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Research paper

Host switching of human lice to new world monkeys in South America

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ABSTRACT

The coevolution between a host and its obligate parasite is exemplified in the sucking lice that infest primates. In the context of close lice–host partnerships and cospeciation, *Pediculus mjobergi*, the louse of New World primates, has long been puzzling because its morphology resembles that of human lice. To investigate the possibility that *P. mjobergi* was transmitted to monkeys from the first humans who set foot on the American continent thousands of years ago, we obtained and compared *P. mjobergi* lice collected from howler monkeys from Argentina to human lice gathered from a remote and isolated village in Amazonia that has escaped globalization.
Morphological examinations were first conducted and verified the similarity between the monkey and human lice. The molecular characterization of several nuclear and mitochondrial genetic markers in the two types of lice revealed that one of the *P. mjobergi* specimens had a unique haplotype that clustered with the haplotypes of Amazonian head lice that are prevalent in tropical regions in the Americas, a natural habitat of New World monkeys. Because this phylogenetic group forms a separate branch within the clade of lice from humans that were of American origin, this finding indicates that human lice have transferred to New World monkeys.

1. Introduction

A close host–parasite association fact that they may speciate in parallel. This phenomenon is called cospeciation and is well exemplified in lice (Insecta: Phthiraptera). Indeed, lice are obligate ectoparasites of birds and mammals, and the partnership with their hosts has existed for over 65 million years (Barker, 1991, 1994; Hafner and Page, 1995; Smith et al., 2011).

Humans can be infested by two types of sucking lice (Anoplura), *Pediculus humanus* and *Phthirus pubis*, the crab louse (Durden, 2001). *P. h. capitis* (head louse) and *P. h. humanus* (body louse) are ecotypes that have spread worldwide as modern humans have moved out of Africa over the past 100,000 years (Ascunce et al., 2013b).

The molecular analysis of the mitochondrial (mt) genes cytochrome oxidase subunit 1 (*cox1*) and cytochrome b (*cytb*) has allowed for their classification into three haplogroups, which are designated A, B and C (Reed et al., 2004). Of these groups, only haplogroup A is distributed worldwide and comprises both head and body lice (Reed et al., 2007; Xiong et al., 2014b). Haplogroup B consists of head lice found in the Americas, Western Europe, Australia and North Africa (Boutellis et al., 2014). Haplogroup C consists of head lice found in Nepal, Thailand, Ethiopia and Senegal (Light et al., 2008b; Sunantaraporn et al., 2015; Veracx et al., 2013; Xiong et al., 2014a, 2014b). Recently, a fourth mitochondrial haplogroup baptized haplogroup D, has been identified in the Democratic Republic of the Congo. Interestingly, as for haplogroup A, haplogroup D includes both head and body lice (Drali et al., 2015). In addition to the inter-haplogroup diversity, human lice also demonstrate intra-haplogroup diversity, which is illustrated by many distinct A and B haplotypes (Ascunce et al., 2013a; Leo et al., 2002; Light et al., 2008a). The molecular analysis of lice collected from Pre-Columbian mummies shows that haplogroups A and B were already present in the New World before the arrival of European settlers (Boutellis et al., 2013a; Raoult et al., 2008).

This finding supports an American origin for haplogroup B, followed by a dispersal into the Old World by European colonists returning to Europe (Boutellis et al., 2014).

So far, the body louse is the only known louse that can transmit at least three deleterious diseases which have killed millions of people, namely epidemic typhus, trench fever and relapsing fever caused by *Rickettsia prowazekii*, *Bartonella quintana*, and *Borrelia recurrentis* respectively (Raoult and Roux, 1999). It is also suspected in the transmission of a fourth lethal pathogen, *Yersinia pestis*, the agent of the plague (Blanc and Baltazard, 1941; Drali et al., 2015; Houhamdi et al., 2006; Piarroux et al., 2013).

In recent years, the DNA of *B. quintana* was found in head lice belonging to haplogroup A (Bonilla et al., 2009; Boutellis et al., 2012; Piarroux et al., 2013; Sangare et al., 2014), haplogroup C (Angelakis et al., 2011; Sasaki et al., 2006) and haplogroup D (Drali et al., 2015). DNA of *B. recurrentis* was found in head lice belonging to haplogroup C

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(Boutellis et al., 2013b), whereas DNA of *Y. pestis* was found in head lice belonging to haplogroup D (Drali et al., 2015).

