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The long and intimate association between humans and parasites through time

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Abstract

While the interaction between humans and their parasites today is well studied, taking the long view of infection throughout human evolution helps to place the current picture in context and identify trends in infection over time. After considering how early technologies may have facilitated parasite transmission to humans, we explore the association between humans and parasites through time using archaeological and genetic evidence. Techniques such as microscopy, immunoenzymatic assays and DNA analysis have identified a range of protozoa, helminths and ectoparasites in our ancestors. Evidence is discussed for the origins and impact upon societies through time for protozoa causing malaria, leishmaniasis, Chagas' Disease and diarrhoeal illnesses, helminths such as schistosomiasis, soil transmitted helminths, *Taenia* tapeworms, fish tapeworms and liver flukes, and ectoparasites such as fleas, body lice and pubic lice. Prevalence studies show widespread infection for some parasites, such as 36% with falciparum malaria in ancient Egypt, and 40% with Chagas Disease in prehistoric Peru and northern Chile. Humans have been responsible for the inadvertent spread of a range of parasites around the world, ranging from African heirloom parasites with early human migrations to the introduction of malaria and schistosomiasis to

the Americas with the transatlantic slave trade in the 1600s-1800s. It is clear that the epidemics due to bacterial pathogens spread by ectoparasites since the Bronze Age must have had major impacts upon past societies, particularly for bubonic plague and epidemic typhus.

Key words

Evolution; Farming; Paleoparasitology; Paleopathology; Population density; Urbanisation; Zoonoses

Introduction

The influence of evolutionary history is well known to have resulted in major consequences for human health and disease (Benton et al., 2021). Theoretical modelling has proposed that the most important factors influencing host-parasite coevolution are population dynamics and the genetic basis for infection, while other factors such as stochasticity (random effects) and whether time proceeds continuously or in discrete steps are also contributors (Buckingham and Ashby, 2021). The Stockholm Paradigm framework adds further complexity to this model by highlighting the role of climate change in triggering pathogen host-switching and ecological fitting (Brookes et al., 2019).

Integrating evidence from a range of disciplines allows the application of our knowledge of parasite genetic origins and archaeological evidence for infection over time across the world (Ferreira et al., 2014; Mitchell, 2015a; Mitchell, 2023). When we couple this data with our understanding of variation in past human population dynamics, lifestyle, changes to the environment and ancient migrations (Mitchell, 2024a) we will be in a position to explore the long and intimate association between people and parasites through time. The protozoan parasites to be investigated are malaria, leishmaniasis, trypanosomiasis and gastrointestinal pathogens such as *Giardia*, *Entamoeba* and *Cryptosporidium*. Helminths to be assessed include schistosomes, soil transmitted nematodes such as whipworm, roundworm and hookworm, and a range of zoonotic tapeworms and flukes. The ectoparasites under scrutiny are fleas, head lice, body lice and public lice as well as the bacterial pathogens they can transmit.

Human population dynamics through time

Changes in the number of people in a population and the density of people in a geographic area can be described through population dynamics (Henderson and Loreau, 2019). Throughout most of human evolution the population density is thought to have been extremely low. Despite this, early human species such as *Homo erectus* and later *H. sapiens* migrated out of Africa colonising Europe, Asia, Australasia and Oceania, and subsequently the Americas (López et al., 2015). The population density seems to have started to increase in a meaningful way with the development of farming (the Neolithic period). Starting around 10,000 years ago, people developed herding of animals and cultivation of crops such as cereals in the Near East, rice, millet and sorghum in East Asia, and maize and squash in the Americas (Bellwood, 2023). It has been proposed that farming provided foods that could be stored for consumption during predictable periods of resource shortages (such as winter) but could also save lives in times of unexpected scarcity following environmental disasters that might otherwise have led to a population crash (Boone, 2002).

This led to some key changes that are sometimes referred to as the first epidemiological transition (Barrett et al., 1998). Low density hunter gatherer groups caught and ate wild animals which put them at risk of infection by the zoonotic parasite species they contained. Unless they chose to remain associated with an environmental asset such as a cave, such groups may have kept on the move in search of new food sources, so leaving their faecal waste behind. In contrast, early farmers had to stay in one location to tend their crops (early urbanisation), keeping them in contact with their faecal waste. The Neolithic period saw the domestication of certain species of wild animals such as sheep, goats, cattle, pigs and horses to become farm animals. Although hunting wild animals remained common in the

Neolithic (Cummings and Harris, 2011), the wild component of the diet typically reduced over time into the Bronze Age and Iron Age. While this process meant a decreasing injury risk from hunting dangerous wild animals as they farmed their own herds, the risk of zoonotic parasite infection from wild animals was gradually taken over by risk of zoonotic parasites from their farm animals (Ledger and Mitchell, 2022). This interpretation has been highlighted by the recent aDNA evidence indicating that the advent of herding in the Neolithic was associated with a notable increase in the infection of human populations by zoonotic bacterial pathogens (Sikora et al., 2025). For farmers, the combination of increased population size and density, coupled with sedentism and the resulting challenges with the disposal of faecal waste, appear to be key factors leading to change in parasitism in human evolution (Mitchell, 2013). However, the way in which these changes affected parasite infection in early human populations seems to have varied in different regions of the world (Reinhard et al., 2013).

