American Journal of Primatology 57:177–188 (2002)

Chromosomal Homologies Between *Cebus* and *Ateles* (Primates) Based on ZOO-FISH and G-Banding Comparisons

F. GARCÍA[1,2], A. RUIZ-HERRERA[1], J. EGOZCUE[1,2], M. PONSÀ[1,2], AND M. GARCIA[1,2]*
[1]*Departament de Biologia Cel.lular, Fisiologia i Immunologia, Barcelona, Spain*
[2]*Institut de Biotecnologia i Biomedicina, Universitat Autònoma de Barcelona, Barcelona, Spain*

ZOO-FISH (Fluorescent ''in vitro'' hybridization) was used to establish the chromosomal homology between humans (HSA) and *Cebus nigrivitatus* (CNI) and *Ateles belzebuth hybridus* (ABH). These two species belong to different New World monkey families (Cebidae and Atelidae, respectively) which differ greatly in chromosome number and in chromosome morphology. The molecular results were followed by a detailed banding analysis. The ancestral karyotype of *Cebus* was then determined by a comparison of in situ hybridization results, as well as chromosomal morphology and banding in other Platyrrhini species. The karyotypes of the four species belonging to the genus *Cebus* differ from each other by three inversions and one fusion as well as in the location and amounts of heterochromatin. Results obtained by ZOO-FISH in ABH are in general agreement with previous gene-mapping and in situ hybridization data in *Ateles,* which show that spider monkeys have highly derived genomes. The chromosomal rearrangements detected between HSA and ABH on a band-to-band basis were 27 fusions/fissions, 12 centromeric shifts, and six pericentric inversions. The ancestral karyotype of *Cebus* was then compared with that of *Ateles.* The rearrangements detected were 20 fusions/fissions, nine centromeric shifts, and five inversions. Atelidae species are linked by a fragmentation of chromosome 4 into three segments forming an association of 4/15, while *Ateles* species are linked by 13 derived associations. The results also helped clarify the content of the ancestral platyrrhine karyotype and the mode of chromosomal evolution in these primates. In particular, associations 2/16 and 5/7 should be included in the ancestral karyotype of New World monkeys. Am. J. Primatol. 57:177–188, 2002.

Key words: primates; ZOO-FISH; *Cebus*; *Ateles*; chromosome evolution

Contract grant sponsor: DGES; Contract grant number: PB96/1170; Contract grant sponsor: DGES; Contract grant number: BXX 2000-0151.

*Correspondence to: Montserrrat Garcia Caldés, Departament de Biologia Cel.lular, Fisiologia i Immunologia, Unitat de Biologia, Facultat de Medicina, Universitat Autonoma de Barcelona, 08193. Bellaterra, Barcelona, Spain. E-mail: montserrat.garcia.caldes@uab.es

Received 7 December 2001; revision accepted 9 May 2002

DOI 10.1002/ajp.10047
Published online in Wiley InterScience (www.interscience.wiley.com).

INTRODUCTION

Although many publications have analyzed the phylogenetic relationships among the Platyrrhini, there is still no definitive consensus. However, most recent interpretations based on DNA sequences [Goodman et al., 1998; Meireles et al., 1999; Schneider et al., 2001] classify these primates into three families: Cebidae (comprising the genera *Cebus*, *Saimiri*, *Aotus*, *Saguinus*, *Leontopithecus*, *Cebuella*, *Callimico*, and *Callithrix* genera); Pithecidae (genera *Pithecia*, *Cacajao*, *Chiropotes*, and *Callicebus*); and Atelidae (genera *Alouatta*, *Ateles*, *Lagothrix*, and *Brachyteles*).

The phylogenetic relationships in the Atelidae are not clearly established. Morphological studies have provided contradictory results: Ford [1986] arranged *Brachyteles*, *Lagothrix*, and *Ateles* in an unresolved trichotomy; Rosenberger et al. [1990] stated that the branching order is *Brachyteles* and *Ateles* forming a clade, followed by *Lagothrix* and then *Alouatta*; Kay [1990] grouped the Atelidae into two sister clades, one grouping *Alouatta* and *Brachyteles*, and the other grouping *Lagothrix* with *Ateles*. However, results based on DNA sequences [Meireles et al., 1999; Schneider et al., 2001] are more homogeneous and group *Brachyteles* with *Lagothrix* in a clade followed by *Ateles* and then *Alouatta*.

The aim of this work is to help clarify the chromosomal phylogeny and evolution of New World monkeys. Cytogenetic data are presented and compared for species from two genera belonging to two New World monkey families: Cebidae (family Cebidae; subfamily Cebinae, genera *Cebus*) and Atelidae (family Atelidae; subfamily Atelinae, genera *Ateles*). These genera differ in chromosome number ($2n = 52–54$ for *Cebus*, and $2n = 32–34$ for *Ateles*) and chromosome morphology. The karyological characteristics of the four species of *Cebus* [Napier and Napier, 1985; Rowe, 1996] are considered to be more conserved with regard to the ancestral karyotype of the Platyrrhini [Dutrillaux and Couturier, 1981; Clemente et al., 1990], while the *Ateles* species appear to have a highly derived karyotype [Turleau et al., 1974; García et al., 1975; Morescalchi et al., 1997].

