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Short communication

Diversity of STLV-1 strains in wild chimpanzees (*Pan troglodytes verus*) from Côte d'Ivoire

Sandra Junglen[a], Claudia Hedemann[a], Heinz Ellerbrok[b], Georg Pauli[b], Christophe Boesch[c], Fabian H. Leendertz[a,*]

[a] *Research Group Emerging Zoonoses, Robert Koch-Institute, Nordufer 20, 13353 Berlin, Germany*
[b] *Center for Biological Safety, Robert Koch-Institute, Nordufer 20, 13353 Berlin, Germany*
[c] *Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*

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ABSTRACT

Simian T-lymphotropic viruses type 1 (STLV-1) are regarded as a highly conserved group of viruses with genotypes clustering according to geographic regions rather than to infected species. In free living West African chimpanzees we have described a variety of STLV-1 strains and suggested that this diversity results from interspecies transmissions. Here we present new data on STLV-1 infections in these chimpanzees with the presence of two new distinct clades, proposing the establishing of two new STLV-1 subtypes. Moreover, in one of the chimpanzees, the Central African STLV-1 subtype B was detected. The STLV-1 strains detected here display a much wider diversity than heretofore reported for STLV-1 with presence of three distinct subtypes in chimpanzees from one distinct geographic region. In conclusion, the hypothesis of primate T-lymphotropic virus type 1 (PTLV-1) clustering by geography rather than host should be reconsidered, at least regarding STLV-1 infections in chimpanzees.

The genomes of simian retroviruses like simian immunodeficiency viruses (SIV) and simian foamy viruses (SFV) are highly diverse, but in general each primate species has its own species-specific strain suggesting virus–host co-evolution (Allan et al., 1991; Beer et al., 1999; Switzer et al., 2005). In contrast, strains of simian T-cell lymphotropic virus type 1 (STLV-1) are considered to be linked to geographic regions rather than host species (Vandamme et al., 1998; Makuwa et al., 2004; Van Dooren et al., 2007). STLV-1 has been characterized from approximately 30 different Asian and African non-human primates (NHPs), including species from *Cercopithecidae*, *Colobidae*, *Cercopithecinae* and *Homonidae*, and the strains cannot be separated into distinct phylogenetic lineages in respect to infected species. Furthermore, cross-species transmission of STLV-1 between different NHPs and from NHPs to humans has been documented (Leendertz et al., 2004b; Wolfe et al., 2005; Van Dooren et al., 2007; Liegeois et al., 2008).

To date four major genomic subtypes have been established, Cosmopolitan subtype A (Miura et al., 1994, 1997), Central African subtype B (Hahn et al., 1984; Vandamme et al., 1994), Melanesian subtype C (Gessain et al., 1991; Bastian et al., 1993) and Central African subtype D (Mahieux et al., 1998). Additional subtypes with few members are subtype E with strains from the Democratic Republic of the Congo (Salemi et al., 1998), subtype F with strains from Gabon and Cameroon (Nerrienet et al., 2001; Van Dooren et al., 2001; Sintasath et al., 2009), Central and West African subtype G (Meertens et al., 2001), Baboon STLV-1 subtype (Voevodin et al., 1997), South African STLV and East African STLV. Recently a putative new African STLV-1 lineage, STLV-1 H, was identified in *Cercopithecus cephus* from Cameroon (Liegeois et al., 2008).

In free living chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire, we have described a high prevalence and surprisingly high variety of STLV-1 strains (Leendertz et al., 2003, 2004a,b). The isolates showed close relationship to STLV-1 sequences detected in red colobus monkeys (*Piliocolobus badius badius*) living in this region, giving evidence for interspecies transmission via hunting and consumption of meat from prey to hunter (Leendertz et al., 2004b).

In order to further investigate the diversity of STLV-1 subtypes in chimpanzees from one defined area, we analyzed blood and various tissue samples from 14 free-ranging chimpanzees (*P. troglodytes verus*) in the Taï National Park that had died of anthrax, respiratory disease, or other causes (Leendertz et al., 2004c, 2006; Kondgen et al., 2008). The chimpanzees of the communities studied are known individually and followed on a daily basis by researchers. In addition, on two different occasions blood was collected from two adolescent chimpanzees bleeding after an encounter with members of a neighbouring community. The blood was collected

* Corresponding author. Tel.: +49 30187542592; fax: +49 30187542181.
E-mail address: LeendertzF@rki.de (F.H. Leendertz).

