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Evolutionary history of chromosome 10 in primates

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Abstract We have tracked the evolutionary history of chromosomes homologous to HSA10 (PHYL-10) in primates using appropriate panels of PCP, YAC, and BAC probes. This approach allowed us to delineate more precisely the PHYL-10 constitution in the ancestor of catarrhine, platyrrhine, and prosimians. The results suggest that (i) in the ancestor of prosimians PHYL-10 was organized in two separate PHYL-10p and PHYL-10q chromosomes; (ii) in the progenitor of New World monkeys PHYL-10p was a separate chromosome, while PHYL-10q was associated with a chromosome homologous to HSA16; (iii) in the ancestor of Old World monkeys PHYL-10 was a unique chromosome with a marker order corresponding to the orang form. We have also analyzed the cat, chosen as an outgroup for its very conserved karyotype. In agreement with published data our experiments show that the PHYL-10 in cat is structured in two blocks, PHYL-10p and PHYL-10q, both as part of larger chromosomes. The overall data indicate that, contrary to common opinion, PHYL-10p and PHYL-10q were distinct chromosomes in the primate ancestor. Analysis of the *Saimiri sciureus* (SSC) PHYL-10q marker order showed that it was isosequential with the *Callithrix jacchus* PHYL-10q, as well as with the PHYL-10q platyrrhine ancestral form. The SSC centromere, nevertheless, was located in a different chromosomal region, therefore suggesting that a centromeric repositioning event occurred in this species.

Introduction

Progress toward sequencing the entire human genome has allowed ever deeper insights into its complex structure. A full understanding of the organization of our genome, however, will be achieved only through the elucidation of its recent evolution, i.e. through a detailed comparison of its architecture with the architecture of the genome of our closest relatives, the primates. However such comparative studies are severely limited by the lack of sequence data on primates. Dutrillaux (1979) presented a comprehensive overview on chromosomal evolution based on chromosome banding. The advent of molecular cytogenetic techniques has considerably expanded our knowledge of primate chromosomal evolution and achievements in this respect have perfectly complemented sequence data. Whole chromosome paints (WCP) and, more recently, reciprocal chromosome painting have been exploited better to delineate primate karyotypic evolution. However, WCPs are of poor resolution and can only detect chromosomal interchanges. They would miss, for instance, intrachromosomal rearrangements. The use of partial chromosome paints (PCP) and, particularly, of probes of small size like yeast and bacterial artificial chromosomes (YACs and BACs) has made the molecular cytogenetic approach more efficient in investigating marker order conservation among chromosomes. Well-characterized contigs of BAC/PAC probes, produced as an intermediate step toward sequencing, now cover almost the entire human genome [see the University of California Santa Cruz Database (SCD, http://genome.ucsc.edu)] and can be advantageously used toward a detailed marker order comparison. Their use has indeed disclosed unpredicted phenomena such as pericentromeric plasticity (Eichler et al. 1999; Jackson et al. 1999) and evolutionary centromeric repositioning (Montefalcone et al. 1999; Ventura et al. 2001).

Here we report evolutionary studies on phylogenetic chromosome 10 (PHYL-10) using appropriate panels of human PCPs, YACs, and BAC probes. The studies were performed in great apes and on representative species of Old World monkeys (OWM), New World monkeys (NWM), and prosimians. Cat (*Felix catus*, FCA) was used as an outgroup, since it has been shown that its conserved karyotype resembles the ancestral karyotype of mammals (Yang et al. 2000). For the cat, in addition,

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a detailed radiation hybrid (RH) map has been published (Murphy et al. 2000; http://rex.nci.nih.gov/lgd/cat/catgenome.htm).

Delineation of the evolution of PHYL-10 in primates can be derived from studies aimed at comparing the whole karyotypes of different primate species (for a review see Murphy et al. 2001). Most of these studies made use of WCPs only, giving a quick and broad view of karyotypic differences among the species under study, but with poor resolving power. The results presented here have defined a more precise evolutionary history of PHYL-10 in primates, disclosed an additional example of centromeric repositioning, and contributed to the definition of the organization of this chromosome in the common ancestor of primates and carnivores. The conclusions on the latter issue diverge from those of the current available studies.

