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Reciprocal chromosome painting between a New World primate, the woolly monkey, and humans

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Abstract

We employed fluorescence-activated chromosome sorting (FACS) to construct chromosome paint sets for the woolly monkey (*Lagothrix lagotricha*) and then FISH to reciprocally paint human and woolly monkey metaphases. Reciprocal chromosome painting between humans and the woolly monkey allowed us to assign subchromosomal homologies between these species. The reciprocal painting data between humans and the woolly monkey also allow a better interpretation of the chromosomal difference between humans and platyrrhines, and refine hypotheses about the genomic rearrangements that gave origin to the genome of New World monkeys. Paints of woolly monkey chromosomes were used to paint human metaphases and forty-five clear signals were detected. Paints specific to each human chromosome were used to paint woolly monkey metaphases. The 23 human paints gave 39 clear signals on the woolly monkey karyotype. The woolly monkey chromosomes painted by human paints produced 7 associations of segments homologous to human chromosomes or human chromosome segments: 2/16, 3/21, 4/15, 5/7, 8/18, 10/16 and 14/15. A derived translocation between segments homologous to human chromosomes 4 and 15 is a synapomorphic marker linking all Atelines. These species may also be linked by fragmentation of homologs to human 1, 4, and 15.

Introduction

We employed FACS to construct chromosome paint sets for the woolly monkey (*Lagothrix lagotricha*) and then FISH to reciprocally paint human and woolly monkey metaphases. Reciprocal painting between humans and the African green monkey, lemurs and tree shrews has recently been reported (Müller *et al.* 1997, 1999, Finelli *et al.* 1999). However, no reciprocal painting has been reported between humans and a New World monkey. Reciprocal chromosome painting between humans and woolly monkey allowed us to assign subchromosomal homologies between these species. The hybridization pattern of the woolly monkey was then compared with that found in other primates.

Woolly monkeys are generally considered to be part of the family Atelidae (comprised of Ateles, Lagothrix, Brachyteles and Alouatta); however, the branching order within the Atelidae is still debated. (Rosenberger 1984, Ford 1986, Kay 1990). However, most recent molecular data suggest that Lagothrix is the sister species of Brachyteles (Hugot 1998, Canavez *et al.* 1999, Horovitz *et al.* 1998, Meireles *et al.* 1999, von Dornum & Ruvolo 1999, Schneider 2000).

Molecular cytogenetic data have shown that Atelidae have experienced a high rate of chromosomal rearrangement (Consigliere *et al.* 1996, Morescalchi *et al.* 1997, Consigliere *et al.* 1998). Therefore, we hoped that cytogenetic data might be informative about evolutionary relationships within these primates.

First reports based on classical staining established that the karyotype of *Lagothrix lagotricha* had a diploid number of $2n = 62$ with 14 pairs of metacentric or submetacentric chromosomes and 16 pairs of acrocentric chromosomes (Chu & Bender 1962, Egozcue & Perkins 1970). Later, banding techniques were used on woolly monkey chromosomes (Garcia *et al.* 1980) and comparisons were made between the chromosomes of the woolly monkey and other species. Homologies to most human chromosomes were proposed (Dutrillaux *et al.* 1980, Viegas Pequignot *et al.* 1985, Clemente *et al.* 1987). Dutrillaux (1986) placed Lagotrix as the sister species to Ateles, but did not include Alouatta in his analysis.

The reciprocal painting data between humans and woolly monkey also allow a better interpretation of the chromosomal difference between humans and platyrrhines and refine hypotheses about the genomic rearrangements that gave origin to the genome of New World monkeys. Finally, establishing chromosomal homologies allows a transfer of gene mapping data from humans to woolly monkey thus aiding both disease and genetic trait analyses (Wienberg & Stanyon 1998).

Materials and methods

A fibroblast cell line from a single female *Lagothrix lagotricha* was used. The cells were from the Coriell Institute for Medical Research (repository number AG05356). Standard tissue culture and chromosome preparation techniques were followed. Sequential G-banding before *in-situ* hybridization was as previously described (Wienberg *et al.* 1990, Wienberg *et al.* 1992, Consigliere *et al.* 1996).