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Table 1
Primate T-lymphotropic virus distribution among wild chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d'Ivoire and Sierra Leone.

Individual	Sex	Age‡	STLV-1 *tax*	STLV-1 LTR	STLV-1 *env*
Côte d'Ivoire					
Candy	F	>15†	neg	nd	nd
Gargantuan	M	10	pos	pos	pos
Giselle	F	5	pos	pos	pos
Ishas's baby	F	1	neg	nd	nd
Nino	M	26	pos	pos	neg
Ophelia	F	2	neg	nd	nd
Oreste	M	6	neg	nd	nd
Sagu	M	Alive	pos	pos	pos
Sumatra	F	Alive	pos	pos	pos
Venus	F	29	neg	nd	nd
Virunga	F	25	pos	pos	pos
Zora's Baby	F	<1	neg	nd	nd
East chimp-48	M	>15†	neg	nd	nd
East chimp-78	M	>15†	neg	nd	nd
Dorry*	F	10	pos	pos	pos
Loukum*	F	27	pos	pos	pos
Leo*	M	29	pos	pos	pos
Kady*	F	30	pos	pos	pos
Rafiki*	F	19	pos	pos	pos
Sierra Leone					
Christo	M	>15	pos	pos	pos

nd = not detected.
* Published in Leendertz et al. (2004a).
† Recently habituated; age could only be roughly estimated.
‡ Age for chimpanzees older than 15 was estimated.

from leaves on the forest floor and stored in liquid nitrogen and afterwards at −70 °C until analyses. Furthermore samples were collected from one chimpanzee anesthetised for surgical intervention (unpublished data). In addition samples from one chimpanzee that died of unknown cause in a sanctuary in Sierra Leone were also included in the study. In order to test the samples for STLV-1 DNA was extracted using either a DNA tissue kit or DNA blood kit (Qiagen, Hilden, Germany), respectively. Samples were tested for proviral DNA by a *tax*-specific real-time PCR. Using the primers Sk43 and Sk44 (Kwok et al., 1988) and a PTLV-1 specific probe (sequences can be obtained on request). STLV-1 was detected in seven of the 15 chimpanzees (Table 1).

For further genome analyses LTR and *env* gene fragments from all *tax*-positive samples were amplified by PCR. PCR products were confirmed by agarose gel electrophoresis, purified and sequenced on both strands as described before (Leendertz et al., 2003, 2004b). A 450 bp LTR fragment was generated from the seven PCR-positive chimpanzees; an 1105 bp *env* fragment could be amplified from six chimpanzees. Despite multiple approaches it was not possible to amplify the *env* fragment from one chimpanzee (Nino). Consensus sequences were generated using SeqMan II (LaserGene software programme; DNAStar) and are available in GenBank under the accession numbers GU168945–GU168957. Sequences generated were compared to published sequences using BLASTn (www.ncbi.nlm.nih.gov/blast/Blast.cgi) indicating that all *tax*-positive samples were STLV-1 infected. Comparison to other PTLV-1 sequences revealed a close relationship of five strains to strains previously found in chimpanzees and red colobus monkeys from the same groups of the Taï National Park (94–99% paired identity). Two of the new STLV-1 strains (Ptr-Nino and Ptr-Christo) were closely related to STLV-1 isolates from captive *P. troglodytes verus* showing 98% paired identity (Ch-Regina, AY899815, Sierra Leone and Ch-Coen, AY899814, born in captivity, Van Dooren et al., 2007).

