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SHORT COMMUNICATION

Massive LINE-1 retrotransposon enrichment in tamarins of the Cebidae family (Platyrrhini, Primates) and its significance for genome evolution

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Abstract

To study heterochromatin distribution differences among tamarins, we applied LINE-1 probes using fluorescence *in situ* hybridization onto chromosomes of *Saguinus mystax*, *Leontocebus fuscicollis*, and *Leontopithecus rosalia* with the aim to investigate possible evolutionary implications. LINE-1 repeats were shown to be involved in genome architecture and in the occurrence of chromosomal rearrangements in many vertebrates. We found bright LINE-1 probe signals at centromeric or pericentromeric areas, GC rich, on almost all chromosomes in three tamarin species. We also found non-centromeric signals along chromosome arms. In a phylogenetic perspective, we analyzed the pattern of LINE-1 distribution considering human chromosomal homologies and C banding patterns. Our data indicate that LINE-1 centromeric expansions and accumulation presumably arose in a common tamarin ancestor and that the presence of LINE-1 at the junction of human chromosome associations is presumably linked to interchromosomal rearrangements. For example, we found bright centromeric signals as well as non-centromeric signals on chromosomes 1 and 2, in all species analyzed, in correspondence to human chromosome associations 13/9/22 and 20/17/13, which are synapomorphic for all tamarins. Furthermore, we found other faint signals that could be apomorphisms linked both to intrachromosomal rearrangements as well as to retro-transposition events. Our results confirm that the three species have similar karyotypes but small differences in LINE-1 and heterochromatin amplification and distribution; in particular on chromosome pairs 19–22, where we show the occurrence of small inversions, in agreement with previous classic cytogenetic hypotheses.

KEYWORDS
heterochromatin, inversions, rearrangements, repetitive sequences

Astratto

Per studiare la distribuzione dell'eterocromatina nei tamarini, si è applicata la sonda LINE-1 mediante l'ibridazione in situ fluorescente sui cromosomi di *Saguinus mystax*, *Leontocebus fuscicollis* e *Leontopithecus rosalia* con l'obiettivo di indagare sulle loro possibili implicazioni evolutive. È stato, infatti, dimostrato che le ripetizioni di LINE-1 sono coinvolte nell'architettura del genoma e nella comparsa di riarrangiamenti

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cromosomici in molti vertebrati. Si sono riscontrati segnali luminosi della sonda LINE-1 nelle aree centromeriche o pericentromeriche, ricche di GC, su quasi tutti i cromosomi in tre specie in analisi ed anche segnali non centromerici lungo i bracci dei cromosomi. In una prospettiva filogenetica, si è analizzato il "pattern" di distribuzione delle LINE-1 considerando le omologie cromosomiche umane e i bandeggi. I dati ottenuti indicano che le espansioni centromeriche e l'accumulo di LINE-1 sono sorte presumibilmente in un antenato comune dei tamarini o di tutti i primati e che la presenza di LINE-1 alla giunzione delle associazioni cromosomiche umane è presumibilmente legata ai riarrangiamenti intercromosomici nei tamarini. Ad esempio, i segnali centromerici non centromerici sui cromosomi 1 e 2, in tutte le specie analizzate, sono in corrispondenza delle associazioni cromosomiche umane 13/9/22 e 20/17/13, che sono sinapomorfiche per tutti i tamarini. Inoltre, sono stati evidenziati altri deboli segnali che potrebbero essere apomorfismi legati sia a riarrangiamenti intracromosomici che a eventi di retrotrasposizione. I risultati confermano che le tre specie hanno cariotipi simili ma con piccole differenze nell'amplificazione e distribuzione di LINE-1 e dell'eterocromatina; in particolare sulle coppie cromosomiche 19-22, dove si dimostrano il verificarsi di piccole inversioni, in accordo con le precedenti ipotesi citogenetiche classiche.

1 | INTRODUCTION

Tamarins (*Saguinus*, *Leontopithecus*), along with marmosets (*Callithrix*, *Cebuella*), are New World monkeys (Platyrrhini), members of the Callitrichinae subfamily of the Cebidae family (Rylands et al., 2016). In Callitrichinae, the traditionally proposed divergence starts with *Saguinus* genus followed by *Leontopithecus*, *Callimico*, *Callithrix*, *Mico*, and *Cebuella*, in agreement with the phyletic dwarfism hypothesis. This hypothesis proposes an evolutionary trend from larger-sized ancestral forms to the smallest platyrrhines, which are the most derived (Perelman et al., 2011).

