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Parasite Diversity and Diversification

Evolutionary Ecology Meets Phylogenetics

Edited by Serge Morand, Boris R. Krasnov, D. Timothy J. Littlewood

Chapter

10 - The study of primate evolution from a lousy perspective pp. 202-2

14

10 The study of primate evolution from a lousy perspective

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10.1   Introduction

The field of primate evolution has long been active, with major fossil discoveries and more recently genetic and genomic studies that enable humans to better understand their place in the world. However, the spottiness of the fossil record and the complicated history of humans have led researchers to look at additional sources of information to study human origins. In particular, evolutionary biologists have examined the parasites and pathogens of humans to glean new insights into our evolutionary past (see Reed *et al.*, 2009 for a review). Some parasites are particularly good at uncovering recent events in human history, such as very recent migrations around the globe. Others are better suited for deep-time evolutionary questions. What is particularly relevant to this book is that parasites help us understand not only their shared evolutionary history with their hosts, but may also help us understand something about the ecology of their hosts. For example, parasites evolve more quickly than their hosts and therefore record evolutionary events in their DNA with greater information. One could use such parasites to study endangered host species, or use gene flow among parasites to study hard-to-track hosts (see Whiteman and Parker, 2005 for other examples). One parasite that has great potential for shedding light on host ecology is the louse.

Lice often cospeciate with their hosts. This is because they have limited vagility (i.e. the ability to move from host to host) and are essentially trapped on host lineages over both short and long timescales. This lack of vagility often leads to the process of cospeciation (parasites speciating more-or-less in tandem with their hosts). Due to the close association between lice and their hosts, lice have been used as a marker of host evolutionary history. This has been particularly useful in studying primate hosts, which have been speciating in tandem with lice for over 25 million years (Figure 10.1). In this chapter we outline how the evolutionary history of lice can shed light on not only the evolutionary history of their primate and human hosts, but also on the ecology of those hosts. The first section in this chapter summarizes how lice were used to determine when humans first began wearing clothing, which is a question that is difficult to answer from archeological evidence alone. The second section addresses how host-switching in
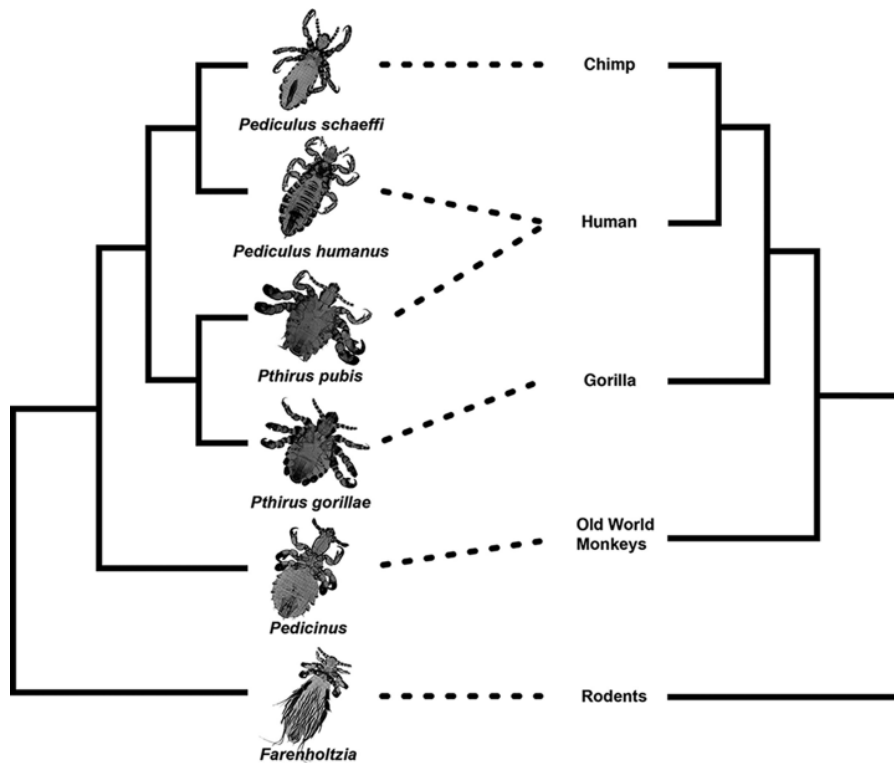
Figure 10.1 Phylogenetic trees of primate lice (left) and their hosts (right) plus an outgroup (adapted from Reed *et al.* 2004). Dashed lines connect lice to the host on which they are naturally found.

