

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.

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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 (Ascunze 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 (Ascunze 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, sub-order 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 Abrahamovich 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 Corrientes (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.

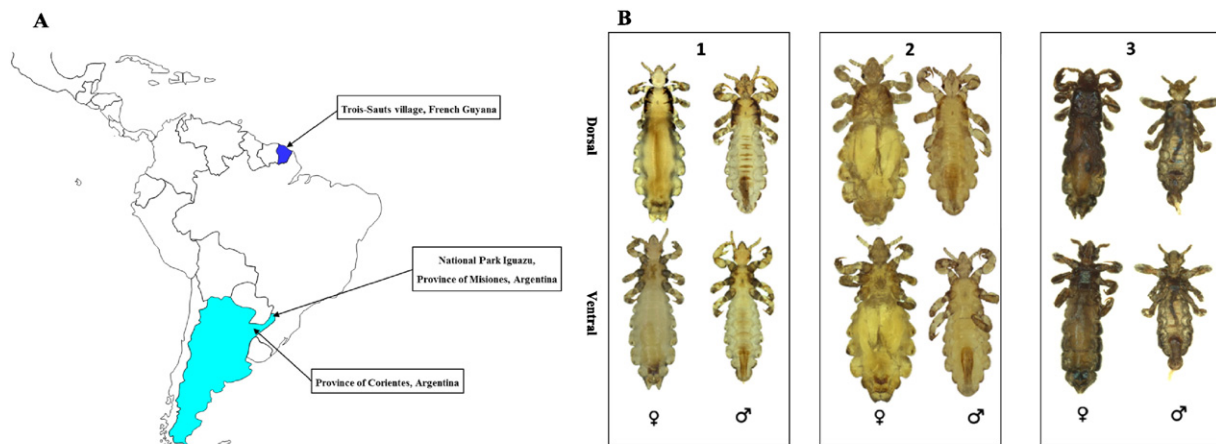


Fig. 1. Morphological ventro-dorsal comparisons show that *P. mjobergi* lice highly resemble human lice. A: Geographical localization of louse sampling. B: (1) Human head lice from USA; (2) *P. mjobergi* (Barker collection) from Argentina; (3) human head lice from Amazonia. ♀ female; ♂ male.

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