Interestingly, humans are not the only species in the Americas that harbor lice of the genus *Pediculus*. In 1916, Ferris reported that New World monkeys harbored a sucking louse of the Pediculidae family, suborder Anoplura (Ferris, 1916). The first description of this louse was reported in 1910 by Mjoberg, who named it *Pediculus affinis* (Durden and Musser, 1994). Ferris suggested replacing the name *affinis* with *mjobergi* (Ferris, 1951). *Pediculus mjobergi* has been found in 11 species, 5 genera and three of the five families of monkeys in the New World: in howler and spider monkeys that belong to the family Atelidae with *Alouatta bekebel* (Linnaeus), *Alouatta caraya* (Humboldt), *Alouatta palliata* (Gray), *Alouatta pigra* Lawrence, *Ateles bekebufh* E. Geoffroy, *Ateles fusciceps* Gray and *Ateles geoffroyi* Kuhl; in capuchin monkeys that belong to the family Cebidae with *Cebus apella* (Linnaeus) and *Cebus capucinus* (Linnaeus); in titi monkeys that belong to the family Pitheciidae with *Cacajao calvus* (I. Geoffroy) and *Pithecia monachus* (E. Geoffroy), (Durden and Musser, 1994; Finstermeier et al., 2013; Price and Graham, 1997).

To investigate the relationship between *P. humanus* and *P. mjobergi* lice, we obtained and compared *P. mjobergi* lice with lice recovered from a remote and isolated village in Amazonia that has escaped globalization.

2. Materials and methods

2.1. Ethics statement

The lice (*P. mjobergi*) from *Alouatta* were a gift from Drs Cicchino Armando and Alberto Abrhamamovich from the Louse Collection of the Museo de La Plata, Buenos Aires Province. The Amazonian human head lice were removed from hair, with the verbal consent of the infested individuals because most of the subjects were illiterate. However, in most instances, local authorities approved and were present when the collecting of lice was performed.

The human lice collected in France were obtained from homeless individuals during a registered epidemiological study (French Bioethics laws n° 2011-814). Informed consent was obtained from these subjects, and the study was approved on January 12, 2011 (ID RCB: 2010-A01406-33).

2.2. Louse samples

In 1993, six adult specimens of *P. mjobergi* were collected from two wild howler monkeys, *A. caraya*, located in northeast Argentina. The first four lice were collected from monkey #B2188 (Barker collection) from the National Park Iguazu, Province of Misiones. The other two lice were found on monkey #B1395 (Barker collection) from the Province of Corientes (Fig. 1A).

For the human lice in the Americas, 19 Amazonian human head lice were included in this study. We recovered these specimens in 2013 from members of the Wayapi community (Woerther et al., 2010) living in "Trois-Sauts", a remote and isolated village on the Oyapock River along the border between French Guyana and Brazil (Fig. 1A).

Collected monkey and human lice studied in this work were stored in 70% alcohol before being transferred in our laboratory following local ethical and legal regulations.

Human head and body lice collected in France were included as positive controls.

Lice were photographed on their dorsal and ventral sides using a fixed camera (Olympus DP71, Rungis, France). The morphological identification of our *P. mjobergi* specimen was done according to Ferris (1951).

2.3. DNA samples

Genomic DNA was extracted using the QIAamp DNA tissue extraction kit (Qiagen, Hilden, Germany) in an EZ1 apparatus following the manufacturer's instructions. DNA from each louse was eluted in 100 μl of TE buffer and stored at −20 °C.

2.4. PCR amplifications

Seven genes, three nuclear genes [18S rRNA, glycerol-3-phosphate dehydrogenase (GPD) and RNA polymerase II largest subunit (RPII)] and four mtDNA [(*cytb*), cytochrome oxidase subunit 1 (*cox1*), 16S ribosomal RNA, and NADH dehydrogenase subunit 2 (*nad2*)] were investigated. We also targeted intergenic regions using two highly polymorphic intergenic spacers (PM1 and PM2) as previously described (Li et al., 2010).

PCR amplifications were conducted in a Peltier PTC-200 model thermal cycler (MJ Research Inc., Watertown, MA, USA). PCR reactions were prepared on ice and contained 3 μl of DNA template, 4 μl of Phusion HF Buffer, 250 μM of each nucleotide, 0.5 μM of each primer, 0.2 μl of high fidelity Phusion DNA Polymerase (Finnzymes, Thermo Scientific, Vantaa, Finland) and water to a final reaction mixture volume of 20 μl. The cycling conditions were 98 °C for 30 s; 35 cycles of 5 s at 98 °C, 30 s at Tm (SI Appendix A), 15 s at 72 °C; and a final extension time of 5 min at 72 °C. PCR positive and negative controls were included in each assay. The success of PCR amplification was then verified by electrophoresis of the PCR product on a 1.5% agarose gels. All primers used for these experiments are described in SI Appendix A.

