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Mapping chromosomal homology between humans and the black-handed spider monkey by fluorescence *in situ* hybridization

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We hybridized human chromosome-specific DNA probes to metaphases of the New World monkey *Ateles geoffroyi* to map the chromosomal homology between these two species. In the haploid *Ateles geoffroyi* karyotype the total number of signals was 51 for the 22 human autosomal probes used. Compared with Old World monkeys, the number of translocations found in the black-handed spider monkey karyotype was quite striking. The majority of these translocations are apparently Robertsonian and no reciprocal translocations were revealed. Nine autosomal human chromosome probes (11, 13, 14, 17, 18, 19, 20, 21, 22) provided only two signals each per metaphase, but six of these were translocated to subregions of different spider monkey chromosomes. The other 13 autosomal human chromosome paints (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, 16) provided fragmented signals. Three human probes (5, 8, 10) provided signals located on two pairs of spider monkey chromosomes. Four human paints (2, 3, 4, 12) provided hybridization signals on three pairs of chromosomes. Probes 6, 7, 15 provided six signals each on two pairs of chromosomes; probe 16 gave eight signals on two pairs of spider monkey chromosomes and probe 1 gave 12 signals on four pairs of chromosomes. The synteny between segments to human 18/8 appears to be an apomorphic ancestral condition for all New World monkeys. A synteny between regions homologous to human 16/10, 5/7 and 2/16 HSA is probably an apomorphic ancestral condition for all Cebidae. The syntenic association 3/15 and 4/1 is an apomorphic condition for the Atelinae.

Key words: *Ateles geoffroyi*, chromosome painting, cytogenetics, evolution, phylogeny, Platyrrhini, taxonomy

Introduction

Chromosomes are a valid tool for evolutionary studies only if homologous chromosomes are compared, and ancestral or primitive (plesiomorphic) conditions are clearly distinguished from derived (apomorphic) conditions. In closely related species, such as humans and great apes, banding patterns have proven to be a good indicator of chromosomal homology (Jauch *et al*., 1992). However, in comparisons between distantly related species, or species that have experienced rapid chromosomal evolution, the correlation between banding and gene content is often tenuous (Wienberg *et al*. 1992, Koehler *et al*. 1995a,b).

Fluorescence *in situ* hybridization (FISH or chromosome painting) with specific whole chromosome probes to metaphases provides a rapid and secure method for establishing homologies between different species (Wienberg *et al*. 1990). Recent FISH results have established homologies between human chromosomes and those of a good number of Old World apes and monkeys (Jauch *et al*. 1992, Wienberg *et al*. 1992, Koehler *et al*. 1995a,b, Bigoni *et al*. 1996a,b) and a few New World monkeys (Consigliere *et al*. 1995, Richard *et al*. 1996, Sherlock *et al*. 1996).

Distinguishing between ancestral or derived karyological characters is necessary, because only apomorphic characters provide reliable phylogenetic information. Therefore, to establish the polarity of chromosomal differentiation, comparison with selected 'outgroups' is fundamental. For the Old World primates the best outgroups are the New World monkeys (Platyrrhinae) and more complete data on chromosome painting in platyrrhines could be used to build a phylogenetic tree or cladogram for Catarrhines, including humans. FISH data from prosimians would in turn allow the construction of the ancestral chromosomal sytenies for all higher primates (New and Old World monkeys, apes and humans).

In this paper we hybridized human chromosome-specific DNA probes to metaphase of the New World monkey *Ateles geoffroyi* (Kuhl 1820) the black-handed spider monkey. The genus *Ateles* (Geoffroyi 1806)

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belongs to the subfamily Atelinae (fam. Cebidae), which includes two more genera, *Lagothrix* (Geoffroyi 1806) or woolly monkey and *Brachyteles* (Humboldt 1812) or woolly spider monkey (Hershkovitz 1977).

At present the number of species and subspecies of the genus *Ateles* is still an open question. The genus *Ateles* is commonly divided into four (Fleagle 1988) or six (Groves 1993) species: *A. paniscus*, *A. belzebuth*, *A. marginatus* (separated from *A. belzebuth*) *A. chamek* (separated from *A. paniscus*), *A. fusciceps* and *A. geoffroyi*. Spider monkeys are distributed from Central to South America including parts of Mexico, Costa Rica, Panama, Colombia and Brazil. The need for a rigorous revision of spider monkey taxonomy is often noted (Kellogg & Goldman 1944, Mittermeier & Coimbra-Filho 1981, Mittermeier *et al*. 1988, Roosmalen and Klein 1988, Silva-Lùpez *et al*. 1996). Unfortunately, spider monkey taxonomy is based almost entirely upon pelage, which is highly variable even within species and therefore does not appear as a sufficiently reliable taxonomic indicator (Silva-Lùpez *et al*. 1996).

