Review

Biology and genetics of human head and body lice

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Head lice and body lice have distinct ecologies and differ slightly in morphology and biology, questioning their taxonomic status. Over the past 10 years many genetic studies have been undertaken. Controversial data suggest that not only body lice but also head lice can serve as vectors of *Bartonella quintana*, and a better understanding of louse epidemiology is crucial. Here, we review taxonomic studies based on biology and genetics, including genomic data on lice, lice endosymbionts, and louse-transmitted bacteria. We recommend that studies of human lice employ morphological and biological characteristics in conjunction with transcriptomic date because lice seem to differ mainly in gene expression (and not in gene content), leading to different phenotypes.

Human lice, an appropriate model of coevolution

Human lice

The order of Phthiraptera (lice) is divided into two main groups: the sucking lice that comprise the Anoplura suborder and the chewing lice that comprise three other suborders: Amblycera, Ishnocera, and Rhynchophthirina (Figure 1) [1]. Lice are obligate ectoparasites, and each host species has its own type of louse [2]. Indeed, parasite speciation often occurs at approximately the same time as speciation of the host (cospeciation). The two genera of sucking lice that parasitize humans are Pthirus and Pediculus (Figure 1), which include two species of medical importance, *Pthirus pubis* (pubic louse) and *Pediculus humanus*. The latter is of great public health concern and consists of two ecotypes: head lice and body lice. Both ecotypes have the same life cycle, beginning with an egg stage of approximately 7 days, followed by three instars of approximately 3 days each before becoming adults that are capable of reproducing. Both lice need to take regular blood meals (approximately five times per day) on human skin to survive. However, they live in different ecological niches. Head lice live in human hair and are very commonly found among children. Due to bite reaction, they are responsible for a very intense pruritus that may lead to high irritation and even wound infection. Body lice live in clothes and are associated with a lack of clothing hygiene and cold weather. They are often found in jails and unstable countries but are also currently re-emerging among homeless populations in industrialized countries [3].

Bacteria found in lice and louse-transmitted diseases

Body lice are responsible for the transmission of at least three bacterial diseases (Figure 1). Of these, two belong to the α subgroup of Proteobacteria (*Rickettsia prowazekii* and *Bartonella quintana*) and one is a spirochete (*Borrelia recurrentis*). *R. prowazekii* is the etiologic agent of epidemic typhus, *B. recurrentis* causes louse-borne relapsing fever, and *B. quintana* causes trench fever [4]. Two other bacteria have been found in body lice, *Acinetobacter* spp. and *Serratia marcescens* [5], but it is not known if they can be transmitted to humans by lice biting. Head lice have not been considered vectors of human diseases. However, recently, they have also been found to be infected by *B. quintana* [6–9]. Nevertheless, their role in trench fever transmission remains undetermined. Head lice were also found to be infected with *Acinetobacter baumannii*, but the clinical significance of this finding is unknown [10]. Body lice and head lice harbor the same endosymbiotic microorganisms (*Candidatus* Riesia pediculicola) that seem to be essential for the production of nutritional components, such as B vitamins, that are lacking in host blood [11,12]. The primary endosymbiont and the bacterial pathogens harbored by body lice all possess genomes that are reduced in size compared to their free-living close relatives [13]. Thus, lice offer an appropriate model for understanding the coevolution of vectors, symbionts, and pathogens in a specific niche in allopatry [13].

Overview

We provide here the first exhaustive review of data on human head lice and body lice. First, we focus on relevant comparative studies on human head and body lice based on their morphology and biology before the advent of molecular biology tools. Second, we present information on the body louse genome, the genome of its symbiont, and some data on the genome of the pathogens transmitted by body lice. Finally, the main genetic studies on human lice performed during the past 10 years are reviewed and discussed, and some inferences are made regarding the evolution of human lice.

Human lice taxonomy before molecular biology

The morphology and biology of head and body lice, as reported over several decades, were used to assess their taxonomic status (Table 1).

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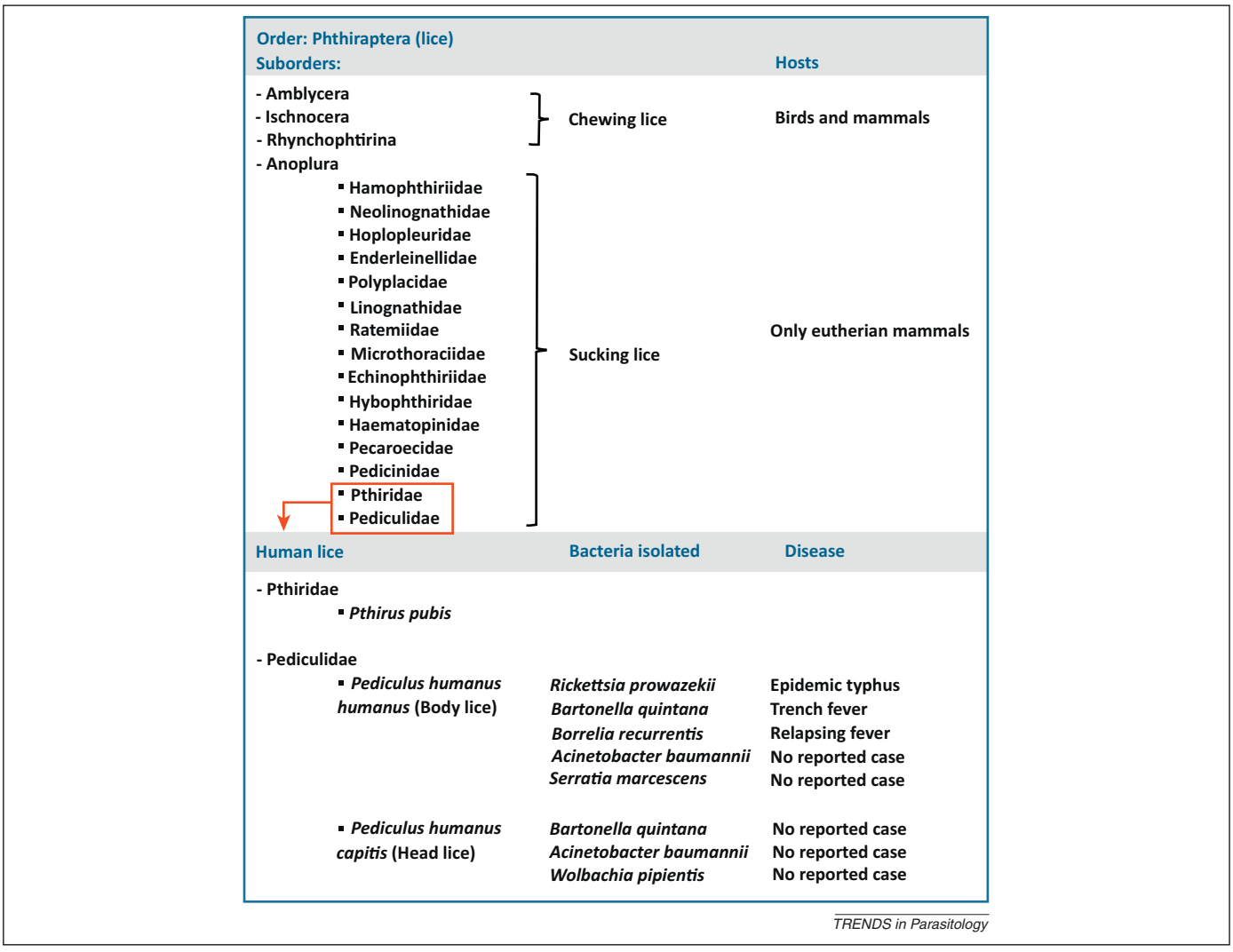