Both molecular (ZOO-FISH) and classical (G-banding) cytogenetic methods were used to: 1) determine the *Cebus* ancestral karyotype; and 2) detect the chromosomal rearrangements that are derived traits in the karyotype of the *Ateles* species by comparing the *Cebus* and *Ateles* ancestral karyotypes, as well as the hybridization results obtained in *Ateles*, with those published in the literature on other Atelidae.

METHODS

G/C-Banded Karyotypes

Sequential G/C-banding in *Cebus albifrons* (CAL), *Cebus apella* (CAP), and *Cebus nigrivitatus* (CNI) chromosomes have been obtained. The *C. capucinus* (CCA) karyotype used in this study was published by Carlà Campa and Stanyon [1992]. The karyotypes of *Cebus* species have been arranged following the ordination proposed for CAP by Matayoshi et al. [1986] and Ponsà et al. [1995].

Sequential G/C-banding in the *Cebus* and *Ateles* was obtained following the methods described by Seabright [1971] for G-banding, and by Sumner [1972] for C-banding. The karyotype of *Ateles belzebuth hybridus* (ABH) was arranged following that proposed by Medeiros et al. [1997].

ZOO-FISH

Human (HSA) chromosome-specific probes (Oncor and Cambio) were used to hybridize CNI and ABH chromosomes following the method described in García et al. [1999, 2000].

RESULTS

Genus *Cebus*

Homologies with the human karyotype were established by ZOO-FISH using whole human-chromosome probes in CNI (Fig. 1). The G/C-banded karyotype of CNI along with the homologies to human chromosomes are shown in Fig. 2a. The homologies established by in situ hybridization were used as a guide in comparing the banding pattern between the four species of *Cebus* (CAP, CNI, CAL, and CCA) (Fig. 2b).

Results show that: 1) CAL and CCA have identical karyotypes; 2) CNI differs from the previous species and CAP by a fusion of chromosomes 12 and 24 (Fig. 2b); 3) CAP karyotype differs from the other three *Cebus* species by

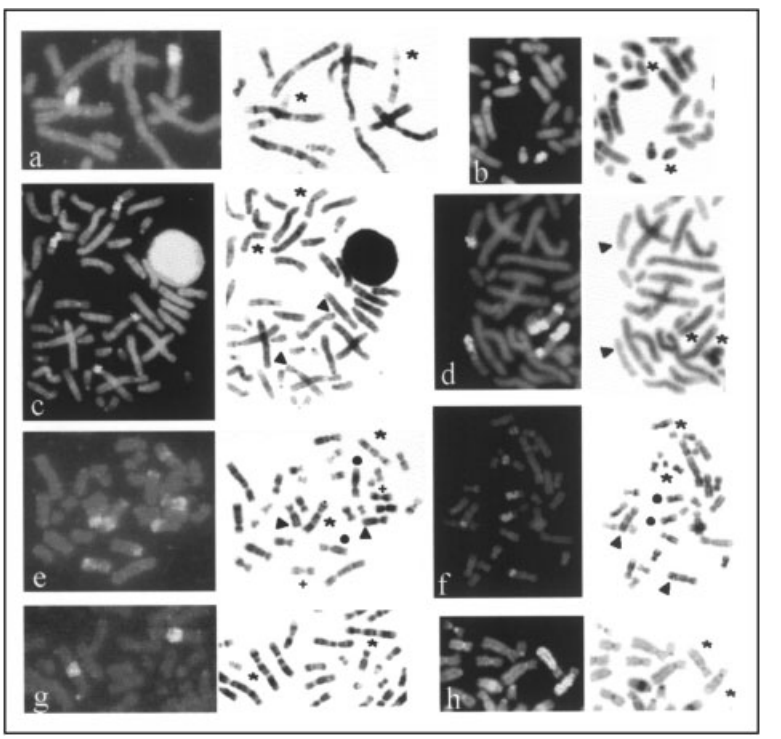

Fig. 1. ZOO-FISH results in CNI and ABH. **a:** The HSA19 probe hybridizes to pair 8 (*) of ABH. **b:** The hybridization signal in CNI chromosome 10 (*) with HSA20 probe. **c:** The HSA15 probe hybridizes on the short arm of pair 12/24 (◀) and on the proximal region of p and q arms of pair 6 (*) in CNI. **d:** The HSA8 probe hybridizes on pair 8 (*) (except for the interstitial heterochromatic region), and on the short arm of pair 7 (◀) in CNI. **e:** The HSA1 probe hybridizes with pairs 2 (*), 4 (●), 6 (◀), and 7 (+) of ABH. **f:** The HSA4 probe hybridizes with pairs 2 (◀), 9 (*), and 15 (●) of ABH. **g**: with the HSA14 probe the hybridization signal can be seen in pair 2 (*) of ABH, and in (**h**) CNI the HSA12 probe hybridizes on the long arm of pair 12/24 (*).