Through morphology as well as cytogenetic and molecular evidence (Matauschek et al., 2011), it has been recently proposed to divide *Saguinus* group into two genera: the small-bodied group of tamarins into the genus *Leontocebus* and the large-bodied group of tamarins into the genus *Saguinus*.

Heterochromatin, including repetitive DNA such as telomeric or rDNA sequences as well as Long Interspersed Elements (LINEs), has been extensively investigated in order to clarify their possible role in genome evolution and organization (Ahmed & Liang, 2012; Biscotti et al., 2015; Dumas et al., 2016; Mazzoleni et al., 2017, 2018; Paço et al., 2019). In primates, repetitive sequences (TEs) constitute about 50% of their genome and are linked to chromosome evolution (Jurka et al., 2007; Kvikstad & Makova, 2010; Xing et al., 2007). Among TEs, transposable elements of the family LINE-1 are the most abundant TEs in Primates and mammalian genomes (Boissinot & Furano, 2001; Richardson et al., 2015).

Molecular cytogenetic studies through chromosomal mapping of LINE-1 show different distribution patterns with the consensus target site for insertion enriched with adenine and thymine (AT-rich), although active elements do not preferentially insert themselves in specific genomic regions in mammals (Ovchinnikov et al., 2001; Waters et al., 2004) and few other species accumulate these elements preferentially in centromeres (Bulazel et al., 2006; Carbone et al., 2012; Kapitonov et al., 1998; Waters et al., 2004). The biological role of this repetitive DNA fraction has been linked to genome structure, evolution, and disease (Dobigny et al., 2017; Klein & O'Neill, 2018): it is involved in genome architecture, including DNA packaging, centromere stability and plasticity, gene expression, and epigenetic mechanisms (Cridland et al., 2014; Garagna et al., 1997; Kim & Han, 2015); these sequences promote genomic evolutionary changes and biological diversity among vertebrates, possibly playing an important role in speciation (Böhne et al., 2008); indeed, TEs have been found in chromosomal breakpoint regions, strongly suggesting that they work as a driving force in the occurrence of chromosomal rearrangements (Belyayev, 2014; Gray, 2000; Paço et al., 2015).

Despite their significant incidence, distribution patterns of TEs on primate chromosomes have been poorly investigated. In the beginning, LINEs-1 were studied using different approaches, including the use of restriction enzymes or whole-genome screening; LINEs-1 were used, respectively, to infer a close phylogenetic link (Seuanez et al., 1989) and a burst of these sequences in simians (Ohshima et al., 2003). In anthropoids including humans, LINE-1 sequence comparisons permitted to group them into subfamilies with a high rate of amplification (Boissinot & Furano et al., 2001; Ovchinnikov et al., 2002). Other studies suggest that rates of LINE-1 amplification differ substantially between the *Homo* and *Pan* lineages, indicating that LINE-1 amplification may have changed rapidly during primate evolution (Mathews et al., 2003). LINE activity has also been shown in *Saimiri*, *Saguinus* (Callitrichinae, Platyrrhini), and *Ateles* lineages (Boissinot et al., 2004; Sookdeo et al., 2018).

In this perspective considering LINE pattern variation, we characterized the karyotype of representative species of tamarins, *Saguinus mystax* (Spix, 1803), *Leontocebus fuscicollis* (Spix, 1823), and *Leontopithecus rosalia* (Linnaeus, 1766), through C banding and fluorescence *in situ* hybridization (FISH) of the LINE-1 sequence probes with the aim to investigate possible evolutionary implications.

Molecular cytogenetic studies by FISH with human probes permitted to show no interchromosomal rearrangements in representative species from *Saguinus* and *Leontopithecus* genera (Gerbault-Serreau et al., 2004; Neusser et al., 2001). On the other hand, intrachromosomal rearrangements have been suggested in part by classic G banding (Nagamachi et al., 1997, 1999) and also by analyses of single locus or BAC probe mapping on tamarins (Dumas & Sineo, 2012, 2014; Dumas et al., 2015; Scardino, Milioto, et al., 2020); indeed inversions, as well as variations in the size and distribution of heterochromatic blocks, are the major cytogenetic differences among tamarin karyotypes.