Figure 1. Classification of the *Phthiraptera*. List of the main suborders of chewing and sucking lice, the main families of sucking lice, and details on the two families of human lice and the diseases that they can transmit.

Early classification

The genus Pediculus was established by Linnaeus in 1758. This genus was applied to both head and body lice, which he termed *P. humanus* varieties 1 and 2 in 1767. In 1778, De Geer proposed naming these varieties *P. humanus capitis* and *P. humanus corporis*, without determining whether these varieties should be considered separate species [14].

One or two species debate: morphological characteristics

Generally, head lice are considered to be more heavily chitinized, smaller, darker, and with more pronounced lateral indentations between segments of the abdomen than body lice [15]. Body lice were shown to have a set of longitudinal muscles on the ventral body wall which is absent in head lice [16]. Another measure that distinguishes between the two ecotypes is the length of antennae, which are longer in body lice, possibly due their adaptation to darkness [17]. However, morphological characteristics were proved to be inconsistent, with the description of many intermediate forms [16,18]. Nevertheless, data from double infestations in Ethiopia support the distinction between the two species because, under conditions where interbreeding could theoretically occur, head lice and body lice possessed distinct and non-overlapping sizes [19].

One or two species debate: physiological characteristics

Head lice live in a different biotope (hair) than body lice (inner part of clothes) and this may have an impact upon physiological characteristics. In general, the two strains show very similar developmental rates, but pre-imaginal mortality of head lice is higher than for body lice [16]. Head lice are also more susceptible to starvation compared to body lice that are adapted to periodically being in clothes discarded by the host [16,17]. Head lice have a lower egg production than body lice, possibly due to their smaller size, and their eggs are also slightly smaller [20]. In addition, the percentage of hatched eggs is higher in body lice [16]. Moreover, head lice are more active at lower temperature, undoubtedly because they normally live on the exposed scalp where the temperature is lower than within clothes [17].

Table 1. Chronology of the main biology-based studies on the taxonomic status of human head and body lice

Date	Author	Main observations	Refs
1758	Linné	The genus Pediculus was established	
1767	Linné	Description of *Pediculus humanus* varieties 1 and 2	
1778	De Geer	Description of *Pediculus humanus capitis* and *Pediculus humanus corporis*	[14]
1861	Murray	Lice imitate the color of the support upon which they live	[26]
1915–1917	Fahrenholz	Human lice description and classification based on various morphological characteristics, including size, shape and pigmentation	[18]
1917	Sikora; Bacot	Evidence that *P. capitis* raised under *P. corporis* conditions become gradually indistinguishable from *P. corporis*	[12,20]
1917	Bacot	In the laboratory, head lice sometimes lay eggs on clothes, but body lice rarely lay eggs on hairs and eggs are badly attached Body lice have a homing instinct, but head lice do not Head and body lice pair freely and their offspring are fertile	[20]
1917	Howlett	When head lice are place on the body, they have a tendency to return to the head, but this tendency is less marked in the next generations	[15]
1918	Nuttall	Feeding habits of *P. capitis* and *P. corporis* They represent extremes in the variation of the species *P. humanus*	[17]
1919	Nuttall	Pigmentation is entirely dependent on the color of the background and is not a genetically transmitted characteristic	[26]
1919	Nuttall	*P. corporis* is a descended from *P. capitis* in nature and some races of *P. capitis* are more labile than others	[17]
1919	Keilin and Nuttall	Occurrence of an abnormal sex-ratio in the progeny of crosses and the appearance of hermaphrodites Review of many cases supporting evidence of intermingling of the two forms of lice	[23]
1920	Nuttall	Fahrenholz: description of human lice criticized Pigmentation is a poor criterion for differentiating lice	[18]
1924 1926 1929	Ewing	Description of American lice and observation that human lice are hybrids Description of mummy lice and comparison with contemporary lice conducted to develop an identification key for American lice In some races of humans, a distinct variety of clothes louse developed from the head louse, whereas this is not the case in other human races	[28–30]
1946	Busvine	Confirmation that lice pigmentation depends on background color	[27]
1948	Busvine	Head lice reared in captivity without any signs of acquiring *P. corporis* characteristics	[16]
1955	Alpatov	Head lice may become body lice under body lice laboratory conditions	[22]
1985	Busvine	Description of head and body lice of distinct non-overlapping sizes in Ethiopia	[19]

Body lice were proved to be vector of several bacterial diseases. *R. prowazekii* and *B. quintana* were shown to be transmitted through the voluminous (blood-contaminated) feces that enter through bite wounds, conjunctiva, and respiratory membranes [21]. The vectorial capacity of head lice is debated, but they also produce voluminous blood-contaminated feces [21]. The vectorial capacity of body lice may reflect their greater blood intake during feeding episodes resulting from the more difficult access to blood for lice in clothes because they must deal with host body movements [17]. This may lead to an increased internal pressure in the *corporis* form that could explain its larger average size, loss of angularity in the abdominal segments, and the more widely separated hairs upon the abdominal surface, compared to the *capitis* form [17]. However, the *capitis* and the *corporis* forms feed in the same way if they are reared under the same conditions [17].