Materials and methods

Metaphase preparations were obtained from lymphoblastoid or fibroblast cell lines of the following species: great apes: common chimpanzee (*Pan troglodytes*, PTR), gorilla (*Gorilla gorilla*, GGO), Borneo orangutan (*Pongo pygmaeus pygmaeus,* PPY); OWM: rhesus monkey (*Macaca mulatta*, MMU), African green monkey (*Cercopithecus aethiops,* CAE), sacred baboon (*Papio hamadrias,* PHA), silvered leaf-monkey (*Presbytis cristata,* PCR); NWM: common marmoset (*Callithrix jacchus*, CJA), dusky titi (*Callicebus molloch*, CMO), squirrel monkey (*Saimiri sciureus,* SSC); prosimians: black lemur (*Eulemur macaco,* EMA), ringtailed lemur (*Lemur catta,* LCA). The domestic cat (*Felis catus*, FCA) has also been investigated.

The YAC probes, from the CEPH megalibrary, were obtained from the YAC Screening Center (Milan, Italy). All BAC probes belong to the RP11 de Jong libraries. The WCPs specific for human chromosomes 10, 16, and 22, derived from flow-sorted chromosomes, were a gift of the Sanger Centre (Dr. N.P. Carter). The PCPs have been constructed in our laboratory (Antonacci et al. 1995; see also our Web site http://www.biologia.uniba.it/rmc). Human PCP no. 177, specific for 10p, and PCP no. 167, specific for almost the entire 10q, will be indicated as PCP-10p and PCP-10q, respectively. The PHYL-10 is indicated with different numbers, according to its relative size, in different primate species (Fig. 1), and it is split in some species.

The human genome sequencing data are derived from the SCD, April 2002 release.

DNA extraction from YACs and BACs has already been reported (Ventura et al. 2001). Fluorescence in situ hybridization (FISH) experiments were performed essentially as described by Lichter et al. (1990). Digital images were obtained using a Leica DMRXA epifluorescence microscope equipped with a cooled CCD camera (Princeton Instruments, N.J.). The Cy3 and 4′,6-diamidino-2-phenylindole fluorescence signals, detected with specific filters, were recorded separately as gray-scale images. Pseudocoloring and merging of images were performed using Adobe Photoshop software.

Results

The specific aim of this work was to define a detailed evolutionary history of PHYL-10 in primates. For this purpose we used: (i) PCP no. 177, specific for human 10p (HSA10p), PCP no. 167 specific for almost the entire 10q; (ii) a panel of 12 YAC probes, reported in Table 1; and (iii) a panel of BAC probe pools that have been mainly used in lemurs and cat, also reported in Table 1. Cohybridization experiments were occasionally performed to assess with certainty the order of close markers.

Great apes and Old World monkeys

The FISH results on great apes (HSA, PTR, GGO, PPY) and representatives of OWM (MMU, PHA, CAE, and PCR) using 12 YAC probes are illustrated in Fig. 1a. Note the splitting of marker F in all species except HSA, PTR, and GGO (insert in Fig. 1d). Additional BACs, identified on the SCD through sequence-tagged sites contained in the YAC 933A3 (marker F) were used on PPY better to define the breakpoint. The most interesting results was obtained with BAC 507K13 (at 52,581–52,780 kb in SCD), giving a signal centromeric to the breakpoint (Fig. 1d), and BAC 96B5 (at 52,941–53,132 kb), whose signal was found distal to the breakpoint (data not shown).

New World monkeys

In all published studies on NWM the human WCP10 library paints two different blocks (Sherlock et al. 1996; Morescalchi et al. 1997; Consigliere et al. 1998; Stanyon et al. 2000, 2001). Use of PCP10p, PCP10q, and the 12 YAC probes showed that in the three NWM we studied (CJA, CMO, and SSC) the two blocks correspond