Cytogenetic studies can often provide essential evolutionary information and make a contribution in resolving taxonomic, phylogenetic and conservation problems (Baker *et al*. 1989, Stanyon *et al*. 1992, King 1993, Wienberg & Stanyon 1995). Further, the high variability in New World monkey karyotypes, in part due to numerous translocations, implies that chromosome painting could be particularly instructive in these primates (Viegas Pèquignot *et al*. 1985, Dutrillaux *et al*. 1986, Clemente *et al*. 1987, Lima & Seuànez 1989, 1991, Ma *et al*. 1991, Stanyon *et al*. 1995).

Spider monkeys appear to be chromosomally variable, both within and between the various species of the genus (Bender & Mettler 1958, Bender and Chu 1963, De Boer & De Bruijn 1990, Kunkel *et al*. 1980, Seuànez *et al*. 1993). Different pericentric and paracentric inversions and a trandem fusion have been found among various species and subspecies of *Ateles* (Kunkel *et al*. 1980, Koiffmann & Saldanha 1981, De Boer & De Bruijn 1990). Spider monkeys have long been considered karyologically derived because distinct regions of homology with human and other primate karyotypes were not found (Turleau *et al*. 1974). This conclusion has recently been supported by gene mapping in the spider monkeys (Seuànez *et al*. 1994).

To provide new data and perspectives on the taxonomic and evolutionary problems relating to chromosomal structure, homologies and rearrangements in Platyrrhinae, we hybridized human whole chromosome-specific DNA probes (chromosome painting) to *Ateles geoffroyi* metaphases. The results were then compared with previous chromosome painting data in primates and other mammals as well as information on gene mapping, radiation-induced chromosomal rearrangements (Hoffschir *et al*. 1988) and DNA sequencing in spider monkeys (Giebel *et al*. 1985, Fitch *et al*. 1988, Maeda *et al*. 1988, Spritz & Giebel 1988, Galili & Swanson 1991, Schneider *et al*. 1993).

Material and methods

Tissue culture, chromosome preparation and banding

The male *Ateles geoffroyi* sample consisted of a low-passage fibroblast cell line obtained from the Institute for Medical Research, Camden, NJ, USA (repository no. AG5352 originally from San Diego Zoological Society). Standard tissue culture and chromosomal preparation techniques were used (Stanyon & Galleni 1991).

Chromosomes were stored in fixative at −20°C; metaphases were trypsin G-banded and photographed before the *in situ* hybridization. Destaining and post-fixation were performed according to Klever *et al*. (1991) and Arnold *et al*. (1992). Briefly, after destaining in fixative and rehydration in an ethanol series and phosphate-buffered saline (PBS), the slides were treated with a 10% formaldehyde solution (diluted in PBS) for 20–30 min and then dehydrated. This method allows chromosomes to be identified on the basis of their G-banding pattern.

In situ hybridization

Chromosomal painting with human whole-chromosome probes was performed as described previously (Wienberg *et al*. 1990). Slides were denatured for 35–45 s at 65°C in 70% formamide/2 × SSC and immediately dehydrated in a cold ethanol series and dried. Probes were made from flow-sorted chromosome followed by DOP-PCR. Paints specific to whole chromosome for all human autosomes were hybridized to metaphases of *Ateles geoffroyi* as follows.

Chromosome-specific probes and human Cot DNA (about 1 μg each) were diluted in 50% formamide buffer and denatured for 10 min at 70°C; they then were preannealed for 30–90 min. Slides were mounted and hybridized for 2 days.

After hybridization the slides were washed twice in 50% formamide/2 × SSC, followed by three times in 2 × SSC, all at 42°C. Biotinylated DNA human chromosome probes were detected with avidin (diluted 1:200) coupled with fluorescein isothiocyanate (FITC) and anti-avidin–biotinylated antibodies. (diluted 1:125), both from Vector; signals were amplified twice. FITC-labelled DNA human chromosome probes were detected using rabbit-anti-FITC diluted (1:200, from Dako) and goat anti-rabbit–FITC-conjugated antibodies (diluted 1:500, from Vector). The detection followed standard procedures with washes in 4 × SSC with 0.05% Tween. Chromosomes were counterstained with a combined DAPI (1 μg/ml) and propidium iodide (2 μg/ml) solution; finally slides were mounted in a p-phenylendiamin anti-fade in phosphate-buffered saline (PBS)/glycerin (1:9).

