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Guns, germs and dogs: On the origin of *Leishmania chagasi*

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ABSTRACT

The evolutionary history of *Leishmania chagasi*, the aetiological agent of visceral leishmaniasis in South America has been widely debated. This study addresses the problem of the origin of *L. chagasi*, its timing and demography with fast evolving genetic markers, a suite of Bayesian clustering algorithms and coalescent modelling. Here, using 14 microsatellite markers, 450 strains from the *Leishmania donovani* complex, we show that the vast majority of the Central and South American *L. chagasi* were nested within the Portuguese *Leishmania infantum* clade. Moreover, *L. chagasi* allelic richness was half that of their Old World counterparts. The bottleneck signature was estimated to be about 500 years old and the settlement of *L. chagasi* in the New World, probably via infected dogs, was accompanied by a thousand-fold population decrease. Visceral leishmaniasis, lethal if untreated, is therefore one more disease that the Conquistadores brought to the New World.

1. Introduction

The origin of *Leishmania chagasi*, the aetiological agent of visceral leishmaniasis in the Americas is associated with contrasting scenarios and intimately linked with our past history (Killick-Kendrick et al., 1980). This protozoan flagellate is a member of the *Leishmania donovani* complex that encompasses two other species from the Old World (*Leishmania infantum* and *L. donovani*). Until recently, based on surface proteins, glycoconjugate ligands and radiorespirometry, *L. chagasi* was considered as a "clear" species (Lainson et al., 1987) indigenous in the New World. However, this situation did not hold longer once polymorphic genetic markers replaced the phenotypic data and different authors suggested that *L. chagasi* is in fact a *L. infantum* subpopulation that arose from imported European strains (Kuhls et al., 2008; Lukes et al., 2007; Mauricio et al., 2000; Momen and Cupolillo, 2000). Though this scenario convinced the "molecularists", there is still an ongoing controversy concerning the age and geographic origin of this pathogen. Moreover, some specialists cast some doubts that the Old World protozoan might have encountered the right vector in the New World (Lainson et al., 1987). This study addresses the problem of the origin of *L. chagasi*, its demography and evolutionary timing with fast evolving genetic markers by applying Bayesian methods, coalescent modelling and phylogenetics. Using data from a set of 14 microsatellite markers (Kuhls et al., 2007), we examined strains from the Mediterranean area, Asia, Africa, South and Central America ($n = 450$) (Kuhls et al., in press). Our results confirm the Old World origin of *L. chagasi*, dramatically improve the detection of the source population and determine a temporal frame for this transcontinental transfer. Finally, we unravel the parallel evolutionary histories and demographies of humans and one of their pathogens.

2. Materials and methods

2.1. Sampling and genotyping

To infer the *L. donovani* complex evolutionary history, we used a sample of 450 strains, from European, African and Asian countries, representative of the species complex diversity. More specifically, according to the topic of this communication we genotyped 106 *L. chagasi* strains from Honduras, Panama, Costa Rica, Colombia, Venezuela, Paraguay and Brazil. Sources, designation, geographical origins, MLEE identification, if known, are provided in Table S1. Most of the samples were of clinical origin; only few were isolated from proven and suspected reservoir animals and from sand fly vectors. DNA was isolated using proteinase K-phenol/chloroform extraction or the Wizard^{TM} Genomic DNA Purification System (Promega, Madison, WI, USA) according the manufacturer's

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protocol, suspended in TE-buffer or distilled water and stored at 4 °C until use. The parasites were genotyped using 14 microsatellite markers as previously described (Kuhls et al., 2007; Ochsenreither et al., 2006). We focused on these nuclear markers because they currently provide the most powerful and discriminative method for strain differentiation and population genetics in this species complex. PCRs were performed with fluorescence-conjugated forward primers. Screening of length variations of the amplified markers was done by automated fragment analysis using capillary sequencers. PCR products from amplified microsatellites were analysed either with the fragment analysis tool of the CEQ 8000 automated genetic analysis system (Beckman Coulter, USA) or the ABI PRISM GeneMapper (Applied Biosystems, Foster City, CA). Microsatellites allelic profiles are available upon request.

2.2. Genetic diversity estimation

The number of alleles (allelic richness) in Old and New World populations was estimated and sample sizes were corrected by the rarefaction procedure using Hp-rare (Kalinowski, 2005). Comparison tests as well as *P*-values were estimated using the Statistica 6.1 package.

2.3. Phylogenetic inferences

Cavalli-Sforza chord distance (Cavalli-Sforza and Edwards, 1967) was used to construct a population tree using a neighbor-joining algorithm (Saitou and Nei, 1987) as implemented in the software POPULATIONS v.1.2.30 (http://bioinformatics.org). Sup-

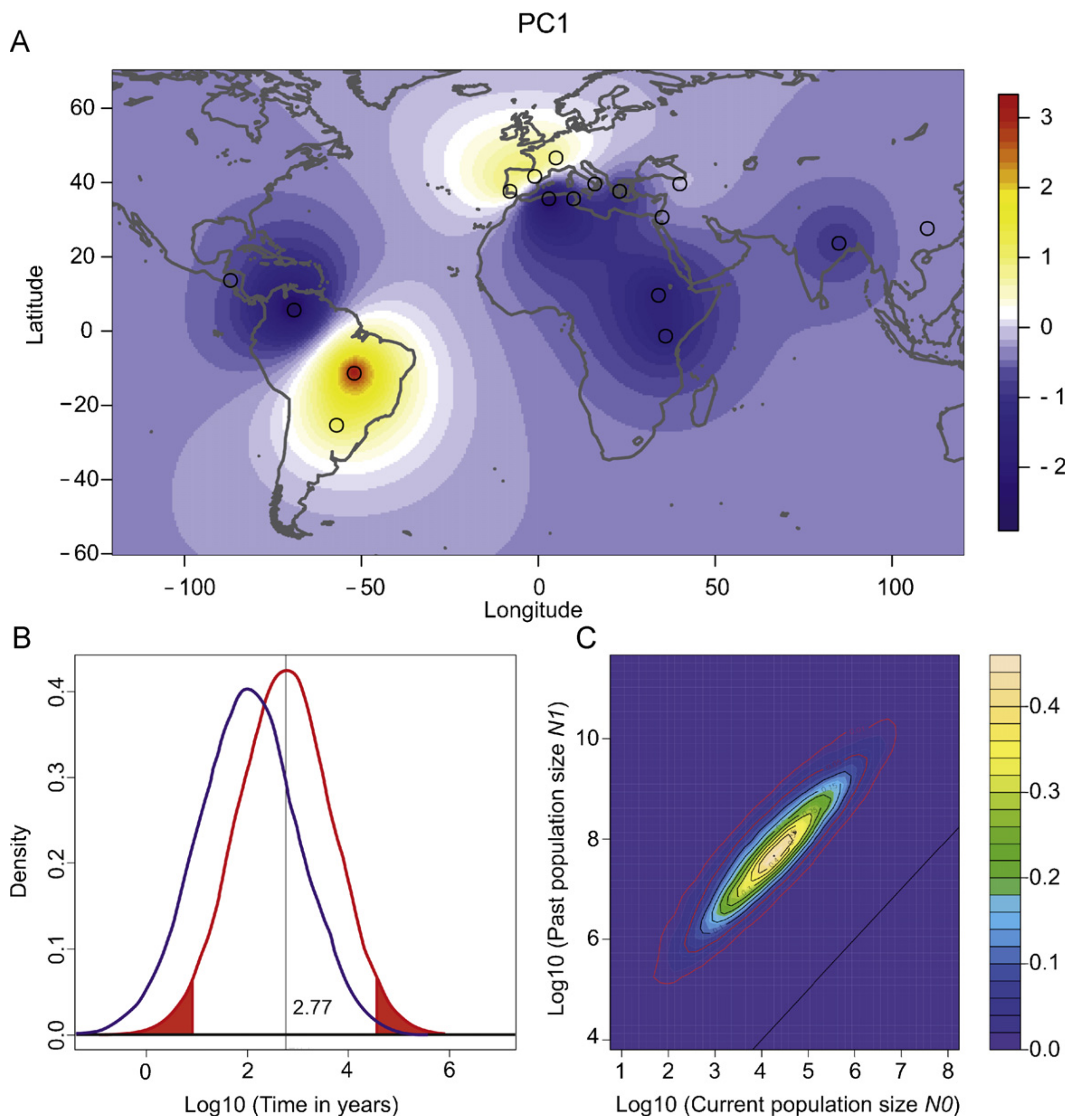

Fig. 1. (A) Synthetic map of the first principal component for *L. donovani* complex populations based on the 14 microsatellite polymorphisms. The first PC accounts for about 99% of the total genetic variation (PC2 accounts for 0.1% and contains the vast majority of the Old World samples). The PC1 map exhibits maximal values for western European and southern American samples confirming the shared ancestry of these populations. (B) Detection of a recent contraction in the *L. chagasi* lineage using the Bayesian methods MsVar. Posterior (red) and prior (blue) distributions of the elapsed time since *L. chagasi* population declined, including the 95% credibility intervals of the posterior distribution (between the two red areas). Time is expressed in years on a log scale and point estimate (mode of the posterior distribution) is indicated with the vertical thin line. (C) Two-dimensional density plot of the marginal posterior distribution of log(N_0) and log(N_1), where N_0 is the current number of individuals and N_1 is the number of individuals before contraction. Red isolines represent 95% and 99% credibility intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

port for the tree nodes was assessed by bootstrapping over individuals (100 iterations).