The second epidemiological transition is a term sometimes used to describe the shift away from infectious diseases towards the chronic diseases associated with industrialisation (Barrett et al., 1998). Industrialisation allowed the development of large cities with even greater population size and density, initially resulting in the spread of gastrointestinal infectious diseases (Nagashima, 2004; Davenport et al., 2019). However, the development of science and technology resulted in an understanding of these pathogens and how they are spread, the development of sanitation infrastructure, clean water, techniques to keep food fresh for longer, synthetic crop fertilizers instead of using faecal waste, and medicines to clear parasite infection (Porter, 1999). In consequence most industrialised countries now have populations where parasite infection is very low, although the consequences of the more meagre industrial intestinal microbiome concerns many (Sonneburg and Sonneburg, 2019).

Early technologies and parasite risk

In the Mesolithic and Neolithic periods humans developed technologies that made daily life easier for them. Examples of early technologies developed include sharper stone tools, pottery vessels, weaving equipment, housing, simple boats and crop irrigation (Baker, 2018). While these technologies allowed early peoples to achieve their goals quicker or with less energy expenditure, some technologies had the potential to increase the risk of parasite infection. Weaving clothes would have made a safe home for ectoparasites such as fleas and body lice (Weiss, 2009). If clothes were shared with others then those ectoparasites could spread too. While woven clothes would have been easier to wash than animals skins, it is likely that until such washing involved the use of hot water and soap-like substances, the potential for the washing process to reduce ectoparasites was probably limited.

A number of parasites such as schistosomiasis and dracunculiasis are spread when a host comes into contact with sources of warm still freshwater. To complete their life cycles these helminths require intermediate hosts that live in the water, such as snails for schistosomiasis and copepods for dracunculiasis (Buonfrate et al., 2025; Galán-Puchades, 2020). Crop irrigation not only increases yields but also allows plants to be grown in regions where natural rainfall alone would be insufficient. Manmade irrigation systems appear to have been developed first by farmers in the Near East (Mesopotamia) about 7,500 years ago (Helbaek, 1974; Wilkinson, 1988). However, crop irrigation was later used by communities across the world such as along the River Nile in Africa, and by those growing rice in southeast Asia (Angelakis et al., 2020). If the warm still fresh water became colonised by suitable intermediate hosts, and if an infected person from a different region entered the water and parasite larvae are released, then a new farming community could have become infected.

If early farmers dammed rivers or cut out cisterns from rock to create reservoirs to store water for crop irrigation or drinking in dry months of the year, this could have allowed them to live in regions where they might otherwise not be able. However, such locations act as suitable breeding grounds for mosquitoes. These mosquitoes had the potential to spread parasites such as malaria and lymphatic filariasis, as well as a range of viruses and bacteria (Dahmana and Mediannikov, 2020).

When humans developed early housing to shield themselves from the elements they would have used whatever materials were available to them, with little idea as to whether the new environments they created would have made good homes for vectors that could transmit parasites to them. It has been argued that one of the factors leading to the significant prevalence of Chagas' disease (*Trypanosoma cruzi*) in the prehistoric populations of Peru and Chile was colonization of the early dwellings made from wood and mud that created plenty of cracks where the triatome bug vectors could hide (Rothhammer et al., 1985). The early earth ovens made by the populations of the Lower Pecos Canyonlands in Texas, USA, have also been proposed as locations where humans inadvertently created homes for triatome bugs. The bugs could live in these baking pits and then intermittently feed on nearby people, so spreading Chagas disease there more than a thousand years ago (Reinhard and Araújo, 2015). Therefore we can see that some early technologies might have clear advantages to early societies who developed them, while they would have been unaware of the health consequences from parasite infection that could then ensue.

Protozoan parasites

Malaria

In modern human populations malaria is mainly caused by *Plasmodium falciparum* and *P. vivax*, with *P. malariae*, *P. ovale* and *P. knowlesi* making up the remainder (World Health Organization, 2024). Genetic analysis suggests that *P. falciparum* likely host switched from gorillas to humans in Africa around 60,000-40,000 years ago (Liu et al., 2010; Otto et al., 2018). Arguments have been made that *P. vivax* host switched to humans from chimpanzees in Africa (Liu et al., 2014; Loy et al., 2017) or from macaques in Asia (Daron et al., 2021). *P. malariae* is also thought to have originated in nonhuman primates in Africa and host switched to humans, although the species involved and timing is less clear (Rutledge et al., 2017). Malaria has been shown to subsequently spread to the Americas with the transatlantic slave trade of the 1600s to 1800s. Strains of falciparum malaria found in the areas of West Africa where the Portuguese obtained their slaves match the strains found in Portuguese colonies in South America (Brazil) today. Similarly, strains found in areas of West Africa where the Spanish obtained their slaves match those found in areas of the Americas previously administered by the Spanish (Caribbean, Mexico, and northern parts of South America) (Yalcindag et al., 2012). More recent work suggests that *P. vivax* was transferred to the Americas by European migrants from the 1500s onwards (Megan et al., 2024).