Flow sorting and preparation of chromosome painting probes

Both human and woolly monkey chromosome-specific probes were made by degenerate oligonucleotide primed PCR (DOP-PCR) from flow sorted chromosomes using PCR primers, amplification and labeling conditions as previously described (Telenius *et al.* 1992, Rabbitts *et al.* 1995, Wienberg & Stanyon 1997, Stanyon *et al.* 1999). Chromosome sorting was performed using a dual laser cell sorter (FACStar Plus; Becton Dickinson). This system allowed a bivariate analysis of the chromosomes by size and base-pair composition. About four hundred chromosomes were sorted from each peak in the flow karyotype. Chromosomes were sorted directly into PCR tubes containing 30 μl distilled water. The same 6MW primer (Rabbitts *et al.* 1995) was used in the primary reaction and to label the chromosomal DNA with biotin dUTP or digoxigenin-dUTP in a secondary PCR. After hybridization and washing of the slides biotinylated DNA probes were detected with avidin coupled with Cy-3 (Amersham) or fluorescein isothiocyanate (FITC; Vector). Digoxigenin-labeled probes were detected with antidigoxigenin antibodies conjugated with FITC or Rodamine (Roche).

Digital images were taken using a cooled CCD camera (Photometrics NU200 equipped with a Kodak KAF1400 CCD chip) coupled to the microscope. Imaging software was SmartCapture (Digital Scientific, Cambridge, UK).

Results

Karyotype

The woolly monkey has a karyotype of $2n = 62$ with 14 pairs of metacentric or submetacentric chromosomes and 16 pairs of acrocentric

chromosomes. The X is a typical mammalian X. We had no data on the Y chromosome because we karyotyped only a single female (Figure 1).

Lagothrix lagotricha *flow karyotype*

The bivariate flow karyotype of the woolly monkey was resolved into 29 peaks. Flow sorting and DOP-PCR provided chromosome paints from each peak. These paints were then hybridized to woolly monkey metaphases to identify the chromosome content of each peak of the flow karyotype. All but two peaks contained single chromosomes (see Figure 2). The X-chromosome was sorted with chromosome 15. Chromosomes 20 and 21 were also contained in a single peak. All peaks provided exceptionally good chromosome paints.

Woolly monkey chromosome paints on human metaphases

Paints to woolly monkey chromosome were used to hybridize human metaphases (Figure 3) and forty-five clear signals were detected on the human karyotype (Figure 4). Thirteen human chromosomes were entirely painted by woolly monkey chromosome paints (6, 9, 11–14, 17–22, and X). However, the woolly monkey chromosome paints that hybridize to chromosomes 14, 18, and 21 also hybridize to other human chromosomes. All remaining woolly monkey chromosome probes also gave multiple signals on one or more human chromosomes. Human chromosomes 2, 5, 7, 8, 10, and 16 were each hybridized by two woolly monkey chromosome paints. The alternating pattern of hybridization signals between woolly monkey probes 11 and 16 on human chromosome 7 probably resulted from at least two inversions after translocation. Likewise, woolly monkey chromosome 29 has two signals on human chromosome 15; these disjunct signals are probably due to an inversion. Three woolly monkey paints hybridized to three human chromosomes: human chromosomes 3, 4, and 15. Human chromosome 3 is divided into 7 segments by probes from woolly monkey chromosomes 20, 22, and 23 due to a series of inversions. Four woolly monkey chromosomes hybridized to human chromosome 1.

Human chromosome paints on woolly monkey metaphases

Paints specific to each human chromosome except the Y were used to paint woolly monkey metaphases (Figure 4). The 23 human paints (autosomes plus X) gave 39 clear signals on the woolly monkey karyotype. Twenty-four woolly monkey chromosomes (1, 3, 5, 7–10, 12–20, 22, 25–30, X) were entirely painted by one single human chromosome paint. The complete synteny of 13 human chromosomes (6, 8, 9, 11–13, 17–22, X) was maintained in the woolly monkey karyotype. However, a segment of human chromosome 8 and all of 21 were translocated to different chromosomes. Seven woolly monkey chromosomes were each hybridized by two human chromosome paints. The woolly monkey chromosome 11 was divided into three segments, signals to human chromosome 7 were localized both on the p arm and on the terminal part of the q arm. A segment homologous to part of human chromosome 5 separated these signals; this pattern is certainly due to a pericentric inversion. The woolly monkey chromosomes painted by more than one human paint produced 7 associations of segments homologous to human chromosomes or human chromosome segments: 2/16, 3/21, 4/15, 5/7, 8/18, 10/16 and 14/15.