2.4. Inferring population structure

Inference of population structure was first performed using principal component analysis (PCA) implemented in the "prcomp" function of the R statistical package on the normalized genotypic matrix. Principal component analysis is a tool for exploring multilocus population genetic data (Cavalli-Sforza et al., 1994; Patterson et al., 2006). The results of the PCA can be visualized using "synthetic maps" that describe how each principal component varies across geographic space. In this representation, each PC is interpolated and displayed on a separate map (Cavalli-Sforza et al., 1994). PCA results were spatially interpolated using the Kriging method and displayed on geographic maps. Two genetic clustering algorithms were run: (i) TESS 2.3 (Chen et al., 2007; Durand et al., 2009) was used by analysing 100 runs of 50,000 iterations for each value of the number of clusters, K, from 2 to 4 using a burn-in period of 2000 sweeps. Admixture coefficients where then averaged over the 10 runs with the smallest values of the deviance information criterion and the values for each cluster were displayed on separate maps. (ii) We also implemented the spatial model of GENELAND 3.1.4 (Guillot et al., 2008) with the Dirichlet model for allelic frequencies for $K = 2$ (first split) and $K = 3$. We used 10 long runs of 10^7 iterations with a thinning of 500 and a burn-in of 50% under the spatial and correlated allelic frequency model.

2.5. Coalescence, TMRCA and demography

We used a Markov chain Monte Carlo Bayesian approach (Beaumont, 1999) that assumes a stepwise mutation model for the microsatellite markers and estimates the posterior probability distributions of the genealogical and demographic parameters under a model of a single population of variable size. This method permits to infer important biological parameters like the past (N_1) and present (N_0) effective population sizes and the time, in years, that has elapsed since the last demographic change (decline or expansion) began (T) (Wirth et al., 2008). The software MSVAR 1.3 (Beaumont, 1999) provides separate estimates of those parameters and was run on the 106 *L. chagasi* strains. The analyses were performed assuming exponential demographic change. A prior mean mutation rate of 10^{-4} per replication was considered based on prokaryotes and *Saccharomyces cerevisiae* experiments (Henderson and Petes, 1992; Vogler et al., 2006, 2007; Wierdl et al., 1997), and uninformative prior means of 10^2 were considered for time and population size parameters. The generation time was set on one day (Chakraborty and Das Gupta, 1962). Three chains of 8×10^8 iterations with a thinning of 20,000 were run for each analysis to confirm the convergence of the analyses. Contraction signatures assessed with a burn-in of 50% were robust and were confirmed with additional runs where an expansion was assumed as a prior.

3. Results and discussion

3.1. Leishmania chagasi origin and genetic structure

We applied three complementary approaches, principal component analysis (PCA), as well as two clustering algorithms, TESS 2.3 (Chen et al., 2007; Durand et al., 2009) and GENELAND 3.1.4 (Guillot et al., 2008). The two Bayesian programs infer population genetic structure based on multilocus genotypes and individual spatial coordinates. TESS infers individual admixture proportions in K ancestral populations, whereas GENELAND tries to assign individuals to K random mating groups. The first PC explained about 99% of the variation in the entire data set and suggested a clear link between *L. infantum* strains from southwest Europe and *L. chagasi* strains from South America (Fig. 1A). The abilities of principal components to estimate admixture proportions have been recently investigated by several studies (Patterson et al., 2006; Francois et al., 2010). Here the PC analysis was in complete agreement with the TESS analysis (Fig. S1), confirming the shared ancestry of the lineages. Moreover, using a hierarchical approach, we investigated the first split ($K = 2$) that could be detected using the spatial model implemented in Geneland (Fig. S2). Interestingly, the vast majority of the *L. chagasi* strains (94 out of 106; 88.7%) clustered with the Portuguese *L. infantum* sample. For $K = 3$, the *L. donovani* complex split accordingly to the accepted nomenclature (*L. donovani*, *L. infantum* with the exception of Portugal, and *L. chagasi*). This result was confirmed when a phylogenetic reconstruction using the Cavalli-Sforza chord distance was implemented (Fig. 2). Indeed, the *L. chagasi* and Portugal lineages were supported by strong bootstrap support (99%) and formed one sister-group within the European *L. infantum* clade. Twelve strains of *L. chagasi* differed from the main pool (data shown elsewhere in Kuhls et al., in press), half of them belonged to Venezuela, and they likely reflect independent minor import events from Spain or Southern-Europe. Those strains differed from the others by their non-MON-1 genotype, confirming a different evolutionary origin. They could not be clearly assigned to their source population due to a lack of statistical power (i.e. sample size to small for accurate allelic frequencies estimates and source population assignment).

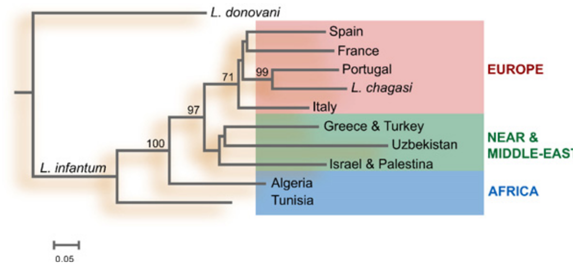

Fig. 2. Neighbor-joining (NJ) phenogram summarizing Cavalli-Sforza & Edwards' (1967) chord distances, D_{CE}, among 11 populations of *Leishmania infantum* strains collected in Europe, the Near and Middle East and in Africa. When the number of strains was too small (<10), we pooled geographically closely related samples in order to avoid statistical discrepancies due to strong allelic variance. The *L. donovani* strains were used as an out-group. Values on the nodes represent the percentage of bootstrap replicates over loci ($n = 100$). Branch lengths are proportional to the genetic distance between the taxa. The scale bar represents a distance D_{CE} of 0.05.

3.2. Demogenetics and dating

Once validated, the status of *L. chagasi* as an emerging pathogen in the New World might leave specific signatures, like a loss of diversity accompanying a founding event. This is exactly what we observed as the mean allelic richness of *L. chagasi* was significantly lower ($P < 0.001$) when compared to the source *L. infantum* populations (Fig. 3). Moreover, the mean number of private alleles in *L. chagasi* was close to 1, achieving a six-fold decrease when compared to the *L. infantum* samples. High levels of genetic diversity are a surrogate indication of ancestral origins as illustrated in African human populations. To estimate and confirm the prior mutation rate, we used Msvar (Beaumont, 1999), a coalescent based method. Indeed a mutation rate of 10^{-4} seems to be realistic since all posterior estimates converged near this initial value. The algorithm indicated that *L. chagasi* populations had undergone a severe and recent decline (Fig. 1C). Inferred current population sizes were extremely small (~15,000) whereas ancestral population sizes were estimated to be close to fifty

Table 1
Bayesian estimates for the actual and ancestral population sizes, the time when the exponential decrease in population size started and the mean mutation rate of the nine loci considered. The analysis was done using the MsVar method; population sizes are expressed as a number of individuals and time in generations. Point estimates correspond to the mode of each marginal posterior distribution and corresponding 95% credibility intervals are given in brackets.