Photographs of metaphases of *Ateles geoffroyi* were taken on a Leitz Orthoplan epifluorescence microscope. G-banded metaphases were photographed with Agfa-Ortho film (25 ASA). Hybridization slides were photographed with an Agfachrome (ASA 1000) colour slide film or a Kodak (ASA 1600) colour slide film. Other metaphases were photographed with a T-max (ASA 400) black and white film.

Results

We found that *Ateles geoffroyi* has a diploid number of $2n = 34$ with a normal XY sex determining system. All chromosomes are biarmed with the exception of one acrocentric pair, n. 16 (Figure 1).

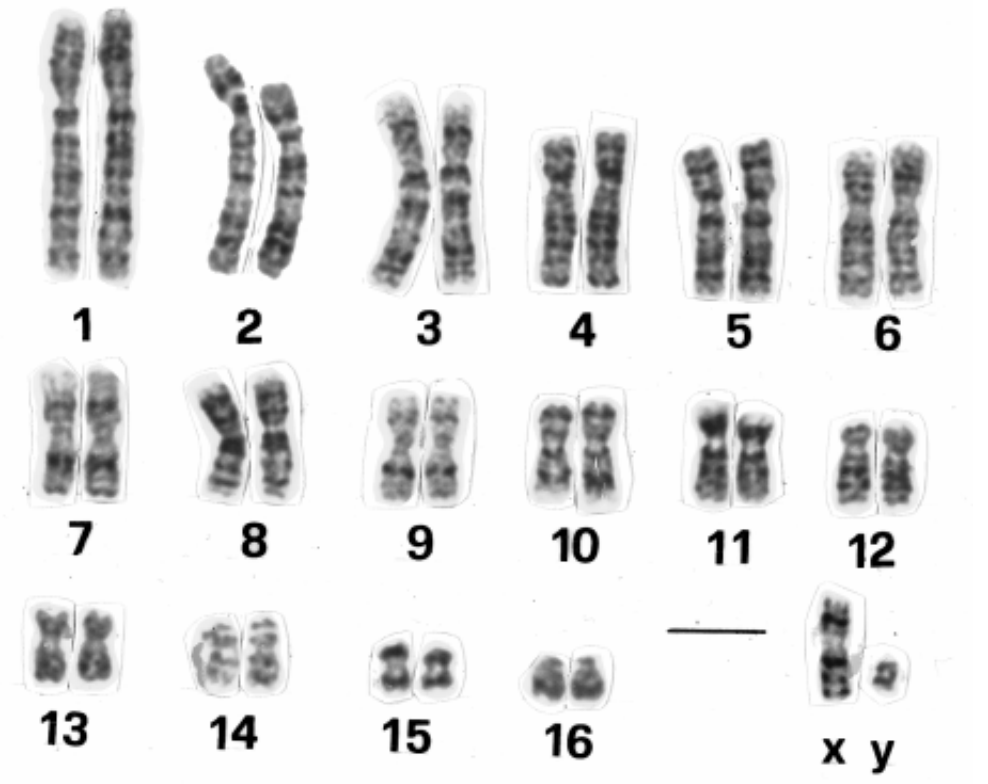

Figure 1. A typical G-banded karyotype for the black-handed spider monkey, *Ateles geoffryoi*. Bar = 10 μm.

Hybridization pattern

Sequential trypsin G-banding followed by *in situ* hybridization allowed us to assign the hybridization signals to specific. *Ateles geoffroyi* whole chromosomes or chromosome subregions (Figure 2). The homology between all human autosomes and those of the black-handed spider monkey were determined (Figure 3, Table 1). In the haploid *Ateles geoffroyi* karyotype the total number of signals was 51 for the 22 whole-chromosome human probes used.

Nine human chromosome probes (11, 13, 14, 17, 18, 19, 20, 21, 22) provided only two signals per metaphase. DNA probes from each of three human autosomes (11, 13, 17) hybridized to only one entire pair of *Ateles* chromosomes: 10, 12, 14 respectively. The hybridization pattern showed that the synteny of regions homologous to the other six human chromosomes (14, 18, 19, 20, 21, 22) was also conserved, but these probes (in contrast to the human condition) appear to be translocated to subregions of different spider monkey chromosomes (2, 1, 9, 9, 11, 3, respectively) (Table 1).