lice three million years ago suggests that early hominins were living in close proximity to gorilla ancestors. This is important because we know little about the lineage leading to gorillas. The third section relates to the use of lice to study patterns of human migration around the world. We have carried lice with us throughout our evolutionary history, and these parasites have recorded a copy of this shared coevolutionary history in their DNA. This parascript of human evolution has the potential to shed new light on routes taken by modern humans out of Africa, the peopling of the Americas and many other questions in human evolution. In the last section of this chapter we look to the future. Genomes of lice are being sequenced in multiple labs, including ours. These genomes will allow us to better understand how lice track their hosts and the depths to which we can plumb their genome for answers to questions of primate and human evolution.

10.2   Dating the origin of clothing use in humans from lice

Humans have migrated out of Africa multiple times over the past two million years (for a review, see Stringer, 2002). Archeological evidence indicates that archaic hominins established long-term populations in cooler regions of Europe (Carbonell *et al.*, 1999) and Central Asia (Krause *et al.*, 2010). Anatomically modern humans (AMHs)

later settled in these same regions and are thought to have outcompeted archaic populations, despite the cooler conditions. While there are a large suite of technologies and behaviors associated with the transition from archaic to modern humans, it is unknown whether clothing use played a key role in the successful expansion out of Africa and the replacement of archaic populations.

Determining the origin of clothing use in AMHs is difficult, since direct evidence, such as animal hides, degrade rapidly and are not preserved in archeological sites. Indirect evidence, such as tools used for scraping, appears in the archeological record 780 000 years ago (780 kya), but these scrapers may have had other uses (Carbonell *et al.*, 2008). Eyed needles have been dated to 40 kya, but these are likely associated with tailored clothing (Delson *et al.*, 2000). Importantly, the development of clothing likely occurred after the loss of body hair. Rogers *et al.* (2004) used human genetic data to estimate the loss of body hair to 1.2 million years ago (mya), and Reed *et al.* (2007) suggested an even older date of 3 mya based on the divergence between head and pubic lice. Therefore, indirect evidence suggests that the development of clothing use could have occurred anywhere between 3 mya and 40 kya.

The human louse *Pediculus humanus* consists of two ecotypes: head and clothing lice. These lice exhibit important ecological, morphological and behavioral differences (Light *et al.*, 2008a). It is hypothesized that the loss of body hair in humans restricted lice to the head region of the human host, and that a subset of these lice moved to the clothing niche once it became available (Kittler *et al.*, 2003). Therefore, dating the divergence between these two ecotypes of lice provides a minimum age for the origin of clothing use since clothing lice could not have evolved prior to the availability of the niche.

Kittler *et al.* (2003, 2004) first attempted to use louse molecular data to date the origin of clothing use through a molecular clock analysis. Using the chimp louse *Pediculus schaeffi* as an outgroup, these studies constructed a phylogenetic tree using both nuclear and mitochondrial loci from a worldwide sample of 40 head and clothing lice. The molecular clock analysis dated the origin of the head and clothing lice clade as 107 kya. However, the Kittler *et al.* (2004) analysis was only able to date the origin of the clade of *P. humanus* that contained both head and clothing lice. Furthermore, subsequent analyses have suggested the age of this clade is considerably older than 107 kya (Reed *et al.*, 2004).

Toups *et al.* (2011) analyzed a multi-locus data set consisting of three nuclear and one mitochondrial gene in a Bayesian isolation-with-migration (IM) coalescent framework. This model jointly estimates divergence time, effective population sizes and effective migration rates of head and clothing louse populations. In this model divergence time refers to the divergence between the head and clothing louse populations, which then split into independent rates of growth and migration between populations. The posterior distribution of divergence time in this analysis is characterized by a mode of 83 kya and a median of 170 kya (Figure 10.2).