Rearing observations

The typical *capitis*, which are raised on humans under conditions that are favorable for *corporis*, gradually become morphologically indistinguishable from *corporis* after four to five generations [22,23]. The typical *capitis* and *corporis* forms may represent the extremes in the variation of the species *P. humanus* [17]. However, similar work could not confirm these observations [16].

Intermingling of capitis *and* corporis *in nature*

Many cases support the intermingling of the two forms of lice when they invade each other's feeding grounds [15,20,23]. *Capitis* and *corporis* were shown to pair freely, and their offspring are fertile [20]. However, there was an abnormal sex-ratio in the progeny of crosses, with a marked decrease in the proportion of females to males and the appearance of hermaphrodites [23]. Interestingly, in our laboratory, we found lice eggs on a cap from a homeless person, confirming that head lice may lay eggs on clothes [24]. Finally, a study undertaken in 2003 further confirmed that head lice may be established on the body [21].

Several subspecies or varieties debate

Fahrenholz classified lice into six subspecies on the basis of lice morphology and pigmentation: three subspecies of *capitis* (*P. capitis angustus*, *P. capitis maculatus*, and *P. capitis capitis*) and three subspecies of *corporis* (*P. nigritarum*, *P. chinensis*, and *P. humanus humanus*). Each of these species occurs on what he referred to as different 'human races' [18]. However, pigmentation as a criterion to describe and differentiate between lice may lead to errors in differentiation because unpigmented structures are difficult to observe and may be reported as being absent even though they are effectively present [18]. Furthermore,

it was reported that lice imitate the color of the skin upon which they live [25,26]. A series of color gradations according to louse origin, ranging from the black louse to the light-gray louse, were described. However, the accuracy of these results has been challenged by several authors who stated that the color difference is inconsistent because a large variety of louse colors can be found on a single host [26]. Moreover, additional experiments showed that the pigmentation was entirely dependent on the color of the background and was not a genetically transmitted characteristic [26]. The variability in louse colors on a single host may be affected not only by the color of the skin but also by the color of the hair and clothing [26,27].

Ewing also used morphological characteristics to propose an identification key for American lice that included five varieties of human lice: *P. humanus nigritarum* Fabricius (also known as *P. humanus corporis* De Geer), *P. humanus marginatus* Fahrenholz, *P. humanus americanus*, a new variety, and *P. humanus humanus* Linnaeus [28–30]. He worked on both contemporary and mummy lice because he was aware that America, a melting pot of human races, had also become a melting pot for hybrid lice from different origins.

First assumptions about the evolution of head and body lice

At the time, the predominant opinion was that *corporis* descended from *capitis* in nature [17,28]. Indeed, it was thought that when primitive humans lost the hair that covered their bodies, and began to wear clothes, lice living in hair evolved to adapt to this new ecologic niche. The variation in the time required for the adaptation of the typical *capitis* form to evolve into the typical *corporis* form illustrates that some varieties of *capitis* are more labile than others [17]. This finding was also stated later by Ewing: 'in certain races of humans a distinct variety of clothes louse developed from the head-louse type for that race, while in other races, no clothes-louse type distinctive from head louse developed' [28]. We will discuss this topic later in this review.

The louse genome

Chromosome structure

Genome sequencing of the human body louse [13] confirmed that body lice and head lice have the smallest genomes of any insect reported to date (108 Mb for females and 109 Mb for males), as previously estimated by flow cytometry in 2007 [31]. Lice are diploid organisms that have six chromosomes (five metacentric chromosomes and one telocentric chromosome) [32]. The average guanine-cytosine (GC) content of the *P. humanus* genome is 28%, making this genome unusually AT rich. Transposable elements represent only 1% of the genome, which is markedly less than for any sequenced insect genome. Both class I and class II mobile elements are present [13]. No genes of prokaryotic origin have been found in the louse genome, suggesting the absence of DNA transfer from *Candidatus* Riesia pediculicola to its host [13].

Gene content and function

The expectation for the reproductive evolution of obligate parasites would be a reduced genome with a reduced basal insect repertoire. However, despite its small size, the body louse genome is functionally complete [13]; 90% of the predicted body louse genes share homology and 80% of the genes show orthology to other sequenced insect genes [33]. The genome contains 10 773 protein-coding genes and 57 microRNAs. Lice belong to the hemimetabolic insects. The louse genome composition is interesting because lice could constitute an outgroup of holometabolic insects and because they share more orthologous genes with this group than with the well-studied *Drosophila melanogaster* model [13]. The genome contains significantly fewer genes associated with environmental sensing and response. First, odorant and gustatory receptors, as well as odorant-binding proteins and chemosensory proteins, do not seem to be necessary for host location and selection because their respective genes are dramatically fewer in number than in other insects [13]. Second, the genome encodes the smallest number of detoxifying enzymes compared with other insect genomes [33]. Its obligate parasitism of a single host species and its simple life history may be indicative of an evolutionary process that resulted in a smaller number of specific gene families. Moreover, the louse has a single insulin-like peptide (ilp) gene, which may reflect its restricted and homogeneous diet [13].

The mitochondrial (mt) genome

In eukaryotes, mt chromosomes are typically circular, approximately 16 kb in length, and contain 37 genes [34]. However, in lice the 37 mt genes are located on 18 minicircular chromosomes instead of one single chromosome. Each of the minicircular chromosomes is 3–4 kb in length and contains one to three genes [35]. The circular chromosomes also contain three blocks of highly conserved regions that may form a stable stem–loop to initiate replication and transcription. The coding regions show single-nucleotide polymorphisms. There is evidence of recombination between minichromosomes that is probably facilitated by the identical sequences present on different minichromosomes, thus explaining the extreme sequence variation in the noncoding regions [35]. The recombination of these minichromosomes may be either homologous or nonhomologous. There are also different types of chimeric mt minichromosomes, in addition to the 18 mt minichromosomes [36]. This novel type of circular mt chromosome is also present in the other sucking lice, but not in chewing lice or the Psocoptera. Blood-feeding appears to have co-evolved with minicircular mt chromosomes in sucking lice [35]. Moreover, the gene content of various eukaryotic mitochondrial genomes (including *P. humanus*) was investigated to determine the origin of each mt gene and reconstitute the origin of mitochondria. This work showed that mitochondria do not have a stable or unique form, and that mitochondria of different organisms do not have the same evolutionary history or the same number of genes [37].