Actual population size (N_0)	Ancestral population size (N_1)	Time when bottleneck started (in years)	Mutation rate/year
15,500 [302; 1.4×10^6]	43,650,000 [0.8×10^6; 3.7×10^6]	537 [7.9; 33,900]	3.8×10^{-7} [5.8×10^{-9}; 2.5×10^{-5}]
Actual population size, θ_0	Ancestral population size, θ_1	Time when bottleneck started $T/2$, N_0	PopSize ratio, N_1/N_0
0.040 [0.007; 0.0930]	74.1 [25; 224]	0.0148 [0.010; 0.023]	3.89×10^{-4} [6.46×10^{-5}; 1.66×10^{-3}]

Settings: Bayes factor bottleneck = infinity, point estimate = mode; [*XX*; *XX*] = 95% credibility intervals; starting values: $N_0 = 1.0 \times 10^6$, $N_1 = 1.0 \times 10^4$, $\mu = 1.0 \times 10^{-8}$, $T = 500$. Thinning 20,000 and 800,000,000 iterations.

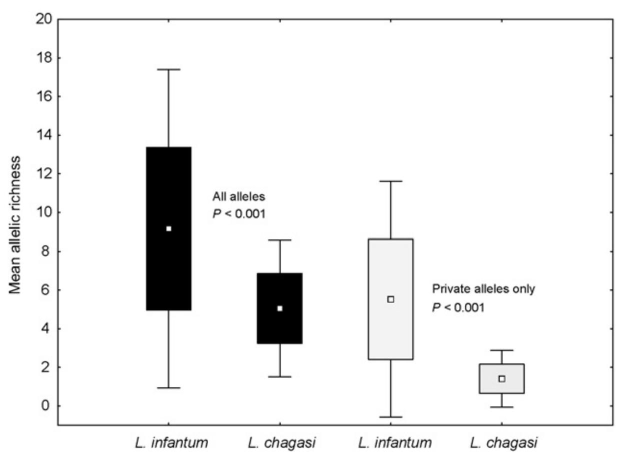

Fig. 3. Genetic variability in the different *L. infantum* lineages. Microsatellite mean allelic richness in *L. infantum* (Old World) and *L. chagasi* (New World) was computed for all alleles and for private alleles only, using the rarefaction algorithm HPrare. Notice that the Central and South American genetic diversity is significantly lower than the African and European genetic diversity ($P < 0.001$).

millions (Table 1). According to Msvar the timing of the population decline occurred 500 years ago (Fig. 1B). However, these numbers must be taken with caution, due to the rather large confidence intervals produced by the method. The differences observed between the PCA/Tess and the Geneland/NJ analyses are probably due to the assumptions of the models and the rather small samples sizes in Central America. The latter models rely on a non-recombining model whereas the two others infer admixture ancestry. Yet the reproductive system of this parasite is intermediate between those models and seems to combine moderately frequent recombinants with clonal expansions (Volf and Sadlova, 2009).

4. Conclusions

From the evidence we cumulate in this report, it is now clear that *L. chagasi* is de facto a *L. infantum* sub-population that emerged from a Portuguese population which had crossed the Atlantic Ocean most probably in the XVIth century via infected dogs and reached Central America and Brazil. The vast majority of the strains came through a first invasion wave, but secondary limited introductions also occurred. Thus, visceral leishmaniasis, lethal if untreated, is one more disease that the Portuguese Conquistadores brought in the New World, like flue and smallpox (Diamond, 1997). This study combines historical, demographic and genetic information to unravel the evolutionary history of an important tropical disease, and illustrates the benefits of Bayesian statistics and multifactorial analyses in the study of non-model pathogens. This study is yet another illustration of how human-bugs can unravel host migrations and origins (Morelli et al., 2010; Wirth et al., 2004, 2005; Wolfe et al., 2007).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.meegid.2011.04.004.

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Supporting Online Material

Table 1: Designation and characteristics of *Leishmania* strains used in this study.

WHO-code	Country	Region	Zymodeme[1]	Clinical picture	Reference
MCAN/PY/2000/L1P	Paraguay	Central Department	nd	CanL	(Kuhls et al. in press)
MCAN/PY/2000/Meka	Paraguay	Central Department	nd	CanL	(Kuhls et al. in press)
MCAN/PY/2000/PB2	Paraguay	Central Department	nd	CanL	(Kuhls et al. in press)
MCAN/PY/2000/L9P	Paraguay	Central Department	nd	CanL	(Kuhls et al. in press)
MCAN/PY/2000/Doberman	Paraguay	Central Department	nd	CanL	(Kuhls et al. in press)
MCAN/PY/2000/Dago	Paraguay	Central Department	nd	CanL	(Kuhls et al. in press)
MCAN/PY/2000/Ringo	Paraguay	Central Department	nd	CanL	(Kuhls et al. in press)
MHOM/PY/2006/AS1	Paraguay	Asuncion	nd	VL	(Kuhls et al. in press)
MHOM/PY/2007/AS6	Paraguay	Asuncion	nd	VL	(Kuhls et al. in press)
MCAN/PY/2008/470	Paraguay	Cordillera Department	nd	CanL	(Kuhls et al. in press)
MCAN/BR/2002/JackCusteau	Brazil	Mato Grosso de Sul	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/2007/JVF	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/1984/CO910	Brazil	Mato Grosso do Sul	MON-1	CanL	(Kuhls et al. in press)
MHOM/BR/2003/BSB	Brazil	Mato Grosso de Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2007/JFVL	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/2002/LVV-136	Brazil	Mato Grosso do Sul	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/2002/LVV-147	Brazil	Mato Grosso do Sul	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/2003/WAZ	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2002/BGC	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/AAS	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/ALX	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/RMJ	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/DDG	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/JHS	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/JBIC	Brazil	Mato Grosso do Sul	IOC/Z1	VL/HIV+	(Kuhls et al. in press)
MHOM/BR/2003/CAS	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/FCM	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/GJR	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2003/MAM	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/2002/LVV-135	Brazil	Mato Grosso do Sul	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/2003/JT	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/2002/LVV-139	Brazil	Mato Grosso do Sul	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/2007/LFSP	Brazil	Mato Grosso do Sul	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/2007/CG2	Brazil	Mato Grosso do Sul	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/2002/CP-TARZAN	Brazil	Espirito Santo	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/1987/HCO-1	Brazil	Espírito Santo	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/1987/HBG-2	Brazil	Espírito Santo	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/1987/HIT-1	Brazil	Espírito Santo	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/2000/CNV-FEROZ	Brazil	Espírito Santo	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/2003/CP-TAISON	Brazil	Espírito Santo	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/2005/CP-40	Brazil	Espírito Santo	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/2005/HRNS-1	Brazil	Espírito Santo	IOC/Z1	VL	(Kuhls et al. in press)
MHOM/BR/2001/HP-EMO	Brazil	Espírito Santo	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/2001/CP-SEMNOME	Brazil	Espírito Santo	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/2003/ACS	Brazil	Pernambuco	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/2005/FACHIDE	Brazil	Pernambuco	IOC/Z1	CanL	(Kuhls et al. in press)

