Origin of Clothing Lice Indicates Early Clothing Use by Anatomically Modern Humans in Africa

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Abstract

Clothing use is an important modern behavior that contributed to the successful expansion of humans into higher latitudes and cold climates. Previous research suggests that clothing use originated anywhere between 40,000 and 3 Ma, though there is little direct archaeological, fossil, or genetic evidence to support more specific estimates. Since clothing lice evolved from head louse ancestors once humans adopted clothing, dating the emergence of clothing lice may provide more specific estimates of the origin of clothing use. Here, we use a Bayesian coalescent modeling approach to estimate that clothing lice diverged from head louse ancestors at least by 83,000 and possibly as early as 170,000 years ago. Our analysis suggests that the use of clothing likely originated with anatomically modern humans in Africa and reinforces a broad trend of modern human developments in Africa during the Middle to Late Pleistocene.

Key words: lice, human evolution, isolation with migration.

Hominins migrated out of Africa numerous times over the last two My (reviewed in Stringer 2002). Through the course of these migrations, archaic hominin populations occupied parts of Europe (e.g., Atapuerca, Spain; Carbonell et al. 2008) and Central Asia (e.g., the Altai Mountains, Siberia; Krause et al. 2010) that were cooler and increased their vulnerability to cold stress. Although evidence suggests that archaic hominins established long-lasting populations in these regions, anatomically modern humans (AMHs) likely outcompeted archaic hominins and were able to thrive despite the more seasonally variable climates (Gilligan 2010). A suite of complex behaviors and technologies associated with the transition of archaic to modern *Homo sapiens*, including improved clothing, are credited with facilitating the successful expansion of AMH out of Africa into higher latitudes. Critically, although clothing was likely a necessary technology for AMH, it is unknown whether clothing use originated early enough to play an important role in the expansion of archaic populations out of Africa.

Determining when clothing use began is challenging because early clothing (i.e., animal hides) would degrade rapidly, erasing any direct evidence of clothing use from the Late Pleistocene archeological record. The first evidence of tools used to scrape hides appears ~780 Ka (Carbonell et al. 1999), but these very old dates do not necessarily signify clothing use. Animal hides had other uses besides clothing (e.g., providing shelter), although clothing is thought to be one of the earliest uses for skins. Eyed needles first appear in the archaeological record ~40 Ka (Delson et al. 2000), but these signal the production of more complex clothing (e.g., tailored multilayered garment assemblages), which is undoubtedly a relatively recent innovation (Gilligan 2010). Importantly, the development of clothing likely occurred after humans lost their covering of body hair. Genetic data suggest that body hair was lost ~1.2 Ma (Rogers et al. 2004), and an even older date (3 Ma) was hypothesized for the loss of body hair based on the origin of pubic lice in humans (Reed et al. 2007; Gilligan 2010). These studies suggest that clothing use may have evolved anywhere from 40 Ka to 3 Ma, and given the vastness of this time-span, alternative approaches for estimating the origin of clothing use are essential.

Parasites offer an ideal source of alternative data for determining when clothing use first began in hominins. Parasites can provide novel insights into the evolutionary history of their hosts, especially when the hosts exhibit low levels of genetic variation (Whiteman and Parker 2005). The parasitic sucking lice of primates (Phthiraptera: Anoplura) have cospeciated with their hosts and track both ancient (e.g., human–chimp split 5–7 Ma) and recent (e.g., expansion of AMHs ~100 Ka) events in human evolution (Reed et al. 2004, 2007). The human louse (*Pediculus humanus*) is a single species that occurs as two ecological

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Table 1. Mean, Median, Mode, and 95% HPD for Parameters Estimated in IM.