The results suggest that lice initially colonized the clothing niche as early as 170 kya, which corresponds to the onset of an ice age, Marine Isotope Stage 6 (190–130 kya; EPICA Community Members, 2004). A cooler climate would have caused cold stress to
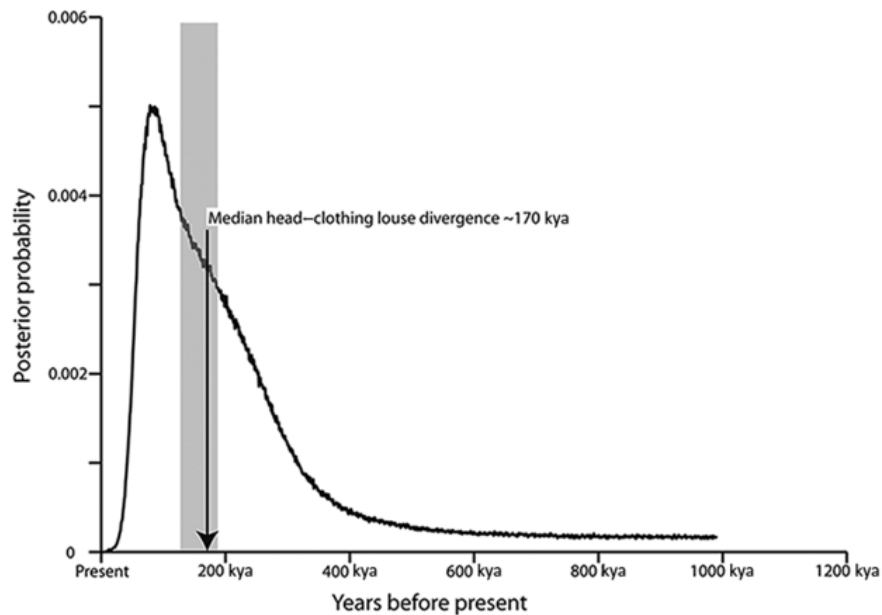
Figure 10.2 Divergence time of human head and clothing lice (Toups *et al.*, 2011). The posterior distribution for the divergence of head and clothing lice (curve) places the median estimate for the origin of clothing lice at 170 kya. The median estimate lies within the Ice Age, coinciding with Marine Isotope Stage 6 130–190 kya, indicated by the shaded region.

populations living in cooler climates, and possibly to AMHs still in Africa. Given that current data tell us that our ancestors left Africa much later than 170–83 kya, we now know that clothing use originated in Africa. It is unknown whether it evolved for adornment, protection or warmth. However, the use of clothing by AMHs was likely instrumental in their success leaving Africa for higher latitudes beginning around 65 kya.

10.3 Inferring the basic ecology of early humans from lice

The pubic louse (*Pthirus pubis*) is a third type of louse that parasitizes humans. Humans and chimpanzees have lice in the genus *Pediculus*, whereas humans and gorillas have lice in the genus *Pthirus* (Figure 10.1). Pubic lice are sexually transmitted and are often found in conjunction with other sexually transmitted diseases (Anderson & Chaney, 2009). They are found in the androgenic hair (hair that grows during puberty) around the pubic region; however, on occasion pubic lice have been found in the eyelashes, eyebrows and edges of the hairline (Meinking, 1999). *Pthirus* spp. are thought to prefer hair that is more widely spaced, which explains why they are not routinely found on the head, but only usually on the edges of the hairline (Waldeyer, 1900; Nuttall, 1918; Fisher & Morton, 1970). These lice can be transmitted on other objects (e.g. towels, clothes, etc.) more easily than *Pediculus* lice, which is one way children get infested with pubic lice (Meinking, 1999). The distribution of *Pthirus* and *Pediculus* on great apes has puzzled scientists for hundreds of years. It is unclear why humans share a louse with both chimpanzees and gorillas.
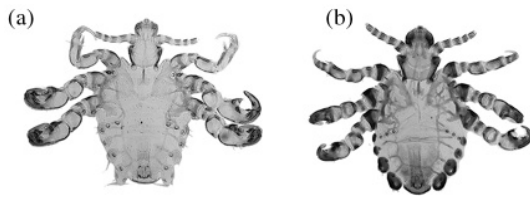
Figure 10.3 (a) Gorilla louse, *Pthirus gorillae*; photo credit J.M. Allen. (b) Human pubic louse, *P. humaus*; photo credit R. Dill.

Molecular evidence suggests that the genera *Pediculus* and *Pthirus* split around 10–13 mya (Reed *et al.*, 2007). This is consistent with recent fossil finds that suggest the split between the chimp–human lineage and the gorilla lineage may be older than previously thought (Suwa *et al.*, 2007; Wilkinson *et al.*, 2011). Furthermore, the sequencing of the gorilla genome suggests that the chimp–human–gorilla split could be as old as ten million years, depending on the mutation rate used (Scally *et al.*, 2012).