MCAN/BR/2006/MAIKE	Brazil	Pernambuco	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/2007/SPOK II	Brazil	Pernambuco	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/1991/1194BAJE	Brazil	Bahia	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/1974/PP75^{T}	Brazil	Bahia	MON-1	VL	(Kuhls et al. in press)
MCAN/BR/1991/1373BAJE	Brazil	Bahia	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/1980/CR3	Brazil	Rio de Janeiro	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/2007/WC	Brazil	Rio de Janeiro	IOC/Z1	VL/HIV+	(Kuhls et al. in press)
MHOM/BR/2007/JFF_BM	Brazil	Rio de Janeiro	IOC/Z1	VL/HIV+	(Kuhls et al. in press)
MHOM/BR/1987/H-136	Brazil	Ceará	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/1984/17.206	Brazil	Ceará	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/1986/H-33	Brazil	Ceará	IOC/Z1	VL	(Kuhls et al. in press)
MCAN/BR/1987/CCC18.406	Brazil	Ceará	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/1986/CCC17.580	Brazil	Ceará	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/1989/M12734	Brazil	Piauí Teresina	nd	VL	(Kuhls et al. in press)
MCAN/BR/1989/M12737	Brazil	Piauí Teresina	nd	CanL	(Kuhls et al. in press)
MCAN/BR/1989/M12727	Brazil	Piauí Teresina	nd	CanL	(Kuhls et al. in press)
MCAN/BR/2002/RN-CEPA2	Brazil	Rio Grande do Norte	IOC/Z1	CanL	(Kuhls et al. in press)
MCAN/BR/2002/RN-CEPA3	Brazil	Rio Grande do Norte	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/BR/1985/M9702	Brazil	Pará Marajó	nd	VL	(Kuhls et al. in press)
MCER/BR/1983/M7633	Brazil	Pará Belém	nd	fox	(Kuhls et al. in press)
MCER/BR/1989/M12085	Brazil	Pará Belém	nd	fox	(Kuhls et al. in press)
MCER/BR/1989/M12084	Brazil	Pará Belém	nd	fox	(Kuhls et al. in press)
MCER/BR/1981/M6445	Brazil	Pará Belém	nd	fox	(Kuhls et al. in press)
MHOM/BR/0000/Edmael	Brazil	nd	MON-1	nd	(Kuhls et al. in press)
MHOM/BR/1984/M8270	Brazil	nd	nd	VL	(Kuhls et al. in press)
MHOM/BR/1973/M1287	Brazil	nd	nd	nd	(Kuhls et al. in press)
MHOM/HN/1994/560	Honduras	El Tigre	nd	CL	(Kuhls et al. in press)
MHOM/HN/1994/419	Honduras	San Juan Bautista	nd	CL	(Kuhls et al. in press)
MHOM/HN/1994/412	Honduras	nd	nd	CL	(Kuhls et al. in press)
MHOM/HN/1988/122	Honduras	El Tigre	nd	CL	(Kuhls et al. in press)
MHOM/HN/1989/167	Honduras	Orcuina	nd	CL	(Kuhls et al. in press)
MHOM/HN/1993/336	Honduras	San Juan Bautista	nd	CL	(Kuhls et al. in press)
MHOM/HN/1994/504	Honduras	El Tigre	nd	CL	(Kuhls et al. in press)
MHOM/HN/1994/556	Honduras	El Tigre	nd	CL	(Kuhls et al. in press)
MHOM/HN/1993/310	Honduras	San Juan Bautista	nd	CL	(Kuhls et al. in press)
MHOM/HN/1988/115	Honduras	El Tigre	nd	CL	(Kuhls et al. in press)
MHOM/HN/1994/421	Honduras	San Juan Bautista	nd	CL	(Kuhls et al. in press)
MHOM/HN/1994/463	Honduras	San Juan Bautista	nd	CL	(Kuhls et al. in press)
MHOM/HN/1994/552	Honduras	El Tigre	nd	CL	(Kuhls et al. in press)
MHOM/HN/1987/29	Honduras	San Francisco de Coray	nd	VL	(Kuhls et al. in press)
MHOM/HN/1993/354	Honduras	Alubaren	nd	VL	(Kuhls et al. in press)
MHOM/PA/1979/WR317	Panama	nd	nd	CL	(Kuhls et al. in press)
MHOM/PA/1978/W285	Panama	nd	nd	CL	(Kuhls et al. in press)
MHOM/CR/199?/LVCR	Costa Rica	Guanacaste	nd	nd	(Kuhls et al. in press)
MCAN/VE/2006/UCNA/LV2	Venezuela	Aragua	nd	CanL	(Kuhls et al. in press)
MHOM/VE/2001/LV10	Venezuela	Carabobo	nd	VL	(Kuhls et al. in press)
MHOM/VE/2004/IB-LAT	Venezuela	Guárico	nd	CL	(Kuhls et al. in press)
MHOM/VE/2000/LV04	Venezuela	Carabobo	nd	VL	(Kuhls et al. in press)
MHOM/VE/2001/LV06	Venezuela	Carabobo	nd	VL	(Kuhls et al. in press)
MHOM/VE/1998/NESA	Venezuela	Nueva Esparta	MON-1	VL	(Kuhls et al. in press)
MCAN/CO/1986/CL-223	Colombia	Huila	IOC/Z1	CanL	(Kuhls et al. in press)
MHOM/CO/1984/CL-044	Colombia	Cundinamarca	IOC/Z1	VL	(Kuhls et al. in press)

MDID/CO/1988/CL-490	Colombia	Tolima	IOC/Z1	*Didelphis*	*(Kuhls et al. in press)*
MHOM/ES/1993/PM1	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1986/BCN16	Spain	Catalonia	MON-1	CL	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-984	Spain	Madrid	nd	VL/transp.	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-983	Spain	Madrid	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-980	Spain	Madrid	nd	VL	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1181	Spain	Madrid	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1212	Spain	Madrid	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1166	Spain	Madrid	nd	VL/HIV+	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1006	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1014	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1037	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1040	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-981	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1122	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-1048	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-1049	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1150	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1109	Spain	Majorca	MON-1	VL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1008	Spain	Majorca	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1007	Spain	Majorca	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1038	Spain	Majorca	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2002/LLM-1149	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2002/LLM-1155	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2002/LLM-1203	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2002/LLM-1139	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2002/LLM-1141	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2002/LLM-1158	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1068	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1106	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2002/LLM-1113	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1116	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1128	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1136	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1148	Spain	Madrid	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1228	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1233	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1238	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1240	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2001/LLM-1215	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1237	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1241	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1226	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MCAN/ES/2003/LLM-1267	Spain	Ibiza	MON-1	CanL	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1220	Spain	Madrid	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1217	Spain	Madrid	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-1036	Spain	Madrid	MON-27	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2003/LLM-1254	Spain	Madrid	nd	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1997/LLM-707	Spain	Madrid	MON-24	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1997/LLM-709	Spain	Madrid	MON-24	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1184	Spain	Barcelona	MON-1	VL	(Kuhls et al. 2008)
MHOM/ES/2003/LLM-1232	Spain	Barcelona	MON-1	VL/HIV+	(Kuhls et al. 2008)

MHOM/ES/1998/LLM-810	Spain	Majorca	MON-24	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1999/LLM-846	Spain	Majorca	MON-24	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1998/LLM-745	Spain	Andalusia	MON-34	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1999/LLM-879	Spain	Andalusia	MN-34	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-1035	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2002/LLM-1167	Spain	Majorca	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1995/LLM-531	Spain	Madrid	MON-34	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/1998/LLM-780	Spain	Madrid	MON-34	VL/HIV+	(Kuhls et al. 2008)
MHOM/ES/2001/LLM-1034	Spain	Madrid	MON-34	VL/HIV+	(Kuhls et al. 2008)
MCAN/ES/1986/LEM935	Spain	Poboleda	MON-77	CanL	(Kuhls et al. 2007)
MHOM/ES/1987/Lombardi	Spain	nd	MON-24	CL	(Kuhls et al. 2007)
MHOM/ES/1988/LLM175	Spain	Madrid	MON-198	VL/HIV+	(Kuhls et al. 2007)
MHOM/ES/1991/LEM2298	Spain	Valencia	MON-183	VL/HIV+	(Kuhls et al. 2007)
MHOM/ES/1992/LLM373	Spain	Madrid	MON-199	VL/HIV+	(Kuhls et al. 2007)
MCAN/PT/1993/IMT193	Portugal	Algarve	MON-1	CanL	(Kuhls et al. 2007)
IPERN/PT/1993/IMT189	Portugal	Algarve	MON-1	sandfly	(Kuhls et al. 2008)
MCAN/PT/1995/IMT205	Portugal	Alentejo	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT328	Portugal	Alentejo	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/89/IMT162	Portugal	Alto Douro	MON-1	CanL	(Kuhls et al. 2008)
IARI/PT/1989/IMT169	Portugal	Alto Douro	MON-1	sandfly	(Kuhls et al. 2008)
IARI/PT/1989/IMT170	Portugal	Alto Douro	MON-1	sandfly	(Kuhls et al. 2008)
MHOM/PT/2002/IMT279	Portugal	Alto Douro	MON-1	VL	(Kuhls et al. 2008)
MHOM/PT/2002/IMT288	Portugal	Alto Douro	MON-1	VL	(Kuhls et al. 2008)
MHOM/PT/2003/IMT337	Portugal	Alto Douro	MON-1	CL	(Kuhls et al. 2008)
MCAN/PT/1997/IMT229	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT300	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT327	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT316	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT329	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT330	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT338	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT339	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MHOM/PT/1989/IMT163	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2002/IMT293	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2003/IMT293-B	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2002/IMT294	Portugal	Lisbon	MON-1	VCL/HIV+	(Kuhls et al. 2008)
MHOM/PT/ 2002/IMT296	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2003/IMT299	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/1998/IMT238	Portugal	Lisbon	MON-80	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2000/IMT262	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2000/IMT262-A	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/1993/IMT184	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/1988/IMT151	Portugal	Lisbon	MON-1	VL	(Kuhls et al. 2008)
MHOM/PT/2004/IMT362	Portugal	Lisbon	MON-1	CL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2004/IMT364	Portugal	Lisbon	MON-1	VL/HIV+	(Kuhls et al. 2008)
MHOM/PT/2004/IMT359	Portugal	Alto Douro	MON-1	VL	(Kuhls et al. 2008)
MHOM/PT/2004/IMT360	Portugal	Alto Douro	MON-1	VL	(Kuhls et al. 2008)
MHOM/PT/2004/IMT363	Portugal	Alentejo	nd	VL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT329	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT331	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2003/IMT354	Portugal	Lisbon	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/1989/IMT160	Portugal	Alto Douro	MON-1	CanL	(Kuhls et al. 2008)