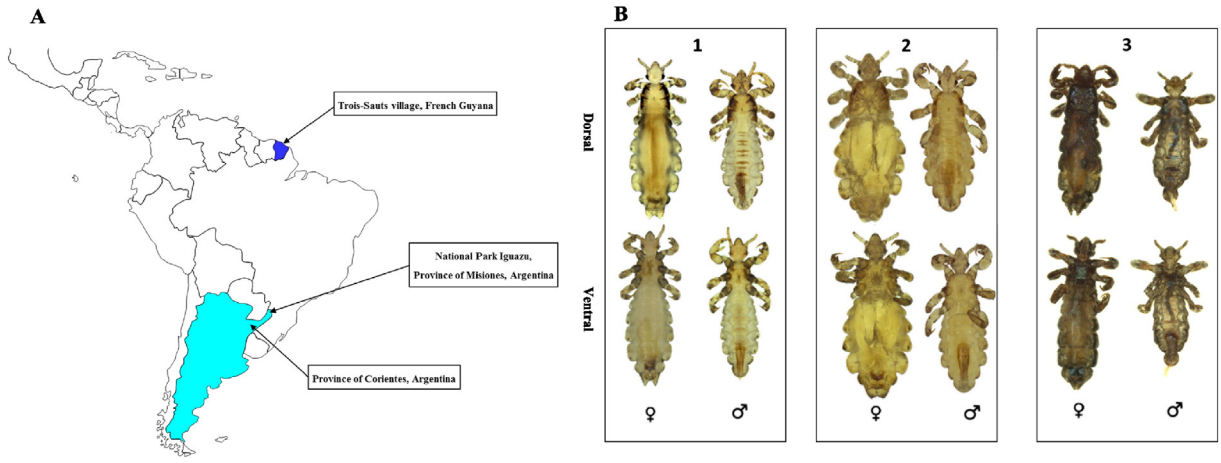

Fig. 1. Morphological ventro-dorsal comparisons show that *P. mjobergi* lice highly resemble human lice. A: Geographical localization of louse sampling. B: (1) Human head lice from USA; (2) *P. mjobergi* (Barker collection) from Argentina; (3) human head lice from Amazonia. ♀ female; ♂ male.

Table 1
Characterization of genetic markers in *P. mjobergi* monkey lice reveals novel sequences.

Targets		Monkey lice					
		#1	#2	#3	#4	#5	#6
Nuclear genes	18S rRNA			II[a]	I[a]		
	GPD				I[a]		
	RPII				I[a]		
Mitochondrial genes	*cytb*	II	II	II	I[a]	II	II
	cox1				I[a]		
	16S rRNA				I[a]		
	nad2				I[a]		
Microsatellites	PM1			II	I		
	PM2				I		

Lice #1–4 were collected from monkey individual B2188. Lice #5 and 6 were collected from monkey individual B1395.
[a] Novel sequence.

2.5. Sequencing

NucleoFast 96 PCR Plates (Macherey-Nagel EURL, France) were used to purify the PCR products before sequencing. The purified PCR products were then sequenced in both directions (with the PCR primers) using a BigDye Terminator version 1.1 cycle sequencing-ready reaction mix (Applied Biosystems, Foster City, CA) and an ABI 3100 automated sequencer (Applied Biosystems). The program Chromas Pro software (Technelysium PTY, Australia) was used to analyze, assemble and correct the sequences.

The sequences obtained in this study and those representing the haplotypes determined from the set of used sequences have been deposited in GenBank (KM579408–KM579584).

For each of the target genes, the nucleotide sequences obtained in this study were aligned with the sequences available in public databases (GenBank) using MUSCLE (Edgar, 2004) and corrected manually. Each gene was analyzed with three methods: maximum-likelihood (ML), NJ and parsimony. NJ analyses were performed with MEGA6 (Tamura et al., 2013) using the Maximum Composite Likelihood method with 200 bootstrap replicates. PAUP*4.0b10 (Swofford, 2001) and the tree bisection-reconnection branch swapping algorithm were used for parsimony analyses with 500 bootstrap replicates and heuristic search. ML analyses were performed with RAXML8 (Stamatakis, 2014) under the GTR + G + I model with 500 bootstrap replicates (rapid bootstrapping (Stamatakis et al., 2008).

To determine the phylogeographic relationships among the lice, median-joining networks were assembled for the louse haplotypes of two mitochondrial markers, *cytb* and *cox1*, using the method of Bandelt with the program Network version 4.6.1.1 (Bandelt et al., 1999). The sequence between nucleotide positions 370–642 of *cytb* and 748–1026 of *cox1* was determined for all the specimens. Partial gene sequences were aligned with the sequences available in GenBank. The percent similarities were determined using MEGA6 (Tamura et al., 2013).