Discussion

This is the first report of reciprocal painting between a New World monkey and humans. All previous reports have been on platyrrhine karyotypes hybridized with human chromosome paints. Reciprocal chromosome painting between woolly monkey and humans allowed a subchromosomal assignment for both species when chromosomes were fragmented by multiple translocations. for instance human chromosome 1 is highly fragmented in the woolly monkey karotype: 4 hybridization signals on 4 different woolly monkey chromosomes were found. With unidirectional painting using only human probes on woolly monkey, the subchromosomal origin of each hybrdization signal is unknown. With

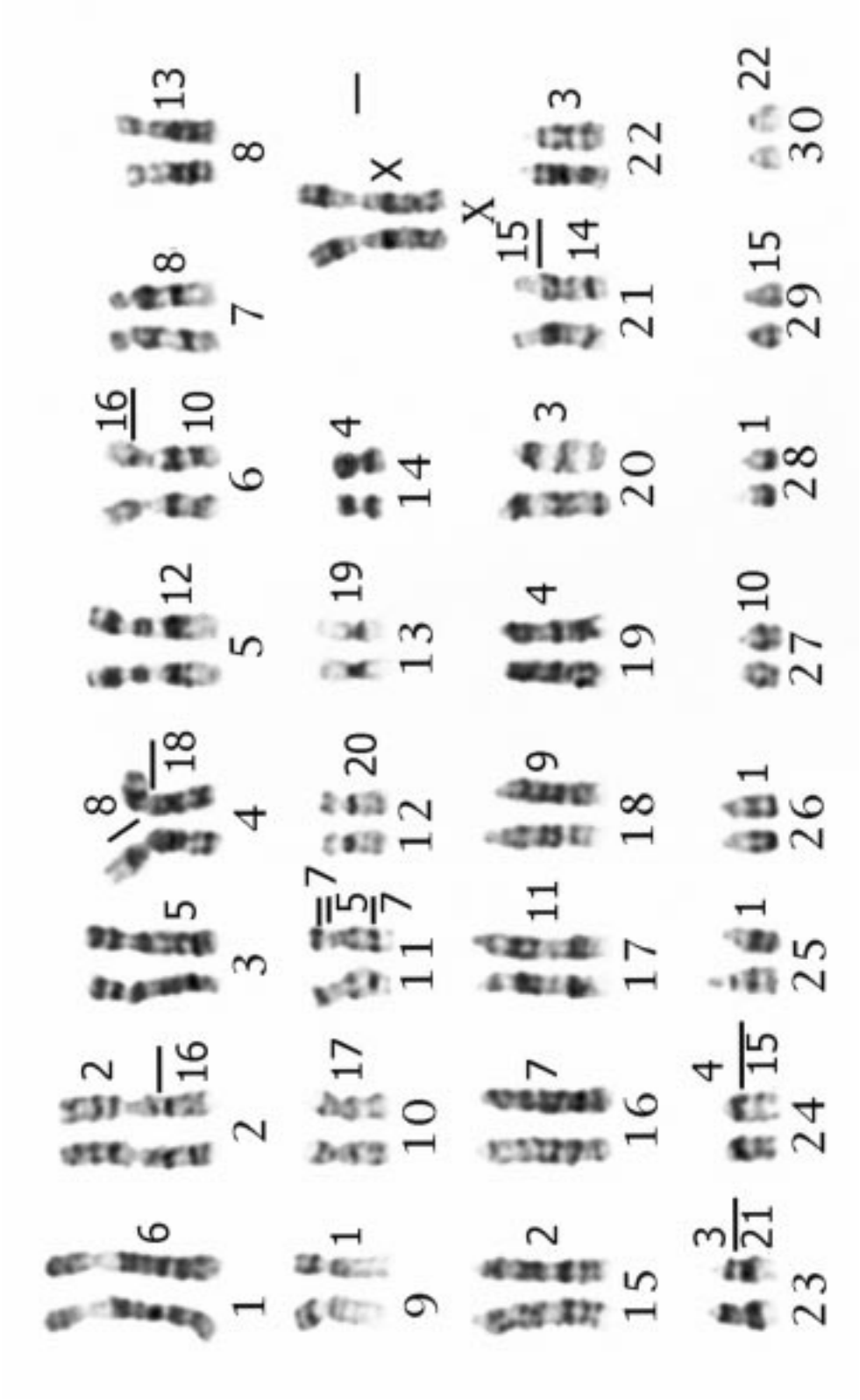


Figure 1. The G-banded karyotype of a female *Lagothrix lagotricha.* The chromosomes are numbered below. Homology with human chromosomes is shown to the right. Bar = 1 μm.

