the gibbon and siamang.

the other while they occupy highly similar niches.

Year-round groups of each species occupy a small territory, of about 0.4 km^2 (*10*), that is defended against conspecifics, yet members of the other species are not excluded. This allows for a siamang family to inhabit an area that is also occupied by a group of gibbons. Interspecific encounters in the wild have been observed although these meetings are usually brief and result in either the immediate retreat of the gibbon group (*10*) or their being chased away by the male siamang (*9*). However, a persistent group of gibbons may cause a male siamang to relinquish a disputed food tree (*9*). Since nonagonistic interactions have not been reported, the occurrence of an interspecific mating in the wild is highly unlikely.

Evolutionary theory has held that speciation generally occurs by a geographic isolating mechanism which prevents gene flow between the separated groups and leads to differential adaptive or random selection of subsequent mutations. According to this view, a genetic barrier gradually accumulates over hundreds, thousands, or millions of years before reaching a level whereby viable offspring could not be produced even if contact were reestablished. The hybrid ape brings into question both (i) the notion that geographic isolation is necessary for speciation and (ii) the form of the genetic barrier between gibbon and siamang. Since these species are geographically contiguous and since the viable hybrids indicate very similar, compatible genes, it appears that the multiple rearrangements rather than any accumulated point mutations may be the primary mechanism by which these species have diverged.

Recently, evolutionary biologists have proposed that speciation of placental animals may indeed proceed primarily by chromosomal rearrangements (*13*). They suggest that shifts in the location of chromosome segments create a new arrangement of genes which, with selective advantage, can become established in only a few generations, given the propensity for inbreeding and low migration rate such as is found for these lesser apes. In this way the social structure eliminates the need for long-term geographic isolation (*13-15*). Since the gibbon and siamang have nearly identical sequences of amino acids (*16*), relatively little structural gene evolution has occurred in the estimated 15 million years (*17*) since divergence. Hence the karyotypic differences between the parental species reported here support a chromosomal theory of evolution. In this view, rearranged chromosomes both create a species difference and provide the mechanism for maintaining it. The rearranged chromosomes would (i) induce morphological species change presumably by position effect (this process can alter the regulation of gene expression without involving mutation of the DNA sequences of the affected genes) and (ii) interfere with the meiotic pairing process during gamete formation. In the latter effect, the high frequency of pairing errors resulting from rearrangements can greatly reduce the reproductive viability of hybrid offspring.

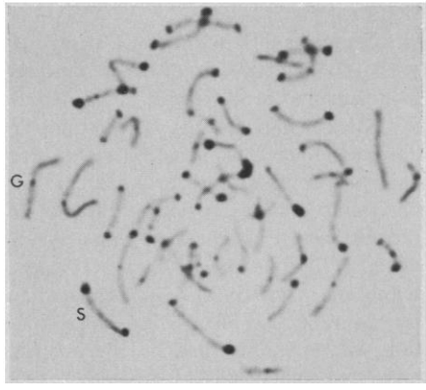

Fig. 2. C-banded siabon chromosomes showing both the gibbon (*G*) type C bands with the usual mammalian location at the centromere and siamang (*S*) type C bands that have a telomeric location. Thus, the structural location and perhaps the function of C bands are different in gibbons and siamangs.

The existence of viable hybrids as well as the evidence of highly similar structural proteins in gibbon and siamang (*16*) indicate little gene divergence between these two parental species. Yet the almost complete lack of banding homology strongly suggests the presence of a meiotic barrier between these species such as described above. A genetic barrier need not impede the production of viable offspring, if it impedes the production of viable grandchildren.

The cross of a gibbon and a siamang is remarkable because of the striking chromosomal dissimilarity between the parental species. While the factors governing the rates of chromosomal evolution are not yet understood, it is clear that, for these species, rearrangements have occurred quite rapidly (*18*). This chromosomal divergence between the lesser apes stands in sharp contrast to the high degree of chromosomal conservatism found in the great apes and man as well as in most of the Old World monkeys (the four major genera of Cercopithecinae with 42 chromosome complements) (*19*). This suggests that, in terms of chromosome structure, there exists a greater genetic distance between these lesser apes than that which distinguishes the great apes from one another and from man.

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20. We thank Dr. Duane M. Rumbaugh and Dr. Arthur Falek for help in preparing this report.

8 November 1978; revised 29 January 1979