Chromosomal relationships and phylogenetic and clustering analyses on genus *Callithrix*, group argentata (Callitrichidae, Primates)

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Abstract. The karyotypes of three species of marmosets of the *Callithrix argentata* group (C. argentata, C. humeralifera and C. chrysoleuca) were studied. Comparisons were made among species and with the previously described karyotypes of *C. emiliae*, *C. mauesi* (argentata group) and *C. jaccus* (jaccus group). Two chromosome rearrangements differentiate the argentata (2n = 44) and jaccus (2n = 46) groups: a fusion or fission and a paracentric inversion. The argentata group is also characterized by the addition of large amounts of distal constitutive heterochromatin (CH) in some chromosomes, while the jaccus group shows mainly centromeric heterochromatin. The five species of the argentata group differ in the amount or location of the distal CH. Interspecific differences were converted to a Basic Data Matrix (BDM), that was submitted to phenetic and cladistic analyses. For cladistic analyses *C. jaccus* was the outgroup. The results agree with morphological and geographical data.

The family Callitrichidae of South American primates includes four genera, *Leontopithecus* and *Saguinus*, the 'tamarins' and *Cebuella* and *Callithrix*, the 'marmosets' (Hershkovitz, 1977, among others). The classification of *Callithrix* at specific and subspecific levels is controversial, but Hershkovitz's (1977) proposed recognition of two species groups, *jaccus* and argentata, is widely accepted (Coimbra-Filho, 1984, 1990; Mittermeier et al., 1988; 1992; Vivo, 1988; 1991; Natori, 1990; Rylands, 1993). The *jaccus* group (aurita, flaviceps, geoffroyi, jaccus, kuhlii and penicillata) occurs in central and western Brazil. According to Vivo (1988, 1991), the argentata group, which inhabits the Amazonian forest (Fig. 1), contains seven species grouped in three subgroups: naked ears and uniformly colored tail (C. argentata, C. emiliae, C. leucippe and C. melanura), tufted ears and annulated tail (C. chrysoleuca and C. humeralifera), and the intermediate marmoset with thinly haired ears and uniformly colored tail (C. intermedia). Recently two new species were described, *C. nigriceps* with naked ears and uniformly colored tail (Ferrari and Lopes, 1992) and *C. mauesi*, closely related to *C. chrysoleuca* and *C. humeralifera* (Mittermeier et al., 1992). Additionally, Vivo (1985) suggested that the animals from Rondonia state were *C. emiliae*, like the specimens from the type locality, Maloca, south Pará state (Thomas, 1920). Rylands (1993) disagrees with this classification because these two populations are geographically separated by the melanura taxon (see Fig. 1).

Cytogenetic studies of *Callithrix* have shown a diploid number (2n) of 46 chromosomes in the *C. jaccus* group and 44 in the *C. argentata* group. Chromosome banding data are available for only two species, both of the *C. jaccus* group: *C. jaccus* (Bedard et al., 1978; Ardito et al., 1983, 1987; Nagamachi and Ferrari, 1984; Seuánez et al., 1988) and *C. penicillata* (Seuánez et al., 1988) and of the argentata group: *C. emiliae* (Barros et al., 1990) and *C. mauesi* (Nagamachi et al., 1994). No chromosomal rearrangement differentiates the karyotype of *C. jaccus* from *C. penicillata* (Seuánez et al., 1988) and the karyotype of *C. emiliae* from *C. mauesi* (Nagamachi et al., 1994), whereas these fast ones differ from *C. jaccus* (2n = 46) by a centric fusion or fission and a paracentric inversion. They
also present large amounts of distal CH in several chromosomes that, in some cases, appear as large blocks (Barros et al., 1990; Nagamachi et al., 1994), a marker absent in C. jacchus. Chimerism with XXXXY line cells is a trait frequently described for representatives of the family Callitrichidae. It is a consequence of the high frequency of fraternal twin births, with placental anastomosis and blood cell exchange between twins. In the present paper the karyotypes of three species of marmosets of the argentata group (C. argentata, C. humeralifera and C. chrysodeluca) are studied. The three species were compared with each other and with the previously described karyotypes of C. emiliae, C. mauesi, and C. jacchus (Barros et al., 1990; Nagamachi et al., 1994; Nagamachi and Ferrari, 1984). The interspecific differences were converted to a basic data matrix that was used for phenetic and cladistic analysis.