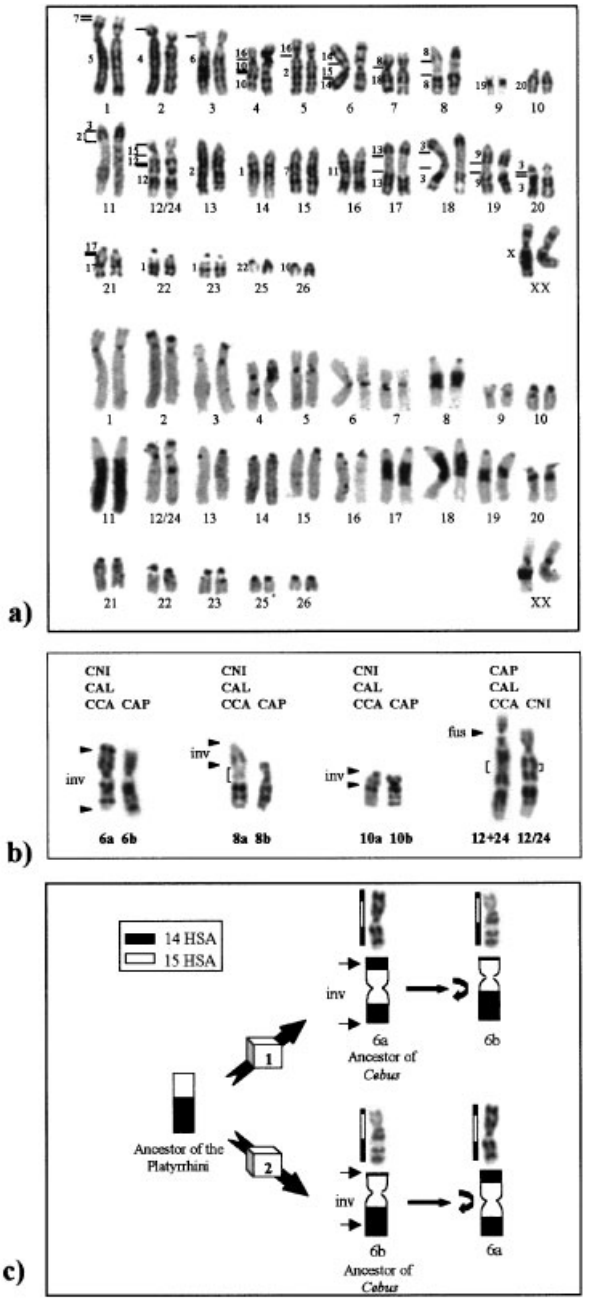

Fig. 2. **a:** Sequential G/C-banded karyotype of CNI. To the left of each G-banded chromosome, the numbers indicate the human probe that hybridizes with each region. Bars indicate the limits of the homologies. **b:** Chromosomal rearrangements detected when the four *Cebus* species are compared: *C. apella* (CAP), *C. nigrivitatus* (CNI), *C. albifrons* (CAL), and *C. capucinus* (CCA). inv, inversion; fus, fusion; [, interstitial heterochromatic regions. **c:** Different possibilities for chromosome 6 in the *Cebus* ancestral karyotype: 1) if the ancestral form is 6a, CAL, CCA, and CNI karyotypes are similar to the ancestor, and CAP would present a pericentric inversion; and 2) if the ancestral form is 6b, CAP has the ancestral form and CNI, CAL, and CCA show a pericentric inversion.

inversions in chromosomes 6, 8, and 10 (Fig. 2b); and 4) variation between the four species in the size and location of constitutive heterochromatin account for differences in morphology and size observed in some homologous chromosomes (Fig. 2b).

Chromosomal Homologies Between HSA and ABH

Results obtained in ABH after ZOO-FISH using human chromosome probes can be seen in Figs. 1 and 3a. The HSA and ABH G-banded chromosomes were compared and homologies were established to determine chromosomal rearrangements that could explain the homologies detected by ZOO-FISH (Fig. 3b). Chromosomal rearrangements that occurred in homologs to human chromosomes can then be grouped into four categories: 1) chromosomes with no rearrangements: X chromosome; 2) chromosomes with only one rearrangement: 13 and 17; 4) chromosomes with more than one known rearrangement: 4, 6, 7, 8, 9, 10, 11, 12, 14, 15, 18, 19, 20, 21, and 22; and 4) chromosomes with unknown rearrangements: 1, 2, 3, 5, and 16.

The rearrangements detected when the ABH and HSA chromosomes were compared included at least 27 fusions/fissions, 12 centromeric shifts, and six pericentric inversions.

DISCUSSION

Ancestral Karyotype of *Cebus*

Comparison of the four *Cebus* species revealed the presence of three inversions (in chromosomes 6, 8, and 10) and one fusion (of 12 and 24 chromosomes) to establish homology among these species. We propose that chromosomes with an identical morphology in the four *Cebus* species are probably present in the putative *Cebus* ancestral karyotype. To determine the ancestral form for chromosomes that show differences between the four *Cebus* species (6, 8, 10, 12, and 24), in situ hybridization results, chromosomal morphology, and G-banding patterns of their homologs in other Platyrrhini species were compared.

Cebus chromosome 6 has two morphologies: forms 6a and 6b (Fig. 2b). In both cases, a 14/15/14 association is observed: 6p proximal+q proximal homologous to human chromosome 15, flanked by two regions (6p distal and 6q distal) homologous to human chromosome 14 (CNI (Fig. 2a); CAP [García et al., 2000]; and CCA [Richard et al., 1996]). Chromosome 6 has the same morphology in CNI, CAL, and CCA (form 6a, Fig. 2b) and a different morphology in CAP (form 6b, Fig. 2b). In *Callithrix jacchus* (CJA) [Sherlock et al., 1996)], *Callicebus moloch* (CMO) [Stanyon et al., 2000)], *Alouatta belzebul* (ABE) [Morescalchi et al., 1997], and *Lagothrix lagothricha* (LLA) [Stanyon et al., 2001], the inversion necessary to internalize the homologous region of HSA15 has not been detected. Therefore, it is not possible to determine which form (6a or 6b) would be present in the ancestral karyotype of *Cebus* (Fig. 2c).