2 | MATERIALS AND METHODS

Following the standard protocol (Small et al., 1985), metaphases were obtained from fibroblast cell line cultures, from one individual each of: *S. mystax* (Spix, 1803), *L. fuscicollis* (Spix, 1823), and *L. rosalia* (Linnaeus, 1766), as detailed in Table 1.

The metaphases obtained through cell culture and chromosome harvesting were stained before and after FISH using CMA3 (staining GC-rich region) and DAPI (staining AT-rich region) according to a recent protocol, with some adjustments (Lemskaya et al., 2018).

DNA extraction from the cell culture pellet derived from the fibroblast cell line was done according to the basic DNA extraction protocol from Invitrogen. The LINE-1 retrotransposon was amplified through Polymerase Chain Reaction (PCR) using the following primers: L1R, 5′-ATTCTRTTC CAT TGG TCT A-3′ and L1F 5′-CCA TGC TCATSGAT TGG −3′ (Waters et al., 2004), and 200 ng of the genomic DNA was amplified in 50 μl reactions using an Applied Biosystems SimpliAmp Thermo Cycler (Thermo Fisher Scientific); products were visualized on 1% agarose gel. The PCR amplification products were labeled through Nick translation using 11-dUTP-Fluorescein.

FISH was performed following previously described protocols (Dumas et al., 2012; Milioto et al., 2019; Scardino, Mazzoleni, et al., 2020; Vizzini et al., 2021); C banding was done sequentially, post-FISH, according to a protocol which includes denaturation with formamide (Fernàndez et al., 2002).

DAPI images were inverted with a photo editing program (Adobe Photoshop) ad karyotypes reconstructed; inverted gray bands generally correspond to dark G bands; indeed, comparing published karyotypes for *L. fuscicollis* and *S. my stax* (Dantas & Barros, 1997; Nagamachi et al., 1997, 1999) and *Leontopithecus* (Gerbault-Serreau et al., 2004; Nagamachi et al., 1999) with our inverted DAPI banding, we showed that they correspond. The chromosomes with the LINE-1 probe signals were identified using inverted DAPI. Homologies with human chromosomes were taken into account by extrapolating painting data for *Saguinus oedipus* (Neusser et al., 2001) and *Leontopithecus chrysomelas* (Gerbault-Serreau et al., 2004) which have been shown to have the same karyotype as the analyzed species.

After FISH, the metaphases were analyzed under a Zeiss Axio2 epifluorescence microscope coupled with a Zeiss digital camera.

3 | RESULTS AND DISCUSSION

All species studied here have the same diploid number of 2n = 46, with almost the same sets of chromosomes: two small metacentric pairs (4–5); 13 pairs of submetacentric chromosomes (1–3 and 6–15); three small variable pairs (16–18) that are either acrocentric or bi-armed, and which also show heteromorphism; four pairs (19–22) that are subtelocentric in all three species but they show differences in their p arm size, which is short in *S. mystax* and *L. fuscicollis*, but longer in *L. rosalia*. The X chromosome in all three species has the standard submetacentric morphology and the G banding of the eutherian X; the Y chromosome is acrocentric in *S. mystax* and very large in *L. rosalia*, whereas it is metacentric/submetacentric and very poorly defined in *L. fuscicollis* (Figure 1).

The post-FISH C banding pattern we obtained was in agreement with previously published ones obtained through classical methods (Dantas & Barros, 1997; Nagamachi et al., 1997): positive C bands are at centromeres on both bi-armed and acrocentric chromosomes in *S. mystax* and, additionally, they were found at the telomeric areas of p arms on submetacentric autosomes 2, 3, 6, 8–15 in *L. fuscicollis* and *Leontopithecus*. Furthermore, in the former species, subtelocentric pairs 16–22 have very small p arms enriched in heterochromatin while *Leontopithecus* chromosome pairs 16–22 have a bigger p arm with distal parts enriched of C bands (Figure 4) in agreement with the previous C pattern study (Nagamachi et al., 1997).