The louse endosymbiont and its genome

Generalities about the endosymbiont

The human louse endosymbiont is a bacterium belonging to the family *Enterobacteriaceae* in the *γ-Proteobacteria class*. Its closest relatives are species in the genus Arsenophonus, and it was termed *Candidatus* Riesia pediculicola

[12]. Many studies were undertaken during the past 5 years on louse endosymbionts [38–40]. The microorganism is primarily located in a disc-shaped organ located on the ventral side of the midgut (the mycetome) and is transmitted from the female louse to its progeny after its migration to the ovaries [39,41,42].

The endosymbiont genome

The genome of the obligatory louse endosymbiont contains less than 600 genes on a short, linear chromosome and a circular plasmid. When compared with the genome of other endosymbionts, only 24 genes are unique to *Candidatus* Riesia pediculicola, including genes coding for transport and binding proteins, as well as enzymes involved in lipopolysaccharide biosynthesis that may be essential for cell-wall stability during extracellular migration [13]. There are 30 genes in all bacteria studied that are absent from *Candidatus* Riesia pediculicola. These genes are mainly exonucleases that are required for conjugation, and enzymes that are involved in energy metabolism, thus reflecting the dependence of the symbiont on its louse host for nutrients. In return, the bacterium is thought to be required by the louse for the production of pantothenic acid (vitamin B5) [43]. The genes encoding this function are situated together on the plasmid, and not on the linear chromosome of the bacteria. The reduction in genome size and the high AT-bias suggest an ancient association between the louse and its primary endosymbiont [13]. However, *Candidatus* Riesia pediculicola is an insect primary endosymbiont (P-endosymbiont) that has been associated with the louse for only 13–25 million years. Moreover, this bacterium was described as the fastest-evolving insect P-endosymbiont, leading to the conclusion that nucleotide substitution rates decrease as the age of the endosymbiosis increases to slow the overall rate of endosymbiont extinction [44].

Genomic data on louse-infesting bacteria

As mentioned above, three main intracellular bacteria are transmitted by lice: *R. prowazekii*, *B. quintana*, and *B. recurrentis* [4]. Interestingly, in addition to all being highly pathogenic, these bacteria share another common characteristic: an unusually reduced genome size compared to close relatives. Hence, *B. recurrentis* appears to be a degraded subset of the tick-borne relapsing fever-causing agent *Borrelia duttonii* [45]. In addition, *B. quintana* is described as a genomic derivative of the zoonotic agent *Bartonella henselae*, which is transmitted among cats by the cat flea and to humans by cat scratches or cat bites [46]. Finally, *R. prowazekii* is also known to have a reduced genome and to contain hundreds of degraded genes [47]. In fact, as bacteria interact with their environment their genetic content varies through gene gain and loss. When a bacterium becomes intracellular the possibility of gene exchange is reduced, leading to gene loss and a reduction in genome size. However, intracellular bacteria of amoebae are in sympatry with many other bacteria and viruses, leading to a very large genome [48]. In cases of intracellular bacteria living in allopatry, new characteristics may not be acquired, and the bacteria can become specialized to their environment and lose the capacity to adapt to a changing environment. A greater reduction in genome size will lead