Fig. 1 Diagrams in **a**, **b**, and **i** summarize the fluorescence in situ hybridization (FISH) results and the hypothesized evolutionary history of phyl-10 in Old World monkeys (OWM) and great apes (**a**); in New World monkeys (NWM) (**b**); in lemurs and cat (**i**). (*CAE Cercopithecus aethiops*, *CJA Callithrix jacchus*, *CMO Callicebus molloch*, *EMA Eulemur macaco*, *FCA Felis catus*, *GGO Gorilla gorilla*, *HSA Homo sapiens*, *LCA Lemur catta*, *MMU Macaca mulatta*, *PCR Presbytis cristata*, *PHA Papio hamadrias*, *PPY Pongo pygmaeus pygmaeus*, *PTR Pan troglodytes*, *SSC Saimiri sciureus*) The chromosome number specific for each species is reported below each chromosome ideogram. The diagram in **j** illustrates the hypothesized arrangement of PHYL-10 in the ancestor of primates and mammals (PHYL-10p in *red*, PHYL-10q in *green*). **c–h** Examples of FISH experiments. **c** Yeast artificial chromosome (YAC) 934C4 (marker M, *green*) cohybridized with whole chromosome paint (WCP) specific for human chromosome 16 (*red*) on a CMO metaphase. Note that WCP16 identifies four distinct homologous regions in CMO: two on CMO7 (*large arrow*) and two on CMO6 (*small arrow*). Note also the polymorphism of the pericentromeric region of CMO7: the signal is on opposite sides in the two homologs; **d** FISH experiment using bacterial artificial chromosome (BAC) 507K13 on PPY metaphase. In the insert are reported the two PPY7 homologs (PHYL-10) showing the split signals of YAC 933A3 (marker F); **e** WCP specific for human chromosome 22 (*red*) cohybridized with BAC 351D16, containing the RET gene (marker R, *green*), on EMA metaphase; **f** BAC pool P on EMA metaphase; **g** BAC 351D16 (RET gene, marker R, *green*) cohybridized with pool S (*red*) on FCA; **h** pool P hybridizing to FCA chromosome B4

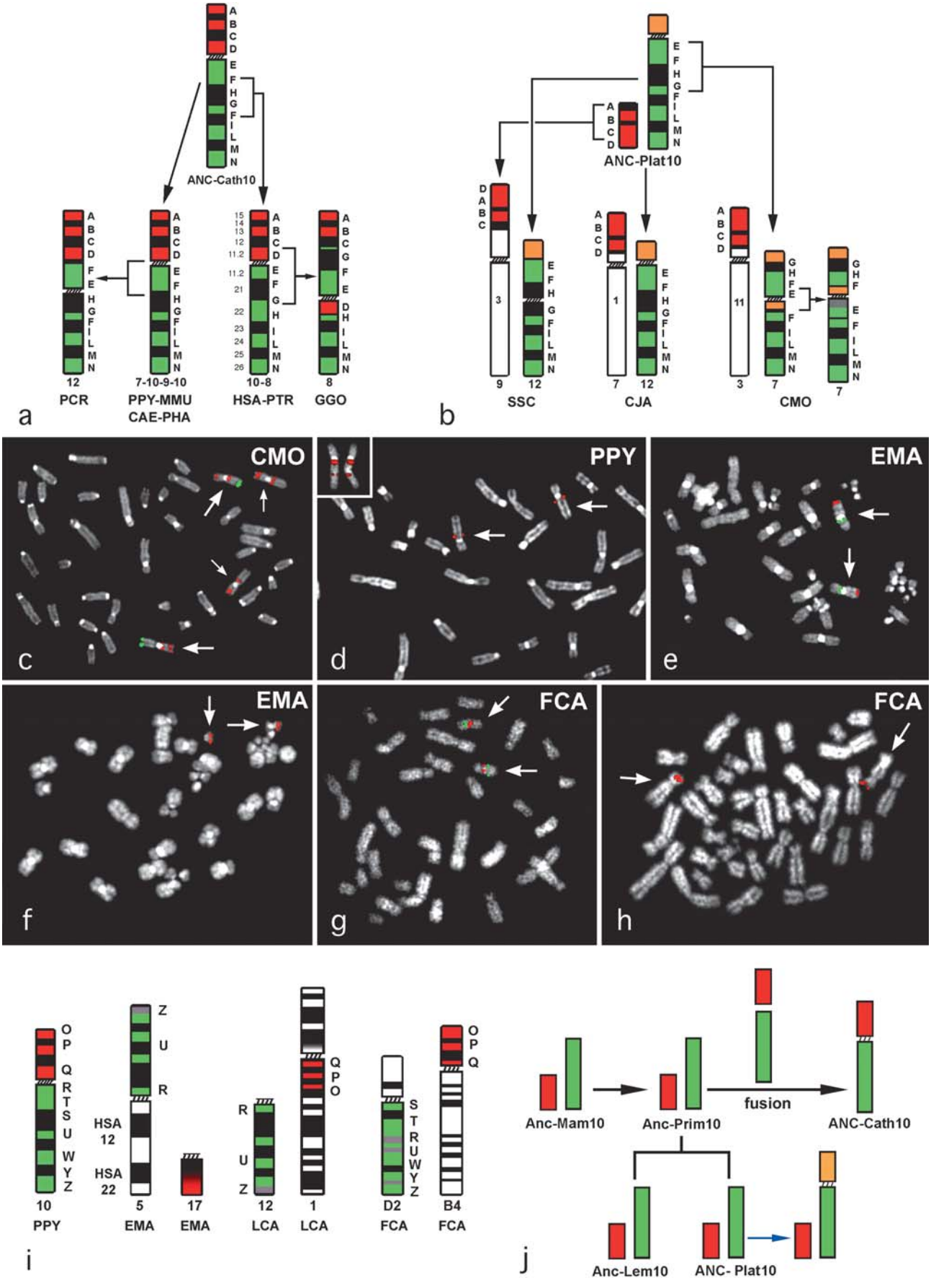
ANC-Cath10
PCR
PPY-MMU
CAE-PHA
HSA-PTR
GGO
a
ANC-Plat10
SSC
CJA
CMO
b
CMO
c
PPY
d
EMA
e
EMA
f
FCA
g
FCA
h
PPY
EMA
EMA
LCA
LCA
FCA
FCA
i
Anc-Mam10
Anc-Prim10
fusion
ANC-Cath10
Anc-Lem10
ANC- Plat10
j