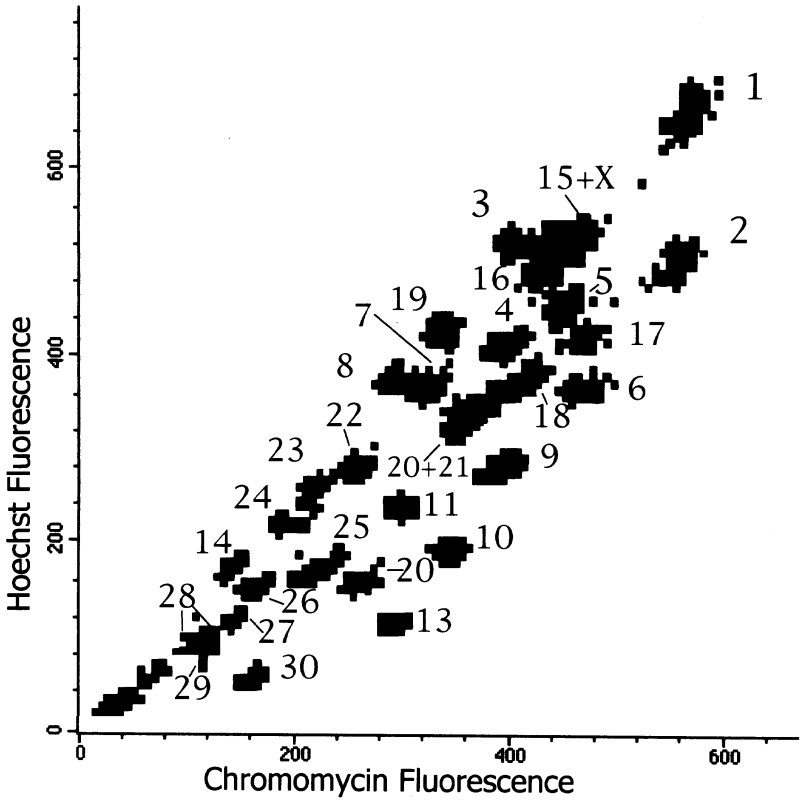
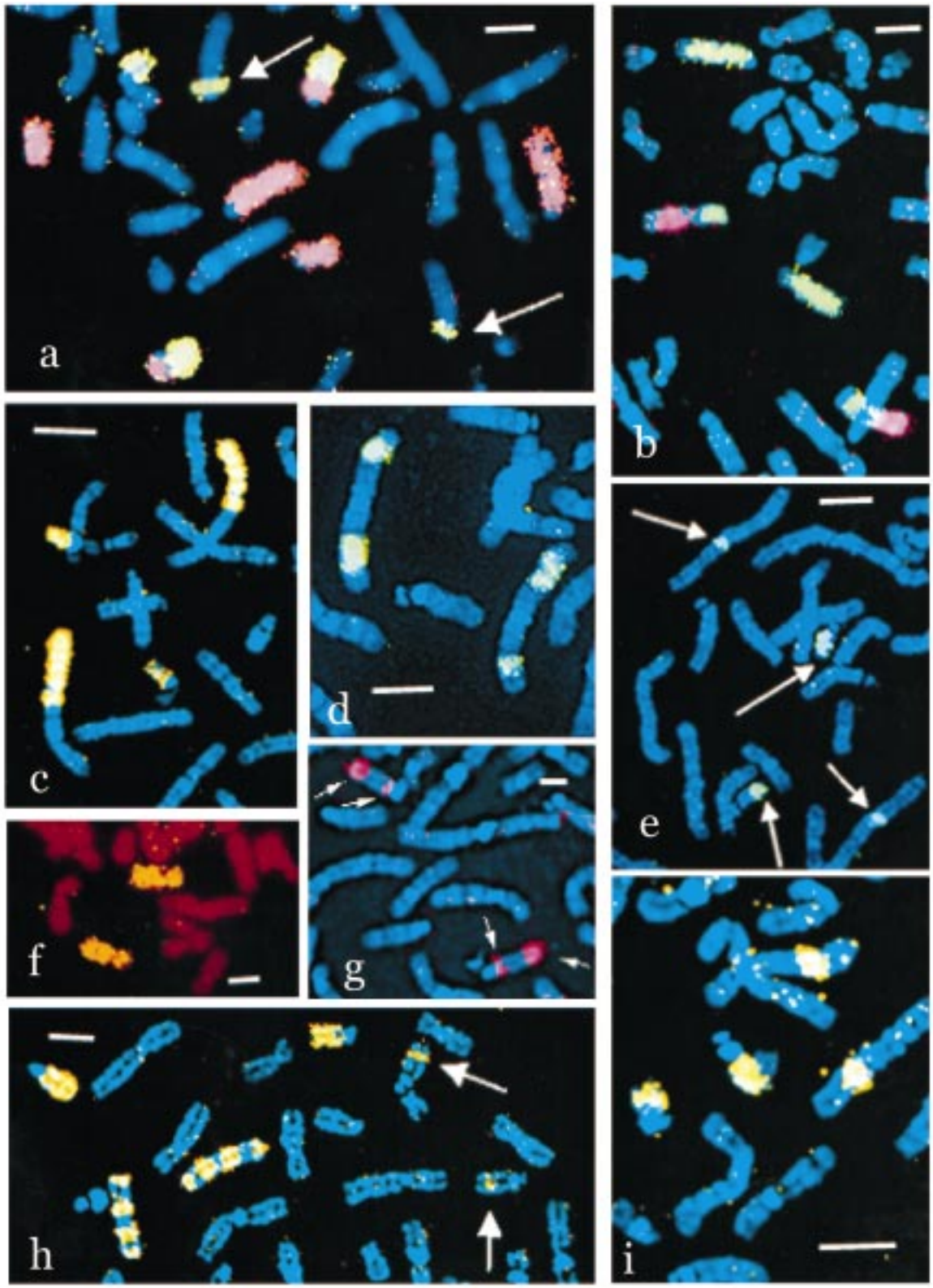