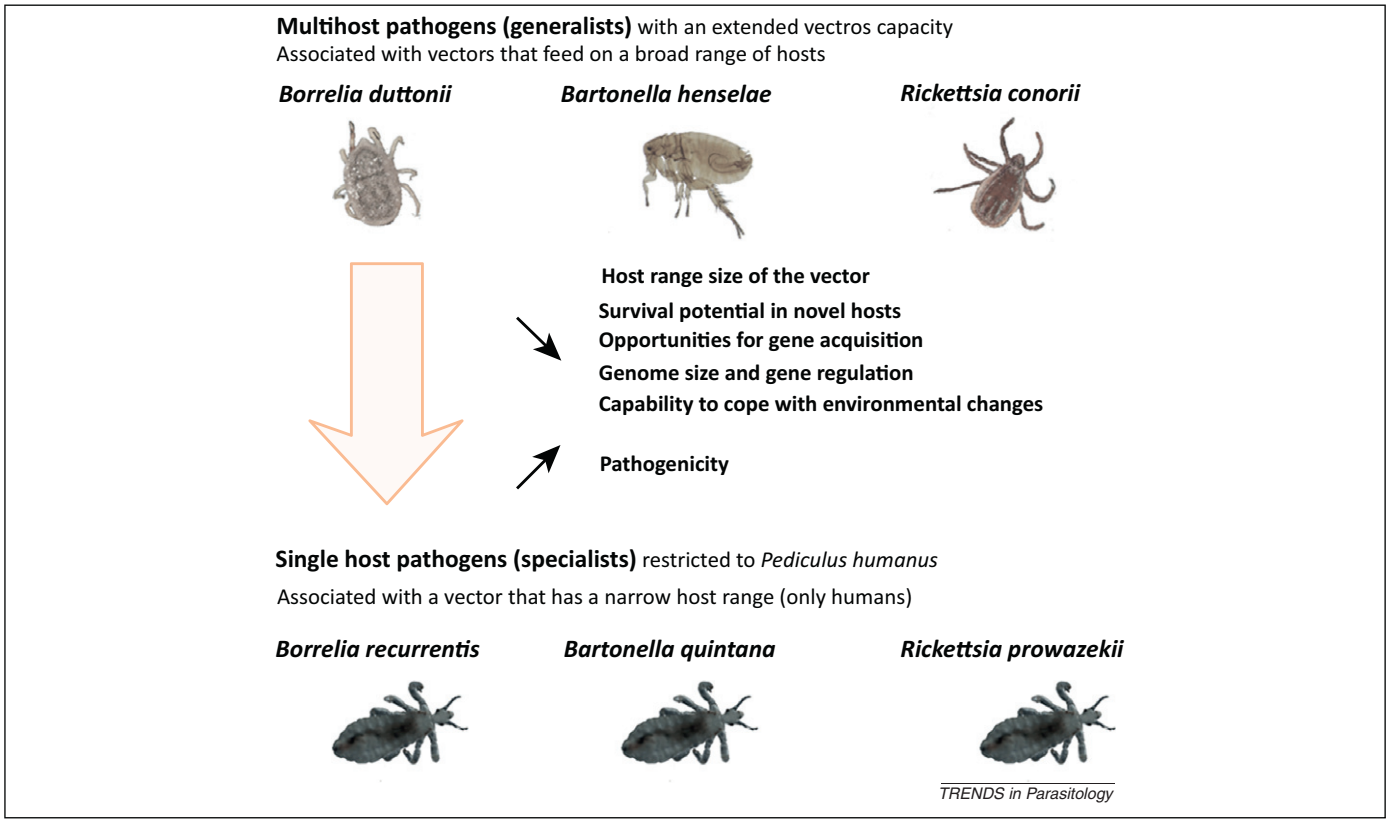

Figure 2. Reductive evolution leading to a higher pathogenicity. Reductive evolution of the highly pathogenic bacteria associated with *Pediculus humanus,* a narrow host-range vector compared to less-virulent closely related bacteria associated with broad host-range vectors.

to deregulation and a higher level of pathogenicity [49–51]. This explains why the bacteria of the genera Borrelia, Bartonella and Rickettsia comprise both highly pathogenic bacteria with small genomes, that are transmitted by a very specific vector (the louse), and less pathogenic bacteria, with larger genomes, that are transmitted by ticks or fleas that feed on a larger variety of hosts (Figure 2) [45].

Genetic studies of human head and body lice

Genetic tools questioned the division of human lice into head lice and body lice (Table 2). The first study was based on the 18S rRNA gene [52], and subsequent studies focused on mt genes [53–56] and intergenic spacers [24,57]. These studies revealed that there are three clades of head lice, one of which may also be body lice (Clade A) [53,54].

Table 2. Summary of the main genetic studies on human head and body lice

DNA Type	Gene	Fragment length	Date	First author	Title	Ref
Mitochondrial DNA	Cytochrome oxidase subunit 1 (COI)	524 bp	2002	Leo	Evidence from mitochondrial DNA that head and body lice of humans are conspecific	[55]
		610 bp	2003	Kittler	Molecular evolution of *Pediculus humanus* and the origin of clothing	[56]
		524 bp	2003	Yong	The geographic segregation of human lice preceded that of *Pediculus humanus capitis* and *Pediculus humanus humanus*	[52]
		854 bp	2004	Reed	Genetic analysis of lice supports direct contact between modern and archaic humans	[54]
		383 bp	2008	Raoult	Molecular identification of lice from pre-Columbian mummies	[53]
		827 bp	2008	Light	Geographic distributions and origins of human head lice based on mitochondrial data	[65]
	Cytochrome *b* (Cyt b)	440 bp	2003	Kittler	Molecular evolution of *Pediculus humanus* and the origin of clothing	[56]
		671 bp	2004	Reed	Genetic analysis of lice supports direct contact between modern and archaic humans	[54]
		356 bp	2008	Raoult	Molecular identification of lice from pre-Colombian mummies	[53]
		316 bp	2010	Li	Genotyping of human lice suggest multiple emergences of body lice from local head louse populations	[24]
	NADH dehydrogenase 4 (ND4)	579 bp	2003	Kittler	Molecular evolution of *Pediculus humanus* and the origin of clothing	[56]
Nuclear DNA	Elongation factor 1α (EF-1α)	485 bp	2003	Kittler	Molecular evolution of *Pediculus humanus* and the origin of clothing	[56]
		348 bp	2003	Yong[a]	The geographic segregation of human lice preceded that of *Pediculus humanus capitis* and *Pediculus humanus humanus*	[52]
	RNA polymerase II (RPII)	601 bp	2003	Kittler	Molecular evolution of *Pediculus humanus* and the origin of clothing	[56]
	18S rRNA gene, small ribosomal subunit rRNA	1474–1493 bp	2003	Yong	The geographic segregation of human lice preceded that of *Pediculus humanus capitis* and *Pediculus humanus humanus*	[52]
		1195 bp	2005	Leo and Barker	Unraveling the evolution of the head and body lice of humans	[66]
	Microsatellites	130–180 bp	2005	Leo	The head and body lice of humans are genetically distinct; evidence from double infestations	[67]
	Intergenic spacers	133–155 bp 323–328 bp 165–185 bp 156–189 bp	2010	Li	Genotyping of human lice suggests multiple emergences of body lice from local head louse populations	[24]
cDNA	Transcript prediction		2012	Olds	Comparison of the transcriptional profiles of head and body lice	[58]
Analysis based on data available in GenBank	Comparison of phylogenetic and population genetic approaches		2008	Light	What's in a name: the taxonomic status of human head and body lice	[68]
	Bayesian coalescent modeling approach for estimation of effective migration rates		2011	Toups	Origin of clothing lice indicates early clothing use by anatomically modern humans in Africa	[69]

[a]The EF-1α sequences of this study are contaminated by fungi [67].

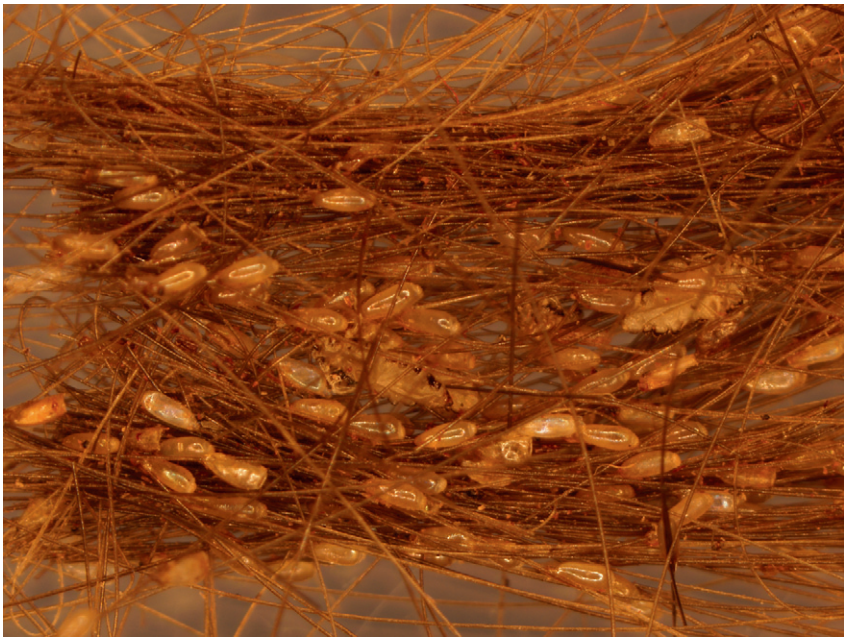

Figure 3. Head lice nits. Picture taken from a highly infested homeless person.