Reed *et al.* (2007) showed that *Pthirus* species from humans and gorillas (*P. pubis* and *P. gorillae*, respectively; Figure 10.3) diverged 3–4 mya, which is much too recent to have resulted from the process of cospeciation. The only explanation for such a recent divergence is that pubic lice switched from an ancestral gorilla to an ancestral human 3–4 mya. While pubic lice are sexually transmitted in humans, it does not necessarily mean that they were acquired that way from an ancestor of gorillas. Humans and gorillas would have been separated for 4–7 million years at this point, so sexual contact between the two species seems highly unlikely. One thing we know about humans is that they are very capable scavengers and they might have fed on recently dead gorillas through the bush-meat trade that persists today. It seems likely that humans were scavenging on gorillas three million years ago and acquired lice in the process. Lice die soon after their host because they require the host's warmth and blood for survival. In fact, lice are known to find a new host when their host body temperature decreases. It seems likely that this process happened frequently enough, meaning there was repeated contact between archaic humans and gorilla carcasses to allow pubic lice to establish successfully on new hominin hosts (Allen *et al.*, 2013).

This host-switch provides clues as to when humans lost their body hair and when they developed androgenic hair. We know that humans had to have lost their hair sometime after the split with chimpanzees (6–7 mya), and there is some molecular evidence that it had happened at least by 1.2 mya (Rogers *et al.*, 2004). The timing of this host-switch gives more resolution to when this might have happened. Androgenic hair is more widely spaced, which is preferred by *Pthirus*. Therefore, it is likely that humans had already not only lost their body hair, restricting head lice to the head, but also developed androgenic hair by 3–4 mya, leaving an open niche available for *Pthirus*.

Finally, this host-switch can tell us something about the ecology of early humans. In particular, it tells us that humans were in close proximity to gorillas 3–4 mya. Gorillas are thought to be relatively conservative in body form and habitat. The few

gorilla fossils that have been found tell us that gorilla diet, and presumably gorilla habitat, has changed little over millions of years (Pickford *et al.*, 1988; Suwa *et al.*, 2007). Gorillas are found in moist tropical forests now and likely were 3–4 mya. Given the host-switch in lice we can now hypothesize that early humans were also present in tropical forests, and that this part of our history might be hidden from us due to poor fossilization in moist habitats. This host-switch adds important information about the habitats that were likely used by early humans, and specifically it suggests that moist tropical forests likely were used by early hominins in addition to the drier savannahs that have produced copious hominin fossils.

10.4   Understanding human dispersal from lice

The questions related to how and when AMHs populated the globe are varied and complex. For example, the genetics of modern populations in the Americas should reflect the two major human settlements of the New World (the first peopling of America and the European colonization after Columbus), yet the timing, geographic routes and number of initial colonizations into the Americas are still debated. The sole consensus is that Native American populations originated somewhere in Asia (e.g. Wallace *et al.*, 1985; Torroni *et al.*, 1993; Kolman *et al.*, 1996; O'Rourke & Raff, 2010). After five centuries of admixture between Native Americans, European, Africans and modern Asians, current populations in the Americas contain great heterogeneity. A researcher can ask a human subject about their ancestry and in so doing make a reasonable assumption about how mixed the heritage of the individual might be. Surprisingly, despite the extensive genetic input from Old World populations (mainly from Europe and Africa), current populations in the Americas retain a substantial fraction of Native American mtDNA (Perego *et al.*, 2010). When an immigrant joins a new population, it can bring its own parasites with it and it can acquire local parasites as well. Interbreeding between parasites from geographically different origins can produce a genetic signal that allows researchers to determine when the contact between these lineages occurred. It is especially beneficial that the parasite might provide greater resolution than the host itself due to faster evolutionary rates. In addition, parasites do not require interbreeding between host populations to provide insight into their inter-actions. The extent to which parasites like lice can inform us of recent and past human migrations is still largely unknown.