Cebus chromosome 8 is homologous to a part of human chromosome 8 (CAP [García et al., 2000], CNI (Figs. 1 and 2a), and CCA [Richard et al., 1996]). In CNI, CAL, and CCA chromosome 8 is acrocentric (form 8a, Fig. 2b), and in CAP it is submetacentric (form 8b, Fig. 2b). In CJA [Sherlock et al., 1996], ABE [Morescalchi et al., 1997], and CMO [Stanyon et al., 2000], the homologous chromosome is similar, in morphology and in its G-banding pattern, to form 8a. Thus, the ancestral form would probably be form 8a.

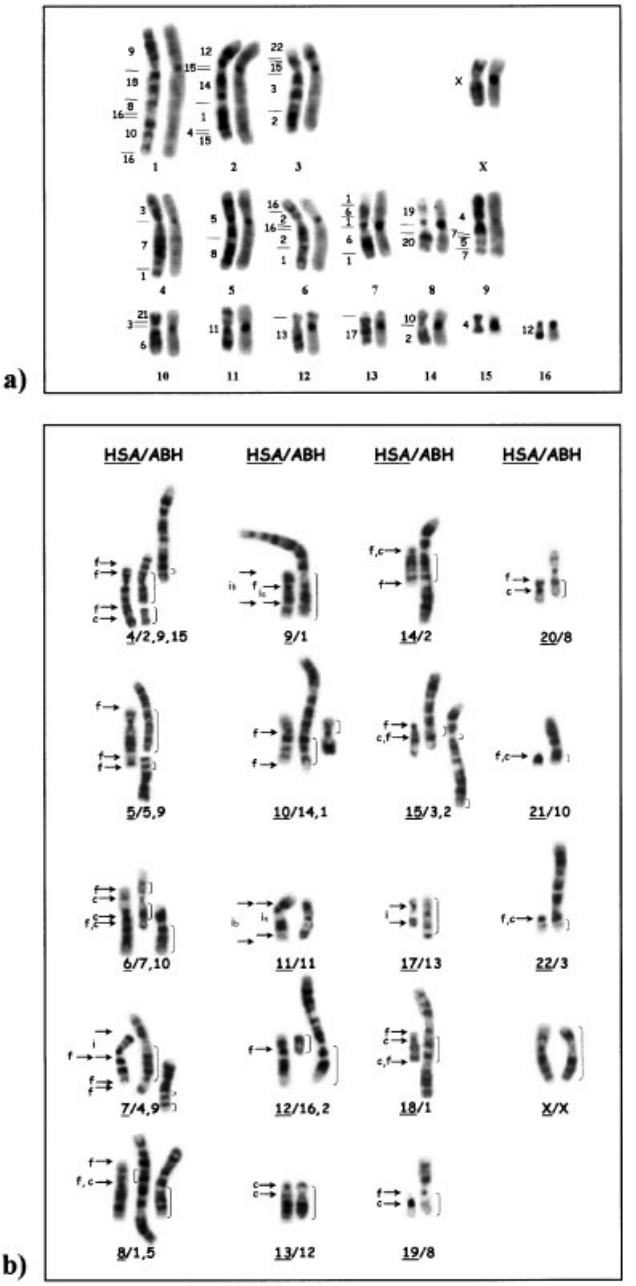

Fig. 3. **a:** Composite ABH karyotype with sequential G/C bands, with a G-banded chromosome on the left and the same C-banded chromosome on the right. To the left of each G-banded chromosome, the numbers indicate the human probe that hybridizes with each region. Bars indicate the limits of the homologies. **b:** Chromosomal rearrangements that explain homologies detected between HSA and ABH chromosomes. f, fusion/fission; i, inversion; c, centromeric shift. Arrows indicate bands involved in the rearrangements. Numbers corresponding to human chromosomes are underlined. Matching between HSA/ABH chromosomes is restricted to regions previously shown to share ZOO-FISH homologies (vertical bars).

Cebus chromosome 10 is homologous to HSA20, as it has been described by ZOO-FISH in CCA [Richard et al., 1996], CAP [García et al., 2000], and CNI (Figs. 1 and 2a). *Cebus* chromosome 10 is acrocentric in CNI, CAL, and CCA (form 10a, Fig. 2b) and submetacentric in CAP (form 10b, Fig. 2b). Although the homologous chromosome to HSA 20 in *Lagothrix lagothricha* [Stanyon et al., 2001] is similar to form 10b, the morphology and the banding pattern of the chromosome homologous to HSA20 in other Platyrrhini species [Sherlock et al., 1996; Consigliere et al., 1995, 1998; Stanyon et al., 2000] and in the Catarrhini *Presbytis cristata* [Bigoni et al., 1997] suggest that the ancestral form in *Cebus* would be 10a.