Figure 2. The density plot of the bivariate flow karyotype of the woolly monkey is shown. Chromosomes were sorted for DNA content and AT to GC base pair ratios into 30 peaks after staining with Hoechst 22358 (vertical axis) and chromomycin-A (horizontal axis). Highly pure sorts of single chromosomes were obtained for 28 woolly monkey chromosomes. Two peaks contained two chromosomes each.

reciprocal painting of woolly monkey paints to human metaphases, the subchromosomal origin is revealed (see Figure 5).

Comparison of homology assignments based on banding patterns and in-situ *hybridization*

Our results confirm previous reports on the diploid number and banding pattern of the woolly monkey (Chu & Bender 1962, Egozcue & Perkins 1970, Dutrillaux *et al.* 1980, Garcia *et al.* 1980). Two publications have proposed chromosomal homologies between woolly monkey and humans (Dutrillaux *et al.* 1980, Clemente *et al.* 1987). These authors agree on many assignments. However, the homologies proposed by Dutrillaux *et al.* are in better agreement with the hybridization data presented here and will be considered in more detail. Indeed, banding appears to have been a good guide to chromosomal homology between these two species yet important data are added by the FISH results. Dutrillaux *et al.* (1980) state that they have assigned 'certain homoeology' between all human chromosomes in the woolly monkey karyotype except for HSA 8 ('probable') and HSA1q and HSA 3 ('possible'). They proposed that 1p was homologous to a single woolly monkey chromosome when in fact it is composed of two woolly monkey chromosomes. We confirmed that human chromosome 7 was homologous to two woolly monkey chromosomes but they missassigned the smaller segment. Dutrillaux *et al.* found a single homolog each for human chromosomes 10 and 15 when in fact both these chromosomes have been fragmented: there are two chromosomes homologous to human 10 and three homologous to chromosome 15. All other 'certain' homologies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proposed by Dutrillaux *et al.* were confirmed by chromosome painting. However, if we consider the interchromosomal rearrangements or translocations which have produced syntenic associations in the woolly monkey, which differ from humans, they correctly identified only 2 out of 7 and Clemente *et al.* (1987) found none of the translocations. These results demonstrate that chromosome painting is a very effective method to track interchromosomal rearrangements. However, chromosome painting is not an efficient method to identify intrachromosomal rearrangements. Banding analysis offers the possibility of tracking intrachromosomal rearrangements, although, it would be best to confirm the banding interpretations with molecularly based methods.