Previous studies showed that the human louse genealogy was composed of three deeply divergent mitochondrial (mtDNA) clades or haplogroups, named A, B and C, that coalesced to a single common ancestor around 2 mya and differ in their geographic distribution (Figure 10.4; Reed *et al.*, 2004). Clade A, which has a worldwide geo-graphic distribution, was most common and showed signs of recent demographic expansion about 100 kya (Reed *et al.*, 2004). This date coincided with the out-of-Africa expansion of AMHs (Reed *et al.*, 2004), reflecting a pattern of coevolution
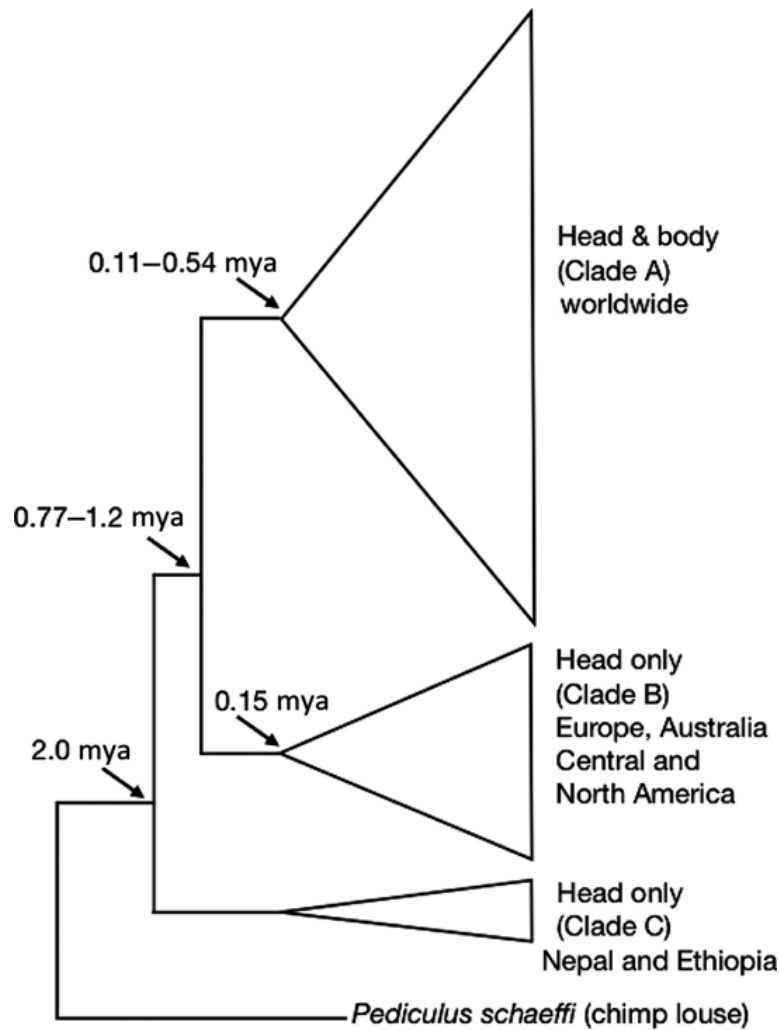
Figure 10.4 Phylogenetic relationships, timing of divergence events (in millions of years; mya) and geographic distribution among human lice based on the mitochondrial *cox1* gene (Reed *et al.* 2004; Kittler *et al.* 2003, 2004). Height of the triangles represents the number of specimens in each clade. Figure modified from Light *et al.* (2008a).

between lice and their human hosts. Clade B has been found in the New World, Europe and Australia, but not in Africa, and Reed *et al.* (2004) suggested that it might have had its evolutionary origins on an archaic hominid (likely *H. neanderthalensis*). Clade C has been found in Nepal and Ethiopia, appears to be over two million years old and probably evolved on archaic hominids in Asia or Africa (Reed *et al.*, 2004).

Ascunce *et al.* (2013a) examined the mitochondrial gene diversity for 450 lice collected from 14 localities throughout North, Central and South America to determine the extent to which the lice reflected patterns of human diversity. Throughout the Americas, Ascunce *et al.* (2013a) found two of the three known louse mitochondrial clades (Clades A and B). The ratios of Clade A to B differed geographically with a ratio

of 58:42 in North America, 18:82 in Central America and 95:5 in South America. Twelve haplotypes were found in Clade A ($n = 333$ lice) and 24 in Clade B ($n = 117$ lice). Haplotype diversity estimates for Clades A and B were 0.605 and 0.795, respectively, whereas nucleotide diversity estimates were 0.0017 and 0.00831, respectively. Clade A and B values were similar to values estimated by Light *et al*. (2008b), suggesting that the New World contains a large fraction of the total worldwide variation found in human lice.