Archaeological evidence for malaria can be found in preserved malarial DNA, antigens, and in the skeletal changes of chronic anaemia (such as cribra orbitalia) caused by malaria. Malaria DNA is best preserved in regions where mummies survive, but is occasionally recovered in human skeletal remains. As falciparum malaria originated in Africa, then we might expect the earliest evidence to come from civilizations in Africa. Mummies from ancient Egypt and Nubia (Sudan) dating from 3200 BCE-124 CE have been found positive for *P. falciparum* using both immunoenzymatic assay and aDNA. If we include studies of both mummies and skeletons (221 individuals), 22% were positive. However, malarial DNA does not survive as well in ancient human skeletal remains compared with in mummified tissues, so if only studies of mummies are included (130 individuals) then 36% were positive (Mitchell, 2024b).

A metagenomic study interrogating the previously sequenced genomes of over 10,000 ancient individuals from across the world has identified 36 early cases of malaria, which then underwent further enrichment. The most widely found species was *P. vivax*, being identified in Europe (Germany and Spain) and Asia (Russia) from the 4th-3rd millennium BCE (Neolithic period). *P. falciparum* was identified in Nepal dating to 804-765 BCE, and Germany in 350-250 BCE (Iron Age). In the last thousand years many more cases of these two species were identified, as well as cases of *P. malariae* in Asia (Megan et al., 2024). It should be noted that ancient Egypt was the only region of Africa included in the study, so we remain unsure of the date of host switching from non-human primates to humans in sub-Saharan Africa.

Analysis of the dental pulp of the teeth of 39 individuals from Versailles in northern France, dating to the 6th century CE (Merovingian period), has also detected malaria. ELISA detected *Plasmodium* antigens in 36% of individuals, with most infections being *P. vivax* but some *P. falciparum* was also present (Boualam et al., 2023). Where genetic and antigen analysis is not possible, skeletal lesions commonly caused by chronic anaemia (such as cribra orbitalia) can sometimes be used as a proxy indicator for the presence of malaria in past populations, as malaria commonly leads to anaemia. Comparison of human skeletal remains of 5,802 individuals from Anglo-Saxon England (410-1050 CE) found those who lived in low-lying marshy regions were significantly more likely to have cribra orbitalia that those who lived at higher elevations where marshes were not present. It was argued that malaria, likely *P. vivax*, led to long term anaemia in those who lived in the marshy regions, so explaining the skeletal changes noted (Gowland and Western, 2012).

Unlike most other parasites that affect humans, malaria has triggered the rise of a range of genetic mutations that reduce the risk of a person dying from infection. These include mutations to HbS, HbC, HbE, alpha and beta globin chains, glucose-6-phosphate dehydrogenase and Duffy-negative allele (Taylor et al., 2012). While being heterozygous for these mutations can reduce the risk of death from malaria, being homozygous will lead to death even in the absence of malaria in cases of sickle cell disease and thalassaemia. The driver for passing on these mutations may well be that malaria tends to kill infants and children (before they can reproduce and pass their genes on to the next generation), while those heterozygous for the mutation survive to adulthood and do pass on those genes to their offspring. Archaeological evidence for these gene mutations can be found in the Roman period. A child from the 5th century BCE cemetery at Lugano was found to have the gene mutation for glucose-6-phosphate dehydrogenase deficiency (G6PD med variant) (Sallares et al., 2004). The genome of an individual from the 1st-3rd century necropolis at Monte Carru in Sardinia included the gene mutation for beta thalassaemia (Viganó et al., 2017).

Chagas disease

Trypanosoma cruzi is spread to humans through the bite of triatome bugs and infection is lifelong. Following a period of acute infection with fever, around 30-40% of people develop chronic disease with eventual death from cardiomyopathy, irregular heart rhythm and megaviscera, as dilated intestines can prevent swallowing or defecation (Pérez-Molina and Molina, 2018; Hochberg and Montgomery, 2023). This zoonosis is only endemic to South and Central America, so must have originated there.

Archaeological evidence takes the form of both mummies with signs of megaviscera such as dilated heart and intestines, and ancient DNA. An autopsy study analysed thirty five mummies dating to 470 BCE to 600 CE from the Atacama Desert in northern Chile (although only 22 were in a good state). They found 41% demonstrated signs of megacolon, 9% had cardiomegaly and 4.5% had megaoesophagus (Rothhammer et al., 1985). If 30-40% of people infected today develop chronic disease with mega-syndromes, this might indicated that virtually everyone in the prehistoric population at Quebrada de Tarapacá had been infected. A more recent large study focussed on aDNA to investigate 283 mummies from southern Peru and northern Chile, dating from 7050 BCE to 1800 CE. In the Chinchorro period (7050-3000 BCE) 39% of the 18 mummies tested were positive for *T. cruzi* aDNA. In the Chiribaya period mummies (1050-1250 CE) 47% of the 70 individuals were positive. In the Inca period mummies (1450-1550 CE) 50% of the 26 individuals were positive. If data for the entire group of 283 mummies from all time periods are amalgamated, the overall prevalence for infection was 40% (Aufdeheide et al., 2004). Bearing in mind many of these samples are extremely ancient, this should be regarded as a minimum prevalence since some individuals may have been infected but the trypanosome DNA not survive well enough to be detected by the study. While the best ancient evidence for Chagas disease comes from the Atacama desert of Peru and Chile due to the large number of naturally preserved mummies there, trypanosomiasis appears to have been endemic in prehistoric populations throughout central America as well. For example, megacolon from Chagas disease has been identified in the mummy from a hunter gatherer population from the Chihuahua Desert on the border between Texas and Mexico dating to 1,150 years ago (Reinhard et al., 2003).