	95% HPD	Mean	Median	Mode
N_{eHEAD}[a]	**1.991–16.998 × 10^6**	**8.033 × 10^6**	**7.008 × 10^6**	**4.893 × 10^6**
N_{eCLOTH}[b]	**0.461–10.676 × 10^6**	**4.742 × 10^6**	**4.038 × 10^6**	**3.274 × 10^6**
$N_{\mathrm{eANCESTRAL}}$[c]	**0.011–3.161 × 10^6**	**1.317 × 10^6**	**0.934 × 10^6**	**0.011 × 10^6**
$t_{\mathrm{Divergence}}$[d]	**29–691 Ka**	**229 Ka**	**170 Ka**	**83 Ka**
$m_{\mathrm{HEADtoCLOTH}}$[e]	**0.005–1.755**	**0.492**	**0.235**	**0.005**
$m_{\mathrm{CLOTHtoHEAD}}$[f]	**0.495–3.785**	**1.836**	**1.615**	**1.335**
s[g]	**0.001–0.879**	**0.325**	**0.242**	**0.001**

[a] Effective population size of modern head lice (N_{eHEAD}).

[b] Effective population size of modern clothing lice (N_{eCLOTH}).

[c] Effective population size of ancestral head lice population ($N_{\mathrm{eANCESTRAL}}$).

[d] Time of clothing and head lice divergence ($t_{\mathrm{Divergence}}$).

[e] Migration from head to clothing lice populations ($m_{\mathrm{HEADtoCLOTH}}$).

[f] Migration from clothing to head lice populations ($m_{\mathrm{CLOTHtoHEAD}}$).

[g] Proportion of the ancestral head lice population that contributes to the modern head lice population (s).

types (head and clothing lice) exhibiting morphological, behavioral, and ecological differences (Reed et al. 2004; Light et al. 2008). The loss of human body hair restricted *P. humanus* to the head, and the subsequent divergence of the two louse types is unlikely to have begun prior to the availability of the new clothing niche (Burgess 1995; Kittler et al. 2003). Thus, determining when head and clothing lice began to diverge provides a date by which clothing must have been in regular use by humans.

In this study, we analyzed a multilocus data set of clothing and head louse DNA sequences from three nuclear genes (18S ribosomal RNA [rRNA], nuclear elongation factor 1-α [EF-1α], and RNA polymerase II [RPII]) and the mitochondrial gene cytochrome *c* oxidase subunit I (COI). After estimating substitution rates for each locus based on the codivergence of human and chimpanzee lice with their primate hosts (Light and Reed 2009), we employed a multilocus Bayesian isolation-with-migration (IM) coalescent method (Nielsen and Wakeley 2001; Hey and Nielsen 2004; Hey 2005) to jointly estimate the divergence time (t), effective sizes (N_{eHEAD}, N_{eCLOTH}, $N_{\mathrm{eANCESTRAL}}$), and effective migration rates ($m_{\mathrm{HEADtoCLOTH}}$, $m_{\mathrm{CLOTHtoHEAD}}$) of head and clothing louse populations from our combined multilocus data set. This model is ideal for estimating the divergence of head and clothing lice because it assumes an ancestral population (i.e., head lice) diverged at some time t into two daughter populations, which then experience independent rates of exponential growth with migration between populations.

Our results indicate a small effective population size for ancestral *P. humanus* ($N_{\mathrm{eANCESTRAL}}$, median $= 0.934 \times 10^6$; 95% highest probability density [HPD] $= 0.011–3.161 \times 10^6$; table 1), which is consistent with either a bottleneck created by the loss of body hair or a bottleneck imposed in the ancestral human host population. The estimates of effective population size for both head and clothing lice were larger ($N_{\mathrm{eHEAD}} = 7.008 \times 10^6$; 95% HPD $= 1.991–16.998 \times 10^6$ and $N_{\mathrm{eCLOTH}} = 4.038 \times 10^6$; 95% HPD $= 0.461–10.676 \times 10^6$) and consistent with postbottleneck expansions. Estimates of s (~0.24) indicate that a large fraction of the ancestral head louse population initially became clothing lice, perhaps rapidly exploiting new niche space.

Parameter estimates showed elevated rates of continuous migration in the direction of clothing to head lice ($m_{\mathrm{CLOTHtoHEAD}} = 1.615$, 95% HPD $= 0.495–3.785$) but notably less migration in the opposite direction ($m_{\mathrm{HEADtoCLOTH}} = 0.235$, 95% HPD $= 0.005–1.755$). These estimates contradict previous studies that found no migration between head and clothing lice based on microsatellite data (Leo et al. 2005). In addition, the direction of gene flow is unexpected given that head lice can readily colonize the clothing niche (Alpatov and Nastjukova 1955; Levene and Dobzhansky 1959; Li et al. 2010).