In general, many mammalian species have deposits of this LINE-1 element in euchromatic regions in G-positive bands, for example on some autosomes and on the X chromosome, where they are usually abundant along the chromosomal length (Acosta et al., 2008; Parish

TABLE 1 Species of the family Cebidae (subfamily Callitrichinae) and fibroblast cell lines used in this study

Latin name/common name	Code	Sample/cell line acknowledgement
Saguinus mystax/Moustached Tamarin	SMY	Melody Roelker-Parker (Leidos, NCI, USA); June Bellizzi and Richard Hahn (Catoctin Zoo, MD, USA)
Leontocebus fuscicollis/Saddleback Tamarin	LFU	
Leontopithecus rosalia/Golden Lion Tamarin	LRO	Stephen O'Brien (Laboratory of Genomic Diversity, National Cancer Institute, Frederick MD, USA)

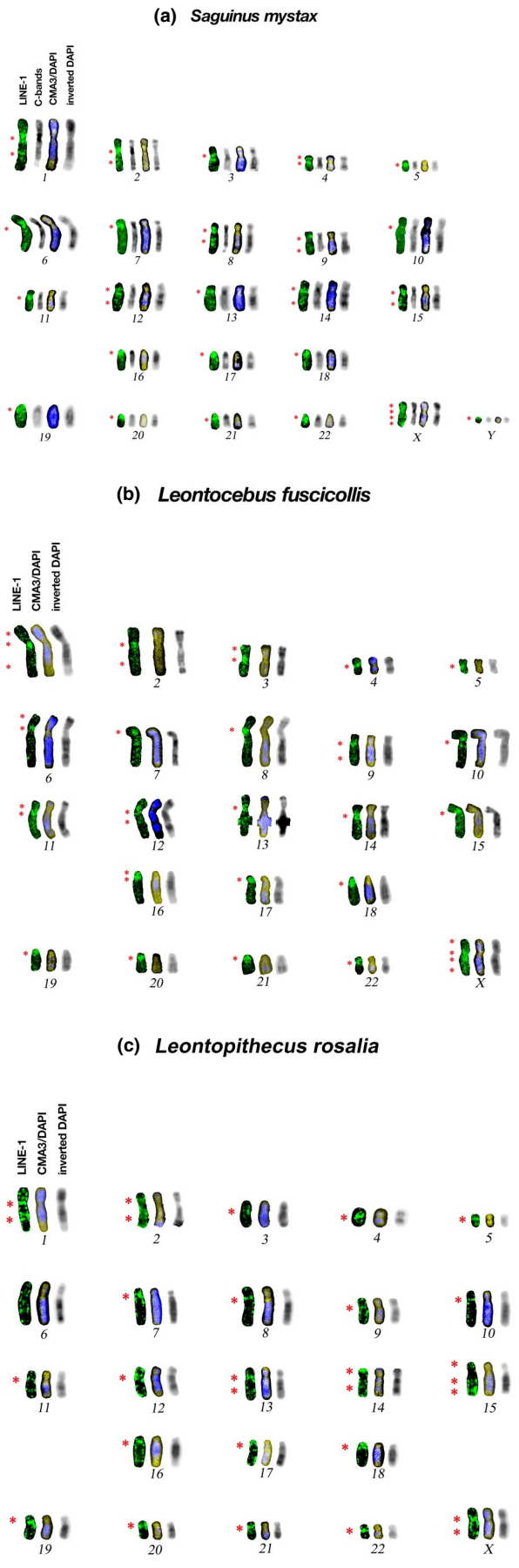

FIGURE 1 (a–c) Haploid species karyotypes; from the center to the sides chromosomes with inverted DAPI (black and white); CMA3/DAPI staining (yellow/blue); inverted CMA3/DAPI staining (C bands post-FISH); LINE probe signals (green). Red asterisks indicate LINE-1-enriched areas

et al., 2002; Waters et al., 2004), while in other species, it occurs in heterochromatic regions, especially in the centromeric regions (Waters et al., 2004). In our work, we found both of these patterns since, in addition to massive centromeric blocks, hybridization signals were observed at non-centromeric region (Figures 1 and 2); the results obtained are summarized in ideograms (Figure 3).