Leishmaniasis

Fossil protozoa from the genus *Paleoleishmania* have been identified in the gut of a sand fly trapped in Burmese amber dating to 100 million years ago, in the early Cretaceous period (Poinar and Poinar, 2004; Poinar, 2007). A further example of *Palaeoleishmania* was found in a sand fly in amber from the Dominican Republic dating to 20-30 million years ago (Poinar, 2008). *Leishmania* is thought to have originated in the Gondwana supercontinent, and then when the land mass broke up to form modern continents during the Jurassic period further evolution of the parasite led to the different species we know today (Steverding, 2017). The modern forms that cause disease in humans are cutaneous, mucocutaneous and visceral leishmaniasis, which can be found in many tropical and subtropical regions of the world today where sand flies are endemic (World Health Organization, 2010, 91-96; Pace, 2014).

Archaeological evidence for leishmaniasis in past populations can be found in mummies, human skeletal remains and pottery sculptures. In mummies from ancient Egypt and Nubia (Sudan) aDNA analysis using PCR identified the kinetoplastid mitochondrial DNA of *L. donovani* (visceral leishmaniasis) (Zink et al., 2006). In the 71 Nubian mummies which dated from 550-1500 CE, nine (12.9%) tested positive. Of the 91 Egyptian mummies which dated to 2050-500 BCE, four tested positive. All of these four were from the Middle Kingdom, a time when there was regular trade between Egypt and Nubia. Egyptian mummies from earlier and later time periods were negative. Therefore it was proposed that leishmaniasis was not endemic in ancient Egypt, but could be contracted by Egyptians who travelled to Nubia where it was endemic (Zink et al., 2006).

Further evidence for visceral leishmaniasis has been found in Italy dating to the renaissance. Eleonora of Toledo (1522-1562) married into the politically powerful Medici family. Her skeletal remains were found to be positive for *L. infantum* using both PCR for the kinetoplastid mitochondrial DNA and also a protein assay detecting IgG against *L. infantum* using Western blot gel electrophoresis. Autopsy performed by doctors immediately after her death reported enlarged liver and spleen, which we now know would be compatible with her visceral leishmaniasis (Nerlich et al., 2012).

In South America a different form of leishmaniasis appears to have infected the ancient populations (Novo et al., 2016). Human skeletal remains from San Pedro de Atacama in Chile, dating to around 1000 years ago, were noted to include individuals with destructive lesions to the nose and maxilla compatible with mucocutaneous leishmaniasis. aDNA was extracted from bone at the margins of the lesions and the analysis indicated *L. viannia* (Costa et al., 2009; Marsteller et al., 2011). The prevalence of individuals with bony lesions was 0.5%, although the overall prevalence including those with only soft tissue lesions would be expected to be higher. Pottery sculptures from the 1st-8th century CE Moche (Mochica) culture from northern Peru include a good number with the appearance of destructive lesions of the nose that have the appearance of mucocutaneous leishmaniasis (Urteaga-Ballon, 1991). The Inca civilization also appears to have been affected by mucocutaneous leishmaniasis. Analysis of 241 individuals from Makatampu dating to the 15th and 16th centuries CE showed five cases (2%) had destructive cranial lesions compatible with leishmaniasis (Altamirano Enciso et al., 2001).

Gastrointestinal protozoa

Diarrhoeal illness can be triggered by a range of protozoa such as *Entamoeba histolytica*, *Giardia duodenalis* and *Cryptosporidium* spp. Genetic analyses have identified a variety of differing genotypes and interplay between human and non-human infection, but so far has not been able to fully understand the evolutionary origins of these protozoa (Weedall and Hall, 2011; Cui et al. 2019; Ryan et al., 2021). However, archaeological evidence employing microscopy and ELISA has determined patterns that would indicate their origins.

Cryptosporidium sp. has been identified in 600-800 CE Mexico (Morrow and Reinhard, 2016) Since tests for the organism have regularly been negative in archaeological faecal samples from Europe and Asia this would suggest the parasite may well have originated in the Americas. The earliest evidence for *Entamoeba histolytica* is from Greece during the Neolithic (5000-2000 BCE)(Le Bailly and Bouchet, 2006) and it has been found in many sites in Europe and the Near East during the Roman and medieval periods (Le Bailly et al. 2016; Wang et al., 2024). This would suggest that this is an Old World parasite and since it is found in non-human primates in Africa it may well have its origins there, before being spread worldwide by human migrations (Mitchell, 2013; Steverding, 2025). The earliest evidence so far found for *Giardia* infection in humans is from two Iron Age latrines in Jerusalem dating to the 7th-6th century BCE (Mitchell et al., 2023). The most ancient written descriptions of diarrhoeal illness come from early texts from Mesopotamia dating to the 2nd and 1st millennium BCE. The Assyrian and Babylonian medical texts include descriptions such as 'his stomach is colicky and has flowing of the bowels', and 'his insides are cramped, his bowels are loose' (Scurlock and Andersen, 2005). While a range of bacteria and viruses can cause diarrhoeal illness, having shown that *Giardia* was present in the Near East in the first millennium BCE this would indicate that a proportion of such cases may have been due to *Giardia*. It has been found at a range of Roman and medieval sites in Europe and the Near East (Williams et al., 2017; Ledger et al., 2021; Rabinow et al., 2024). *Giardia* has also been detected in a coprolite from a cave in Tennessee, USA, dating to 600-0 BCE (Faulkner et al., 1989). As *Giardia* is found in many different mammal species, it possible that it spread around the world long ago and as a zoonosis was able to transfer between animals and humans wherever humans migrated.