Table 1 Human YAC and BAC pool probes used in the study and cat radiation hybrid (RH) markers. The YACs belong to the CEPH megalibrary. Their position on the University of California Santa Cruz Database (SCD), in megabases is derived from the sequence-tagged sites (STSs) they contain. All BAC probes belong to the RPCI-11 de Jong library (http://www.chori.org/bacpac). The SCD map position of the first and last BAC of each pool is reported. A selection of cat RH markers (http://rex.nci.nih.gov/lgd/cat; Murphy et al., 2000) is listed. Their position on the cat RH map (cR) is compared with their position on the SCD human sequence map

YACs					BACs				Cat RH	
	Code	Mapping	STS	Mb	Pool	Code	Mapping	Mb	Cat marker (cR)	HSA (Mb)
A	946G12	10p15.3	WI-6177	1	**O**	10D13–195B3	10p15	0–3	IL2RA (0)	4
B	808A2	10p13	D10S223	13	**P**	454I3–379F12–397O4–120C13	10p14	7–11	NMT2 (64)	15
C	875B4	10p12.1	D10S197	26	**Q**	30A6–241I20–60H16–134A8	10p11.2	33–39	BMI1 (146)	22
D	837B5	10p11.21	D10S1791	41		**CEN**			ITGB1 (188)	34
CEN					**R**	351D16 (RET gene)	10q11.2	44	**CEN**	
E	895D3	10q11.21	D10S604	45	**S**	118J22–550M24–97A17	10q21	58–63	EGR2 (328)	65
F	933A3	10q11.22	WI-6188	52	**T**	227H15–222G7	10q22	72–78	Hs.182470 (443)	87
G	876B5	10q22.2	D10S188	77	**U**	337H16–402D21–119K6–7D5	10q24.1	95–99	CHAT (462)	52
H	807D4	10q22.3	D10S551	87	**W**	548K23–316M21–411B6	10q24.3	103–106	RET (475)	44
I	744D4	10q24.1	D10S1736	100	**Y**	348N5–159K22–357H24	10q25	114–116	CYP17 (504)	103
L	926A7	10q26.3	D10S1201	122	**Z**	88I10–296H2–283C16	10q26	127–133	Hs.93667 (530)	107
M	935F11	10q25.3	D10S1748	130					ADRA2A (616)	114
N	934C4	10q26.2	D10S214	135					Hs.23620 (645)	126
	Total length			138						

exactly to the human HSA10p and HSA10q (Fig. 1b). In all these three species, furthermore, the phyl-10q block is associated with sequences homologous to HSA16. The PHYL-10p, on the contrary, is associated with different counterparts in all three species: with HSA1 in CJA (CJA7), with HSA11 in CMO (CMO3), with HSA3 in SSC (SSC9). Figure 1c reports the finding that the two CMO7 homologs differ, in all cells, for a pericentric inversion involving marker E and the heterochromatic block adjacent to the centromere. Marker F gave split signals in all NWM species.