The posterior probability distribution for the head and clothing louse divergence time is characterized by a mode (i.e., the single estimate with the highest posterior probability) of 83 Ka and a median value of 170 Ka (95% HPD = 29–691 Ka; fig. 1). These dates are largely consistent with those estimated by Kittler et al. (2003, 2004), who analyzed a single mitochondrial gene using a distance-based method. However, the Bayesian multilocus IM method accounts for uncertainty in the model parameters as well as stochastic variation between loci, which provides a more robust and accurate parameter estimate (Edwards and Beerli 2000).

During the latter part of the Middle Pleistocene (e.g., 83–170 Ka), archaic hominins lived in cold climates in Eurasia, whereas *H. sapiens* was still in Africa. Whether these archaic hominins had clothing is unknown because they left no clothing louse descendents that we can sample among living humans. All modern clothing lice are confined to a single mitochondrial clade that shows a contemporaneous population expansion with modern humans ~100 Ka (Reed et al. 2004, 2007). Therefore, we are left to conclude that regular clothing use must have occurred in *H. sapiens* at least by 83 Ka and possibly as early as 170 Ka. Whether archaic hominins used clothing cannot be assessed from these lice and may require the collection of lice from archaic human remains, which is unlikely.

Even though archaic hominins dispersed into cold climates hundreds of thousands of years before AMH, modern humans are often credited with outcompeting contemporary archaic species due to increased fitness stemming from a suite of "modern" behaviors and technologies that include the use of clothing (Gilligan 2010). Interestingly, we estimated that clothing may have been in use as early as 170 Ka, which corresponds to the rapid onset of

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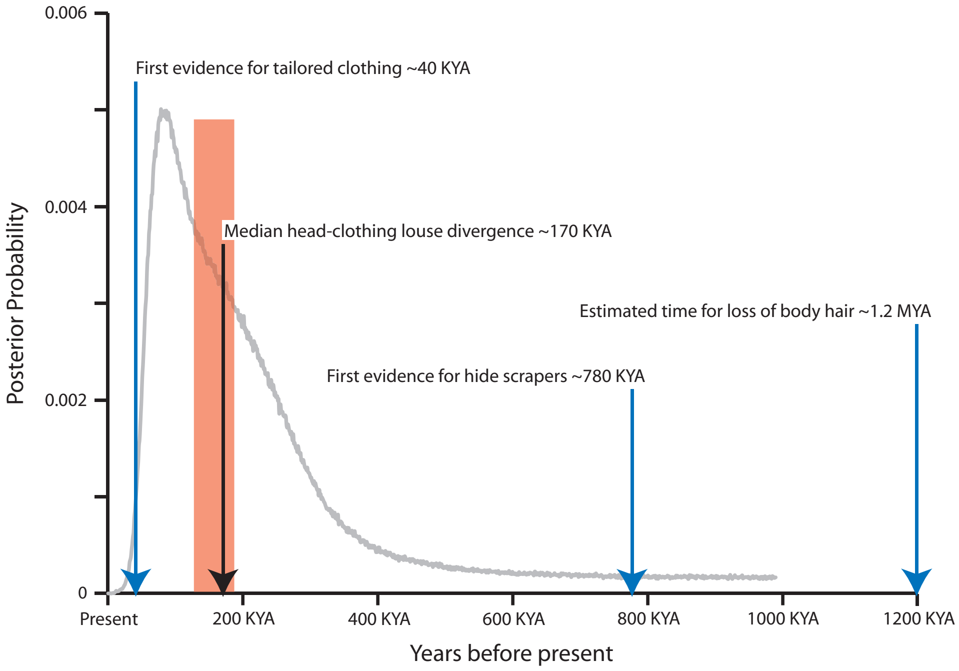