In contrast, probes for all the other 13 human chromosomes (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, 16) provided multiple, fragmented signals in the black-handed spider monkey karyotype. Human probe 9 mapped to AGE 1p, but the hybridization signal was split by a chromosome segment that was not hybridized by any human probe. Three human probes (5, 8, 10) provided four signals located on two pairs of AGE chromosomes. The signals of human probe for chromosome 5 were localized on *Ateles* chromosomes 5p and 8q. Signals for human probe 8 were clear on *Ateles* chromosome 5q and 1q. Human chromosome probe 10 hybridized a single region of the q arm of chromosome AGE 1 and the whole p arm of AGE 13.

Four human probes (2, 3, 4, 12) provided hybridization signals on three pairs of *Ateles* chromosomes; multiple translocation events are proposed for all these probes. Human probe 2 showed two signals on both arms of AGE chromosome 6, one signal on AGE chromosome 3q and on AGE chromosome 13q. Human probe 3 provided two different signals on AGE chromosome 3q and one signal on AGE chromosomes 4p and 11p. Human probe 4 exhibited one signal on AGE chromosome 2q and on AGE 8p, and hybridized the whole AGE chromosome 15. Human probe 12 provided two signals on AGE chromosome 2p, one signal on AGE chromosome 5q and hybridized the entire AGE chromosome 16.

Three human probes (6, 7, 15) provided six signals each on two pairs of AGE chromosomes, whereas human probe 16 gave eight signals on two pairs of AGE chromosomes. Human chromosome probe 6 gave two signals on both arms of AGE chromosome 7 and one signal on AGE chromosome 11q. Human probe 7 provided one signal on AGE chromosome 4q and two

