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Tracing Zoonotic Parasite Infections Throughout Human Evolution

Marissa L. Ledger

Department of Archaeology, University of Cambridge, The Henry Wellcome Building,
Fitzwilliam Street, Cambridge CB2 1QH, UK
mll45@cam.ac.uk

Piers D. Mitchell*

Department of Archaeology, University of Cambridge, The Henry Wellcome Building,
Fitzwilliam Street, Cambridge CB2 1QH, UK
pdm39@cam.ac.uk

*corresponding author

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ABSTRACT

Parasites are useful pathogens to explore human-animal interactions because they have diverse life cycles that often rely on both as hosts. Moreover, some species are not host specific and are transmitted between animals and humans. Today most emerging infections are zoonoses. Here, we take a specific look at the emergence and re-emergence of zoonotic parasites throughout hominin evolution and consider evolutionary, cultural, and ecological factors involved in this. We combine genetic studies focused on molecular phylogenetic reconstructions, most often using the ribosomal RNA gene unit and mitochondrial genes from modern parasites, archaeological evidence in the form of preserved parasite eggs and antigens in skeletal and mummified remains, and modern epidemiological data to explore parasite infections throughout hominin evolution. We point out the considerably ancient origins of some key zoonotic parasites and their long coevolutionary history with humans, and discuss factors contributing to the presence of many zoonotic parasites in the past and today including dietary preferences, urbanization, waste disposal, and the population density of both humans and domesticated animals.

1. Introduction

Zoonoses can be defined as those infections which are naturally transmitted from nonhuman animals to humans. In the case of intestinal parasites, these may be infections where humans are a necessary or sole definitive host for a parasite that needs other animals as intermediate hosts (e.g. *Taenia* tapeworms). They may also be infections that occur when humans interact with animals and incidentally become infected with generalist parasites that these animals carry. In the twenty first century the majority of emerging infectious diseases are zoonotic (Jones et al., 2008). Similarly some re-emerging zoonotic diseases such as cysticercosis and echinococcosis are becoming increasingly problematic (Webster et al., 2016). Despite a long evolutionary history with humans, many zoonotic parasites have low host specificity. This allows them to infect different mammalian species, including humans, relatively easily. Many of the more specialized parasites that prefer humans as their definitive host nevertheless require one or more animal intermediate hosts to complete their life cycle. A list of some of the more common zoonotic parasites today is given in Table 1. Perrin et al. (2010) estimated that only 15% of parasites known to infect humans are human specific, and the remaining 85% are shared with animals. Here we explore evidence for zoonotic endoparasites globally throughout hominin evolution to identify evolutionary, cultural, and ecological factors involved in the emergence and re-emergence of zoonotic parasite

infections. Genetic evidence for parasite evolution using analysis of specific genes sequenced from modern samples gives us evidence for the significantly ancient origins for many zoonotic species, while archaeological evidence for zoonotic parasites further supports the long history of humans and zoonotic parasites. Here we have chosen to only include archaeological evidence for parasites found in unequivocally human contexts (those from mummified remains and soil from the pelvis of skeletons), to avoid errors due to uncertainty of human or animal origins of eggs in latrines, coprolites, and sediment from occupation areas.

Table 1: Hosts of some major zoonotic parasites, and risks for transmission to humans.

Disease	Parasite	Intermediate Hosts/Vector	Definitive Hosts	Risks for Transmission to Humans
Chagas disease	<i>Trypanosoma cruzi</i>	Triatomine bugs	Humans, wild/domestic animals	Feces from bug in bite wound
Chinese liver fluke	<i>Clonorchis sinensis</i>	Snail, freshwater fish	Mammals	Consumption of undercooked fish
Hydatidosis	<i>Echinococcus granulosus</i>	Sheep, goats, swine, cattle	Dogs, canids	Ingestion of eggs from dog feces
Fascioliasis	<i>Fasciola</i> sp.	Snails	Humans, sheep, cattle	Ingestion of encysted larvae on water plants
Fish tapeworm	<i>Diphyllobothrium pacificum</i>	Marine fish	Mammals	Consumption of undercooked fish
	Other Diphyllobothrids (<i>D. latum</i> , <i>D. dendriticum</i>)	Freshwater fish		
Dwarf Tapeworm	<i>Hymenolepis nana</i>	Beetles, fleas	Humans, rodents	Ingestion of eggs or intermediate hosts
Leishmaniasis	<i>Leishmania</i> spp.	Sand flies	Dogs, rodents, humans	Bite of a sand fly
Schistosomiasis	<i>Schistosoma mansoni</i>	Freshwater snails	Humans, rodents, baboons	Human contact with water
	<i>Schistosoma haematobium</i>		Humans, monkeys, baboons	
	<i>Schistosoma mekongi</i>		Humans, dogs	
	<i>Schistosoma japonicum</i>		Humans, cattle, swine, dogs, cats, rodents, horse, goats	

Taeniasis (cysticercosis)	<i>Taenia asiatica</i>	Pigs	Humans	Consumption of undercooked pork or beef
	<i>Taenia saginata</i>	Cattle		
	<i>Taenia solium</i>	Pigs		
Trichinellosis	<i>Trichinella spiralis</i>	Carnivores and omnivores	Carnivores and omnivores	Consumption of undercooked meat

2. Tracing Human Parasitic Infection Through Time

The earliest fossil evidence for helminths comes from the Middle Permian (275 mya) where cestodes were found in a shark coprolite (Dentzien-Dias et al., 2013). The earliest evidence for parasites in humans comes much later from the Pleistocene (30,000 ya), where an egg of roundworm (*Ascaris* sp.) was found in a cave in France (Bouchet et al., 1996). However, it is expected that the origins of many human parasites are much earlier (Poinar, 2015). Many parasites of humans are shared with modern primates and are thought to have been phylogenetically inherited from hominin ancestors, these are called heirloom parasites (Mitchell, 2013). Those parasites that we acquired more recently as humans moved out of Africa and interacted with new vectors, and animals, are sometimes termed souvenir parasites.