Lemurs (prosimians) and cat (*Felis catus*)

In EMA, LCA, and cat, the PCP libraries and YAC probes turned out not to be very efficient in FISH experiments. For these species we decided to use a pool of BACs close to each other as a single probe (see Table 1). The BAC probes were carefully selected for their gene richness, as reported in SCD, because greater sequence conservation could be predicted. To track the evolutionary history of PHYL-10 better in these species the BAC pools were also hybridized to PPY (see Fig. 1i) because the marker order of both PHYL-10p and PHYL-10q in PPY corresponds to the ancestral form of OWM and NWM (see Discussion). Examples of FISH experiments in EMA are reported in Fig. 1e, f. Overall results are summarized in Fig. 1i. In both EMA and LCA, as in NWM, the PHYL10p and PHYL-10q blocks are localized apart. The PHYL-10q corresponds to a unique chromosome in both EMA (EMA5) and LCA (LCA12). In EMA also the PHYL-10p forms a unique chromosome (EMA17), while in LCA it is part of a larger chromosome (LCA1). The marker order of both blocks appears roughly conserved (Fig. 1i). A more detailed analysis was hampered by failure of some pools in FISH.

In the cat both PHYL-10p and phyl-10q are part of a larger chromosome, FCA-B4 and FCA-D2, respectively. Some FISH examples are shown in Fig. 1g, h.

Discussion

In previous papers we have presented details of the structure and evolution of the pericentromeric regions of human chromosome 10 (Jackson et al. 1999; Guy et al. 2000). In this paper we have delineated its evolutionary history using the cat as an outgroup. The use of the latter species substantially contributed to the definition of the ancestral primate form of this chromosome, since its karyotype appears as one of the most highly conserved among mammals (O'Brien et al. 1997).

Great apes and Old World monkeys

In great apes and OWM the PHYL-10 appears as a single chromosome. The marker order analysis defined four different groups: [PPY-MMU-CAE-PHA], [HSA-PTR], [GGO], and [PCR], as reported in Fig. 1a. The orang appears to conserve the ancestral hominoid form shared with the ancestor of African apes (Anc-Cath10 in Fig. 1a). The HSA-PTR form can be reconciled with Anc-Cath10 by assuming a paracentric inversion. A single additional inversion of the HSA-PTR form leads to GGO. A pericentric inversion differentiated the PCR form from PPY-MMU-CAE-PHA. Note that in PCR and GGO the PHYL-10 is a metacentric chromosome as a consequence of two distinct apomorphic pericentric inversions. Marker F splits in all examined species, with

the exception of HSA, PTR, and GGO. These findings suggest that marker F in HSA spans the chromosomal segment where two regions that were localized apart joined after the paracentric inversion event in the ancestor of HSA-PTR-GGO, thus confirming that the HSA-PTR-GGO PHYL-10 form is derivative with respect to the ancestral arrangement. The PPY breakpoint identified by marker F was found to fall between BACs 507K13 and 96B5, which are 161 kb apart.

New World monkeys

Data from the literature on NWM (see Introduction), obtained by the use of human WCP10, have shown that this painting library recognizes two distinct blocks in all platyrrhines, and that in all species a 10/16 association is present. Stanyon et al. (2001) have reported, using reciprocal paintings, that in woolly monkey (*Lagotrix lagotrica*, LLA), PHYL-10p is a separate chromosome, while PHYL-10q is associated with chromosome 16. We found the same 10q/16 association in SSC, CJA, and CMO. Very likely, the 10/16 association is ancestral to platyrrhine. We have also found that in these species the PHYL-10p is not a single chromosome and that in all the three species it is associated with different partners. These overall data indicate that PHYL-10 in the platyrrhine ancestor was separated in PHYL-10p and PHYL-10q, which we designate as ANC-Plat10p and ANC-Plat10q. The constant partner chromosome of ANC-Plat10q could be positively identified as chromosome 16 (see also below). The finding that ANC-Plat10p has different partners in SSC, CJA, CMO (Sherlock et al. 1996; Morescalchi et al. 1997; Consigliere et al. 1998; Stanyon et al. 2000; present study), and that it is a single chromosome in LLA (Stanyon et al. 2001) strongly suggest that the latter form is ancestral.