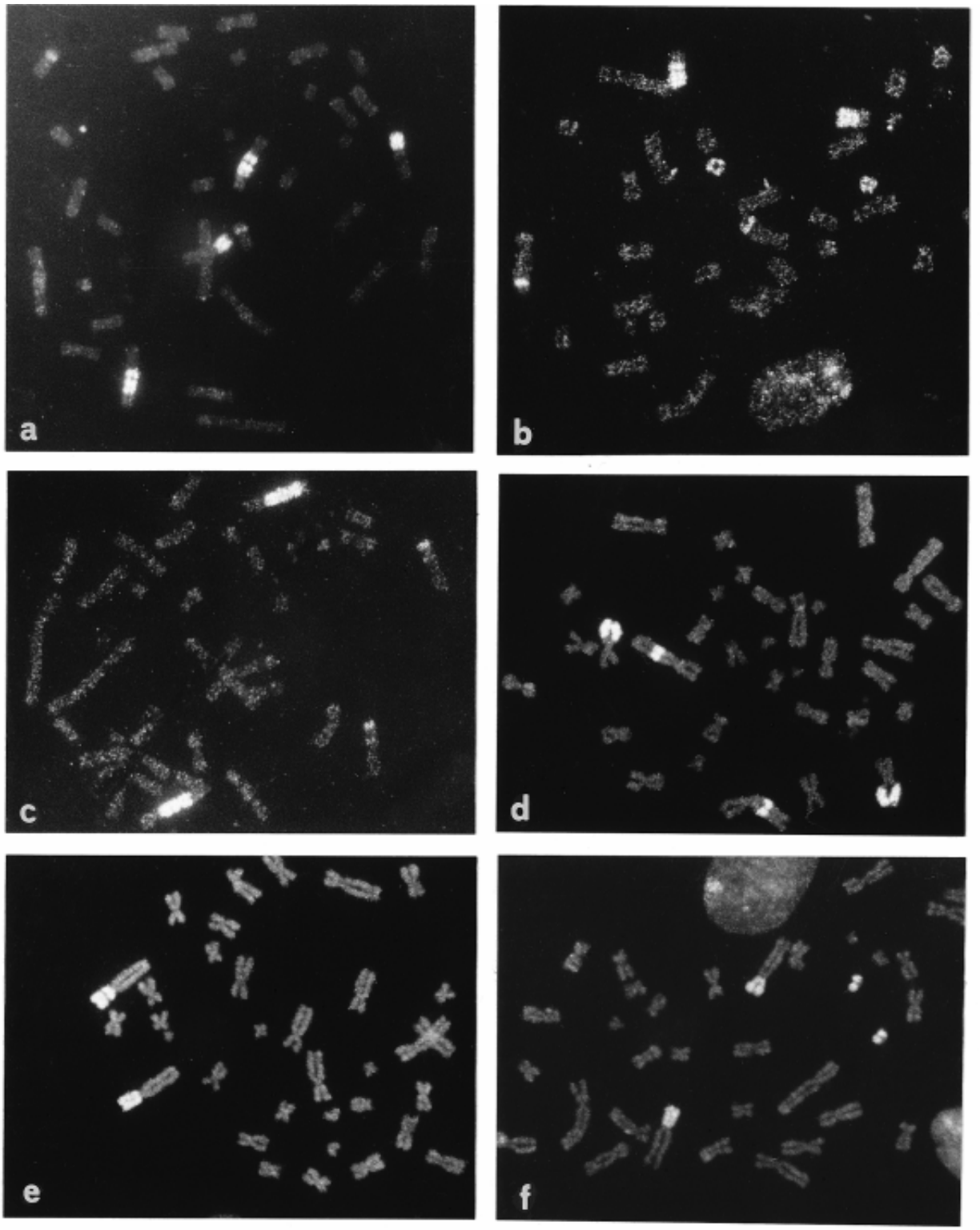

Figure 2. Examples of hybridization of DNA probes specific to individual whole human chromosomes to metaphases of *Ateles geoffryoi* (AGE). **a** Probe for human chromosome 3 signals homologue of 3 pairs of AGE chromosomes (3, 4, 11). **b** Human paint 4 hybridizes to three pairs of AGE chromosomes (2, 8, 15). **c** Human paint 7 hybridizes to two pairs (4 and two small signals on 8). **d** Human 8 signals two pairs (1, 5). **e** Human probe 9 signals short arm of chromosome 1. **f** Human paint 12 hybridized to two pairs (2, 5). Note that the signal from some probes is interrupted by a chromosome segment that is composed of heterochromatin (probe 3 on AGE 3 in **a**, and probe 9 on AGE 1 in **e**). All hybridizations were photographed directly from the microscope on Kodax T-Max 400 without image processing.