Helminths

Schistosomiasis

Blood flukes of the *Schistosoma* genus infect a range of animals across the world, with some species damaging the urological system and others the gastrointestinal system. Genetic analysis of ribosomal RNA genes indicates an ancient origin in Asia and a basal lineage of *Schistosoma japonicum* (Attwood et al., 2007). It has been proposed that during the middle Miocene (16-11 million years ago) mammals moved from Asia to Africa, transferring the genus there and allowed the development of *S. mansoni* and *S. haematobium* that affect humans and other primates (Lawton et al., 2011). Schistosomes were only introduced into the Americas with the transatlantic movement of enslaved people from Africa to the New World between the 1600s and 1800s. Analysis of the genomes of *S. mansoni* in Africa with that of *S. mansoni* endemic in the islands of the French Caribbean indicates that the strains found in former French colonies in west Africa matches those in the Caribbean (Crellen et al., 2016). This spread was made possible by the presence of *Biomphalaria glabrata* freshwater snails in

Caribbean islands that were physiologically close enough to the African intermediate host *B. pfeifferi* snails for *S. mansoni* to complete its life cycle (Morgan et al., 2001).

Archaeological evidence for schistosomiasis includes their eggs, antigens, aDNA and the skeletal changes of chronic anaemia. The earliest evidence so far identified dates from 4500-4000 BCE, from the site of Tell Zeidan in Syria (Anastasiou et al., 2014). This was an early farming settlement in the Euphrates river valley. An egg of a terminal spined schistosome was noted on microscopy of pelvic sediment of a child buried at the site, and subsequent aDNA analysis at the McMaster University Ancient DNA Laboratory identified 73 reads matching *S. haematobium*. Man-made crop irrigation systems were first developed in the Middle East around 5,500 BCE to improve crop productivity (Haelbeck, 1972). As schistosomiasis can be contracted by people wading in fresh water where *Bulinus* sp. intermediate host snails are present, the development of crop irrigation appears to be the earliest evidence so far for a manmade technology resulting in increased risk of infectious disease in humans (Mitchell, 2023, p.19). Further evidence for early schistosomiasis in the Near East region comes from the ancient civilizations of Egypt and Nubia, where crop irrigation was used by farmers along the River Nile. The first ever published paleoparasitological study reported the eggs of *S. haematobium* during microscopic analysis of the kidneys of two out of three 20th Dynasty mummies (Ruffer, 1910). Subsequent research employing microscopy, aDNA and ELISA for schistosome antigens in over 200 mummies has shown how widespread schistosomiasis appears to have been, with prevalence ranging from 10%-65% in different populations (Mitchell, 2024b).

In East Asia the earliest evidence for oriental schistosomiasis comes from naturally preserved mummies from ancient China. For example, *S. japonicum* eggs have been identified in the Phoenix Hill mummy and the Changsha mummy in Huibei Province, both dating to the Han Dynasty (206 BCE-220 CE) (Yeh and Mitchell, 2016). Although the region's schistosomiasis is named *S. japonicum*, this evidence would suggest that the disease did not originate in Japan but only spread there at a later date.

Soil transmitted helminths

Whipworm (*Trichuris trichiura*) has been found in the faecal remains of most early human populations around the world, and *Trichuris* sp. is also found in non-human primates in Africa. Early archaeological examples in humans include 7800-7300 BCE Cyprus (Harter-Lailheugue et al., 2005), 6410-6300 BCE Turkey (Ledger et al., 2019a), 5840-5620 BCE Britain (Dark, 2004) and 7830-7630 BCE Argentina (Fugassa et al., 2010). This would suggest that whipworm is an heirloom parasite that evolved in primates and early human ancestors in Africa and then spread around the world as humans migrated (Mitchell, 2013).

The species of whipworm typically found in humans is very similar to *T. suis*, the form typically found in pigs. Pigs are known for coprophagy, where they eat their own faeces or those of other animals to gain nutrients from them (Soave and Brand, 1991). This has the potential to act as a mode of spread for intestinal parasites. Genetic analysis of modern strains of whipworm in humans and pigs across the world has shown many similarities. However, interpretation of the genetic differences identified indicates that when humans domesticated pigs, their similar physiology meant that pigs contracted human whipworm, probably in China. *T. suis* appears to then have been spread around the world when humans transported infected pigs to other continents (Hawash et al., 2016).