Comparison of the woolly monkey hybridization pattern with other New World monkeys

We then compared the hybridization pattern of human on the woolly monkey with other primates and non-primate mammals. There is *in-situ* hybridization data of human paints on 9 New World primate species (Consigliere *et al.* 1996, Richard *et al.* 1996, Sherlock *et al.* 1996, Consigliere *et al.* 1998, Garcia *et al.* 2000, Stanyon *et al.* 2000).

The signals of woolly monkey paints on human alternate on three human chromosomes, 3, 7 and 15. Chromosomes 3 and 7 are known to have undergone multiple inversions during the evolution of hominoids (Müller *et al.* 2000, Richard *et al.* 2000). The alternating signals of woolly monkey chromosome 29 on human 15 also provide evidence that an inversion has taken place on this chromosome in the human line sometime after the divergence of New World monkeys. Four syntenic associations of human homologs are present in most platyrrhine primates. Associations of homologs to human 3/21 and 14/15 are present in all orders of placental mammals and are clearly ancestral. Associations 8/18 and 10/16 are present in all playtyrrhines and are surely derived traits linking all New World monkeys. Association 5/7 may also be a phylogenetic landmark for the origin of New World monkeys. Its apparent absence in some species could be secondary (Consigliere *et al.* 1998, Stanyon *et al.* 2000). A number of Atelines have been studied with chromosome paints: Three species of howler monkey, the black-handed spider monkey and with this report the woolly monkey. A number of derived cytogenetic features that link these species were revealed by chromosome painting. A derived translocation between segments homologous to human chromosomes 4 and 15 is found only among Atelines. There are 4 segments homologous to human chromosome 1 while in other platyrrhines there are 3. There are 3 segments homologous to human 4 while, in other New World monkeys, the synteny of this chromosome is usually conserved. There are 3 segments homologous to human 15 while, in other neotropical primates, there are usually two. Further chromosome painting with woolly monkey painting probes within these species would confirm whether these chromosome fragments are indeed homologous. At present, the molecular cytogenetic data cannot determine the phylogenetic branching order with the Atelines. To determine the phylogeny within Ateline we need to at least study the chromosome painting pattern of the woolly spider monkey, Brachyteles. However, Brachyteles is now considered one of the most

Figure 3. (opposite) This figure shows examples of the reciprocal hybridizations between humans and woolly monkeys. Double hybridizations of human probes on Lagothrix metaphases are shown in (**a**) human 4 in red and human 15 in yellow and (**b**) human 8 in yellow and 18 in red. Other hybridizations show woolly monkey probes painted to human metaphases: (**c**) woolly monkey 2 hybridizes parts of human 2 and 16; (**d**) woolly monkey 22 hybridizes human chromosome 3; (**e**) woolly monkey 23 hybridizes human 21 and a small part of human 3 near the centromere; (**f**) woolly monkey 5 hybridizes human 12; (**g**) woolly monkey chromosome 29 gives two signals on human 15; (**h**) a woolly monkey paint which contains two woolly monkey chromosomes (20, 21) hybridizes with 4 signals on human chromosome 3, most of human 14 and a small segment of chromosome 15, arrow; (**i**) woolly monkey chromosome 24 hybridizes to segments of human 4 and 15. Bar = 2 μm