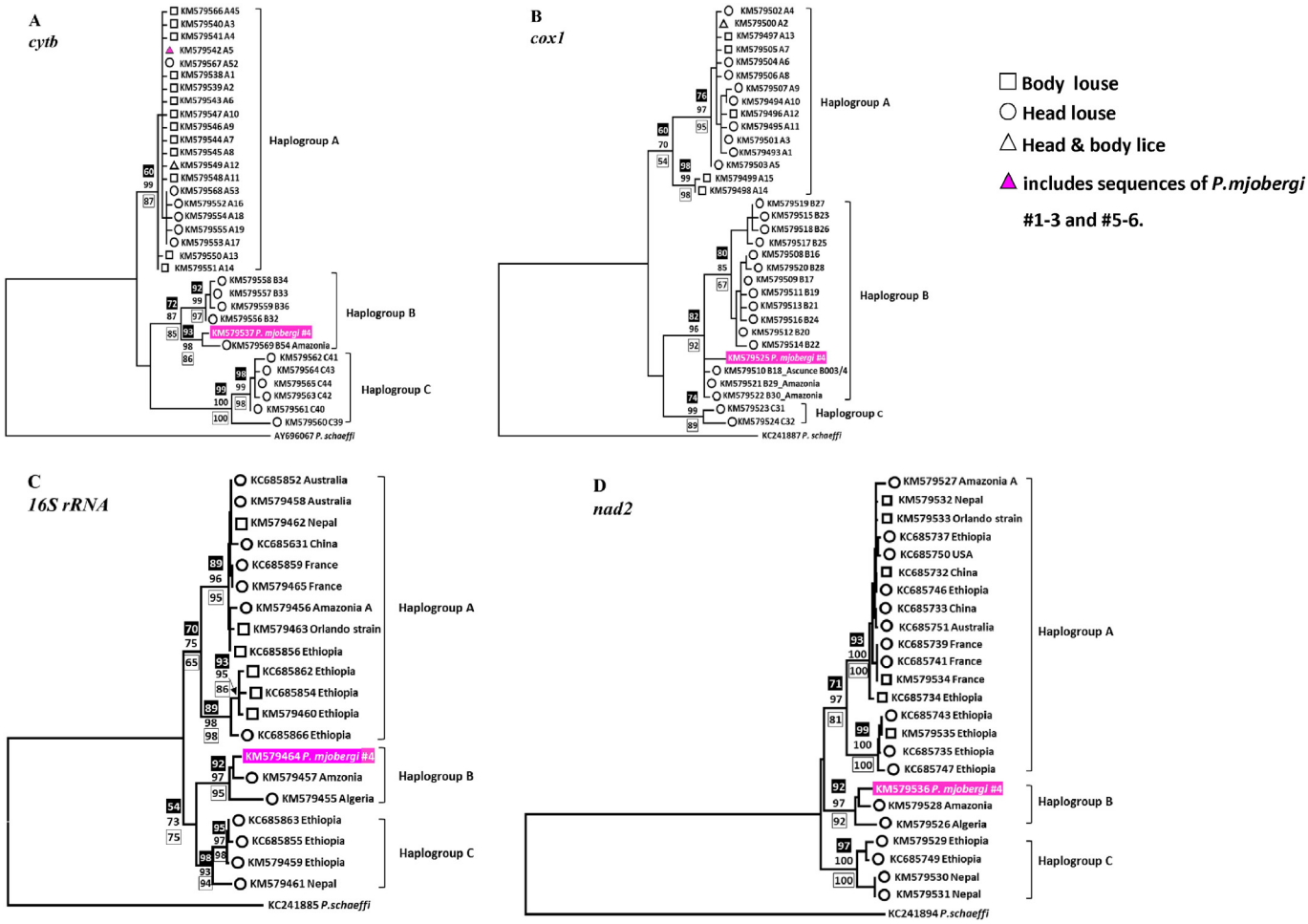

Fig. 2. *P. mjobergi* sequences are highly related to sequences obtained from human lice. Maximum-likelihood (ML), neighbor-joining (NJ) and parsimony analyses of mt gene sequences: *cytb*, *cox1*, *16S rRNA* and *nad2*. The NJ tree topology is used for the display and bootstrap support values are given for the main groups when support ≥50 with the three methods (from top to bottom: ML, NJ, and parsimony). mt clade memberships are indicated to the right of each tree.

Ancestral sequences were reconstructed for each node of the *cytb* phylogenetic tree using the marginal reconstruction approach with BASEML of the PAML4 software package (Yang, 2007).

3. Results

3.1. P. mjobergi specimens highly resemble human lice

A comparison between the six adult *P. mjobergi* specimens from two wild howler monkeys and 19 Amazonian human head lice showed that the *P. mjobergi* specimens are morphologically similar to human lice (Fig. 1B). In particular, *P. mjobergi* have the same gray color as the contemporary head lice recovered in the USA and were not the darker color of the Amazonian head lice (Fig. 1B).

3.2. P. mjobergi mtDNA sequences belong to the mtDNA clades of human lice

To determine whether the morphological similarities between the *P. mjobergi* specimens and human lice are the result of convergent evolution or a recent common ancestor, we evaluated four mtDNA markers (*cytb*, *cox1*, *16S rRNA*, and *nad2*). Although each marker was targeted for amplification from each of the six *P. mjobergi* specimens, only one marker was amplified from all six individuals (*cytb*), and the remaining three markers (*cox1*, *16S rRNA*, and *nad2*) were only amplified from *P. mjobergi* individual #4 (Table 1). Because the positive and negative PCR amplification controls worked well in all of the amplification experiments, this finding suggests that for *P. mjobergi* individuals #1–3 and #5–6, either the DNA extracted was not of sufficient quality or the targeted genes had a sequence at the primer sites that was too divergent.