3.1 | LINE-1 distribution at centromeres

Although the absence of LINE-1 signals in centromeres is often reported, for example, in rodent species (Acosta et al., 2008; Dobigny et al., 2004; Vieira-da-Silva et al., 2016) or other taxa, including xenarthrans, afrotherians and ungulates (de Sotero-Caio et al., 2017; Dobigny et al., 2006; Waters et al., 2004), we have shown a massive accumulation of LINE-1 elements in CMA3 GC-rich bands in the centromeres of the three tamarin species on both bi-armed and acrocentric chromosomes co-localizing with heterochromatin (Figures 1 and 4), in agreement with what was previously shown in many other mammals, such as bats, some rodents, and other *Saguinus* species (de Sotero-Caio et al., 2017; Paço et al., 2019; Serfaty et al., 2017). Indeed, LINE-1 has been previously mapped at centromeres on other *Saguinus* species such as *S. midas* (Linnaeus, 1758) and *S. bicolour* (Spix, 1823) (Serfaty et al., 2017). These signals' location is in contrast to results describing a preference for the accumulation of this element in AT-rich G band regions in other mammals (Korenberg & Rykowski, 1988). The finding of the centromeric enrichment of LINEs in all the analyzed species indicates that this accumulation may have occurred early in the radiation of the group, in the common ancestor of all tamarins or in all Platyrrhini; LINEs are linked to the inter-chromosome rearrangements characterizing the group and contributing to the current features of the tamarin karyotype, which is considered to be conservative.

Furthermore, we show the C positive bands on the 16–22 homologues in *L. fuscicollis* and *Leontopithecu rosalia* clearly overlapping with LINE-1 amplified signals (Figures 1b,c, 3, and 4); however, the comparison of the LINE-1 localization patterns on these homologues among species reveals a different distribution of repetitive sequences respectively on the q and p arms in *L. fuscicollis* and *L. rosalia*, presumably due to the occurrence of amplifications and inversions that could have dislocated both the repetitive sequences from a q arm position to a p arm position, where both sequences show a double band in *Leontopithecus* (Figures 3 and 4). This evidence explains the different morphology of these p arms among tamarin species in agreement with the different DAPI inverted banding pattern and the previously C, G banding and

rDNA probe mapping of these species (Gerbault-Serreau et al., 2004; Nagamachi et al., 1997); indeed, rDNA loci map on the chromosomes 19–22 in the q arms in *Saguinus* while on p arms in *Leontopithecus*.

3.2 | LINE-1 in non-centromeric position

We also found non-centromeric LINE-1 signals along chromosomal arms (Figures 1–3), in agreement with what was previously observed in other groups (de Sotero-Caio et al., 2017; Kapitonov et al., 1998; Paço et al., 2015; Rebuzzini et al., 2009; Serfaty et al., 2017).

LINE mapping on the X chromosome of tamarins confirms the evidence of abundant LINE distribution along the X from other eutherian orders (Acosta et al., 2008; Waters et al., 2004). Further, we also observed some fainter signals at non-centromeric positions in euchromatic regions either in DAPI-positive bands or in CMA3-positive regions (Figure 1). The localization of LINE-1 in CMA3-positive areas is in accordance with other studies, suggesting that young and active elements do not preferentially insert themselves in specific AT-rich genomic regions (Ovchinnikov et al., 2001; Waters et al., 2004). These LINE-1 signals found along chromosomes at non-centromeric regions, through a comparison with the human chromosomal homologies reported for *S. oedipus* (Neusser et al., 2001) and *L. chrysomelas* (Gerbault-Serreau et al., 2004), led us to hypothesize that these repetitive elements may be located in breakpoint regions at the junction of human syntenic blocks; these elements may be linked to ancestral fusion events, correlated to the rise of the tamarin lineage, and in agreement with previous evidence about the link between LINE-1 location and evolutionary rearrangements (Bulazel et al., 2007; Paço et al., 2015). For example, we found bright centromeric signals as well as non-centromeric signals on chromosomes 1 and 2, in all tamarin species here analyzed (Figures 1a–c and 3); those chromosomes correspond to human chromosome associations 13/9/22 and 20/17/13 (Gerbault-Serreau et al., 2004; Neusser et al., 2001), which are synapomorphic for all tamarins (De Oliveira et al., 2012; Dumas & Mazzoleni, 2017); the LINE-1 localization pattern appears to correspond to junction areas of human syntenic blocks (Figure 3), supporting the previous hypothesis (Bulazel et al., 2007; Paço et al., 2015).