Recently, a transcriptome study of human head and body lice revealed that there is only one gene that is present in body lice but not in head lice. Otherwise, the main differences identified between head lice and body lice concern gene expression levels [58]. Indeed, 14 putative differentially expressed genes were identified by comparing head louse and body louse data. Nine head louse genes were more highly expressed: genes encoding a putative

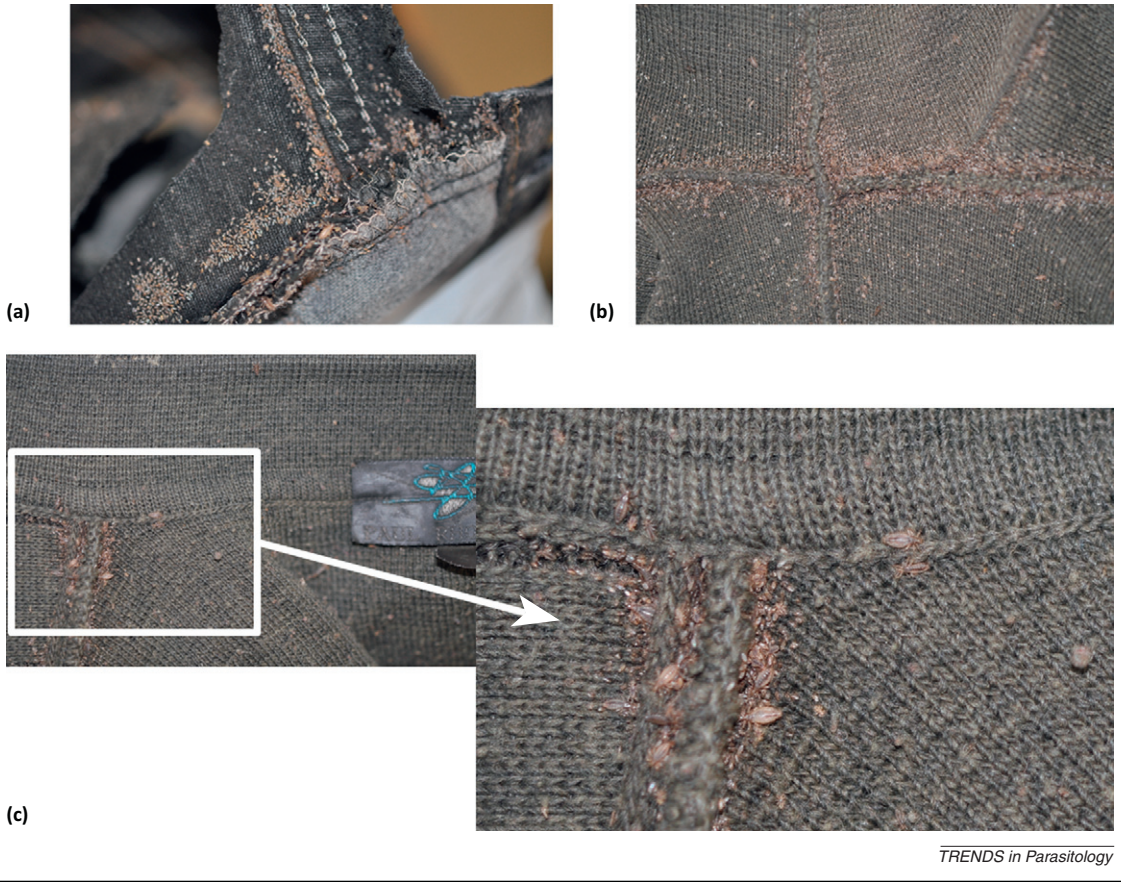

Figure 4. Body lice nits. Pictures taken from clothes of a highly infested homeless person: **(a)** a piece of pants, **(b)** the armpit, and **(c)** the collar.

enzymatic polyprotein, a putative cuticle protein, a cytochrome P450, a putative triadia, a putative glucose dehydrogenase precursor, a putative trypsin-4 precursor, a putative parathyroid precursor, and two hypothetical proteins. Five other genes were expressed at lower levels and encode an agglutinin isolectin 2 precursor, a putative Bardet–Biedl syndrome 4 (bbs4), a histone H2B.3, as well as a predicted protein and a hypothetical protein of unknown function. Thus, head lice and body lice have almost the same genomic content but are phenotypically different (different ecotypes) as a result of differential gene expression.

Concluding remarks

Body lice are only found in one lineage (Clade A). The theory that body lice evolved from head lice when humans began to wear clothes [56] is incompatible with genetic studies. The data suggest that evolution of body lice from head lice, and vice versa, takes place constantly among Clade A lice, and that this evolution is facilitated by mass infestations (Figures 3 and 4). This finding is strengthened by the identification of body louse nits in the cap of a homeless person that may have originated from a head louse [24]. We now know that among Clade A lice, head lice and body lice are two ecotypes of the same species that, with the exception of one gene, differ only in gene expression and not in gene content. The reported morphological and behavioral differences between head and body lice [16] could be the result of epigenetics. Epigenetics is the study of inherited changes in phenotype or gene expression that are caused by mechanisms other than changes in the underlying DNA sequence [59]. Such phenotypic modification in insects has been reported to occur in termites and migratory locusts. In termites, the descendants of a female 'queen' may develop into different phenotypic forms, such as 'workers', 'soldiers', or two sexual forms, under genetic influences as well as in response to environmental and social factors [60]. In locusts, when the population increases to a specific level, the locust phenotype changes and the population starts to migrate [61–63]. These changes also accumulate across generations through a maternal effect [62]. It is possible that something equivalent takes place in body lice when they proliferate at high levels, perhaps because of the influence of physical contact and/or of pheromones that play the role of quorum sensing [64]. In conclusion, studying the phenotypic characteristics of lice and their genetic data provides crucial information for understanding lice epidemiology. Obtaining data on these parasites is essential for preventing re-emerging diseases because body lice are vectors for very severe diseases, and head lice can serve as potential reservoirs for disease. In conclusion, there are three major clades of head lice, one of which can also generate a body louse that is phenotypically but not genotypically different from the head louse form.