The targets that could be amplified by PCR were sequenced, and the sequences generated were aligned with the publicly available sequences. The *P. mjobergi* sequences obtained were highly similar to the sequences obtained from human lice. To investigate their precise relationship, we performed phylogenetic analyses. Maximum-likelihood (ML), neighbor-joining (NJ) and parsimony phylogenetic analyses were performed for each of the four mtDNA genes and showed that, in all four analyses, the human and *P. mjobergi* sequences split into three well-supported haplogroups that corresponded to haplogroups A, B and C (Fig. 2). In all four analyses, the sequences of the monkey louse *P. mjobergi* #4 clustered with the Amazonian head lice in haplogroup B. Similarly, the analysis of the *cytb* gene revealed that the remaining monkey lice (*P. mjobergi* #1–3 and #5–6) have the widespread haplotype A5 of haplogroup A (Fig. 2A).

To investigate the geographical distribution of the haplotypes more precisely, we assembled a dataset of 707 *cytb* sequences of body and head lice (424 from GenBank and 283 from our laboratory) (SI Appendix B). These 707 sequences span 36 worldwide geographic locations on five continents and represent 32 distinct haplotypes, 21 from haplogroup A (66%), five from haplogroup B (16%) and six from haplogroup C (SI Appendix B). While *P. mjobergi* #1–3 and #5–6 have haplotype A5, which is common worldwide (80% of locations and 49% of the 707 analyzed human lice), the *P. mjobergi* #4 haplotype is closely

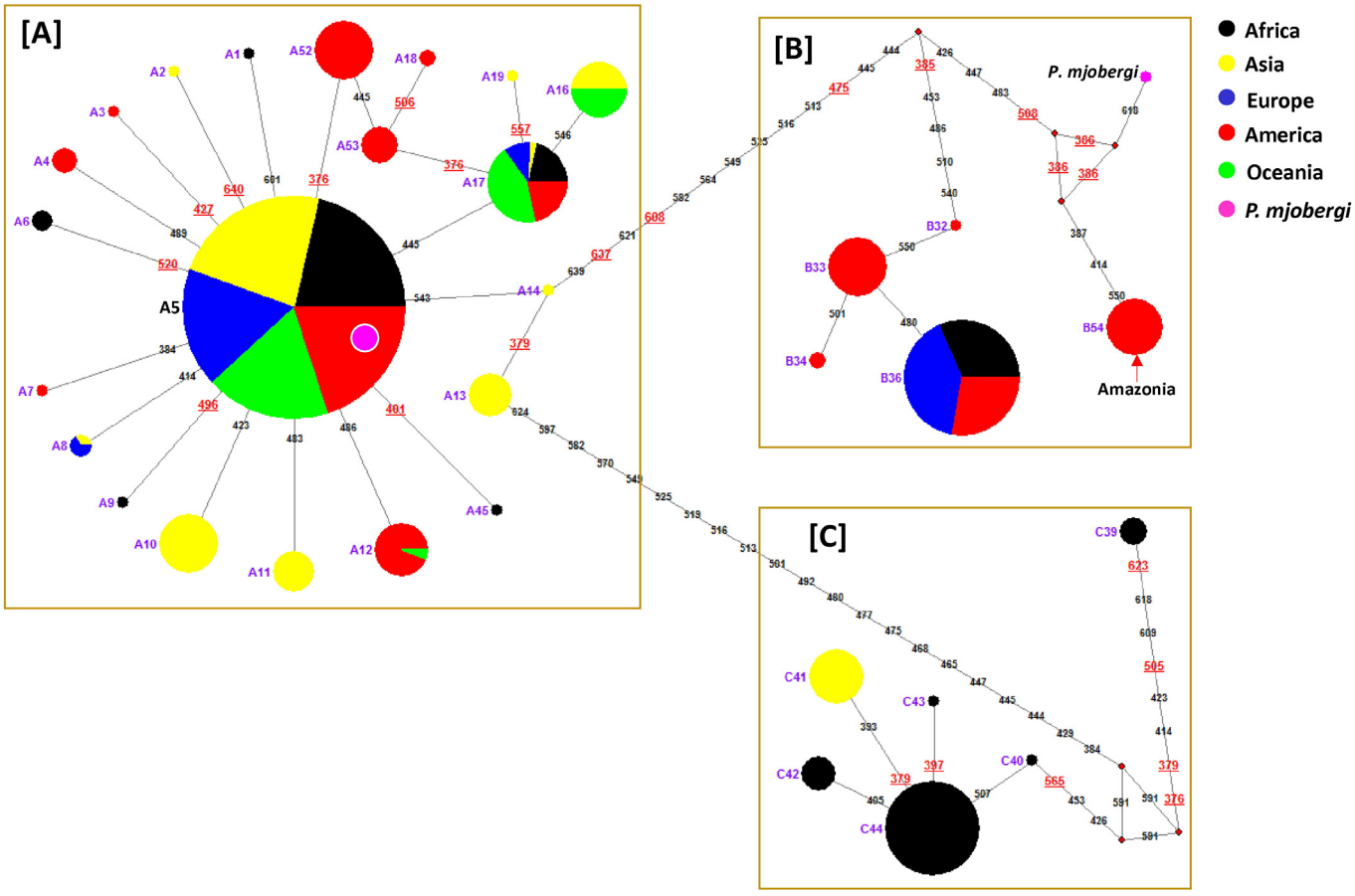

Fig. 3. *P. mjobergi* shows a novel haplotype that belongs in a group with Amazonian head lice. Statistical parsimony network for the *cytb* gene haplotypes found in haplogroup A, haplogroup B and haplogroup C. *P. mjobergi* #1–3 and 5–6 that belong to the haplotype A5 are included in the portion representing American lice. They are indicated with purple circle. Each connecting branch represents a single mutational step. Sizes are scaled and represent relative frequencies. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