MCAN/PT/1989/IMT161	Portugal	Alto Douro	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2004/IMT355	Portugal	Alentejo	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/2004/IMT356	Portugal	Alentejo	MON-1	CanL	(Kuhls et al. 2008)
MCAN/PT/1994/IMT204	Portugal	Algarve	MON-1	CanL	(Kuhls et al. 2008)
MVUL/PT/1982/IMT108	Portugal	Lisbon	MON-1	fox	(Kuhls et al. 2008)
MHOM/PT/2000/IMT260	Portugal	Lisbon	MON-1	CL	(Kuhls et al. 2007)
MHOM/FR/1978/LEM75	France	Languedoc	MON-1	VL	(Kuhls et al. 2007)
MHOM/FR/1995/LPN114	France	Côte d'Azur	MON-1	VL	(Kuhls et al. 2007)
MHOM/FR/1997/LSL29	France	Languedoc	MON-1	CL	(Kuhls et al. 2007)
MCAN/FR/1987/RM1	France	Marseille	MON-108	CanL	(Kuhls et al. 2007)
MHOM/FR/1962/LRC-L47	France	nd	nd	VL	(Kuhls et al. 2007)
MHOM/FR/1996/LEM3249	France	Roussillion	MON-29	CL	(Kuhls et al. 2007)
MHOM/FR/1980/LEM189	France	Roussillion	MON-11	CL	(Kuhls et al. 2007)
MHOM/FR/1985/LPN24	France	Corsica	MON-1		(Kuhls et al. in press)
MHOM/FR/1987/LEM1163-CL	France	Cévennes	MON-1		(Kuhls et al. in press)
MHOM/FR/1987/LEM1224	France	Cévennes	MON-1		(Kuhls et al. in press)
MHOM/FR/1988/LEM1345	France	Cévennes	MON-1		(Kuhls et al. in press)
MHOM/FR/1988/CRE2	France	Corsica	MON-1		(Kuhls et al. in press)
MHOM/FR/1989/LEM1614	France	Cévennes	MON-1		(Kuhls et al. in press)
MHOM/FR/1989/LPN58	France	Côte d’Azur	MON-1		(Kuhls et al. in press)
MCAN/FR/1989/LPN57	France	Côte d’Azur	MON-1	CanL	(Kuhls et al. in press)
MHOM/FR/1990/LPN61	France	Côte d’Azur	MON-1		(Kuhls et al. in press)
MHOM/FR/1990/LPN62	France	Côte d’Azur	MON-1		(Kuhls et al. in press)
MHOM/FR/1990/LPN66	France	Côte d’Azur	MON-1		(Kuhls et al. in press)
MHOM/FR/1990/LEM2191	France	Cévennes	MON-1		(Kuhls et al. in press)
MHOM/FR/1991/LEM2327	France	Pyrénées-Orientales	MON-1		(Kuhls et al. in press)
MHOM/FR/1993/LEM2652	France	Pyrénées-Orientales	MON-1		(Kuhls et al. in press)
MHOM/FR1994/LEM2859	France	Pyrénées-Orientales	MON-1		(Kuhls et al. in press)
MHOM/FR/1995/LEM2982	France	Pyrénées-Orientales	MON-1	HIV-	(Kuhls et al. in press)
MHOM/FR/1995/LEM3003	France	Pyrénées-Orientales	MON-1		(Kuhls et al. in press)
MHOM/FR/1996/LPM138	France	Provence	MON-1		(Kuhls et al. in press)
MHOM/FR/1996/LPM154	France	Provence	MON-1		(Kuhls et al. in press)
MHOM/FR/1996/LEM3276	France	Provence	MON-1		(Kuhls et al. in press)
MHOM/FR/1996/LPM161	France	Provence	MON-1		(Kuhls et al. in press)
MHOM/FR/1996/LEM3285	France	Provence	MON-1		(Kuhls et al. in press)
MHOM/FR/1997/LPN154	France	Corsica	MON-1		(Kuhls et al. in press)
MHOM/FR/1999/CRE103	France	Corsica	MON-1		(Kuhls et al. in press)
MHOM/FR/1999/LPM190	France	Corsica	MON-1		(Kuhls et al. in press)
MHOM/MT/1985/BUCK	Malta	Malta	MON-78	CL	(Kuhls et al. 2007)
MHOM/IT/1994/ISS1036	Italy	nd	MON-228	VL	(Kuhls et al. 2007)
MHOM/IT/1993/ISS800	Italy	Sicily	MON-188	VL/HIV+	(Kuhls et al. 2007)
IPRF/IT/1985/ISS174	Italy	Abruzzo	MON-1	sandfly	(Kuhls et al. in press)
IPER/IT/1986/ISS231	Italy	Puglia	MON-1	sandfly	(Kuhls et al. in press)
MHOM/IT/1998/ISS1779	Italy	Puglia	MON-1	VL/HIV+	(Kuhls et al. in press)
MHOM/IT/2006/ISS2826	Italy	Puglia	MON-1	VL/HIV+	(Kuhls et al. in press)
MCAN/IT/1993/ISS949	Italy	Sicily	MON-1	CanL	(Kuhls et al. in press)
MHOM/IT/1996/ISS1435	Italy	Sicily	MON-1	CL	(Kuhls et al. in press)
MHOM/IT/2002/ISS2179	Italy	Sicily	MON-1	VL/HIV+	(Kuhls et al. in press)
MCAN/IT/2002/ISS2420	Italy	Sicily	MON-1	CanL	(Kuhls et al. in press)
MHOM/IT/2004/ISS2653	Italy	Sicily	MON-1	CL	(Kuhls et al. in press)
IPER/IT/2005/2805	Italy	Sicily	MON-1	sandfly	(Kuhls et al. in press)
MFEL/IT/2005/ISS2814	Italy	Sicily	MON-1	Feline L	(Kuhls et al. in press)