In the same study, Ascunce *et al*. (2013a) estimated the mean date of demographic expansions, which varied from about 16 000 years ago to 20 000 years ago for each clade and are contemporaneous with estimates of demographic expansions in Native Americans (Tamm *et al*., 2007; Fagundes *et al*., 2008; Goebel *et al*., 2008; Kitchen *et al*., 2008; Mulligan *et al*., 2008; Reich *et al*., 2012). Based on the mitochondrial louse diversity in the Americas, Ascunce *et al*. (2013a) found no clear signature of the recent European louse colonization (those that arrived within the last 500 years), which is not unexpected since that colonization was from widespread European origins and occurred in many waves.

In a separate study, Ascunce *et al*. (2013b) examined nuclear genetic diversity based on microsatellite data among human head and body louse populations ($n = 93$ lice) from four main geographic regions (North America, Central America, Asia and Europe). They showed that the populations were structured geographically, where one cluster included head lice from North America and Europe, a second cluster contained head lice from Central America, a third cluster was made up of Asian head lice and the fourth was a cluster of clothing lice from Canada (Ascunce *et al*., 2013b). Principal coordinate analysis and measures of gene flow indicated a close relationship between the clusters from Central America and Asia, suggesting that the Central America cluster is probably of Native American origin (Torroni *et al*., 1993; Kolman *et al*., 1996).

The parallel timing of demographic expansions of human lice and Native Americans, plus the contrasting pattern between the distribution of Clade A and Clade B through the Americas, suggests that human lice have additional information to provide about the peopling of the Americas. Although sampling is somewhat limited, it is also clear that both mitochondrial and microsatellite data support the idea that current populations of human lice in the Americas retain human louse genetic diversity brought by the first peoples. Additionally, sampling lice from Mongolia and Siberia will be particularly important since they are potential source populations for the first peoples in the Americas (Torroni *et al*., 1993; Kolman *et al*., 1996).

10.5   Genomics and the future of studies of host–parasite coevolution

The genomic era provides the ability to tackle new questions about primate/louse evolution due to the reduced cost of next-generation sequencing and access to publicly available genomes. In 2010, Kirkness *et al*. published the genome sequence of the human clothing louse, providing a new perspective of the louse genome (Kirkness *et al*., 2010). Subsequently, Olds *et al*. (2012) published the two human louse transcriptomes

and Shao *et al.* (2012) published additional human louse mitochondrial genomes, providing greater depth to our view of the louse genome. As described in this chapter, we have gained insights from their lice into human migration, contact between extinct and modern human species and use of clothing by humans. Similarly, the study of lice in the genomic era will provide new insights to both louse and human evolution, and in a few cases the interplay between evolution and ecology. In this section we summarize the findings of the human louse genome and transcriptome projects and discuss how genomic data are being applied to understand louse evolution.

Human clothing lice (*Pediculus humanus humanus*) have the smallest known insect genome at 108 megabases (Mb), encoding for 10 773 predicted proteins, 57 microRNAs and 161 tRNAs (Kirkness *et al.*, 2010). The mitochondrial genome of the clothing louse is unique among animals. The typical insect mitochondrial genome is composed of a single circular chromosome encoding 37 genes. However, the clothing louse mitochondrial genome is composed of 18 circular chromosomes, each of which is 3000–4000 bp in length, circular and contains 1–3 genes per chromosome (Shao *et al.*, 2009; Kirkness *et al.*, 2010). Similarly, human head and pubic lice (*Pediculus humanus capitus* and *Phthirus pubis*) also have mitochondrial genomes consisting of 18 circular chromosomes (Shao *et al.*, 2012). This fragmentation of the louse mitochondrial genome is likely caused by the loss of mitochondrial single-stranded binding protein (Cameron *et al.*, 2011; Shao *et al.*, 2012). Olds *et al.* (2012) sequenced the transcriptome of the head and clothing lice. Of the 10 773 genes predicted from the human clothing louse genome, 10 771 were expressed in the human clothing louse and 10 770 in the human head louse. They also detected all predicted microRNAs and one additional one, suggesting gene and microRNA predictions by Kirkness *et al.* (2010) were largely complete and accurate. Olds *et al.* (2012) surveyed transcriptomes for differential expression and found 14 genes with differential expression between human head and clothing lice. Additionally, Olds *et al.* (2012) determined nucleotide sequence divergence between human head louse and clothing louse orthologous protein-coding sequences, finding a rate of 5–15% nucleotide sequence divergence in a few genes, while most showed much lower nucleotide diversity at 0.1–1.3%.