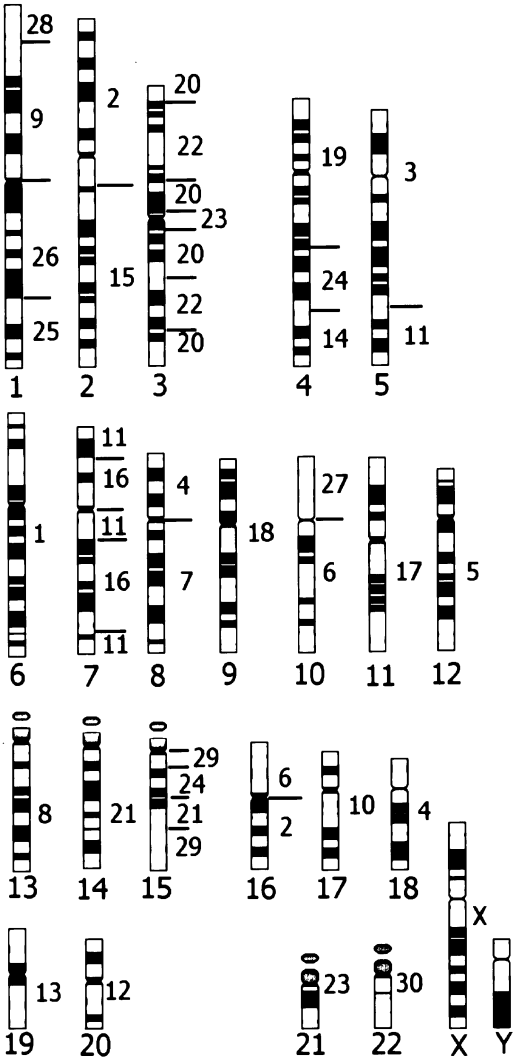

Figure 4. An idiogram of the human karyotype numbered below with the homology to woolly monkey chromosomes to the left.

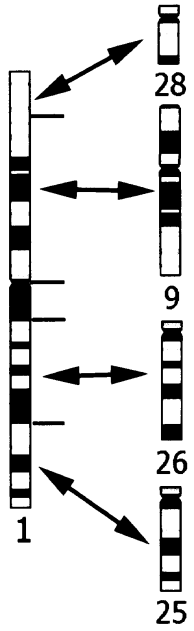

Figure 5. Illustrates how reciprocal painting provided additional data on the subregional homology between human and woolly monkey chromosomes. The paint from human chromosome 1 hybridizes 4 woolly monkey chromosomes (left to right), but the subregional homology is unknown until the woolly monkey chromosome probes are painted to human chromosome 1 (right to left).

endangered New World monkey species with a total population size of probably less than 400 individuals (Kinzey 1997); we have not yet been able to obtain a sample.

A simple statistical parameter to describe the differences between karyotypes was recently introduced (Cavagna & Stanyon in press), the diversity index or Z statistic. $Z = (1 - K/T)$, where K is the number of completely and uniquely conserved chromosomes and T is the total number of homology segments (i.e. hybridization signals). Greater genome conservation results in higher K and lower T values. Sex chromosomes are not considered in the analysis. The Z statistic is a measure of phenetic distance, which is not necessarily related to phyletic distance. For the comparison of human/woolly monkey, $Z = (1 - 12/38)$ or 0.68; human/spider monkey $Z = 0.80$; human/howler $Z = 0.69$; human/cebus $Z = 0.58$; and human/macaque $Z = 0.26$. From this comparison, we can conclude that, among the Ateline, *Ateles geofroyii* is karyologically more derived than *Lagothrix lagotricha* or *Alouatta belzebul* which are similar to the human karotype.

Recent publications report that intrachromosomal rearrangements may be 3–4 times more frequent than interchromosomal rearrangements (Müller *et al.* 2000, Murphy *et al.* 2000). It can be easily appreciated that intrachromosomal rearrangements are therefore a

potentially plentiful source of cladistic data for reconstructing primate phylogeny. Chromosome painting, however, is only rarely informative about intrachromosomal rearrangements (i.e. inversions). Chromosome banding is a first approach for comparing intrachromosomal rearrangements. FISH methods can detect and confirm intrachromosomal rearrangements with subchromosomal probes of decreasing size. The set of painting probes from the woolly monkey provides subchromosomal painting probes for a number of human chromosomes which may be of use in the initial phase of the molecular dissection of chromosomes in other species. Other subchromosomal probes, such as YACs, BACS and cosmids, are of much smaller size. Current size limitations of heterologous FISH are of the order of 1–2 MB which is about the resolution of one high resolution chromosome band. Such high resolution molecular methods should allow cytogenetics to make a significant contribution to many evolutionary questions in primates in the near future.

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