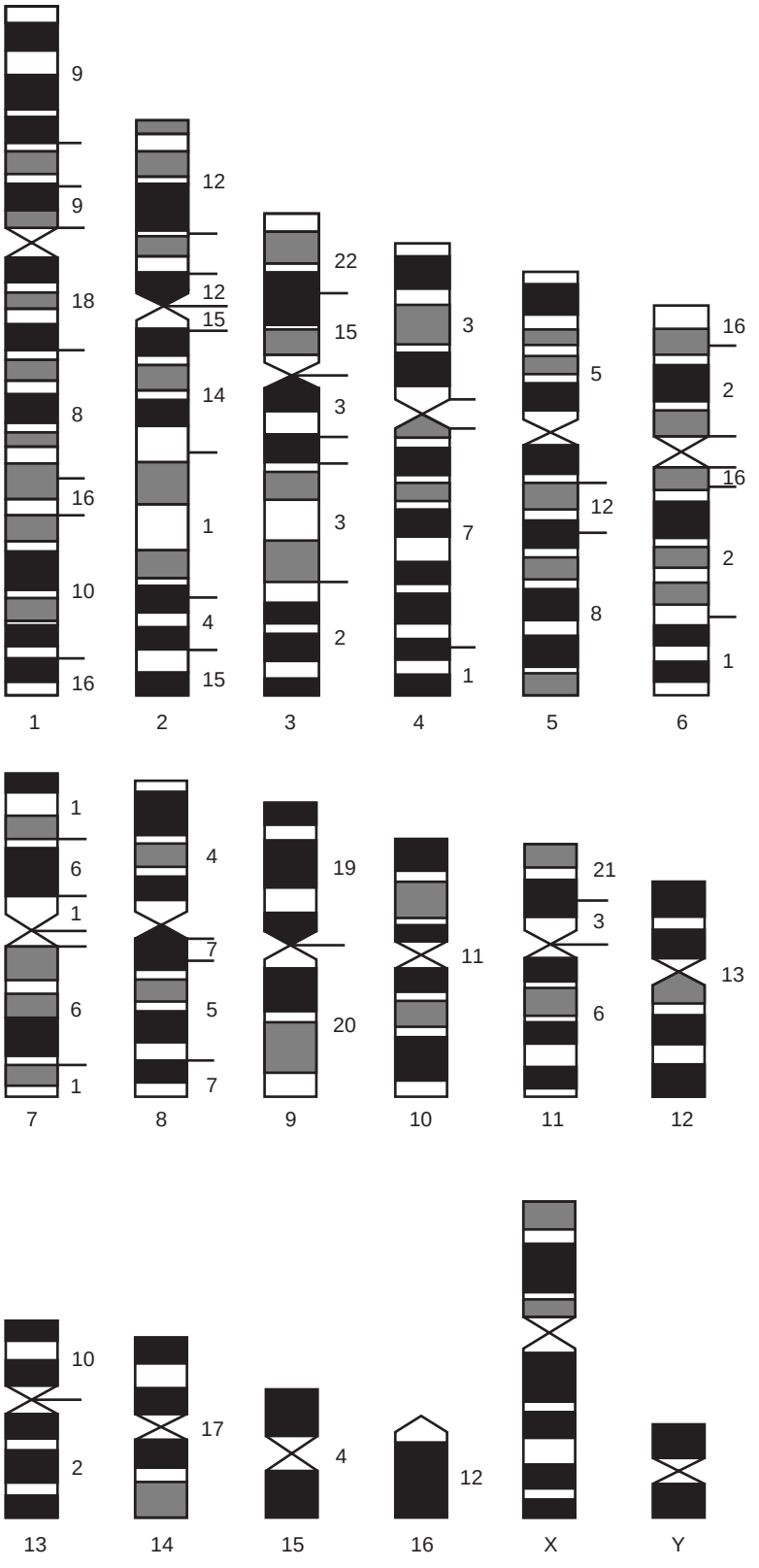

Figure 3. Ideogram of *Ateles geoffroyi* with the human chromosome-specific hybridization pattern. The black-handed spider monkey chromosomes are numbered below and the hybridization pattern with human chromosomes probes is numbered on the right.

Table 1. Summary of the hybridization results using whole human chromosome probes on *Ateles geoffroyi* metaphases. From left to right, the human chromosome probe, the number of hybridization signals per metaphase and the number of homologous chromosome pairs hybridized, the spider monkey chromosome hybridized and in parentheses the number of signals per homologue

Whole human chromosome probe	No. of hybridization signals/ chromosome pairs	*Ateles* chromosome hybridized (no. of signals)
1	12/4	2 (1), 4 (1), 6 (1), 7 (3)
2	8/3	3 (1), 6 (2), 13 (1)
3	8/3	3 (2), 4 (1), 11 (1)
4	6/3	2 (1), 8 (1), 15
5	4/2	5 (1), 8 (1)
6	6/2	7 (2), 11 (1)
7	6/2	4 (1), 8 (2)
8	4/2	1 (1), 5 (1)
9	4/1	1 (2)
10	4/2	1 (1), 13 (1)
11	2/1	10
12	6/3	2 (2), 5 (1), 16
13	2/1	12
14	2/1	2 (1)
15	6/2	2 (2), 3 (1)
16	8/2	1 (2), 6 (2)
17	2/1	14
18	2/1	1 (1)
19	2/1	9 (1)
20	2/1	9 (1)
21	2/1	11 (1)
22	2/1	3 (1)

different signals on AGE chromosome 8q. Human probe 15 gave two signals on AGE chromosome 2q and one signal on the AGE chromosome 3p.

Human chromosome probe 1 showed 12 signals on four pairs of AGE chromosomes: one signal on *Ateles* chromosome pairs 2q, 4q, 6q, and three signals on AGE chromosome 7.

Some areas in the *A. geoffroyi* karyotype were not covered by FISH signals. These regions include centromeric areas and interstitial segments on AGE chromosomes 1p, 2p, 3p and 3q. The lack of hybridization on 1p, 3p and 3q appears to be related to the presence of different DAPI-positive heterochromatic bands. The lack of hybridization on 2p may be related to other repetitive sequences not DAPI positive or to sequences absent in the human probes.

Discussion

We confirmed that *Ateles geoffroyi* had a diploid number of $2n = 34$ (Bender & Mettler 1958, De Boer 1974, Garcia *et al*. 1975, Kunkel *et al*. 1980) and mapped the homology of all human chromosomes to their respective spider monkey chromosome or chromosome segments.

Chromosome paints are a very effective method for mapping interchromosomal rearrangements. The large number of translocations we mapped in the spider monkey karyotype is quite striking in contrast to Old World primates, which appear much more karyologically conservative. For example *Macaca fuscata* has two FISH signals per metaphase for all the human probes with the exception of human probe 2, which has four signals as expected, because human chromosome 2 originated from an apomorphic translocation (Wienberg *et al*. 1992).

Types of translocations and homology of centromeres

The FISH data reported here allowed us to hypothesize about the type of translocations and the fate of the centromeric regions of human chromosomes in the *Ateles geoffroyi* karyotype. The majority of translocations are Robertsonian (centromere fusions/fissions) and apparently the majority of human centromeres are conserved. No reciprocal translocations were found in the AGE karyotype. Robertsonian translocations can be inferred from the pericentromeric position of signals of human probes 1, 5, 6, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19 and 20 in the *Ateles* karyotype, and we propose that the human centromeric areas may be conserved on the spider monkey chromosomes 7, 5, 11, 1, 10, 13, 12, 2, 3, 6, 14, 1 and 9.