Cebus chromosome 12 is homologous to HSA12, and *Cebus* chromosome 24 is homologous to a part of HSA15 (CCA [Richard et al., 1996] and CAP [García et al., 2000]). Chromosomes 12 and 24 of *Cebus* are fused only in CNI to form a submetacentric chromosome, where the long arm is homologous to HSA12 and the short arm is homologous to a part of HSA15 (Figs. 1 and 2a and b). Although *Ateles* presents the HSA 12/15 association (ABE [Morescalchi et al., 1997] and ABH (present work)), this association has not been described in the other Platyrrhini species analyzed in the literature [Sherlock et al., 1996; Consigliere et al., 1998; Stanyon et al., 2000, 2001]. This fact seems to indicate that the morphology present in CNI would be a derived morphology and not an ancestral characteristic of *Cebus*.

The ancestral karyotype of *Cebus* would be: 1–5, 6a or 6b, 7, 8a, 9, 10a, 11–26, and X ($2n = 54$).

Ancestral Form of 14/15 Association in the *Cebinae*

As noted above, the Platyrrhini species *Callicebus moloch*, *Callithrix jacchus*, *Alouatta seniculus sara, A. seniculus arctoidea*, *A. belzebul*, *Ateles geoffroyi*, *A. belzebuth hybridus*, and *Lagothrix lagothricha* present a 14/15 association, but without the 14/15/14 hybridization pattern. However, in *Saimiri sciureus* the 14/15 New World monkey ancestral association has undergone two more inversions than those observed in *Cebus*, and thus the hybridization pattern detected is 14/15/14/15/14/15 [Stanyon et al., 2000]. *Cebus* and *Saimiri* are the two genera that form the subfamily Cebinae [Schneider et al., 2001]. It appears to be probable that in the ancestor of this group (Cebinae), at least one inversion in the 14/15 ancestral association was produced. If this assumption is correct, the Cebinae ancestral form would be *Cebus* 6a or 6b, and different inversions would be produced in the *Cebus* and *Saimiri* genera. It is important to note that these inversions have not been observed in Platyrrhini genera with highly derived karyotypes. This fact seems to indicate that this region shows a high degree of cytogenetic instability in Cebinae, and thus it is more prone to break and invert.

Comparison of the Ancestral Karyotypes of *Cebus* and *Ateles*

Results obtained by ZOO-FISH in ABH are in agreement with gene-mapping data for *A. paniscus chamek* [Moreira et al., 1997; Seuánez et al., 1997; Canavez et al., 1998], and for *Ateles geoffroyi* [Morescalchi et al., 1997] (Stanyon, personal communication), which presents the same karyotype as ABH. The ABH karyotype differs only by inversions in chromosomes 6 and 7 from the ancestral *Ateles* karyotype described by Medeiros et al. [1997]. Because of this similarity, the ABH karyotype (bearing in mind the differences in chromosomes 6 and 7,

with regard to the *Ateles* ancestral karyotype) and the ancestral *Cebus* karyotype were compared, and the results can be seen in Fig. 4.

Taking the homologies detected into account, G-banded chromosomes were compared in order to determine chromosomal rearrangements that could explain these homologies (Fig. 4b). *Cebus* and *Ateles* ancestral karyotypes were compared in reference to the homologies detected by ZOO-FISH with the human karyotype (CCA [Richard et al., 1996], CAP [García et al., 2000], CNI (Figs. 1 and 2a), and ABH (Figs. 1 and 3a). However, G-band homologies between ABH and some *Cebus* chromosomes have not been determined: 1) *Cebus* chromosomes 4p, 5, 6, 13, 14, 22, and 23, because of the high degree of fragmentation of human chromosomes 1, 2, and 16 in the ABH karyotype; and 2) *Cebus* chromosome 6, because of unknown rearrangements.

The G-banding comparison of the proposed *Cebus* ancestral karyotype and ABH show a great number of rearrangements: 20 fusions/fissions, nine centromeric shifts, and five inversions. Results revealed at least three different kinds of relationships between *Cebus* and ABH chromosomes (Fig. 4b): 1) synteny maintained between *Cebus* chromosomes and a single whole ABH chromosome: 16, 17, 21, and X; 2) synteny maintained between *Cebus* chromosomes, but in ABH associated with region or regions homologous to other *Cebus* chromosome: 7, 8, 9, 10, 11, 15, 18, 19, 20, 24, 25, and 26; and 3) synteny of *Cebus* chromosomes disrupted in ABH: 1, 2, 3, and 12 are found on more than one ABH chromosome while chromosome 6 is found disrupted on a single ABH chromosome. The homology between chromosomes 4, 5, 13, 14, 22, and 23 of *Cebus* and their homologs in ABH remains unclear.

Considering intrachromosomal rearrangements in addition to synteny, the *Cebus* ancestral chromosomes can be grouped as follows: 1) chromosomes with no rearrangements: the X chromosome; 2) chromosomes with only one rearrangement: 11, 16, 17, 19, 20, 21, 24, and 26; 3) chromosomes with more than one rearrangement: 3, 4q, 7, 8, 9, 10, 12, 15, 18, and 25; and 4) chromosomes with undetermined rearrangements: 1, 2, 4p, 5, 6, 13, 14, 22, and 23.