Materials and methods

The karyotypes of three species of Callithrix argentata group (Table I) were studied from peripheral blood cultures prepared according to the method of Moorhead et al. (1960). The karyotypes were analyzed by G-(Sehers, 1972), C- (Sunner, 1972), sequential G/C-, and NOR-banding (Howell and Black, 1980) techniques. For sequential G/C-banding, the G-banded metaphases were photographed, destained with Carnoy fixative (methanol, glacial acetic acid 3:1) for 5 min, C-banded, and rephotographed. Karyotypes were arranged according to Nagamachi and Ferrari (1984) for C. jacchus. The phenetic and cladistic analyses were performed with the NTSYS-pc, version 1.80 (Rohlf, 1993) and PAUP/Mac version 3.1.1 (Swoford, 1993) programs.

Results and discussion

The karyotypes of C. argentata (CAR), C. chrysodeluca (CCH) and C. humeralifera (CHU) reveal a diploid number of 44, with 10 acrocentric autosomes and 32 autosomes plus X chromosome bi-armed. This karyotype is similar to those of C. emiliae (CEM, Barros et al., 1990) and C. mauesi (CMA, Nagamachi et al., 1994). The Y chromosome of the three species is small, bi-armed and similar to the Y of C. emiliae (Barros et al., 1990). However, in one specimen of C. humeralifera from our sample, the Y was acrocentric, and its size was similar to that of the Y of C. mauesi (Nagamachi et al., 1994).

C. jacchus has 2n = 46, with 14 acrocentric and 30 bi-armed autosomes. The X chromosome is submetacentric (Nagamachi and Ferrari, 1984). The karyotype of C. jacchus is similar to that of C. penicillata (Scuínzé et al., 1988) and other taxa from the jacchus group (Nagamachi, 1995). G-banding shows that no chromosomal rearrangement differentiates the karyotypes of the five species from that of the argentata group (C. argentata, C. chrysodeluca, C. emiliae, C. humeralifera and C. mauesi). Figure 2 shows the sequential G/C-banding patterns of C. humeralifera as a representative of the argentata group. Similar to C. emiliae and C. mauesi, the three species studied here diverge from C. jacchus (2n = 46) by a paracentric inversion in pair number 19 and a fusion or fission, in which the acrocentric autosomes 16 and 22 correspond to the submetacentric chromosome named t(22/16) in the argentata group (Barros et al., 1990; Nagamachi et al., 1992). The five species of the argentata

![Fig. 1. Geographic distribution of the taxa of the argentata group of Callithrix in the eastern Amazon region, according to Hershkovitz, 1977; Vivo, 1991; Ferrari and Lopes, 1992; Mittmeier et al., 1992. * = C. argentata; △ = C. humeralifera; V = C. leucite; ♻ = C. mauesi; ♦ = C. chrysodeluca; ○ = C. intermedia; ◆ = C. nigritae; ♠ = C. emiliae; ♠ = C. melanura. The dotted region on the right side corresponds to part of the geographic distribution of the jacchus group.](image-url)
group vary in the amount or location of distal G-light segments in many chromosomes (Fig. 3). These G-light segments (Figs. 2 and 3) are dark C-banded (Figs. 2 and 4), composed of constitutive heterochromatin. A detailed analysis of Fig. 4 shows that the five species differ in the amount or location of this heterochromatin. The following patterns were observed:

1) Features shared by the five species: a) a small centromeric C-band in all the chromosomes except the Y; b) the long arm of the Y entirely heterochromatic, and the intra- and interspecific variations in its size due to the differences in the amounts of heterochromatin; c) a small distal band in the short arm of chromosomes 3, 6, 8, 10, 15, t(22/16); and d) a large heterochromatic block of variable size on the short arm of chromosome 2 and on the long arm of 3.

2) Features shared by some species: a) a small distal band on the short arm of chromosomes 9, 11, 12 (absent only in CEM) and 14 (shared by CAR, CHU and CMA); b) a large heterochromatic block on the long arm of chromosome X (CHU, CMA, and CCH) and 21 (CEM, CAR, and CHU).

3) Species-specific characteristics: a) a small distal band in the short arm of chromosome 13 (CHU) and the long arm of X (CAR); b) a large heterochromatic block on chromosome 20 (CEM) and on the short arm of chromosome 14 (CCH).