The centromeres homologous to human chromosomes 8, 21 and 22 could not be clearly identified. The centromere homologous to human 8 may have been inactivated after a tandem fusion with 5/12 (AGE 5). Another hypothesis is that a 5/8 translocation was followed by an insertion of a segment homologous to 12 in proximity to the centromere. The presence of a 5/8 association in howler monkeys supports the second hypothesis (Consigliere 1995). Comparisons with distant outgroups (artiodactyls and carnivores) suggest that centromeres for chromosome regions homologous to 21 and 22 originated during catarrhine evolution.

Given the tandem fusion origin of human 2, we expect to find two centromeres in other primates, and AGE chromosomes 6 and 13 probably have homologous ancestral centromeres. FISH with subregional probes would be needed to determine which AGE chromosome has the centromere homologous to that now active in human chromosome 2 (cf. Arnold *et al*. 1996).

The fate of centromeres homologous to human centromeres 3, 4, 7 and 12 is less clear. However, these centromeres could be homologous to those found on AGE 4, 15, 8 and 16 respectively.

Intrachromosomal rearrangements

Although whole chromosome probes provided only limited information on intrachromosomal rearrangements, the hybridization pattern for some probes permits some hypotheses to be formulated. Human probes

1, 2, 6, 7, 12, 15 and 16 provided multiple FISH signals on the same individual spider monkey chromosomes. Such a pattern can be interpreted as translocation events followed by pericentric inversions. For instance, human probe 16 gave two signals on AGE chromosome 1q and two signals on both arms of AGE chromosome 6, indicating a pericentric inversion following translocation on both these spider monkey chromosomes.

Chromosomal syntenies found in *Ateles* compared with other primates and non-primate mammals

The chromosomal syntenies found in the *A. geoffroyi* karyotype were compared with the chromosome painting data previously reported for other primate and non-primate mammals for the following species (Table 2): *Alouatta s. arctoidea* and *Alouatta s. sara* (Consigliere 1995), *Cebus capucinus* (Richard *et al*. 1996), *Callitrix jacchus* (Sherlock *et al*. 1996), *Macaca fuscata* (Wienberg *et al*. 1992), *Felis catus* (Rettenberger *et al*. 1995a), *Equus caballus* (Raudsepp *et al*. 1996), *Sus scrofa* (Rettenberger *et al*. 1995b) and *Bos taurus* (Hayes 1995, Solinas-Toldo *et al*. 1995).

The synteny between segments to human 8/18 appears to be an apomorphic ancestral condition for all New World monkeys, because this synteny was found in all platyrrhines with the exception of ASA, but not in other taxa. The association between regions homologous to 10/16 HSA is an apomorphic ancestral condition for the Cebidae because it is found in all Cebidae studied, but not in *Callithrix jacchus*. The syntenic association 5/7 and 2/16 could also be a common Cebidae apomorphism that was lost in howlers. The syntenic assocations 3/15 and 4/15 are probably apomorphic ancestral conditions for the subfamily Atelinae because they are present in both spider and howler monkeys.

The synteny between regions homologous to human 15/14 and 3/21 is probably ancestral to all primates and many mammalian orders as it was found in both Old and New World monkeys, carnivores and many artiodactyls. The association between regions homologous to 2 and 1 found in the spider monkey and in the cat may simply represent a convergence.

Single chromosomes homologous to human 11, 13, 17 present in the spider monkey appear to have considerable antiquity, because they are found intact in a wide range of primate and non-primate karyotypes. Various ancestral syntenic groups that form individual chromosomes in other primates and distant outgroups appear to be disrupted or translocated in AGE, including 4, 6, 9, 10, 18, 20 and either 2p or 2q. The synteny of a single chromosome homologous to human 12 appears to be a new character restricted to primates which has, however, been disrupted in the Atelinae.

Table 2. A comparison of chromosome painting data using human whole chromosome-specific DNA probes between the black-handed spider monkey, and various other primates and non-primate mammals. Chromosomal syntenies are listed in the left hand column. Chromosome numbers separated by a slash indicate a syntenic association between regions homologous to these chromosomes; a single chromosome number indicates the presence of a single, whole individual homologous chromosome. New World monkeys: *Ateles geoffroyi* (AGE) *Alouatta s. arctoidea* (ASA) *Alouatta s. sara* (ASS), *Cebus capucinus* (CCA) and *Callitrix jacchus* (CJA). An Old World monkey *Macaca fuscata* (MFU), and distant outgroup species: *Felis catus* (FCA), *Sus scrofa* (SSC) and *Bos taurus* (BTA). See text for references