Chromosomal Rearrangements in Primate Evolution

In the present report, the chromosomal rearrangements seen in different species of the same genus are predominantly inversions. When different genera are compared, at least in these cases, fusions/fissions appear predominant.

For instance, chromosome comparison of the *Cebus* species shows a low number of rearrangements in this genus. The same observation was made by Medeiros et al. [1997] between species of the genus *Ateles*. In both genera, inversions are the most frequent rearrangement detected. Inversions (with, in some cases, heterochromatin variations and centromeric shift) are also the most frequent rearrangement detected when karyotypes of other Cebidae species are compared [Dutrillaux and Couturier, 1981; Clemente et al., 1987; Mudry et al., 1994].

Comparisons between the genera *Cebus* and *Ateles* have revealed that fusions/fissions are the most frequent rearrangement detected. Comparisons of the human karyotype with that of CAP and ABH have revealed that the most frequent rearrangements are also fusions/fissions [García et al., 2000] (present report).

When HSA and CAP are compared [García et al., 2000], the number of rearrangements is lower than that detected when *Cebus* and *Ateles* ancestral karyotypes (both Platyrrhini) are compared, indicating that *Ateles* species have

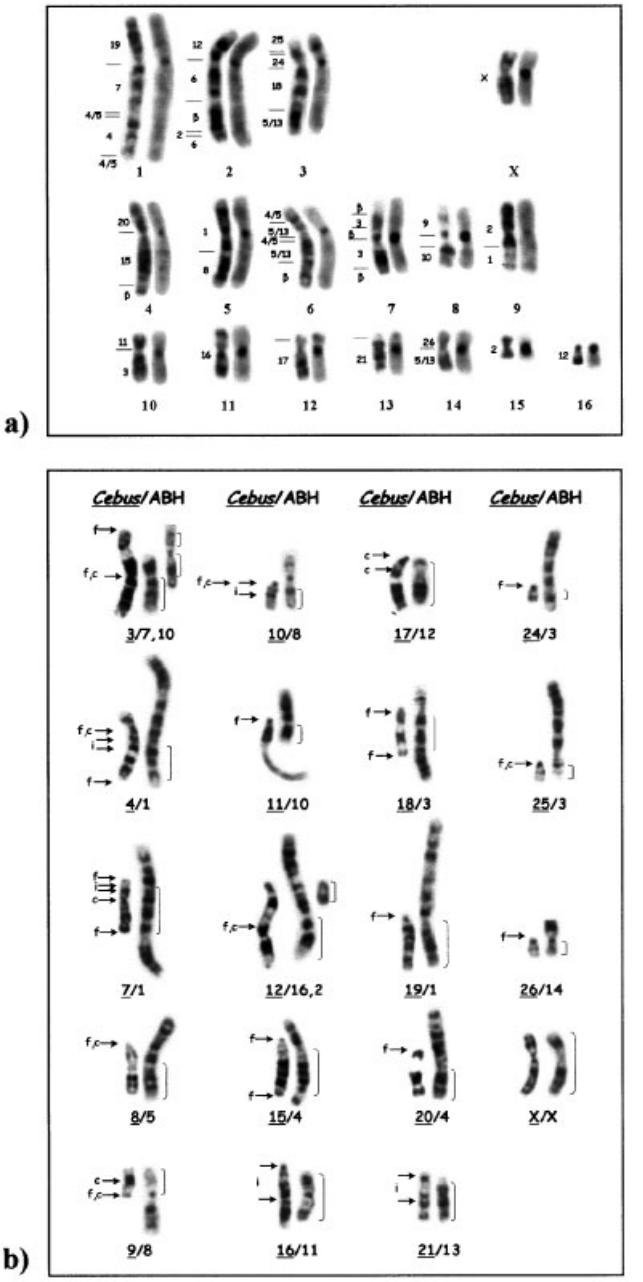

Fig. 4. **a:** Chromosomal homologies between the ancestral karyotype of *Cebus* and ABH based on ZOO-FISH with human probes. Numbers on the left correspond to *Cebus* chromosomes homologous to each pair. Bars indicate the limits of the homologies. β on the left of ABH chromosomes 2, 4, 6, and 7 indicates that all of these regions are homologous to *Cebus* chromosomes 14, 22, and 23. **b:** Chromosomal rearrangements that could explain homologies detected between *Cebus* and ABH. f, fusion/fission; i, inversion; c, centromeric shift. Arrows indicate bands involved in the rearrangements. The vertical bar on the right of ABH chromosomes shows the homologous region to the *Cebus* chromosome placed on the left. Regions of homology correspond to regions painted by the same human probe.

very derived karyotypes compared with those of *Cebus* species. These data show that the number of rearrangements and the phylogenetic distance are not always correlated. That was also the conclusion when human and gibbon species were compared [Jauch et al., 1992; Koehler et al., 1995].

Implications for the Ancestral Karyotype of the Platyrrhini

In the New World monkeys, there are some chromosomes that conserve the synteny to entire human chromosomes: 4, 6, 9, 11, 12, 13, 14, 17, 18, 19, 20, 21, 22, and X. These syntenies were proposed as ancestral for the Platyrrhini by Clemente et al. [1990] and Stanyon et al. [2000]. In Cebinae, only the synteny of HSA14 is disrupted by inversions (see above). In all the Atelidae, ancestral chromosome 4 is fragmented, showing hybridization signals in three different chromosomes. This synteny disruption links all the Atelidae, and it was probably produced in the Atelidae ancestor. Synteny of the chromosome homologous to HSA12 appears disrupted only in *Ateles* and *Callicebus moloch*. This latter case could be a convergence, but it could be useful to confirm that the two derived chromosomal segments homologous to HSA12 are the same in *Ateles* and *Callicebus*, by using *Ateles* and *Callicebus* reciprocal painting or subchromosomal painting probes from HSA12.