An additional LINE-1 probe signal is present on chromosome pair 4 in a DAPI-positive region with no C bands on the distal p arm of *S. mystax* (Figures 1a, 3, and 4). This evidence is in agreement with LINE-1 signals found on the homologues of chromosome 4 in *S. midas* and *S. bicolour* (Serfaty et al., 2017), and presumably representing a synapomorphic feature. Chromosome 4 of *Saguinus*

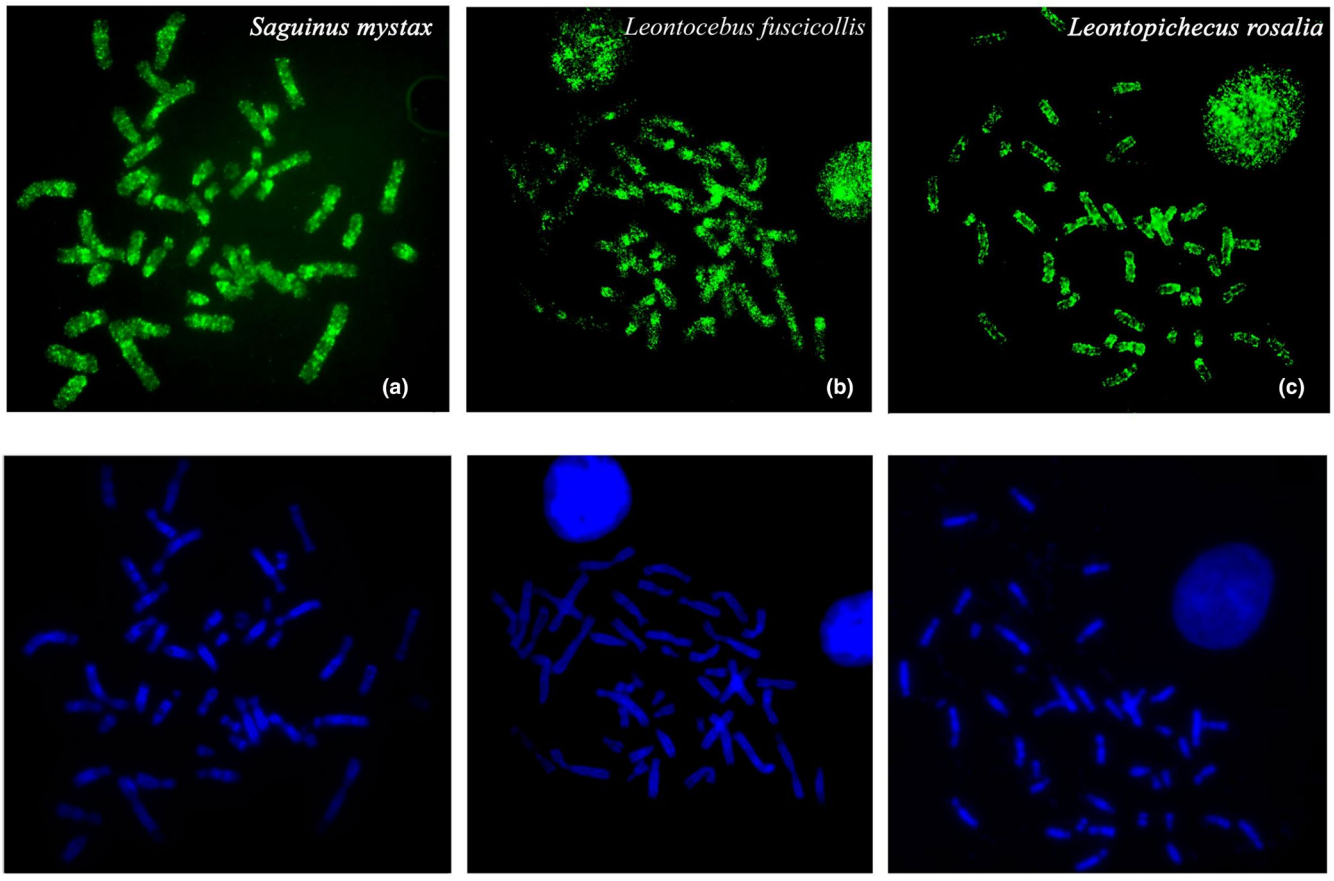

FIGURE 2 (a–c) *In situ* hybridization of LINE-1 probe onto mitotic metaphases of tamarins. The LINE-1 probe localization pattern (green); below are the same metaphase spreads with DAPI stain (blue)