MHOM/IT/1995/ISS1268	Italy	Sardegna	MON-1	VL/ HIV+	(Kuhls et al. in press)
MCAN/IT/1996/ISS1457	Italy	Sardegna	MON-1	CanL	(Kuhls et al. in press)
MCAN/IT/2002/ISS2379	Italy	Lazio	MON-1	CanL	(Kuhls et al. in press)
MHOM/IT/2002/ISS2434	Italy	Lazio	MON-1	VL/ HIV+	(Kuhls et al. in press)
MHOM/IT/2002/ISS2384	Italy	Campania	MON-1	VL	(Kuhls et al. in press)
MHOM/IT/2002/ISS2426	Italy	Campania	MON-1	VL	(Kuhls et al. in press)
MHOM/IT/2002/ISS2429	Italy	Campania	MON-1	CanL	(Kuhls et al. in press)
MCAN/IT/2003/ISS2609	Italy	Campania	MON-1	CanL	(Kuhls et al. in press)
MHOM/IT/2003/ISS2615	Italy	Campania	MON-1	VL	(Kuhls et al. in press)
MHOM/IT/2003/ISS2641	Italy	Campania	MON-1	VL	(Kuhls et al. in press)
MHOM/IT/2005/ISS 2786	Italy	Campania	MON-1	VL	(Kuhls et al. in press)
MCAN/IT/2002/ISS2427	Italy	Calabria	MON-1	CanL	(Kuhls et al. in press)
MHOM/IT/2002/ISS2452	Italy	Molise	MON-1	VL	(Kuhls et al. in press)
MCAN/IT/2003/ISS2611	Italy	Piemonte	MON-1	CanL	(Kuhls et al. in press)
MHOM/IT/2002/ISS2508	Italy	Piemonte/ Lombardia	MON-1	VL/HIV+	(Kuhls et al. in press)
MCAN/IT/2004/ISS2658	Italy	Lombardia	MON-1	CanL	(Kuhls et al. in press)
MHOM/IT/2002/ISS2524	Italy	Liguria	MON-1	VL	(Kuhls et al. in press)
MHOM/GR/2001/GH1	Greece	Athens	MON-1	VL	(Kuhls et al. 2008)
MHOM/GR/2001/GH2	Greece	Athens	MON-1	VL	(Kuhls et al. 2008)
MHOM/GR/2001/GH3	Greece	Crete	MON-1	VL	(Kuhls et al. 2008)
MHOM/GR/2001/GH5	Greece	Crete	MON-1	VL	(Kuhls et al. 2008)
MHOM/GR/2001/GH6	Greece	Athens	MON-98	VL	(Kuhls et al. 2008)
MHOM/GR/2001/GH8	Greece	Athens	MON-1	VL	(Kuhls et al. 2008)
MHOM/GR/2001/GH9	Greece	Athens	MON-1	VL	(Kuhls et al. 2008)
MHOM/GR/2001/GH10	Greece	Athens	MON-1	VCL/HIV+	(Kuhls et al. 2008)
MHOM/GR/2001/GH11	Greece	Athens	MON-1	VL	(Kuhls et al. 2008)
MCAN/GR/2001/GD3	Greece	Crete	MON-98	CanL	(Kuhls et al. 2008)
MCAN/GR/2001/GD4	Greece	Crete	MON-98	CanL	(Kuhls et al. 2008)
MCAN/GR/2003/GD5	Greece	Crete	MON-1	CanL	(Kuhls et al. 2008)
MCAN/GR/2001/GD7	Greece	Crete	MON-1	CanL	(Kuhls et al. 2008)
MCAN/GR/2001/GD8	Greece	Crete	MON-98	CanL	(Kuhls et al. 2008)
MHOM/GR/2002/GH12	Greece	Crete	MON-1	VL	(Kuhls et al. 2008)
MCAN/TR/1996/EP16	Turkey	nd	nd	CanL	(Kuhls et al. 2007)
MHOM/TR/1994/EP3	Turkey	nd	nd	nd	(Kuhls et al. 2007)
MCAN/IL/1994/LRC-L639	Israel	cIL / Nataf	MON-1	CanL	(Kuhls et al. 2007)
MCAN/IL/1996/LRC-L685	Israel	cIL / Nataf	nd	CanL	(Kuhls et al. 2007)
MCAN/IL/1996/LRC-L695	Israel	cIL / Nili	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L709	Israel	nIL/ Klil	nd	CanL	(Amro et al. 2009)
MCAN/IL/1997/LRC-L716	Israel	cIL / Nataf	nd	CanL	(Amro et al. 2009)
MCAN/IL/1997/LRC-L717	Israel	cIL / Nataf	nd	CanL	(Amro et al. 2009)
MCAN/IL/1997/LRC-L718	Israel	cIL / Nataf	nd	CanL	(Amro et al. 2009)
MCAN/IL/1997/LRC-L719	Israel	cIL / Rishon Lezion	nd	CanL	(Amro et al. 2009)
MCAN/IL/1997/LRC-L720	Israel	cIL / Tzur Natan	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L689	Israel	cIL / Sataf	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L699	Israel	nIL / Klil	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L700	Israel	cIL / Nataf	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L705	Israel	nIL / Klil	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L706	Israel	nIL / Klil	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L708	Israel	nIL / Klil	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L692	Israel	cIL / Nili	nd	CanL	(Amro et al. 2009)
MCAN/IL/1991/LRC-L613	Israel	nIL / Avtalyon	nd	CanL	(Amro et al. 2009)
MCAN/IL/2005/LRC-L1252	Israel	cIL / Na'ale	nd	CanL	(Amro et al. 2009)

MCAN/IL/2005/LRC-L1253	Israel	cIL / Bet Shemeh	nd	CanL	(Amro et al. 2009)
MCAN/IL/2005/LRC-L1257	Israel	cIL / Bet Nehemia	nd	CanL	(Amro et al. 2009)
MCAN/IL/2005/LRC-L1275	Israel	cIL/ Ben Shemen	nd	CanL	(Amro et al. 2009)
MCAN/IL/2006/LRC-L1278	Israel	cIL / Yehud	nd	CanL	(Amro et al. 2009)
MCAN/IL/2005/LRC-L1280	Israel	nIL / Kedarim	nd	CanL	(Amro et al. 2009)
MCAN/IL/1997/Lychee8849	Israel	nd	nd	CanL	(Amro et al. 2009)
MCAN/IL/1996/LRC-L693	Israel	cIL / Nili	nd	CanL	(Amro et al. 2009)
MHOM/IL/1998/LRC-L742	Israel	cIL / Barkan	nd	VL	(Amro et al. 2009)
MCAN/IL/1998/LRC-L741	Israel	cIL / Alei Zahav	nd	CanL	(Amro et al. 2009)
MHOM/JO/0000/JCL24	Jordan	nd	nd	VL	This study
MHOM/EG/1987/RTG2	Egypt	nd	MON-98	nd	This study
MHOM/PS/1999/LRC-L773	Palestine	Jenin	MON-281	VL	(Amro et al. 2009)
MHOM/PS/2000/SL7	Palestine	Hebron	nd	VL	(Amro et al. 2009)
MHOM/PS/2000/SL8	Palestine	Hebron	nd	VL	(Amro et al. 2009)
MHOM/PS/2000/SL18	Palestine	Hebron	nd	VL	(Amro et al. 2009)
MHOM/PS/1993/SL20	Palestine	Hebron	nd	VL	(Amro et al. 2009)
MHOM/PS/2004/SL21	Palestine	Hebron/Betola	nd	VL	(Amro et al. 2009)
MHOM/PS/2005/SL22	Palestine	Hebron/Noba	nd	VL	(Amro et al. 2009)
MHOM/PS/2005/SL23	Palestine	Hebron/Dersamet	nd	VL	(Amro et al. 2009)
MHOM/PS/2006/SL26	Palestine	Hebron	nd	VL	(Amro et al. 2009)
MHOM/PS/2006/LRC-L1296	Palestine	Hebron/Samoa	MON-1	VL	(Amro et al. 2009)
MHOM/DZ/1982/LIPA59	Algeria	nd	MON-24	CL	(Seridi et al. 2008)
MCAN/DZ/1998/LIPA882	Algeria	Tizi Ouzou	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/2000/LIPA1086	Algeria	Boumerdes	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA1066	Algeria	Alger	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/1998/LIPA881	Algeria	Tizi Ouzou	MON-24	VL	(Seridi et al. 2008)
MHOM/DZ/1995/LIPA459	Algeria	Lakhdaria	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA1058	Algeria	Lakhdaria	MON-80	CL	(Seridi et al. 2008)
MCAN /DZ/2000/LIPA1118	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1323	Algeria	Tizi Ouzou	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/2001/LIPA1140	Algeria	Boumerdes	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/2000/LIPA1087	Algeria	Béjaia	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1996/LIPA477	Algeria	Ain Defla	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/2001/LIPA1226	Algeria	Alger	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA977	Algeria	Tizi Ouzou	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/1995/LIPA 440	Algeria	Alger	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/1995/LIPA452	Algeria	Boumerdes	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1338	Algeria	Lakhdaria	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/2001/LIPA1233	Algeria	Béjaia	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/2001/LIPA1227	Algeria	Bejaia	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/2001/LIPA1148	Algeria	Bouira	MON-1	VL	(Seridi et al. 2008)
MCAN/DZ/2001/LIPA1179	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MCAN/DZ/2001/LIPA1213	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MCAN/DZ/2000/LIPA1109	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/1998/LIPA842	Algeria	Ain-Defla	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1998/LIPA851	Algeria	Blida	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1998/LIPA867	Algeria	Alger	MON-1	VL	(Seridi et al. 2008)
MCAN/DZ/1998/LIPA904	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MCAN/DZ/1998/LIPA911	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA979	Algeria	Tizi Ouzou	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA1002	Algeria	Tizi Ouzou	MON-1	VL	(Seridi et al. 2008)