Fig. 1. Divergence time of human head and clothing lice. The posterior distribution for the divergence of head and clothing lice (gray curve) places the median estimate for the origin of clothing lice at 170 Ka (black arrow). This estimate is substantially older than a previous estimate of 30–112 Ka from molecular data (Kittler et al. 2003) and is consistent with the relative antiquity of the first archaeological evidence for hide scrapers ~780 Ka (Carbonell et al. 1999), the loss of human body hair by ~1.2 Ma (Rogers et al. 2004), and the first evidence for tailored clothing ~40 Ka (Delson et al. 2000), which are indicated by blue arrows. Furthermore, the median estimate lies within the ice age coincident with Marine Isotope Stage 6 ~130–190 Ka (EPICA Community Members 2004), indicated by the red-shaded region.

an ice age, Marine Isotope Stage 6 (~190–130 Ka; EPICA Community Members 2004), that would have caused cold stress for populations living outside the tropics and could have led to the initial use of clothing by modern humans. Our estimate for the origin of clothing use suggests that one of the technologies necessary for successful dispersal into colder climates was already available to AMH prior to their emergence out of Africa.

Methods

All available DNA sequences for COI (108 head and 58 clothing lice), 18S rRNA (10 head and 12 clothing lice), EF-1α (25 head and 9 clothing lice), and RPII (25 head and 10 clothing lice) for *P. humanus* and the outgroup *P. schaeffi* (chimpanzee louse) were downloaded from GenBank (available as supplementary table S1, Supplementary Material online). All sequences were aligned by hand using Se-Al v2.01a11 (http://tree.bio.ed.ac.uk/software/seal/), with the 18S rDNA aligned to secondary structure (Gillespie 2004; Gillespie et al. 2005).

Substitution rates (table 2) for the four genes were estimated in BEAST v.1.5.3 (Drummond and Rambaut 2007). Rates were calibrated by placing an exponential prior distribution (lower bound = 5 Ma, mean = 5.5 Ma) on the divergence of *P. humanus* (human) and *P. schaeffi* (chimpanzee) lice that reflects conservatively recent estimates for the divergence of their hosts (Kumar and Hedges 1998). Each gene was analyzed using a range of substitution and clock models, as well as tree priors, with posterior estimates made from the model that best fit the data as determined by marginal likelihoods estimated in the program

Table 2. Models of Substitution, Likelihood Scores, and Mean Substitution Rates Per Gene Calculated in BEAST.

Gene	Substitution Model	Clock Model	Tree Prior	Marginal Likelihood	Mean Substitution Rate (95% HPD)
COI	GTR + CP[a]	UCED[b]	BSP[c]	−1318.728	6.28×10^{-8} ($3.36–9.64 \times 10^{-8}$)
18s rDNA	HKY + G[d] + I[e]	UCED	BSP	−3087.519	7.19×10^{-9} ($3.64–11.01 \times 10^{-9}$)
EF-1α	GTR + CP + G	UCED	BSP	−853.401	7.89×10^{-9} ($3.90–12.622 \times 10^{-9}$)
RPII	GTR + CP + G	UCED	Constant[f]	−1144.325	1.26×10^{-8} ($0.46–2.34 \times 10^{-8}$)

[a] Between site rate variation partitioned by codon position (CP).

[b] Uncorrelated exponentially distributed relaxed clock (UCED, Drummond et al. 2006).

[c] Bayesian skyline plot tree prior (BSP, Drummond et al. 2005).

[d] Gamma distribution of between site rate variation (G).

[e] Invariate proportion of sites (I).

[f] Constant population size tree prior.

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Tracer v1.5 (http://tree.bio.ed.ac.uk/software/tracer). Markov chains were run for at least 100 million generations, sampled every 10,000 generations, and the first 10% of samples were discarded as burn-in. All runs were duplicated to ensure convergence.

Multilocus Bayesian IM coalescent analysis was performed on the *P. humanus* sequences using the program IM (Hey 2005). All analyses used the HKY substitution model, whereas priors on model parameters were broad uniform distributions conservatively estimated from preliminary runs. Markov chains were run for $>$200 million generations and replicated 8 times to ensure convergence. A louse generation time of 21 days (18 generations per year) and the substitution rates in table 2 were used to convert parameter estimates from mutational to demographic units.

Supplementary Material

Supplementary table S1 is available at *Molecular Biology and Evolution* online (http://www.mbe.oxfordjournals.org/).

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