References

1 Johnson, K.P. *et al.* (2004) Multiple origins of parasitism in lice. *Proc. Biol. Sci.* 271, 1771–1776
2 Weiss RA (2009) Apes, lice and prehistory. *J. Biol.* 8, 20
3 Brouqui, P. (2011) Arthropod-borne diseases associated with political and social disorder. *Annu. Rev. Entomol.* 56, 357–374
4 Badiaga, S. and Brouqui, P. (2012) Human louse-transmitted infectious diseases. *Clin. Microbiol. Infect.* 18, 332–337
5 La Scola, B. *et al.* (2001) Detection and culture of *Bartonella quintana*, *Serratia marcescens*, and *Acinetobacter* spp. from decontaminated human body lice. *J. Clin. Microbiol.* 39, 1707–1709
6 Angelakis, E. *et al.* (2011) Altitude-dependent *Bartonella quintana* genotype C in head lice, Ethiopia. *Emerg. Infect. Dis.* 17, 2357–2359
7 Angelakis, E. *et al.* (2011) *Bartonella quintana* in head louse nits. *FEMS Immunol. Med. Microbiol.* 62, 244–246
8 Bonilla, D.L. *et al.* (2009) *Bartonella quintana* in body lice and head lice from homeless persons, San Francisco, California, USA. *Emerg. Infect. Dis.* 15, 912–915
9 Sasaki, T. *et al.* (2006) First molecular evidence of *Bartonella quintana* in *Pediculus humanus capitis* (Phthiraptera: Pediculidae), collected from Nepalese children. *J. Med. Entomol.* 43, 110–112
10 Bouvresse, S. *et al.* (2011) No evidence of *Bartonella quintana* but detection of *Acinetobacter baumannii* in head lice from elementary schoolchildren in Paris. *Comp. Immunol. Microbiol. Infect. Dis.* 34, 475–477
11 Buchner, P. (1920) Zur Kenntnis der Symbiose niederer pflanzlicher Organismen mit Pedikuliden. *Biol. Zentbl.* 39, 535–540 (in German)
12 Sikora, H. (1919) Vorläufige Mitteilung über Myzetome bei Pediculiden. *Biol. Zentbl.* 39, 287–288 (in German)
13 Kirkness, E.F. *et al.* (2010) Genome sequences of the human body louse and its primary endosymbiont provide insights into the permanent parasitic lifestyle. *Proc. Natl. Acad. Sci. U.S.A.* 107, 121168–121173
14 De Geer, C. (1778) *Mémoires Pour Servir à l'Histoire des Insectes*, Hesselberg, pp. 62–68 (in French)
15 Howlett, F. (1917) Notes on head- and body-lice and upon temperature reactions of lice and mosquitos. *Parasitology* 10, 186–188
16 Busvine, J.R. (1948) The head and body races of *Pediculus humanus* L. *Parasitology* 39, 1–16
17 Nuttall, G. (1919) The systematic position, synonymy and iconography of *pediculus humanus* and *phthirus pubis*. *Parasitology* 11, 329–346
18 Nuttall, G. (1920) On Fahrenholz's purported new species subspecies and varieties of *Pediculus*. *Parasitology* 12, 136–153
19 Busvine, J. (1985) Biology of the Parasites. In *Cutaneaous Infestations and Insect Bites* (Orkin, M. and Maibach, H.I., eds), pp. 163–173, Marcel Dekker
20 Bacot, A.W. (1917) A contribution to the bionomics of *Pediculus humanus* (*vestimenti*) and *Pediculus capitis*. *Parasitology* 9, 228–258
21 Bailey, A.M. *et al.* (2003) Head lice and body lice: shared traits invalidate assumptions about evolutionary and medical distinctions. *Aust. J. Med. Sci.* 24, 48–62
22 Alpatov, W.W. (1955) Transformation of the head form of *Pediculus humanus* L. into the body form under the influence of changed living conditions. *Bull. Soc. Nat.* 60, 79–92
23 Keilin, D. and Nuttall, G. (1919) Hermaphroditism and other abnormalities in *Pediculus humanus*. *Parasitology* 11, 279–328
24 Li, W. *et al.* (2010) Genotyping of human lice suggests multiple emergencies of body lice from local head louse populations. *PLoS Negl. Trop. Dis.* 4, e641
25 Shipley, A.E. (1915) The louse (*Pediculus*), In *The Minor Horrors of War*, Smith and Elder, pp. 1–29
26 Nuttall, G. (1919) The biology of *Pediculus humanus*. *Parasitology* 10, 201–220
27 Busvine, J. (1946) On the pigmentation of the body louse *Pediculus humanus* L. *Proc. R. Entomol. Soc. Lond.* 21, 98–103
28 Ewing, H.E. (1926) A revision of the American lice of the genus *Pediculus*, together with a consideration of the significance of their geographical and host distribution. *Proc. U.S. Natl. Museum* 68, 1–30
29 Ewing, H. (1924) Lice from human mummies. *Science* 9, 389–390
30 Ewing, H. (1929) Anoplura, or sucking lice, In *A Manual of External Parasites*, CC Thomas, pp. 143–152
31 Johnston, J.S. *et al.* (2007) Body lice and head lice (Anoplura: Pediculidae) have the smallest genomes of any hemimetabolous insect reported to date. *J. Med. Entomol.* 44, 1009–1012
32 Hindle, E. and Pontecorvo, G. (1942) Mitotic divisions following meiosis in *Pediculus corporis* males. *Nature* 149, 668
33 Lee, S.H. *et al.* (2010) Decreased detoxification genes and genome size make the human body louse an efficient model to study xenobiotic metabolism. *Insect Mol. Biol.* 19, 599–615