related to haplotype B54 (Fig. 3), which is unique to Amazonian head lice; these two haplotypes only differ in five nucleotides that result in only a single amino acid difference (Lys129Ile) (SI Appendix C).

We performed a similar analysis for the *cox1* gene. Even though the sequences included in this analysis were primarily collected from across the America (Ascunce et al., 2013a), we were also able to include 79 sequences from head and body lice from other parts of the world as well as the 33 lice sequences obtained in this study (SI Appendix D). The 562 sequences collected represent 37 haplotypes, fifteen from haplogroup A, fifteen from haplogroup B and two from haplogroup C. As for *cytb*, *P. mjobergi* #4 has a unique haplotype that is part of a subgroup of haplogroup B that contains haplotype B18 from Argentina and Mexico and haplotypes B29–B30 from Amazonia (Fig. 4).

The results of this analysis indicate that the *P. mjobergi* mtDNA sequences belong to the mtDNA clades of human lice. In particular, specimen *P. mjobergi* #4 had, for all four markers, sequences belonging to the B haplogroup, a haplogroup that most likely originated in the Americas (Boutellis et al., 2014). Therefore, in addition to the morphological similarities, *P. mjobergi* lice and human lice also share highly related mtDNA genomes, which suggests that their morphological similarities are not the result of convergent evolution but are the result of their close genetic relationship.

3.3. *P. mjobergi* nuclear sequences are closely related to the sequences of human lice

To further investigate whether *P. mjobergi* and human lice are closely related, we extended our analysis to include nuclear markers, three genes and two intergenic spacers (Table 1). All three nuclear genes were amplified from *P. mjobergi* #4 as well as one gene from *P. mjobergi* individual #3 (18S rRNA), but no PCR product was obtained for specimens #1–2 and #5–6 (Table 1). A comparison of the sequences obtained in these amplifications with publicly available human louse sequences showed that the *P. mjobergi* sequences are highly related to the human louse sequences but are unique sequences in all cases. In particular, the 18S rRNA sequences from *P. mjobergi* individual #3 and *P. mjobergi* #4 are both unique (SI Appendix E (1)).

The intergenic spacers PM1 and PM2 could be amplified from *P. mjobergi* #4, and PM1 was also amplified from *P. mjobergi* #3 (Table 1). Both spacers were also amplified from the 19 Amazonian head lice included in this study (see Section 2). For PM1, 15 of the 19 Amazonian head lice shared genotype 13 (G13) with human lice from Africa and Europe belonging to a group that also includes *P. mjobergi* #3 (Fig. 5A). The *P. mjobergi* #4 PM1 sequence, however, belongs to genotype 21 (G21), which was previously characterized in Mexico. The remaining Amazonian head lice belong to either genotype 36 (G36), which was already characterized in Amazonia, or a new genotype that is highly related to G36 (Fig. 5A). For the PM2 marker, *P. mjobergi* #4 and Amazonian head lice share genotype 47 (G47) with human lice from Africa, Oceania and America (Fig. 5B).

This analysis of nuclear markers supports the results from the mtDNA analysis and shows that the *P. mjobergi* specimens are closely related to human lice.

4. Discussion

In this study, we report for the first time, to our knowledge, molecular data for *P. mjobergi*, which is known as the louse of New World monkeys. The six individual lice analyzed were morphologically similar to *P. humanus*, the human lice (Fig. 1B). This observation supports two previous descriptions reported in 1938 and 1983 (Ewing, 1938; Maunder, 1983).