In order to gain insights into the evolution of PTLV-1 in wild primates, sequences were aligned with representative primate T-lymphotropic virus type 1 (PTLV-1) strains using the ClustalW software programme in BioEdit (software version 7.0.9) and phylogenetic analyses were performed using the PHYLIP package 3.573C (Felsenstein, 1981). Partial sequences of the LTR region (422 bp) corresponding to nucleotides 8331–8745 and a 516 bp *env* fragment corresponding to nucleotides 6046–6561 (nucleotide positions are based on the HTLV-1 ATK sequence, accession number J02029) were used for phylogenetic tree analysis using Neighbour-Joining (NJ) and Maximum Likelihood (ML) methods. Robustness of the trees was tested by bootstrap analysis with 1000 replicates (Thompson et al., 1994). Similar tree topologies were achieved for both trees (data for ML are not shown). Tree analysis confirmed that five of the chimpanzee sequences clustered with those found previously in the Taï chimpanzees, forming two new larger STLV-1 groups (Fig. 1a and b). The new strains Ptr-Sumatra and Ptr-Sagu clustered in the LTR region together with the previously described strains Ptr-Loukum and Ptr-Leo. This cluster of *P. troglodytes verus* STLV-1 strains was supported by high bootstrap values and was clearly distinct and distant from other PTLV-1 subgroups, suggesting a new STLV-1 subtype tentatively named STLV-1 subtype I. The isolates Ptr-Gargantuan, Ptr-Giselle and Ptr-Virunga clustered in the LTR region together with the previously reported strains Ptr-Dorry, Ptr-Rafiki-II, Ptr-Kady, STLV-wrc, Ptr-Rafiki-I and cb14/97. Like STLV-1 subtype I this cluster was supported by high bootstrap values and clearly distinct from other isolates and we propose a new STLV-1 subtype for these sequences, tentatively named STLV-1 subtype J. These clusters of STLV-1 strains were also present in the *env* region, except for Ptr-Sumatra which grouped with subtype J. The clustering of the LTR and *env* strains derived from Sumatra suggests a double infection with STLV-1 subtypes I and J. For confirmation a 516 bp *env* fragment with primers specific for subtype I (S1env 5′ TCCTTAACACCGAACCCAACC and R1env 5′ GTAGTTGACGGAG TGATGCATGGT) was amplified and sequenced. Sequence comparison revealed the presence of two different *env* fragments with 95% homology, Ptr-Sumatra-I and Ptr-Sumatra-II. Phylogenetic analyses displayed significant clustering of Ptr-Sumatra-I with STLV-1 subtype I and Ptr-Sumatra-II with STLV-1 subtype J. Multiple approaches to amplify a larger *env* fragment or a LTR fragment clustering with STLV-1 subtype J were not successful.

Interestingly, two of the characterized isolates, Ptr-Nino and Ptr-Christo, clustered most likely with the Central African subtype B, which comprises several HTLV-1 isolates from Sierra Leone, Equatorial Guinea, Central Africa, Cameroon and the Democratic Republic of Congo. Ptr-Nino is the first strain identified in Côte d'Ivoire that clustered with an STLV-1 subtype which comprises strains from other African regions.

Few studies have been performed on STLV-1 strains in defined groups of wild primates. Most data on PTLV prevalence and diversity among NHPs are based on samples derived from animals that were born in captivity or wild caught when they were still very young and kept in captivity for extended periods of time before analysis was performed. In recent years more studies were done on samples originating from wild primates, mostly bushmeat samples that were collected by hunters or bought at local markets in Cameroon (Courgnaud et al., 2004; Liegeois et al., 2008; Sintasath et al., 2009). However, for those samples contamination with infectious material from other species cannot be excluded. Hunters and people handling the bushmeat mostly use the same equipment for butchering and primates are often piled up together. In order to understand the natural transmission cycle and to shed light on prevalence and diversity of PTLV, the investigation of wild NHPs is crucial. The samples investigated here are especially valuable as they originate from wild but habituated groups of chimpanzees which are known individually and have been studied for more than 25 years (Boesch and Boesch-Achermann, 2000). Samples were collected at different time points using single use materials excluding any cross contamination. Furthermore, samples were handled separately for laboratory analyses. New aliquots were used to re-test positive samples for confirmation.