In some chromosomes, the size of the distal CH is highly variable both among and within species, ranging from a small band, or even absent, to a large block. Many animals are heteromorphic for these CH regions. This high intra-individual, intra- and interspecific heterochromatin variability in the *argentata* group suggests that regions with large amounts of highly repetitive DNA can tolerate losses or gains without any phenotypic effect.
Fig. 3. Comparative G-banding patterns of the five species of the *argentata* group. Each chromosome pair is represented by one of the homologs.

In situ restriction enzymes studies in *C. emiliae*, *C. argentata* and *C. humeralifera* (Pieczarka et al., 1996) show that the distal CH of these three species reacts homogeneously to the action of the enzymes, independent of its size or location in the chromosomes. The exceptions are the distal CH of the Y chromosome of the three species and the X chromosome of *C. argentata*, indicating a distinct composition from the other distal heterochromatin. In the case of the small distal dark C-band found on the long arm of the X chromosome, *C. argentata* presents a different composition from the heterochromatic block found on the X chromosome of *C. humeralifera*, while the X chromosomes of *C. mauesi* and *C. chryssoleuca* show a heterochromatic block similar to the X of *C. humeralifera*, suggesting that these blocks have a homogeneous composition and that chromosomally these species are closely related. These results agree with the morphological classification of *C. humeralifera*, *C. mauesi* and *C. chryssoleuca* proposed by Vivo (1988) and Mittermeier et al. (1992). Since the X chromosome of higher primates is highly conservative (Dutrillaux, 1979), this distal CH occurs as a unique trait in the primates. The euchromatic portion of the Y chromosome is located on the short arm and is conserved in the *argentata* group. The difference in size and, consequently, in morphology (Figs. 2 and 4) is due to the difference in the amount of distal CH on the long arm. These CH should have a common origin, since they react in a homogeneous way to restriction enzymes (Pieczarka et al., 1996).

The constitutive heterochromatin of *C. jacchus* (Nagamachi, 1982) occurs mainly in the centromeric region of all the chromosomes. A small telomeric band is found in the short arm of pair number 6 and, in some cases, on the long arm of 22. Other species of the *jacchus* group have a small amount of constitutive heterochromatin, mainly centromeric (Nagamachi, 1995).

Cytogenetic studies of representatives of the family Callitrichidae (Nagamachi and Ferrari, 1984; Nagamachi and Pieczarka, 1988; Nagamachi et al., 1990; Barros et al., 1990; Nagamachi et al., 1992; 1994) identify a C-banding pattern typical of each group or genus. As discussed in Nagamachi et al. (1992), these data suggest that addition, rather than differential loss of CH occurred in these different groups of Callitrichidae, this...
Fig. 4. Comparative C-banding pattern of the five species of the argentata group. Each chromosome pair is represented by one of the homologs.

Table II. Number and types of chimeric animals observed in this study

<table>
<thead>
<tr>
<th>Species</th>
<th>Number analyzed</th>
<th>Number of chimeras</th>
<th>Chimerism</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>XX/XY</td>
<td>XXX/XX</td>
</tr>
<tr>
<td>C. argentata</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>C. humeralifera</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>C. mauesi</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>C. chrysoleuca</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>C. emiliae</td>
<td>16</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>C. jacchus</td>
<td>26</td>
<td>17</td>
<td>17</td>
</tr>
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</table>

being a process that happened after the cladogenesis of the groups or genera.

Ag-NOR staining shows labeling on the short arm of the acrocentric autosomes of the five species of the argentata group, similar to that of C. jacchus, which also shows NOR activity on the telomeric region of the long arm of the Y chromosome (Nagamachi and Ferrari, 1986).

Dizygous twins are common in Callitrichidae with the cotwins sharing a unique placenta with anastomosis during embryogenesis (Wislocki, 1939), that allows blood cell exchange between twins, leading to chimerism (Benirschke et al., 1962). This chimerism was found in animals of the three species described here (C. argentata, C. humeralifera and C. chrysoleuca) and in C. emiliae, C. mauesi, and C. jacchus (Table II). XX/XY chimeras have been extensively described (Benirschke and Brownhill, 1962; Benirschke et al., 1962; Hsu et al., 1970; Nagamachi and Ferrari, 1984; Nagamachi and Pieczarka, 1988; Barros et al., 1990; Nagamachi et al., 1990). Chimeras with cell lines of the same sex (XX/XX or XY/XY) can be found when two lines present autosomal differences. This type of chimerism was first described in C. mauesi (Nagamachi et al., 1994) and in the three species studied here (Table II). This is an important finding because it is a situation in which an autosomal marker region can permit the precise identification of co-twin lines, even in the case of dizygous twins of the same sex (Barros et al., 1990). In these four species the two lines were identified by differences in the amount of distal CH. Figure 5 shows, for each of the four species, the chromosome pairs...
which allowed the identification of the cell lines of the same sex. These pairs are as follows:

a) C. argentina: the XX/XX lines of the female differ in the size of the heterochromatic block of pair number 2. This block is heteromorphic in one of the lines and homomorphic for a small band in the other line (Fig. 5a).