Chromosomal syntenies	Species								
	AGE	ASE	ASS	CCA	CJA	MFU	FCA	SSC	BTA
2/1	+	−	−	−	−	−	+	−	−
3/21	+	−	−	+	−	−	+	+	+
14/15	+	−	−	+	+	+	+	+	+
8/18	+	−	+	+	+	−	−	−	−
10/16	+	+	+	+	−	−	−	−	−
2/16	+	−	−	+	−	−	−	+	−
5/7	+	−	−	+	−	−	−	−	−
3/15	+	+	+	−	−	−	−	−	−
4/15	+	+	+	−	−	−	−	−	−
4	−	−	−	+	+	+	−	−	−
6	−	+	+	+	+	+	+	−	−
9	−	+	+	+	−	+	+	−	−
10	−	−	−	−	−	+	+	−	−
11	+	−	−	+	+	+	+	−	−
12	−	−	−	+	+	+	−	−	−
13	+	+	+	+	−	+	−	+	+
17	+	−	−	+	−	+	+	+	+
18	−	−	−	−	−	+	−	−	+
20	−	−	−	+	−	−	−	−	+

Comparison with gene mapping data

Based on a comparison of both G-banding and mapping data previously reported for *Ateles paniscus chamek* chromosomes, homologies between *A. paniscus* and *A. geffroyi* can be recognized for most of the karyotype (Seuànez *et al*. 1993, 1994). Chromosomes 1, 2, 3, 4, 5, 6, 7, 13, 14, 15 and 16 seem to be the same in both karyotypes. *A. p. chamek* chromosomes 9, 10 and 11 appear homologous to *A. geoffroyi* 11, 9 and 10. However, no certain homology was found for *A. p. chamek* autosomes 8 and 12 and *A. geoffroyi*.

Gene mapping is equivocal for complete homology between *A. Geoffroyi* and *A. p. chamek* chromosome 7. In fact Seuànez (1994) reported that the synteny of human genes *MPI* and *HEXA* (HSA 15q22–qter; HSA 15q23–q24) was retained on chromosome 2 of APC. On the same chromosome he found the presence of two other human genes, *PEPB* (HSA 12q21) and *NP* (14q11.2). The same association (human chromosome 12/14/15) is revealed by our FISH data on AGE chromosome 2.

Two human genes, *IDH2* (HSA 15q21–qter) and *ACY1* (HSA 3p21), were found by Seuànez on APC chromosome 3; this association (human chromosome probes 15/3) is confirmed by FISH data on AGE chromosome 3.

Different human single genes and gene syntenies were found on APC chromosome 6: *PEPC* (HSA 1q25), *APC1* (HSA 2p25) and *MSH1* (HSA 2p23), *DIA4* (HSA 16q12–q22) and *GOT2* (HSA 16q12–q22). The same association of human chromosome 1/2/16 was revealed by the FISH data on AGE chromosome 6.

Human genes *PGD* (HSA 1p36.3–p36.13), *ME1* (HSA 6q12) and *AK1* (HSA 9q34.1–q34.2) were found on APC chromosome 7. We found that human chromosome probes 1 and 6 hybridized to AGE chromosome 7, but no signal for human probe 9 was detected on this chromosome.

There is a limited number of reports on gene sequencing in *A. geoffroyi* (Giebel *et al*. 1985, Fitch *et al*. 1988, Maeda *et al*. 1988, Spritz and Giebel 1988, Schneider *et al*. 1993, Galili & Swanson 1991). Most of these genes are located on human chromosome 11: *HBG2* (HSA 11p15.5), *HBB* (HSA 11p15.5), *HBD* (HSA 11p15.5), *HBE1* (HSA 11p15.5), *HBG1* (HSA 11p15.5). Our FISH data indicate that AGE 10 is equivalent to human chromosome 11 and that these genes should all map to this spider monkey chromosome. ABO was also sequenced in the spider monkey; this gene maps to HSA 9q34.1–q34.2 and therefore should be on AGE 1p (Craig & Rawlings 1990).

Conclusions

A comparison of the hybridization pattern in *Ateles geoffroyi* with those of other species show that the genomes of many New World primates have experienced a remarkable reorganization. Clearly, the whole scheme of chromosomal phylogeny in Neo-tropical primates needs to be restudied with the aid of molecular cytogenetics. In particular, for precise phylogenetic reconstruction, it is essential that the chromosomal homology of additional species is determined by FISH. Further, data on chromosome painting in platyrrhines would also provide such information for biomedical researchers using thee primates as models. The results could also be used to test assumptions about chromosome evolution and clarify the role of chromosomes in speciation.

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