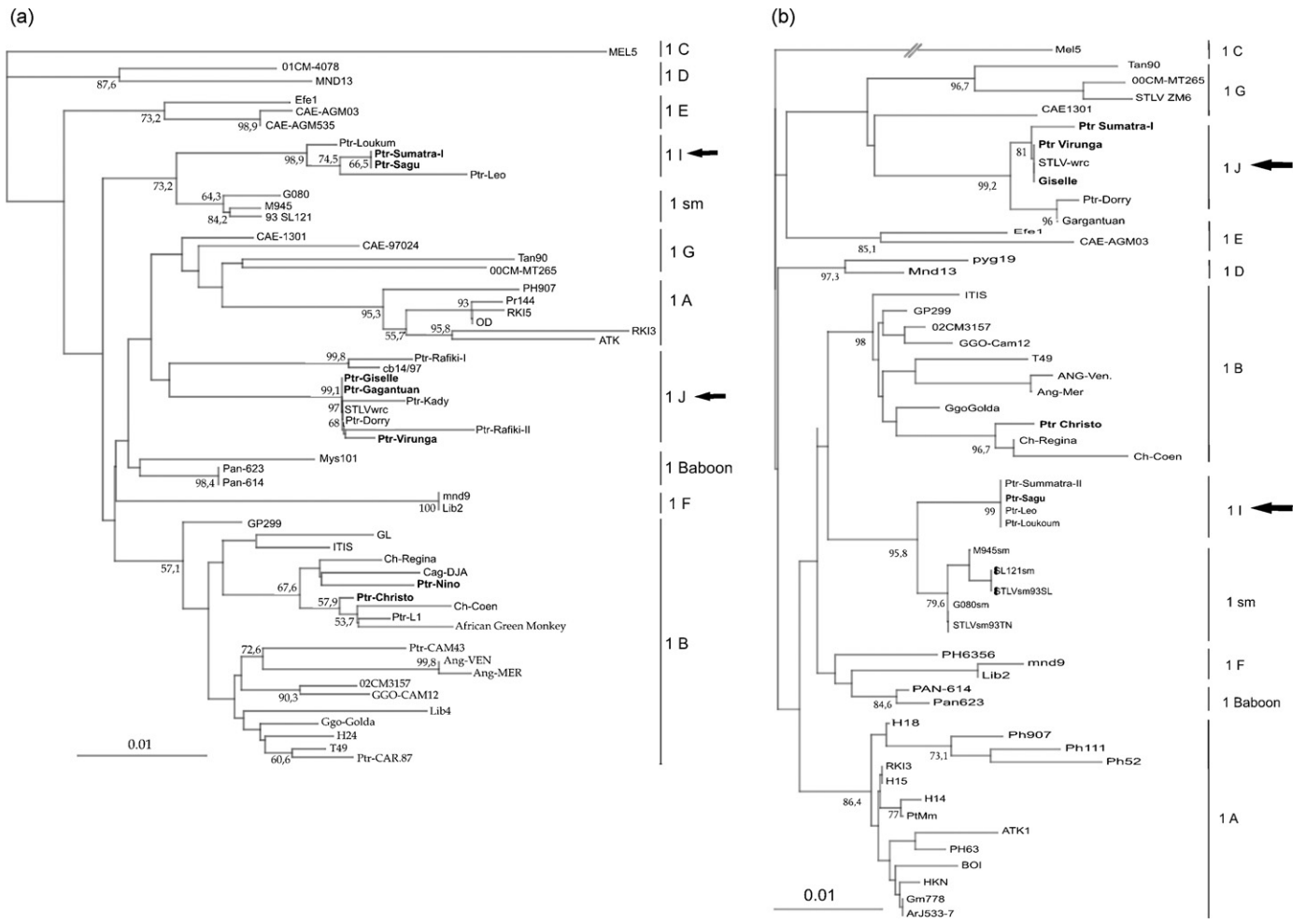

Fig. 1. Rooted phylogenetic trees of PTLV sequences. The trees are generated with the Neighbour-Joining method based on a 422 bp fragment which corresponds to the LTR (a) and a 516 bp *env* fragment (b). The HTLV-1 isolate Mel 5 was used as an outgroup. The trees were statistically evaluated with bootstrap analysis with 1000 replicates. Bootstrap values for the major branch points are given in percent. The suggested new subtypes are indicated by arrows and strains from chimpanzees of this study are indicated in bold.

Clustering by geographic origin rather than by host species is suggested to mirror cross-species transmission of PTLVs among NHPs and potentially also transmission to humans (Mahieux et al., 1998; Vandamme et al., 1998; Slattery et al., 1999; Gessain et al., 2000; Van Dooren et al., 2001; Wolfe et al., 2005). Five of the STLV-1 sequences characterized here cluster with two distinct and phylogenetically distant lineages described earlier for STLV-1 isolates found in NHPs of the Taï National Park (Leendertz et al., 2004b). These two STLV-1 clusters originate from one restricted tropical rainforest area and are clearly distinct from other STLV-1 subtypes described and clearly distinct from each other. Thus, we propose that additional subtypes of STLV-1 should be defined as STLV-1 subtype I and STLV-1 subtype J. A similar high diversity of STLV-1 in one species was previously suggested for *Cercopithecus nictitans* and *C. cephus* in a bushmeat study from Cameroon (Liegeois et al., 2008).