Roundworm (*Ascaris lumbricoides*) was present in humans from early prehistory, as demonstrated by palaeolithic evidence for human infection found in layers dated to 28,000-22,000 BCE in a cave at Arcy-sur-Cure in France (Bouchet et al., 1996). Roundworm eggs have also been recovered from the pelvic sediment of burials from China dating to 770-403 BCE (Wei et al., 2012), 620-290 BCE America (Fry, 1974), and 6860-6740 BCE Brazil (Leles et al., 2008).

Infection by roundworm in humans and pigs share many similarities. Some have argued that *A. lumbricoides* and *A. suum* are the same species (Leles et al., 2012), and genetic analyses indicate that they represent a genetic complex with considerable hybridisation (Easton et al., 2020). In the same way that occurred with whipworm, it seems likely that *Ascaris lumbricoides* originated in primates and early humans in Africa, was spread around the world with early human migrations, and host switched to pigs once they were domesticated by humans (Mitchell, 2013).

Hookworm (*Ankylostoma duodenalis* and *Necator americanus*) produce fragile eggs that do not survive as well in archaeological contexts as do the robust eggs of helminths such as *Ascaris*, *Trichuris* and *Taenia*. However, they have been identified in some early societies such as in Chile, Brazil and Argentina dating to several thousand years ago (Gonçalves et al., 2003). *Necator* and *Ancylostoma* infect gorillas, chimpanzees, baboons and a range of monkeys in Africa (Seguel and Gottdenker, 2017). This would suggest that it is an heirloom parasite that has infected humans throughout our evolution (Mitchell, 2013).

Lifestyle has been identified as having a significant effect upon infection rates by whipworm, roundworm, hookworm and pathogenic amoebae. Modern research has shown that when nomadic hunter-gatherer groups settle to take up farming, all these intestinal parasites become much more common (Dounias and Froment, 2006). The same pattern is seen in past populations, where from the Bronze Age onwards zoonotic parasites from eating wild animals become less common, and helminths spread by poor sanitation, such as whipworm and roundworm, are much more widespread (Mitchell, 2017; Reinhard et al., 2013; Yeh and Mitchell, 2016). In the Americas pinworm has also been shown to become much more widespread with the development of farming and crowded settlements with communal sleeping arrangements (Camacho and Reinhard, 2020)

Infections with high worm burdens of whipworm, roundworm and hookworm may cause chronic anaemia, abdominal cramps, diarrhoea, and affect growth in children (Jourdan et al., 2018). Therefore we would expect these parasites to have had a considerable impact upon those living in past civilizations across the world that practiced farming, underwent urbanisation, and experienced increasing population density (Mitchell, 2023).

Taenia tapeworms

Taenia are contracted by humans when they consume raw or undercooked meat. *T. solium* and *T. asiatica* are transmitted in pork, while *T. saginata* is in beef. These species are specific to the human host, but understanding their relationship with other species of *Taenia* can help determine their origins. Molecular phylogenetic studies indicate that *T. saginata* and *T. asiatica* are closely related to species of *Taenia* that infect hyenas in Africa, while *T. solium* is more closely related to *T. arctos* which infects brown bears. Therefore it has been suggested that beef and Asiatic tapeworms in humans probably originated in Africa, while pork tapeworm may have originated separately in Asia (Terefe et al., 2014). Comparison of the genomes of *T. saginata* and *T. asiatica* has estimated that the two species diverged around 1.1 million years ago. Therefore *T. saginata* may have been carried to Asia from Africa by migrating archaic humans (such as *Homo erectus*), becoming introduced to wild pig populations there, and evolved into *T. asiatica* (Wang et al., 2016). The archaeological evidence supports such a hypothesis, as *Taenia* eggs have been recovered in human contexts from ancient Egypt and Nubia in Africa (Mitchell, 2024b) as well as across Europe and Asia in prehistory (Anastasiou, 2015; Seo and Shin, 2015).

Fish tapeworms

Broad tapeworms (Diphyllobothriidae) affecting humans can be caused by a range of species in different regions of the world, including those in the genus *Dibothriocephalus*, *Diphyllobothrium* and *Adenocephalus*. They are contracted by eating raw, smoked, pickled, dried or undercooked fish. These parasites can infect a range of fish eating mammals and birds as well as humans (Scholz et al., 2019). Archaeological evidence for fish tapeworm infection in human faeces has been found in early societies in Africa, Europe, Asia and the Americas, indicating that humans have been at risk of infection throughout our history (Le Bailly and Bouchet, 2013). Both geography and dietary preferences had significant impact upon transmission in past societies. Those species relying on freshwater fish for their life cycle (such as *Dibothriocephalus dendriticus and D. latus*) were much more common throughout history in well-watered regions of northern Europe compared with the hotter, dryer regions of southern Europe (Knorr et al., 2019). Trends in fish tapeworm infection over time have also been noted. It was relatively widespread in Europe during the Neolithic and Bronze Age when people had a mixed diet from farming and hunting wild foods, but then appears to have been less common as parasites spread by poor sanitation dominated during the Roman Period, before becoming more common again in the medieval period (Ledger et al., 2025). In the medieval period fish tapeworm infection was noteworthy in populations living along the river systems of northern Europe (Graff et al., 2020; Rabinow et al., 2024; Rocha et al., 2006; Yeh et al., 2014). These trends over time might reflect changes in preferences for eating fresh water fish compared with sea fish, or the consumption of fish in medieval Europe on fast days when meat consumption was not permitted by the catholic church (Mitchell, 2015b).