The marker order arrangement in SSC is identical to CJA and, as stated, could reflect the ANC-Plat10q arrangement. However, the centromeric position in SSC is unequivocally different. Indeed it is located between markers H and G in this species, while being close to marker E in CJA, CMO, and in all OWM (Fig. 1b). These data suggest that in SSC repositioning of a centromere occurred. We have recently described this biological phenomenon (Montefalcone et al. 1999; Ventura et al. 2001), which does not appear to be a rare event. Other examples, in primates and in mammals, have been envisaged (Iannuzzi et al. 2000; Müller et al. 2000), and several examples have been identified in cattle (Band et al. 2000).

Surprisingly, the marker order of the two CMO homologous chromosomes shows a pericentric inversion in heterozygous status (Fig. 1b). We do not know which is the most common form nor its distribution in the population. We cannot discard the possibility that the inversion occurred in cell culture. However the latter hypothesis seems unlikely since the same polymorphism was detected in all the 50 analyzed metaphases.

Lemurs and cat

Müller et al. (1997, 1999), using WCP10 and reciprocal painting, have reported that in EMA and in *Eulemur fulvus fulvus* (EFU) the WCP generates two distinct blocks, corresponding to PHYL-10p and PHYL-10q. Our data show that this same distinction is present in LCA. It can be assumed, therefore, that the PHYL-10 was organized in two distinct chromosomes in the ancestor of prosimians (Fig. 1e, f). This conclusion is reinforced by the comparison with the cat (Fig. 1i). The analysis of overall data in NWM and prosimians strongly suggests that the PHYL-10p and PHYL-10q were organized as distinct and unique chromosomes in the primate ancestor, contrary to the hypotheses reported by Chowdhary et al. (1998) and Murphy et al. (2001), as illustrated in Fig. 1j. Comparison of the PHYL-10p internal marker order among PPY, sharing the form of ancestral OWM and NWM ancestors, LCA, and FCA excludes gross rearrangements and suggests that marker order is conserved. This conclusion is also supported by the RH data in the cat (Table 1 c). The PHYL-10q comparison is more complex and detailed analysis was only possible in cat. The FISH data indicate the presence of a paracentric inversion differentiating the position of pool markers R, S, and T in PPY and cat. The analysis of the corresponding region in the cat RH map confirms the presence of a paracentric inversion (Table 1 c). The mapping data of the CHAT gene in cat, HSA, and PPY turned out to be very useful in comparing the cat and PPY forms of PHYL-10q. This gene, 52 kb in size (SCD) and covering the interval 52,572–52,624 kb, spans the first 42 kb of the centromeric part of BAC 507K13, located at 52,581–52,780 kb (from SCD). The use of this probe in FISH experiments on PPY (Fig. 1d) indicates that the CHAT marker is located centromeric to the breakpoint. This conclusion clarifies that the cat and PPY forms of PHYL-10q can be perfectly reconciled by assuming a single paracentric inversion involving RH markers EGR2, Hs.182470, CHAT, and RET. We cannot discriminate, at present, which of these two forms is ancestral. Some hints, however, were derived from the following data. Marker R in EMA and LCA is close to the centromere, as in PPY, indicating that the PHYL-10q forms of EMA and LCA are more close to the PPY than to the cat. Furthermore, we mined mammalian databases looking for data helpful in this respect (http://www.thearkdb.org; http://www.toulouse.inra.fr/lgc/pig/cyto/cyto.htm). The only useful information concerns the location of markers OAT and CHAT in the pig (*Sus scrofa*) chromosome 14, of which the PHYL-10q is an uninterrupted portion. OAT is telomerically located as in PPY and cat, while CHAT is localized on the central part of PHYL-10q, as in the cat. The conclusion that the cat marker arrangement of PHYL-10q is ancestral, however, is only tentative.

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