b) C. humeralifera: the XY/XY lines of the male are differentiated by the heterochromatic blocks of pairs 2 and 21. One of the lines is heteromorphic in both pairs. In pair number 21 only one of the homologues has a block. The other line is homomorphic in pair number 2 and heteromorphic in pair number 21, which has one homologue without distal CH and the other with a small heterochromatic C-band (Fig. 5b).

c) C. mauesi: the XY/XY lines of the male can be distinguished by the heterochromatic block of pair number 2, which is heteromorphic in one of the lines and homomorphic in the other (Fig. 5c).

d) C. chrysoleuca: the XY/XY lines of the male are differentiated by the heterochromatic blocks of pairs 2 and 3. One of the lines is heteromorphic in both pairs and the other is heteromorphic in pair number 2 and homomorphic in pair number 3 (Fig. 5d).

A Basic Data Matrix (BDM, Table III) was made for both analyses (phenetic and cladistic), in which the characters considered were the interspecific distal C-band variations and two autosomal rearrangements: the paracentric inversion in chromosome 19 and the centric fusion or fission involving chromosomes 16 and 22 of the jacchus group. Variations in the size of the C-bands were not considered, only its presence ("1") or absence ("0").

In both analyses, phenetic and cladistic (NTSYS-pc), the BDM was used to obtain a similarity matrix (Table IV) through the SIMQUAL program, using the DICE coefficient. In pheno-

<table>
<thead>
<tr>
<th>Number</th>
<th>Trait†</th>
<th>CJA</th>
<th>CEM</th>
<th>CAR</th>
<th>CHU</th>
<th>CMA</th>
<th>CCH</th>
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<td>1</td>
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</tr>
<tr>
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<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
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<td>CH block in 3q</td>
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<td>1</td>
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<td>1</td>
</tr>
<tr>
<td>4</td>
<td>CH block in 4q</td>
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<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>Small CH band in Xq</td>
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<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>6</td>
<td>Absence of CH in Xq</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
</tr>
<tr>
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<td>Small CH band in 8p</td>
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<tr>
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<td>Small CH band in 9p</td>
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</tr>
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<tr>
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</tr>
<tr>
<td>17</td>
<td>Parac inv in 19q</td>
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<tr>
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</tr>
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</table>

SIMQUAL: coeff = DICE + 1.000000, = 0.000000

In cladistic analysis, both by PAUP and NTSYS-pc (Neighbor-Joining) programs, C. jacchus, representative of the jacchus group, was the outgroup for determination of the relationships among the taxa of the argentina group. The PAUP analysis pro-

anism, the similarity matrix was used to obtain a graphic tree matrix by the UPGMA clustering method of the SAHN program. The phenogram obtained by the TREE program using the tree matrix (Fig. 6) shows two branches which distinguish the jacchus group from the argentina group. In the argentina group, C. mauesi and C. humeralifera are most closely related and are joined by C. chrysoleuca, followed by C. argentina and C. emiliae. In the argentina group, C. emiliae is the species closest to the jacchus group. The cophenetic correlation was r = 0.99288.

In cladistic analysis, both by PAUP and NTSYS-pc (Neighbor-Joining) programs, C. jacchus, representative of the jacchus group, was the outgroup for determination of the relationships among the taxa of the argentina group. The PAUP analysis pro-