Interestingly, one isolate (Ptr-Nino) is the only strain so far from the Taï National Park that clustered with the common Central African subtype B which includes most of the STLV-1 strains reported from chimpanzees. The closest relationship was found to isolates from chimpanzees of the *P. troglodytes verus* subspecies: to Ptr-Christo, Ch-Regina wild caught in Sierra Leone, to Ch-Coen born in captivity (Van Dooren et al., 2007). Christo was kept in the same sanctuary as Regina and Coen. As the bootstrap values for Ptr-Nino are around 70% statistical support is not high enough to exclude clustering with other clades. STLV-1 subtype B also includes strains from other primate species, like strains from *Allenopithecus nigroviridis* that were wild caught in the Democratic Republic of Congo (Meertens et al., 2001), strains from *Gorilla gorilla gorilla* that were wild caught in Cameroon (Van Dooren et al., 2007) and from *Papio anubis* that were wild caught in Kenya (Meertens et al., 2001). However, STLV-1 subtype B is generally not well supported by bootstrap values and includes various African primate species, widely distributed across Africa. Further sequence information is needed to clarify the structure of this cluster.

There are no commonly used criteria to define clusters in STLV-1 phylogeny. Distant related strains are found to be grouped within established subtypes or can be found as ungrouped lineages. Also, strains distantly related to each other are grouped together despite low bootstrap values or defined as new lineages. Thus, there is an eminent need for clarifying such definitions.

It has been speculated previously that the chimpanzees were infected by interspecies transmission from red colobus monkeys and sooty mangabeys (Leendertz et al., 2004b), with red colobus monkeys hunted and consumed frequently by chimpanzees and sooty mangabeys representing a rare prey (Boesch and Boesch-Achermann, 2000). The possible mode of transmission of the different strains between chimpanzees still requires further investigation. However, the few data available point towards rare sexual transmission events (Leendertz et al., 2004a). It is known that the chimpanzees Leo and Kady had sexual contact but were

infected with STLV strains from different clusters (Leendertz et al., 2004b). The strains analysed here from Sagu and Virunga who also had sexual contact were shown to be different. In contrast, two STLV-1 strains obtained from offspring of the same mother (Ptr-Gargantuan and Ptr-Gisele) were identical in the LTR region but divergent in the *env* region (98% paired identity). The mother was tested positive for STLV-1 using a non-invasive method established for the detection of STLV-directed antibodies in urine (Leendertz et al., 2004a); sequence information is not available.

In general, transmission from prey to hunter is supported by the phylogenetic analysis of STLV-1 sequences determined in the different species (Leendertz et al., 2004b). Mother-to-offspring transmission cannot be excluded but sexual transmission seems to be a rather uncommon infection route for primates. This hypothesis is likely to be true for STLV-1 subtypes I and J, but it seems to be more complex regarding the origin of Central African subtype B. Whereas the subtypes I and J consist of local strains, subtype B includes strains from chimpanzees and other monkey species from Sierra Leone, Côte d'Ivoire, Equatorial Guinea, Cameroon and the Democratic Republic of Congo. It is possible that strains clustering with subtype B have entered the chimpanzee population through interspecies transmission in the distant past before chimpanzees were split into subspecies.

The diversity reported in the study presented here is so far only been described for *C. cephus*, *C. nictitans* and *Piliocolobus badius* (Liegeois et al., 2008; Leendertz et al., 2004b). The low diversity described in other studies may imply that this is rather an effect of sample selection or sample origin, e.g. from sanctuaries. For example, populations held in captivity have probably undergone bottle neck events since only young primates with few infected individuals are the founders of these populations. We suggest that the natural STLV-1 diversity might depend on the primate species studied and on their social behaviour, for example STLV-1 diversity of different primate species living in close contact and often have aggressive intergroup encounters should be higher than of species having rarely direct contact to other primates. In order to understand the epidemiology of STLV-1 in wild primates, further analyses on well-characterised wild primate groups will be necessary to understand the complex picture seen in STLV-1 phylogeny. Our data suggest that some of the chimpanzees (Rafiki and Sumatra) may carry multiple STLV-1 genome sequences, bearing the risk of possible recombination events between genomes potentially resulting in altered pathogenicity and transmissibility. It would therefore be of major interest to identify recombinant STLV-1 isolates. Furthermore, humans in close contact to these chimpanzee populations or those handling and/or consuming chimpanzees are at risk to get infected by such altered viruses.

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