It is unclear if sequence divergence and/or regulatory changes in the louse genome may have influenced shift in louse ecology between head and clothing lice, but it does provide important information on rates of mutation in coding sequences. Rates of nucleotide divergence can be estimated from the most orthologous coding sequence using Olds *et al.*'s (2012) transcriptome sequences and the divergence date for human head and clothing lice (83–170 kya; Toups *et al.*, 2011). This means we can confidently select slow-evolving coding genes and fast-evolving non-coding genes for specific evolutionary questions.

Members of the Reed Lab (University of Florida) are currently employing next-generation sequencing and genomic methods to explore questions about louse population biology and evolutionary history. As described above, there are ancient clades of human head lice and Reed *et al.* (2004) proposed that these clades cospeciated with extinct human species and then moved to modern humans during recent evolutionary history. If true, barriers to reproduction between these lice might have arisen in isolation

that would prevent subsequent interbreeding on modern humans. As described from the human head and clothing louse project, there is 0.1–15% nucleotide diversity between orthologous genes of recently diverged human head and clothing lice (83–170 kya; Toups *et al*., 2011; Olds *et al*., 2012). Consequently, we might expect to see higher levels of nucleotide diversity between clades of human head lice that diverged 900 kya (Reed *et al*., 2004) if barriers to reproduction were present. Microsatellite data from Ascunce *et al*. (2013b) suggest that no such barrier exists. We are re-sequencing thousands of coding markers using next-generation sequencing to determine whether gene flow is occurring between these divergent clades of lice, which will allow us to better determine human migration patterns worldwide. This project uses a reference-based genome assembly not possible prior to the publication of the human body louse genome. Subsequently, we are also using these data to identify additional non-coding and rapidly evolving markers. These genomic data will provide a large set of genomic markers to expand on the questions of evolution and ecology described in this chapter.

10.6   Conclusions

The use of parasites may reveal aspects of host evolution that are not preserved in the archeological record or are poorly resolved in the host DNA. However, great care must be taken not to over-interpret data. Because lice in particular are so closely tied to their host in both ecological and evolutionary time, they have the potential to shed light on not only the host's evolutionary past, but also on host ecology. Two examples of that were given in this chapter. Lice were used to determine when humans began wearing clothing, a technological innovation that changed their ecology dramatically by allowing them to successfully leave Africa for higher latitudes and eventually disperse worldwide. In addition, a host-switch in lice was used to infer that archaic hominids, such as *Australopithecus*, were in close contact with gorillas 3 mya. Traditionally it was thought that humans evolved in a savannah/grassland habitat. Evidence from lice suggests that archaic hominids were using moist tropical forests. Interestingly, upon re-examination of hominin fossils other habitats (woodlands and dry forests) have been suggested as important during hominin evolution (WoldeGabriel *et al*., 1994, 2009; Reed, 1997; Brunet, 2010; Luca *et al*., 2010). No fossils from moist tropical forest habitats have yet been discovered, which is likely due to the difficulty of fossilization in these habitats. Therefore, these lice provide a new hypothesis suggesting the importance of yet another habitat for hominins. It will be interesting to see if this is validated in time by new fossil or other direct human evidence. Great care must be taken not to overreach with interpretations from the parasites of hosts. We are recreating events that took place in the past with data that are known for their stochastic variation. Our subject, the parasite, is one step removed from the host that we are investigating and the parasite is an animal with its own ability to move and adapt, no matter how much we downplay its vagility.

The number of exciting questions in human evolution that lice can address is endless. Human migrations out of Africa occurred through either a northern or southern route.

These routes amounted to a superhighway of humans heading out of Africa and into the Middle East and beyond. Once a better understanding of the current distribution of louse haplotypes is attained, specific questions such as routes out of Africa can be addressed. Testing these questions with molecular data from lice allows us to examine another written record of patterns of human evolution. The genomic tools currently in use by louse researchers worldwide will permit us to move rapidly toward deeper, more meaningful answers to questions of human origins.

Acknowledgments

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