The association of New World monkey homologs to human chromosomes 3/21, 8/18, 10/16, and 14/15 are present in the Atelidae and Cebidae species and in other Platyrrhini, indicating that they are ancestral traits, in agreement with the Platyrrhini ancestral karyotype proposed by Stanyon et al. [2000].

In spite of the fact that associations 2/16 and 5/7 seem to be derived traits that link *Ateles* and *Lagothrix*, the following observations can be made: 1) the 2/16 association is also present in the Cebidae species, and 2) the 5/7 association appears to be ancestral in the New World monkey group, because it is present in the Cebidae and Atelidae species analyzed by ZOO-FISH in the literature [Richard et al., 1996; García et al., 2000; Stanyon et al., 2000, Morescalchi et al., 1997; Consigliere et al., 1998; Stanyon et al., 2001; this report] (Fig. 2a).

Highly Derived Karyotype of *Ateles*

Association 4/15 is a derived trait that links the Atelidae species (it is not present in the other New World monkeys studied). Finally, while *Cebus* does not show any association different from those present in the hypothetical Platyrrhini ancestor, in *Ateles* the associations 1/2, 1/4, 1/6, 1/7, 1/14, 2/3, 2/10, 3/6, 3/7, 4/7, 9/18, 12/15, and 19/20 seem to be derived in this genus, confirming that the *Cebus* species present a conserved karyotype with regard to the ancestral karyotype of the Platyrrhini, while the *Ateles* species present a highly derived karyotype.

Further studies using ZOO-FISH, reciprocal painting, and subchromosomal painting probes in different Cebidae and Atelidae species are required to achieve a better understanding of the Platyrrhini chromosomal evolution.

ACKNOWLEDGMENTS

The authors are grateful to the staffs of the Zoo de la Casa de Campo (Madrid), Parc Zoològic de Barcelona, and Marineland Catalunya, S.A., and to the BIOEVO group of the Universidad Simón Bolívar (Caracas) for providing primate blood samples. We also thank Mr. Chuck Simmons, an English instructor of this

university, for reviewing the English of this manuscript. The authors are also grateful to the Associate Editor of the *American Journal of Primatology* for his helpful comments.

REFERENCES

Bigoni F, Stanyon R, Koehler U, Morescalchi AM, Wienberg J. 1997. Mapping homology between human and black and white colobine monkey chromosomes by fluorescent *in situ* hybridization. Am J Primatol 42:289–298.

Canavez F, Moreira MAM, Bonvicino CR, Parham P, Seuánez HN. 1998. Comparative assignment in *Ateles paniscus chamek* (Platyrrhini, Primates) and man: association of three separate human syntenic groups and evolutionary considerations. Chromosoma 107:73–79.

Carlà Campa MC, Stanyon R. 1992. Sequence of late replication in *Cebus capucinus* chromosomes and a standardized G-banded karyotype. Am J Primatol 28:205–212.

Clemente IC, Garcia M, Ponsà M, Egozcue J. 1987. High-resolution chromosome banding in *Cebus apella*, *Cebus albifrons* and *Lagothrix lagothricha*: comparison with the human karyotype. Am J Primatol 13:23–36.

Clemente IC, Ponsà M, Garcia M, Egozcue J. 1990. Evolution of the Simiiformes and the phylogeny of human chromosomes. Hum Genet 84:493–506.

Consigliere S, Stanyon R, Koehler U, Agoramoorthy G, Wienberg J. 1996. Chromosome painting defines genomic rearrangements between red howler monkey subspecies. Chromosome Res 4:264–270.

Consigliere S, Stanyon R, Koehler U, Arnold N, Wienberg J. 1998. *In situ* hybridization (FISH) maps chromosomal homologies between *Alouatta belzebul* (Platyrrhini, Cebidae) and other primates and reveals extensive interchromosomal rearrangements between howler monkey genomes. Am J Primatol 46:119–133.

Dutrillaux B, Couturier J. 1981. The ancestral karyotype of platyrrhine monkeys. Cytogenet Cell Genet 30:232–242.

Ford SM. 1986. Systematics of the New World monkeys. In: Swindler DR, Erwin J, editors. Comparative primate biology. Vol. I. Systematics, evolution and anatomy. New York: A.R. Liss. p 73–135.

García F, Nogués C, Garcia M, Egozcue J, Ponsà M. 1999. Characterization of constitutive heterochromatin in *Cebus apella* (Cebidae, Primates) and *Pan troglodytes* (Hominidae, Primates). Comparison with human chromosomes. Am J Primatol 49:205–221.

García F, Nogués C, Ponsà M, Ruiz-Herrera A, Egozcue J, Garcia M. 2000. Chromosomal homologies between humans and *Cebus apella* (Primates) revealed by ZOO-FISH. Mamm Genome 11:399–401.