MCAN/DZ/2000/LIPA1113	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1342	Algeria	Blida	MON-1	VL	(Seridi et al. 2008)
MCAN/DZ/2000/LIPA1117	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MCAN/DZ/2002/LIPA1341	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1343	Algeria	Blida	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1995/LIPA448	Algeria	Setif	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1996/LIPA529	Algeria	Tizi Ouzou	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1996/LIPA482	Algeria	Médéa	MON-1	VL	(Seridi et al. 2008)
MCAN/DZ/2001/LIPA1246	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1313	Algeria	Lakhdaria	MON-1	VL	(Seridi et al. 2008)
MCAN/DZ/2000/LIPA1139	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/1995/LIPA454b	Algeria	Médéa	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1996/LIPA466	Algeria	Médéa	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1996 /LIPA487	Algeria	Boumerdes	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1996/LIPA509	Algeria	Sétif	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA992	Algeria	Ain Defla	MON-1	CL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA1057	Algeria	Alger	MON-80	CL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1319	Algeria	Tipaza	MON-80	VL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1285	Algeria	Bouira	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1318	Algeria	Biskra	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1337	Algeria	Alger	MON-1	VL	(Seridi et al. 2008)
MCAN/DZ/2002/LIPA1281	Algeria	Alger	MON-1	CanL	(Seridi et al. 2008)
MHOM/DZ/1999/LIPA1067	Algeria	Tizi Ouzou	MON-80	VL	(Seridi et al. 2008)
MHOM/DZ/1996/LIPA504	Algeria	Boumerdes	MON-24	CL	(Seridi et al. 2008)
MHOM/DZ/2002/LIPA1339	Algeria	Ain Defla	MON-1	VL	(Seridi et al. 2008)
MHOM/DZ/1998/LIPA815	Algeria	Boumerdes	MON-24	CL	(Seridi et al. 2008)
MHOM/TN/1980/IPT1^{T}	Tunisia	nd	MON-1	VL	(Kuhls et al. 2007)
MHOM/TN/2001/Tus167	Tunisia	Monastir	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/27M	Tunisia	Tunis	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/246M	Tunisia	Tunis	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/20S	Tunisia	Beja	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/22MO	Tunisia	Seliana	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/21S	Tunisia	Béja	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/Tus221	Tunisia	Monastir	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/Tum222	Tunisia	Monastir	MON-1	VL	(Chargui et al. 2009)
MCAN/TN/2002/LCnJ20S	Tunisia	Tunis	MON-1	CanL	(Chargui et al. 2009)
MCAN/TN/2002/GGCH1/02	Tunisia	Monastir	MON-1	CanL	(Chargui et al. 2009)
MCAN/TN/2002/FCH2/02	Tunisia	Monastir	MON-1	CanL	(Chargui et al. 2009)
MCAN/TN/2002/LCnJ20G	Tunisia	Tunis	MON-1	CanL	(Chargui et al. 2009)
MHOM/TN/2004/LC78	Tunisia	Tunis	MON-1	VL	(Chargui et al. 2009)
MHOM/TN/2002/Tus227	Tunisia	Monastir	MON-24	VL	(Chargui et al. 2009)
MHOM/TN/2005/PLV11	Tunisia	Kairouan	MON-24	VL	(Chargui et al. 2009)
MHOM/TN/2005/PLV15	Tunisia	Kairouan	MON-24	VL	(Chargui et al. 2009)
MHOM/TN/2005/PLV28	Tunisia	Kairouan	MON-24	CL	(Chargui et al. 2009)
MHOM/TN/2002/LC148	Tunisia	Bizerte	MON-24	CL	(Chargui et al. 2009)
MHOM/TN/2004/LC64	Tunisia	Tunis	MON-24	CL	(Chargui et al. 2009)
MHOM/TN/2002/LC95	Tunisia	Béja	MON-24	CL	(Chargui et al. 2009)
MHOM/TN/2002/SFC89	Tunisia	Sfax	MON-24	CL	(Chargui et al. 2009)
MHOM/TN/2005/SFC51	Tunisia	Sfax	MON-24	CL	(Chargui et al. 2009)
MHOM/TN/2004/TLC3	Tunisia	Siliana	MON-24	CL	(Chargui et al. 2009)
MHOM/TN/2005/PLV14	Tunisia	Kairouan	MON-24	VL	(Chargui et al. 2009)
MHOM/TN/2005/PLV36MO	Tunisia	Kairouan	MON-80	VL	(Chargui et al. 2009)

MHOM/TN/2005/PLV26	Tunisia	Kairouan	MON-24	VL	(Chargui et al. 2009)
MHOM/TN/2005/PLV13	Tunisia	Kairouan	MON-24	VL	(Chargui et al. 2009)
MCAN/UZ/2007/LRC-L1307	Uzbekistan	Namangan	nd	CanL	This study
MCAN/UZ/2007/LRC-L1310	Uzbekistan	Namangan	nd	CanL	This study
MCAN/UZ/2007/LRC-L1308	Uzbekistan	Namangan	nd	CanL	This study
MCAN/UZ/2007/LRC-L1309	Uzbekistan	Namangan	nd	CanL	This study
MCAN/UZ/2007/LRC-L1313	Uzbekistan	Namangan	nd	CanL	This study
MCAN/UZ/2007/LRC-L1311	Uzbekistan	Namangan	nd	CanL	This study
MCAN/UZ/2007/LRC-L1312	Uzbekistan	Namangan	nd	CanL	This study
MCAN/UZ/2007/LRC-L1315	Uzbekistan	Namangan	nd	CanL	This study
MHOM/UZ/2007/MUA	Uzbekistan	Namangan	nd	VL	(Alam et al. 2009)
MHOM/UZ/2007/KOM	Uzbekistan	Namangan	nd	VL	(Alam et al. 2009)
MHOM/UZ/2007/ERD	Uzbekistan	Namangan	nd	VL	(Alam et al. 2009)
MHOM/UZ/2007/OBA	Uzbekistan	Namangan	nd	VL	(Alam et al. 2009)
MHOM/UZ/2007/KU	Uzbekistan	Namangan	nd	VL	(Alam et al. 2009)
MHOM/UZ/2007/KOM2	Uzbekistan	Namangan	nd	VL relapse	(Alam et al. 2009)
MHOM/CN/1978/D2	China	nd	nd	VL	(Kuhls et al. 2007)
MHOM/CN/1954/Peking	China	nd	nd	VL	(Kuhls et al. 2007)
MHOM/CN/1980/StrainA	China	nd	MON-34	nd	(Kuhls et al. 2007)
MHOM/IN/1980/DD8[T]	India	nd	MON-2	VL	(Kuhls et al. 2007)
MHOM/IN/0000/DEVI	India	Bihar	MON-2	VL	(Kuhls et al. 2007)
MHOM/IN/1996/THAK35	India	Bihar	MON-2	nd	(Kuhls et al. 2007)
MHOM/IN/2001/BHU20140	India	Bihar	nd	VL	(Kuhls et al. 2007)
MHOM/IN/2002/BHU6	India	Bihar	nd	VL	(Kuhls et al. 2007)
MHOM/KE/1983/NLB 189	Kenya	nd	MON-37	PKDL	(Kuhls et al. 2007)
MHOM/KE/1984/NLB 218	Kenya	nd	nd	PKDL	(Kuhls et al. 2007)
MHOM/KE/1985/NLB 323	Kenya	nd	MON-37	VL	(Kuhls et al. 2007)
MHOM/KE/1955/LRC-L53	Kenya	nd	nd	nd	(Kuhls et al. 2007)
MHOM/KE/0000/LRC-L445	Kenya	nd	nd	nd	(Kuhls et al. 2007)
MHOM/ET/1967/HU3	Ethiopia	nd	MON-18	VL	(Kuhls et al. 2007)
MHOM/SD/1962/LRC-L61	Sudan	nd	MON-82	nd	(Kuhls et al. 2007)
MHOM/SD/1968/1 S	Sudan	nd	nd	VL	(Kuhls et al. 2007)
MHOM/SD/1992/51-band	Sudan	Gedaref	MON-30	VL	(Kuhls et al. 2007)
MHOM/SD/1993/AEB	Sudan	Gedaref	MON-82	VL	(Kuhls et al. 2007)
MHOM/SD/1993/GE	Sudan	Gedaref	MON-82	VL	(Kuhls et al. 2007)
MHOM/SD/1997/LEM3429	Sudan	Gedaref	MON-257	VL	(Kuhls et al. 2007)
MCAN/SD/0000/LEM3946	Sudan	Gedaref	MON-274	VL	(Kuhls et al. 2007)
MHOM/SD/1997/LEM3463	Sudan	Gedaref	MON-258	VL	(Kuhls et al. 2007)
MHOM/ET/0000/HUSSEN	Ethiopia	nd	MON-31	VL	(Kuhls et al. 2007)