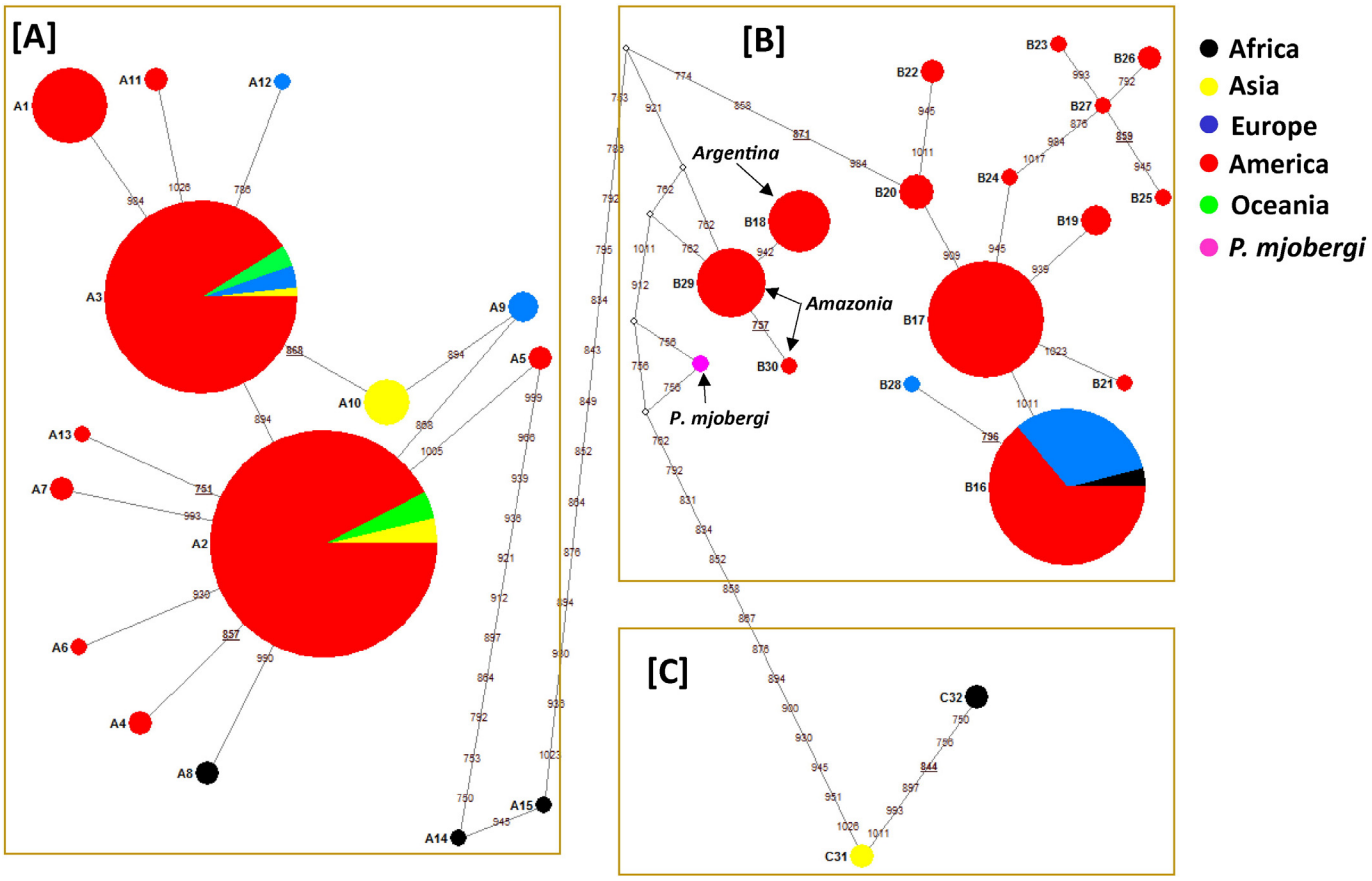

Fig. 4. *P. mjobergi* shows a novel haplotype that belongs in a group with head lice that are prevalent in tropical areas in the Americas. Statistical parsimony network for the *cox1* gene haplotypes found in haplogroup A, haplogroup B and haplogroup C. Each connecting branch represents a single mutational step. Sizes are scaled and represent relative frequencies.