34 Boore, J.L. (1999) Animal mitochondrial genomes. *Nucleic Acids Res.* 27, 1767–1780
35 Shao, R. *et al.* (2009) The single mitochondrial chromosome typical of animals has evolved into 18 minichromosomes in the human body louse, *Pediculus humanus*. *Genome Res.* 19, 904–912
36 Shao, R. and Barker, S.C. (2010) Chimeric mitochondrial minichromosomes of the human body louse, *Pediculus humanus*: evidence for homologous and non-homologous recombination. *Gene* 473, 36–43
37 Georgiades, K. and Raoult, D. (2011) The rhizome of *Reclinomonas americana*, *Homo sapiens*, *Pediculus humanus* and *Saccharomyces cerevisiae* mitochondria. *Biol. Direct* 6, 55
38 Allen, J.M. *et al.* (2007) Evolutionary relationships of '*Candidatus* Riesia spp.', endosymbiotic enterobacteriaceae living within hematophagous primate lice. *Appl. Environ. Microbiol.* 73, 1659–1664
39 Perotti, M.A. *et al.* (2007) Host-symbiont interactions of the primary endosymbiont of human head and body lice. *FASEB J.* 21, 1058–1066
40 Sasaki-Fukatsu, K. *et al.* (2006) Symbiotic bacteria associated with stomach discs of human lice. *Appl. Environ. Microbiol.* 72, 7349–7352
41 Buchner, P. (1965) *Endosymbiosis of Animals with Plant Microorganisms*, Interscience Publishers
42 Ries, E. (1931) Sie Symbiose der Läuse und Federlinge. *Zeitschrift für Morphologie und Ökologie der Tiere* 20, 233–267 (in German)
43 Perotti, M.A. *et al.* (2009) Endosymbionts of lice. In *Insect Symbiosis* (Bourtzis, K. and Miller, T.A., eds), pp. 205–220, CRC Press
44 Allen, J.M. *et al.* (2009) Mutational meltdown in primary endosymbionts: selection limits Muller's ratchet. *PLoS ONE* 4, e4969
45 Lescot, M. *et al.* (2008) The genome of *Borrelia recurrentis*, the agent of deadly louse-borne relapsing fever, is a degraded subset of tick-borne *Borrelia duttonii*. *PLoS Genet.* 4, e1000185
46 Alsmark, C.M. *et al.* (2004) The louse-borne human pathogen *Bartonella quintana* is a genomic derivative of the zoonotic agent *Bartonella henselae*. *Proc. Natl. Acad. Sci. U.S.A.* 101, 9716–9721
47 Andersson, S.G. *et al.* (1998) The genome sequence of *Rickettsia prowazekii* and the origin of mitochondria. *Nature* 396, 133–140
48 Moliner, C. *et al.* (2010) Genome analysis of microorganisms living in amoebae reveals a melting pot of evolution. *FEMS Microbiol. Rev.* 34, 281–294
49 Merhej, V. *et al.* (2009) Massive comparative genomic analysis reveals convergent evolution of specialized bacteria. *Biol. Direct* 4, 13
50 Georgiades, K. and Raoult, D. (2011) Genomes of the most dangerous epidemic bacteria have a virulence repertoire characterized by fewer genes but more toxin–antitoxin modules. *PLoS ONE* 6, e17962
51 Georgiades, K. and Raoult, D. (2010) Defining pathogenic bacterial species in the genomic era. *Front. Microbiol.* 1, 151
52 Yong, Z. *et al.* (2003) The geographical segregation of human lice preceded that of *Pediculus humanus capitis* and *Pediculus humanus humanus*. *C. R. Biol.* 326, 565–574
53 Raoult, D. *et al.* (2008) Molecular identification of lice from pre-Columbian mummies. *J. Infect. Dis.* 197, 535–543
54 Reed, D.L. *et al.* (2004) Genetic analysis of lice supports direct contact between modern and archaic humans. *PLoS Biol.* 2, e340
55 Leo, N.P. *et al.* (2002) Evidence from mitochondrial DNA that head lice and body lice of humans (Phthiraptera: Pediculidae) are conspecific. *J. Med. Entomol.* 39, 662–666
56 Kittler, R. *et al.* (2003) Molecular evolution of *Pediculus humanus* and the origin of clothing. *Curr. Biol.* 13, 1414–1417
57 Veracx, A. *et al.* (2012) Evidence for an African cluster of human head and body lice with variable colors and interbreeding of lice between continents. *PLoS ONE* 7, e37804
58 Olds, B.P. *et al.* (2012) Comparison of the transcriptional profiles of head and body lice. *Insect Mol. Biol.* 21, 257–268
59 Bossdorf, O. *et al.* (2008) Epigenetics for ecologists. *Ecol. Lett.* 11, 106–115
60 Hayashi, Y. *et al.* (2007) Sex-linked genetic influence on caste determination in a termite. *Science* 318, 985–987
61 Islam, M.S. *et al.* (1994) Effects of population density experienced by parents during mating and oviposition on the phase of hatchling desert locusts, *Schistocerca gregaria*. *Proc. Biol. Sci.* 257, 93–98
62 Simpson, S.J. *et al.* (2001) Gregarious behavior in desert locusts is evoked by touching their back legs. *Proc. Natl. Acad. Sci. U.S.A.* 98, 3895–3897
63 Sword, G.A. (2005) Local population density and the activation of movement in migratory band-forming Mormon crickets. *Anim. Behav.* 69, 437–444
64 Applebaum, S.W. and Heifetz, Y. (1999) Density-dependent physiological phase in insects. *Annu. Rev. Entomol.* 44, 317–341
65 Light, J.E. *et al.* (2008) Geographic distributions and origins of human head lice (*Pediculus humanus capitis*) based on mitochondrial data. *J. Parasitol.* 94, 1275–1281
66 Leo, N.P. and Barker, S.C. (2005) Unravelling the evolution of the head lice and body lice of humans. *Parasitol. Res.* 98, 44–47
67 Leo, N.P. *et al.* (2005) The head and body lice of humans are genetically distinct (Insecta: Phthiraptera, Pediculidae): evidence from double infestations. *Heredity* 95, 34–40
68 Light, J.E. *et al.* (2008) What's in a name: the taxonomic status of human head and body lice. *Mol. Phylogenet. Evol.* 47, 1203–1216
69 Toups, M.A. *et al.* (2011) Origin of clothing lice indicates early clothing use by anatomically modern humans in Africa. *Mol. Biol. Evol.* 28, 29–32