\[ \begin{array}{cccccc}
1 & CH block in 2p & 0 & 1 & 1 & 1 \\
2 & Small CH band in 3p & 0 & 1 & 1 & 1 \\
3 & CH block in 3q & 0 & 1 & 1 & 1 \\
4 & CH block in 4q & 0 & 0 & 0 & 1 \\
5 & Small CH band in Xq & 0 & 0 & 0 & 0 \\
6 & Absence of CH in Xq & 1 & 1 & 0 & 0 \\
7 & Small CH band in 8p & 0 & 0 & 1 & 1 \\
8 & Small CH band in 9p & 0 & 0 & 1 & 1 \\
9 & Small CH band in 10p & 0 & 1 & 1 & 1 \\
10 & Small CH band in 11p & 0 & 0 & 1 & 1 \\
11 & Small CH band in 12p & 0 & 0 & 1 & 1 \\
12 & Small CH band in 13p & 0 & 0 & 0 & 1 \\
13 & Small CH band in 14p & 0 & 0 & 0 & 0 \\
14 & CH block in 14p & 0 & 0 & 0 & 0 \\
15 & Small CH block in 15p & 0 & 1 & 1 & 1 \\
16 & Fusion 22/16 & 0 & 1 & 1 & 1 \\
17 & Parac inv in 19q & 0 & 1 & 1 & 1 \\
18 & Absence of the small band in 22q & 1 & 0 & 0 & 0 \\
19 & CH block in 20q & 0 & 1 & 0 & 0 \\
20 & CH block in 21q & 0 & 1 & 1 & 0 \\
21 & Absence of CH in 21q & 1 & 0 & 1 & 1 \\
\end{array} \]

\[ \begin{array}{cccccc}
1.000000 & 1.000000 & 1.000000 & 1.000000 & 1.000000 & 1.000000 \\
0.1538462 & 0.6153846 & 0.8666667 & 1.000000 & 1.000000 & 1.000000 \\
0.000000 & 0.6666667 & 1.000000 & 1.000000 & 1.000000 & 1.000000 \\
0.1052632 & 0.6153846 & 0.8666667 & 1.000000 & 1.000000 & 1.000000 \\
0.1176471 & 0.5833333 & 0.8571429 & 0.9333333 & 1.000000 & 1.000000 \\
0.1176471 & 0.5833333 & 0.7857143 & 0.8666667 & 0.9285714 & 1.000000 \\
\end{array} \]
duced two equally parsimonious trees, both with a tree length of 24 and a consistency index of 0.875. One of the trees (not shown) is identical to the only tree obtained using Neighbor-Joining method (Fig. 7) and is consistent with the morphological and geographic data. This tree shows that, from the out-group (C. jacchus), C. emiliae diverged first, followed by C. argentata, C. humeralifera, and the branch that originated C. mauesi and C. chrysotis, that are closely related to each other and to C. humeralifera.

The results obtained by the phenetic (Fig. 6) and cladistic (Fig. 7) analyses differ from each other only with regard to the position of C. humeralifera and C. chrysotis in relation to C. mauesi. In both analyses, nevertheless, these three species are closely grouped, reflecting their high chromosomal affinity. These results agree with the morphological classification, which groups these three species (Vivo, 1988; Mittermeier et al., 1992). These results also agree with the geographic distributions, since these three species are more closely geographically located than those of the argentata group (Fig. 1). The karyotypes of only two (C. argentata and C. emiliae) of the five species of naked eared marmosets are studied. Of these species, C. argentata shows a higher affinity with the tufted ears group than with C. emiliae. This reflects the geographic proximity of C. argentata to C. humeralifera (Fig. 1) in comparison with C. emiliae (from Samuel, Rondonia) studied here. It would thus be interesting to study the karyotype of C. emiliae from the type locality (Maloca, Pará) to see if these two populations differ from each other in the distribution of CH. The chromosome distance observed between C. argentata and C. emiliae from Samuel (Figs. 6 and 7) may be clarified through cytogenetic studies of the other species of the naked eared group, that occur in the intermediate geographic regions. Of all the species of the argentata group, C. melanura is geographically closest to the jacchus group. Taking into account that there is a chromosomal and geographical correlation among the species, one can suppose that the karyotype of C. melanura shows a distal CH distribution that is more similar to that of the jacchus group.

The chromosomal data obtained for the species of the argentata group show that these taxa diverge by variations in the amount and distribution of distal CH without affecting the euchromatic portion of the chromosomes. This suggests that the addition of CH has played an important role in the karyotypic evolution of this primate group. This addition seems to be a recent phenomenon that is occurring after the differentiation of the genus Callithrix into two groups, jacchus and argentata. The ancestral form of the argentata group may have had a karyotype with a distribution of heterochromatin similar to that of the jacchus group, but including the rearrangements that differentiate the two groups, i.e., a fusion or fission and a paracentric inversion. The results of phylogenetic and clustering analyses suggest that the mechanism of addition of CH could be associated with the differentiation process (cladogenesis) of the taxa in this group.

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