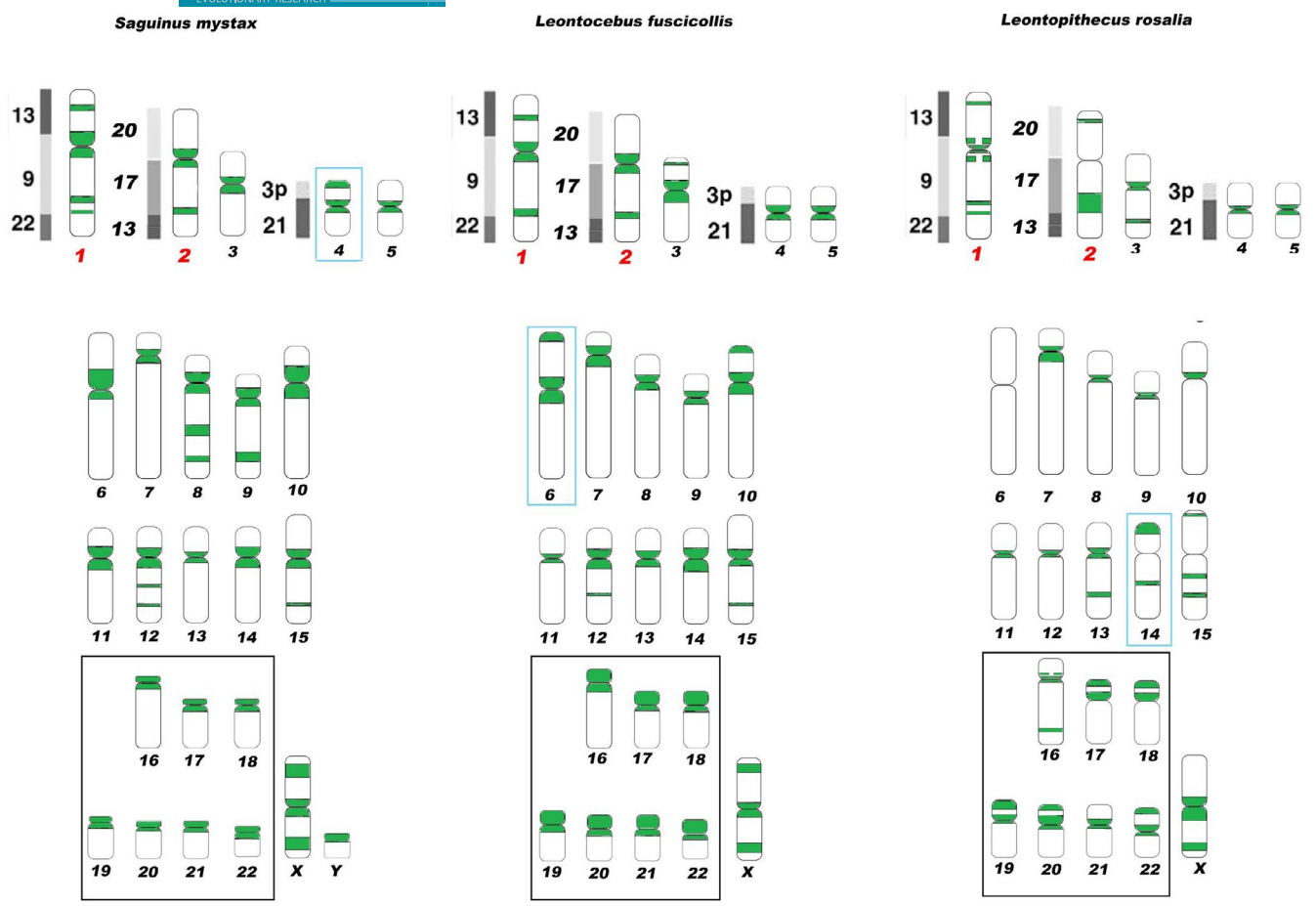

FIGURE 3 The three species ideograms with the haploid set of chromosomes showing the localization of LINE-1: (numbers and bars indicate human syntenies at the left of chromosomes); note LINE on chromosome pairs 16–22 (in the box), on chromosome 4 in *Saguinus mystax*, on pair 14 in *Leontopithecus* (in light blue box), and on chromosomes 3, 6 in *Leontocebus*