Liver flukes

A range of flukes are known to have infected past human populations, such as the intestinal fluke *Echinostoma* in Bronze Age Britain and medieval Belgium (Ledger et al., 2019b; Rabinow et al. 2023), *Fasciolopsis buski* in Ming Dynasty China (Yeh and Mitchell, 2016) and the lung flukes *Paragonimus and Metagonimus* in first millennium CE Korea and Japan (Matsui et al., 2003; Seo et al., 2017). However, here we will consider the group of flukes that have evolved to infect the liver, as they are linked with a number of fascinating stories (Wang and Mitchell, 2022).

Some are contracted by eating raw or undercooked freshwater fish, the most important being Chinese liver fluke (*Clonorchis sinensis*), Southeast Asian liver fluke (*Opisthorchis viverrini*) and Cat liver fluke (*O. felineus*). Others are contracted by eating plants where the intermediate form of the parasites are located, such as sheep liver fluke (*Fasciola hepatica*), giant liver fluke (*F. gigantica*), and the lancet liver fluke (*Dicrocoelium dendriticum*) (Harrington et al., 2017). All these flukes are zoonoses that infect wild mammals, but were also able to infect humans when early migrations led them out of Africa to regions of the planet where these helminths are endemic.

Many have speculated over the years that the two thousand year old Silk Route from China to the Eastern Mediterranean might have been responsible for the spread of infectious diseases (Monot et al., 2009; Simonson et al., 2009; Schmid et al., 2015). However, the first archaeological proof we have for the movement of people along the Silk Route with pathogens is that of Chinese liver fluke. The Silk Route was established during the Han Dynasty, and numerous relay stations were constructed to act as accommodation for government officials and provide a change of horses for the postal service (Hansen, 2012). Xuanquanzhi relay station dates from 111 BCE to 109 CE, and was located at Dunhuang, in the arid northwest of China (He, 2000). Being next to the Taklamakan Desert, the area is so dry that the personal hygiene sticks recovered from excavation of its latrines still has cloth and dried faeces adherent to them. Microscopy showed the eggs of roundworm, whipworm, *Taenia* tapeworm and Chinese liver fluke. The closest regions of China with wetlands where Chinese liver fluke could complete its life cycle are 1500km away from Dunhuang. This indicates that someone who used the latrine at this relay station as they travelled the Silk

Route had previously eaten raw or undercooked fish in eastern or southern China, when they must have become infected with the liver fluke (Yeh et al., 2016).

Chinese liver fluke has also been involved with trans-oceanic migrations. In the 1800s a shortage of manual labour on the west coast of America led to migrants from China traveling across the Pacific to work in hotels, laundries and farms. Wong Nim was a businessman of Chinese ancestry who in 1900 owned property in San Bernardino in California, where he housed Chinese migrants. Analysis of the latrines there showed the eggs of roundworm, whipworm and Chinese liver fluke (Reinhard et al., 2008). As the type of water snails required for Chinese liver fluke to complete its life cycle are not present in the Americas, the fluke could not become endemic there. However, the presence of the eggs in a property associated with Chinese migrants acts as a record of this long distance migration.

Cat liver fluke eggs have been recovered at a series of archaeological sites in northern Siberia (Russia) during the medieval period onwards, indicating the consumption of raw or undercooked fish by the populations living there (Slephchenko et al. 2019). One intriguing site is that of Stadukhinsky Fort in eastern Siberia, which dates from the 17th and 18th centuries. This fort was located at a summer port so fur trappers could export their animal furs before the winter ice cut off the sea route. The appearance of the Opisthorchiidae eggs found at its excavation would be compatible with either cat liver fluke or Chinese liver fluke. Cat liver fluke is endemic in western Siberia but not eastern Siberia. If these eggs were those of cat liver fluke, it would indicate the migration of trappers and sailors from western Siberia to eastern Siberia to staff the fort. However, Chinese pottery, smoking pipes and other material culture were recovered during the fort’s excavation. If Chinese merchants came to trade at the fort, or if Russians headed south to trade in China, it is possible that these Opisthorchiidae eggs represent Chinese liver fluke (Slepchenko et al., 2022).

Ectoparasites

Fleas, head lice, body lice and pubic lice have infected humans and their ancestors through deep time. Some of these have the ability to transmit pathogens that have led to major health consequences for past societies. Genome sequencing leads to estimations that around 11.5 million years ago the lineage that would become the human pubic louse (*Pthirus pubis*) diverged from an ancestor of the chimpanzee and human body louse and head louse in Africa. The lineage that would later become the human body louse (*P. humanus*) is thought to have then diverged from the chimpanzee body louse (*P. schaeffi*) around 5.6 million years ago (Reed et al., 2004). Different lineages (clades) of head lice are found in different geographic regions, which has been interpreted to indicate that one lineage was spread from Africa by archaic human species (such as *Homo erectus*) before modern humans (*H. sapiens*) evolved and spread with their own lice lineages (Reed et al., 2004; Light et al., 2008; Boutellis et al., 2014). The potential effect of the introduction of clothing by early modern humans upon the success of body lice has also been considered (Weiss, 2007).