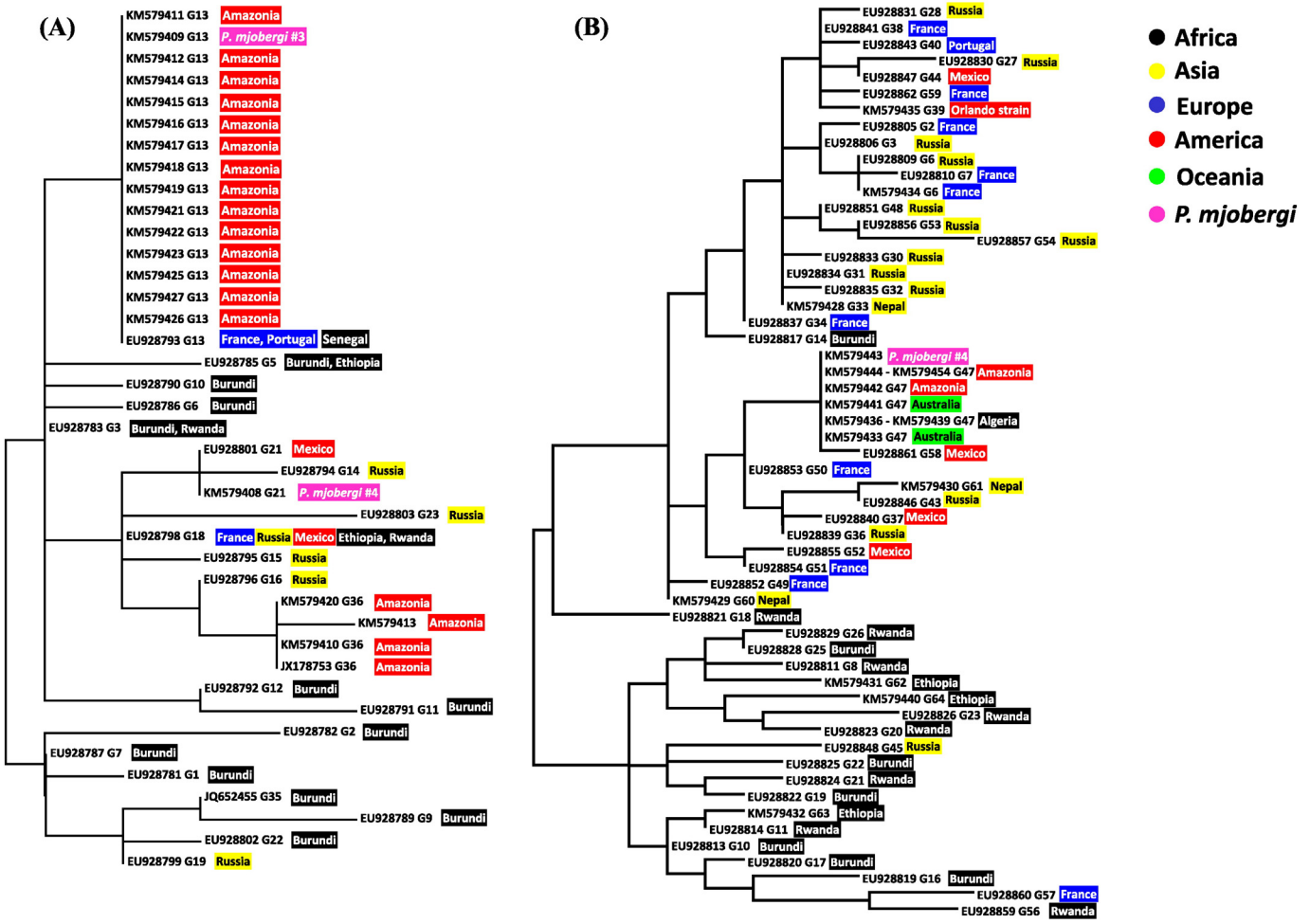

Fig. 5. Analyses of the nuclear intergenic spacers show that the *P. mjobergi* specimens are closely related to human lice. Maximum-likelihood phylogenetic analyses of the sequences of two nuclear intergenic spacers (PM1, panel A; PM2, panel B) of human and *P. mjobergi* lice.

The mtDNA analysis revealed that the New World monkey lice analyzed in this study have *cytb* haplogroup A and B haplotypes, whereas the Amazonian head lice only have haplogroup B haplotypes. Interestingly, while five *P. mjobergi* had a haplogroup A haplotype (A5) that is prevalent (49% of analyzed human lice) and well distributed (80% of locations), *P. mjobergi* #4 had a novel haplogroup B haplotype. This novel haplotype belongs in a group with Amazonian head lice (Fig. 3) that are prevalent in tropical areas in the Americas (Mexico, Amazonia and northeast Argentina), a natural habitat of New World monkeys.

Furthermore, the results obtained here showed that in one of the two howler monkeys (host individual B2188), two different genetic lineages of lice (one lineage from haplogroup A and the other lineage from haplogroup B) were characterized. This result reinforced the hypothesis that the lice recovered from this monkey were possibly the product of at least one host switch from humans. The presence of different genetic lineages of human lice in the same individual was already reported in the literature, this is the case for haplogroups A and B (Boutellis et al., 2013a, 2015; Xiong et al., 2014a), for haplogroups A and C (Veracx et al., 2013; Xiong et al., 2014a) and also for haplogroups A and D (Drali et al., 2015).

Because of the genetic and geographic proximity of the lice evaluated in this study, this finding suggests that an exchange of genetic material has taken place between human lice and New World monkey lice during their casual encounters. Consistent with this model, contact between monkeys and humans has never been interrupted in South America. For example, when monkeys are not hunted for their meat, they can become pets (Horwich, 1998).

In blood sucking insects, including mosquitoes, host preference demonstrates a high degree of flexibility when the favorite host species becomes scarce or is not accessible (Takken and Verhulst, 2013). Under these conditions, physiological factors (hunger) and the physical abundance of available new hosts may contribute to host switching (Takken and Verhulst, 2013). Similarly, geographical proximity is a factor as, among closely related mammals, louse–host cospeciation primarily results from allopatry (Mayr, 1942, 1963).

Conversely, the sympatric life of related hosts can result in an exchange, a host switching that we show here has occurred with human lice transmitted to monkeys. That two different mitochondrial genotypes (Clade A and Clade B) are prevalent in *P. mjobergi* is also consistent with the *P. humanus–P. mjobergi* shift having occurred at least twice.

5. Conclusion

We can conclude that these host switching events are thus exceptions to the strict louse–host coevolution paradigm and can lead to recombination between divergent types of lice, which in turn would contribute to hiding a pattern of strict codivergence.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.meegid.2016.02.008.

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