[T] – Microsatellite profiles are available on request (GS). Microsatellite data were obtained at all loci and for all strains, null alleles were not encountered. Most of the microsatellite genotypes had been the subject of previous publications and collaborations. The allelic diversity of the different loci is described in the different references given. Reference strain of the species; 1 – zymodemes according to the Montpellier system – MON- (Rioux et al. 1990) or the CLIOC system – IOC/Z (Cupolillo et al. 1994), MON-1 and Z1 are corresponding zymodemes; - VL –

visceral leishmaniasis; CL – cutaneous leishmaniasis; PKDL – post Kala-Azar dermal leishmaniasis; CanL – canine leishmaniasis; cIL – central Israel, nIL – north Israel; nd – not defined.

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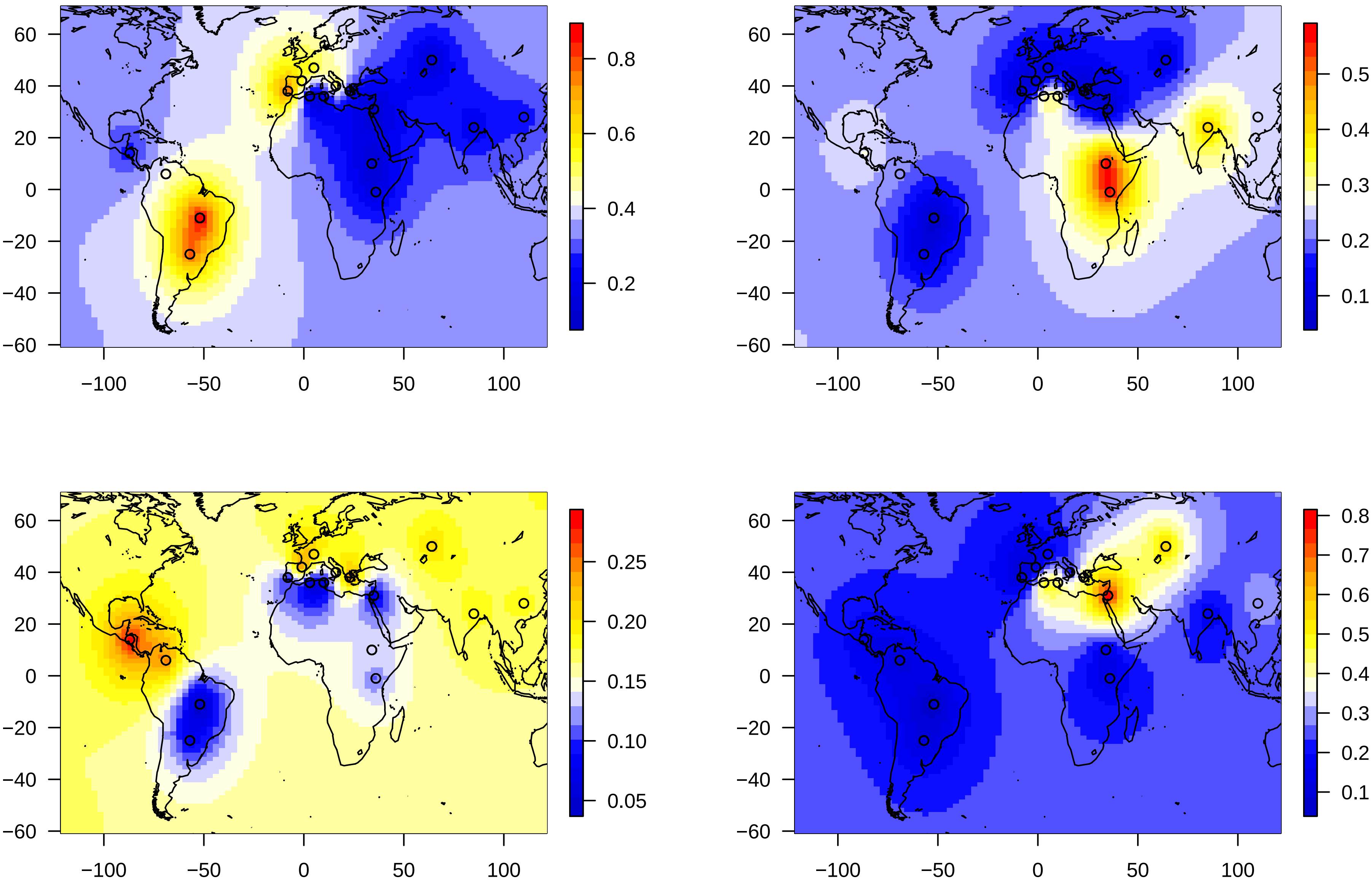
Supporting Figure legends:

Supplementary Figure 1: Inference of individual admixture proportions using *K* = 4 genetic clusters. Each map displays the admixture proportions inferred by the program for the 4 genetic clusters. The map for the first cluster is similar to the map of PC1, and supports a shared ancestry of western European and southern American samples.

Supplementary Figure 2: Maps of GENELAND individual assignments to clusters for *K* = 2 for a total of 17 populations of strains belonging to the *L. donovani* complex, this analysis clearly supports the "out of Portugal scenario" to the New world. The *L. donovani* populations are underlined. The highest membership values are in light yellow and the level curves illustrate the spatial changes in assignment values.



60
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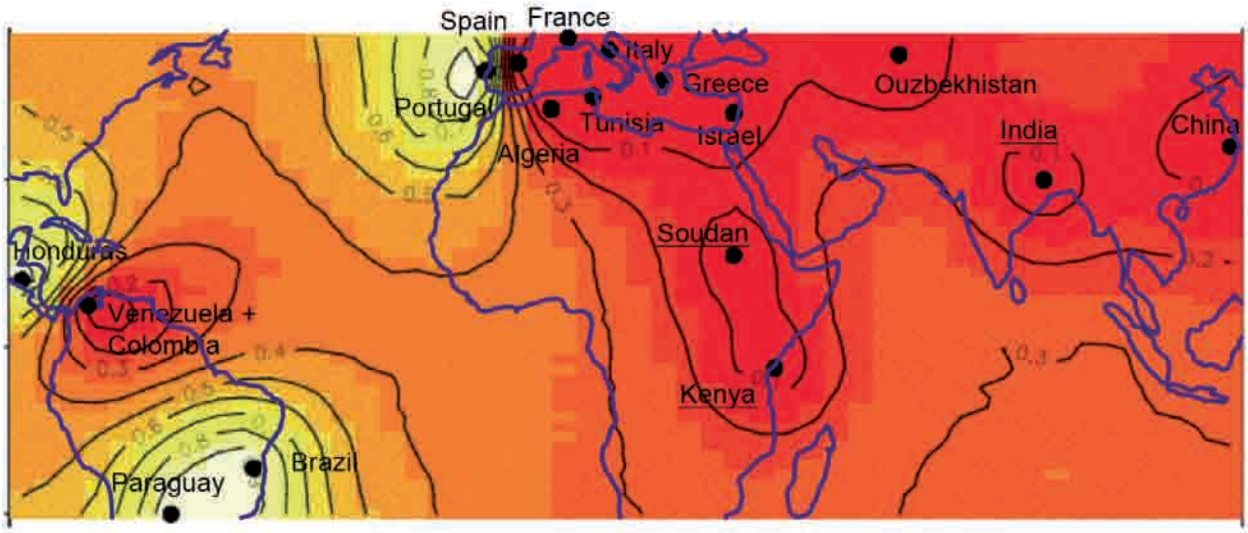
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