García M, Caballín MR, Aragonés J, Goday C, Egozcue J. 1975. Banding patterns of the chromosomes of *Ateles geoffroyi* with description of two cases of pericentric inversion. J Med Primatol 4:108–113

Goodman M, Porter CA, Czelusniak J, Page SL, Schneider H, Shoshani J, Gunnell G, Groves CP. 1998. Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. Mol Phylogenet Evol 9:585–598.

Jauch A, Wienberg J, Stanyon R, Arnold N, Tofanelli S, Ishida T, Cremer T. 1992. Reconstruction of genomic rearrangements in great apes and gibbons by chromosome painting. Proc Natl Acad Sci USA 89: 8611–8615.

Kay RF. 1990. The phyletic relationships of extant and fossil Pitheciinae (Platyrrhini, Anthropoidea). J Hum Evol 19:175–208.

Koehler U, Arnold N, Wienberg J, Tofanelli S, Stanyon R. 1995. Genomic reorganization and disrupted chromosomal synteny in the Siamang (*Hylobates syndactylus*) revealed by fluorescence *in situ* hybridization. Am J Phys Anthropol 97:37–47.

Matayoshi T, Howlin E, Nasazzi N, Nagle C, Gadow E, Seuanez H. 1986. Chromosome studies of *Cebus apella paraguayanus*. Am J Primatol 10:185–193.

Medeiros MA, Barros RMS, Pieczarka JC, Nagamachi CY, Ponsà M, Garcia M, García F, Egozcue J. 1997. Radiation and speciation of spider monkeys, genus *Ateles*, from a cytogenetic viewpoint. Am J Primatol 42:167–178.

Meireles CM, Czelusniak J, Schneider MPC, Muñiz JAPC, Brigido MC, Ferreira HS, Goodman M. 1999. Molecular phylogeny of Ateline New World monkeys (Platyrrhini, Atelinae) based on γ-globine gene sequences: evidence that *Brachyteles* is the sister group of *Lagothrix*. Mol Phylogenet Evol 12:10–33.

Moreira MAM, Canavez F, Parham P, Seuánez HN. 1997. Assignment of TCF1, TGM1, CALM1, CKB, THBS1, B2M, and FES in *Ateles paniscus chamek* (Platyrrhini, Primates). Cytogenet Cell Genet 79:92–96.

Morescalchi MA, Schempp W, Consigliere S, Bigoni F, Wienberg J, Stanyon R. 1997. Mapping chromosomal homology between humans and the black-handed spider monkey by fluorescence *in situ* hybridization. Chromosome Res 5:527–536.

Mudry M, Ponsà M, Borrell A, Egozcue J, Garcia M. 1994. Prometaphase chromosomes of the howler monkey *Alouatta caraya*: G, C, NOR, and restriction enzyme (Res) banding. Am J Primatol 33:121–132.

Napier JR, Napier PH. 1985. The natural history of the primates. Bull Br Mus. 200p.

Ponsà M, Garcia M, Borrell A, García F, Egozcue J, Gorostiaga MA, Delprat A, Mudry M. 1995. Heterochromatin and cytogenetic polymorphisms in *Cebus apella* (Cebidae, Platyrrhini). Am J Primatol 37:325–331.

Richard F, Lombard M, Dutrillaux B. 1996. ZOO-FISH suggests a complete homology between human and capuchin monkey (platyrrhini) euchromatin. Genomics 36:417–423.

Rosenberger AL, Setoguchi T, Shigehara N. 1990. The fossil record of callitrichine primates. J Hum Evol 19:209–236.

Rowe N. 1996. The pictorial guide to the living primates. Charlestown, RI: Pogonias Press. 863p.

Schneider H, Canavez FC, Sampaio I, Moreira MAM, Tagliaro CM, Seuánez HN. 2001. Can molecular data place each neotropical monkey in its own branch? Chromosoma 109:515–523.

Seabright M. 1971. The use of proteolitic enzymes for the mapping of structural rearrangements of man. Chromosoma 36:204–210.

Seuánez HN, Lachtermacher M, Canavez F, Moreira MAM. 1997. The human chromosome 3 gene cluster ACY1-CACNA 1D-ZNF64-ATP2B2 is evolutionarily conserved in *Ateles paniscus chamek* (Platyrrhini, Primates). Cytogenet Cell Genet 77:314–317.

Sherlock JK, Griffin DK, Delhanty JDA, Parrington JM. 1996. Homologies between human and marmoset (*Callithrix jacchus*) chromosomes revealed by comparative chromosome painting. Genomics 33:214–219.

Stanyon R, Consigliere S, Muller S, Morescalchi A, Neusser M, Wienberg J. 2000. Fluorescence *in situ* hybridization (FISH) maps chromosomal homologies between the dusky titi and squirrel monkey. Am J Primatol 50:95–107.

Stanyon R, Consigliere S, Bigoni F, Ferguson-Smith M, O'Brien PCM, Wienberg J. 2001. Reciprocal chromosome painting between a New World primate, the woolly monkey, and humans. Chromosome Res 9:97–106.

Sumner AT. 1972. A simple technique for demonstrating centromeric heterochromatin. Exp Cell Res 75:304–306.

Turleau C, de Grouchy J, Klein M. 1974. Caryotype d'un atèle male (*Ateles paniscus*). Ann Génét 17:213–215.