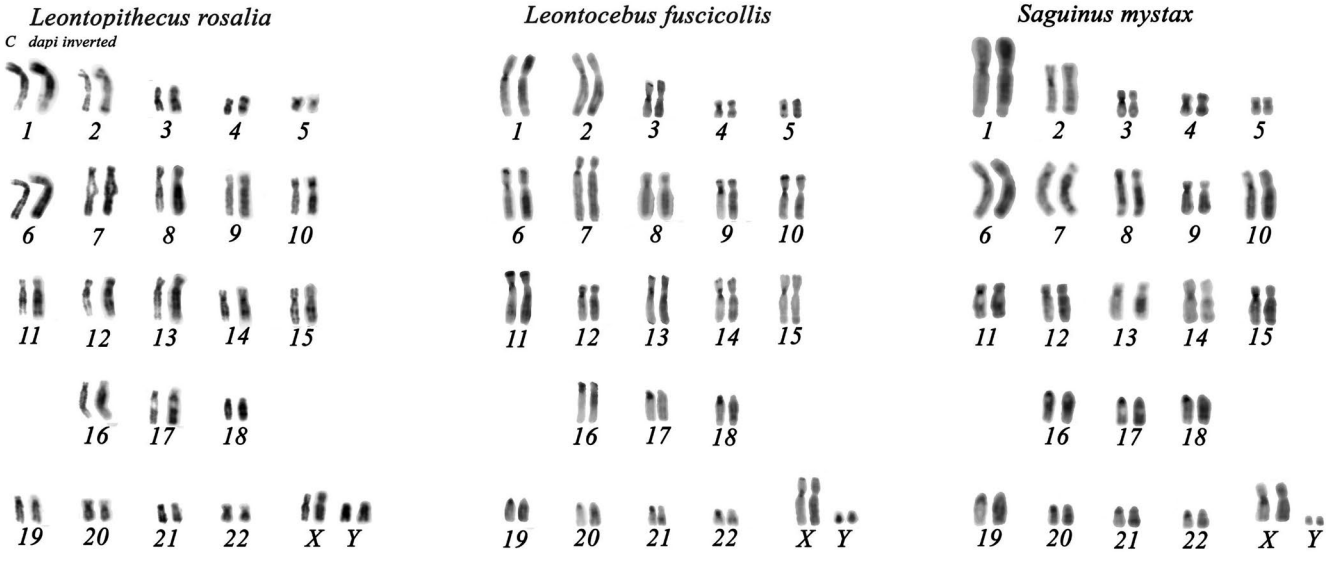

FIGURE 4 Haploid C/DAPI inverted karyotypes of *Leontocebus fuscicollis*, *Saguinus mystax*, and *Leontopithecus rosalia*. From left to right: C and DAPI inverted chromosomes for each pair; dark regions correspond to constitutive heterochromatin blocks/DAPI bands, respectively

corresponds with the human ancestral primate association 3/21 (Gerbault-Serreau et al., 2004; Neusser et al., 2001) that among tamarins has been shown to be prone to inversions. Thus, the evidence of LINE-1 on the distal p arm of *S. mystax* chromosome 4 could be linked to the inversion affecting this ancestral primate association, dislocating a fragment of the LINE-1 centromeric original sequences to the terminal position (Figure 3).

Another case in which the signal is not present at the centromere occurs on chromosome 14 in *Leontopithecus*; two other faint non-centromeric signals are along arms, one bright signal is at the distal p arm and the second is interstitial on the q arm (Figures 1c and 3); this pattern could be explained as the result of a previously hypothesized apomorphic inversion which characterized *L. rosalia* (Nagamachi et al., 1997) and that we confirm at the molecular level.

Some other small differences are presumably species-specific apomorphic features supporting the hypothesis that LINE-1 distribution across chromosomes could also have a species-specific pattern (Vieira-da-Silva et al., 2016; Waters et al., 2004); such as for example, LINE signals on chromosome 3 and 6 in *Leontocebus* (Figures 1b and 3).

4 | CONCLUSIONS

Tamarins show centromeric and pericentromeric regions enriched with LINE-1 sequences when compared to other mammals; this evidence let us to hypothesized they contributed to the karyotype evolution of tamarins. Our data analysis in a phylogenetic framework suggests that LINE-1 is closely linked to rearrangements; some LINEs represents a synapomorphisms in tamarins while other LINE signals are apomorphisms.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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