The prevalence of head lice in past populations has been estimated from careful examination of the scalp and hair of mummies. One project looked at 218 mummies from Wadi Halfa in ancient Nubia (Sudan) dating from 350-550 CE, and found that 40% were positive for head lice (Armelagos, 1969). In prehistoric Peru 79% of 63 Chinchorro period mummies (3000-1000 BCE) were positive for head lice (Arriaza et al., 2013) and 44% of 75 Chiribaya period mummies (1000-1250 CE) were positive (Reinhard and Buikstra, 2003). This highlights how widespread head lice must have been in ancient cultures.

Human fleas (*Pulex irritans*) and body lice have been shown to be efficient transmitters of *Yersinia pestis*, the pathogen responsible for bubonic plague (Bland et al., 2024). Plague genomes from the Neolithic dating to around 3,000 BCE do not appear to have the necessary features for flea-based transmission (Susat et al., 2021), but the *ymt* flea adaptation locus was present by the Bronze Age (Spyrou et al., 2018; Valtueña et al., 2022). Moving between wild rodent reservoirs and human populations, plague has resulted in at least three worldwide pandemics, with the Plague of Justinian in the 6th century CE, the Black Death in the 14th century, and the third pandemic from the late 19th century (Barbieri et al., 2021).

Another pathogen spread by human ectoparasites is that of *Borrelia recurrentis*, which causes louse-borne relapsing fever. This spirochaete is spread when the human body louse feeds or when its faeces are rubbed into areas of broken skin. Untreated fatality rates can reach 40% in some epidemics (Warrell, 2019). Ancient DNA analysis of human skeletal remains has identified cases of *B. recurrentis* across Asia dating back to 3,000 BCE, becoming fairly widespread in Europe during the medieval period (Sikora et al., 2025).

Individuals buried in a medieval mass grave at Bondy in France have been analysed for the aDNA of pathogens to determine the cause of the fatalities. From 14 skeletons whose teeth were tested, two were positive for the aDNA of *Yersinia pestis*, making it likely that the mass grave dates to a bubonic plague outbreak. Interestingly, three individuals were positive for *Bartonella quintana*, the bacteria that causes trench fever which is spread by the bites of body lice (Tran et al., 2011a). Further work by the same team studied 173 individuals from mass graves dating to the 14th and 16th centuries from Venice, Italy. *Y. pestis* aDNA was identified in three individuals and *B. quintana* in five individuals (Tran et al., 2011b). Such findings highlight how ectoparasites were spreading multiple bacterial pathogens in medieval and renaissance Europe.

Head lice have been found trapped between the teeth of Roman period wooden combs recovered from the Dead Sea and Judean Desert in Israel. A study analysing the aDNA of twenty four such head lice identified *Acinetobacter baumannii* in three of them (12.5%) (Amanzougaghene et al., 2016). Infection by this bacterium can cause fevers, sweats, a rash and septicaemia, and is a challenging cause of multidrug resistant hospital acquired infection today (Antunes et al., 2014).

Body lice were extracted from mass graves of French soldiers dug at Vilnius in Lithuania during their retreat from Russia in 1812 during the Napleonic Wars. From five lice recovered, three were found positive for the aDNA of *Bartonella quintana* (trench fever). Thirty five burials of French soldiers underwent DNA analysis of their teeth. Seven were positive for *B. quintana*, and three were positive for *Rickettsia prowazeckii* which causes epidemic typhus (Raoult et al., 2006). Such results highlight how human ectoparasites have acted as significant vectors for the spread of bacterial pathogens at major events during history.

Conclusion

Here we have explored the evidence showing how there has been a long and intimate association between humans and parasites throughout our evolution. It can be seen that a range of heirloom parasites infected early humans and non-human primates, while other zoonotic parasites host switched from a range of mammals to humans as early people migrated to new regions of the planet. This interconnectedness between humans and other animals remains a focus for the One Health approach to medicine today. Changes in lifestyle associated with the three epidemiological transitions had major impacts upon risk of parasite transmission to and between our ancestors. Mobile hunter-gatherers, settled farmers, urbanised town-dwellers and modern industrialised societies all experienced different patterns of parasite infection. Early technologies allowed humans to live in new regions and protected them against environmental catastrophes such as droughts and crop failures, but sometimes these technologies also allowed new parasite species to become introduced in those societies. We can track how past human migrations have moved parasites around the planet by exploring genetic variation in modern parasites and also assessing patterns in space and time in the archaeological evidence for key species. Where they were endemic, protozoan parasite infections such as malaria, leishmaniasis and Chagas Disease likely caused a greater disease burden to early societies than did intestinal helminths. In contrast to the relatively mild health impact of human ectoparasites themselves, from the Bronze Age we see how bacterial pathogens utilised ectoparasites to infect millions of humans over the millennia, leading to numerous deaths from a range of epidemic diseases such as bubonic plague, louse-borne relapsing fever, trench fever and epidemic typhus. The burden of parasite infection upon the success of ancient civilizations seems to have been notable, and helps us to understand the ways in which parasites have moulded human history.

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Graphical Abstract