The typical approach of studying human disease using skeletal remains is often not applicable when looking for evidence of parasite infection. This is because most parasitic infections do not result in skeletal lesions or leave behind their DNA in skeletal tissue. However, soil from the pelvic region of a burial will contain the remains of decomposed intestines including helminth and protozoa eggs and cysts that can be used to diagnose infection (Reinhard et al., 1992; Le Bailly et al., 2006; Mitchell et al., 2013). This process is simplified when working with mummified remains, as intestinal contents can be identified and directly studied, and parasites in other tissues can be preserved (Camacho et al., 2018).

The earliest evidence for zoonotic parasite infection to come from an unequivocally human context (i.e. soil from the pelvis or mummified remains) is from Cyprus 8300–7000 BCE (Harter-Lailheugue et al., 2005). As such, the first direct evidence for zoonotic parasites in humans is only 10,000 years old. Since we expect the origins of many zoonotic parasite species in humans to predate human dispersals out of Africa, 50–100 kya (Reyes-Centeno et al., 2015), indirect evidence is necessary to understand early zoonotic parasite infection. These data come from modern genetic studies on zoonotic parasites.

3. Genetic Evidence for Origins of Human Zoonotic Parasites

A good example of the use of DNA analysis of modern parasites to determine their evolutionary origins is found in *Taenia* tapeworms. There are three main species of *Taenia* that infect humans, *Taenia solium* (pork tapeworm), *Taenia saginata* (beef tapeworm), and *Taenia asiatica* (Asian tapeworm). These *Taenia* tapeworms are host specific, with humans as their only definitive host, and requiring specific intermediate mammalian hosts. To become infected, humans must eat poorly cooked tissue from pigs (*T. solium* and *T. asiatica*) or cows (*T. saginata*) that contains the larval form of the parasite. Once ingested the larvae develop into adult worms in the human intestines and reproduce by excreting eggs in the feces that are in turn eaten by pigs or cattle. Phylogenetic studies using mitochondrial genes, whole mitochondrial genomes, and select nuclear DNA sequences from modern specimens of *Taenia* species, found in human and animal hosts, have revealed that *T. solium* is most closely related to *Taenia* species infecting hyaenids, while *T. saginata* and *T. asiatica* are most closely related to the species that infects lions (Terefe et al., 2014). This indicates that host switching allowing *Taenia* spp. to infect humans was likely a result of hominins scavenging on the same animals as hyenas, in the case of pork tapeworm, and large cats, in the case of beef tapeworm. The phylogenetic evidence suggests that *Taenia* tapeworms began to infect hominins in sub-Saharan Africa 1–2.5 mya, prior to the domestication of animals. This makes them heirloom parasites that have coevolved with humans.

Another helminth widely found in past populations is the *Fasciola* sp. liver fluke, which is a trematode (flatworm). Human infection is acquired when larval forms encysted on water plants are eaten. However, the most common definitive hosts are sheep and cattle, which are often responsible for transmitting the parasite to humans when their feces contaminate aquatic plants or drinking water (Garcia, 2016). Phylogenetic reconstructions using 28S, internal transcribed spacer (ITS) regions, and *nad1* gene sequences from modern samples of fasciolid parasites (including *Fasciola hepatica* and *Fasciolopsis buski*) suggest that the basal species originated in African proboscideans (such as elephants) which migrated into Eurasia where the parasite then evolved to infect other herbivores. It appears that *Fasciola hepatica* has its origins in Eurasia and was spread around the world from there (Lotfy et al., 2008). Molecular evidence, based on ITS regions and nuclear ribosomal DNA, lends support to recent dispersals of *Fasciola hepatica* from Europe into South America, with Spanish colonists, where it has since become hyperendemic (Mas-Coma et al., 2001). The earliest archaeological cases of *Fasciola* sp. in human remains come from Cyprus between 8300–6000 BCE (Harter-Lailheugue et al., 2005) and it has been found in Africa between

2400–1750 BCE (Harter, 2003). It is possible that hominins first acquired *Fasciola hepatica* when they moved into Eurasia, or that it had already been introduced into Africa by animal hosts and acquired by hominins in Africa.

There are many zoonotic species of schistosomiasis known to have animal reservoirs (Standley et al., 2012). Comparison of genetic sequences from modern schistosomes, mainly using small and large ribosomal RNA genes, has supported an “Out-of-Asia” model for the origins of schistosomiasis, with the most basal lineage being *Schistosoma japonicum* (Attwood et al., 2007). It is proposed that schistosomiasis then spread to Africa in the Middle Miocene with the movement of mammals, and it is within Africa that we see the emergence of *S. mansoni* and *S. haematobium*, which are responsible for many human infections in Africa today (Lawton et al., 2011). Thus we would expect that early hominins became exposed to these species in East Africa. When hominins reached East Asia they would have been exposed to the Asian species *S. japonicum*, still a major cause of human infections in Asia today. Schistosomiasis was not introduced into the New World until the African slave trade in the 15th to 19th centuries (Morgan et al., 2005). The archaeological evidence for zoonotic schistosomiasis from Africa and Asia fits with this pattern, early cases of *S. mansoni* and *S. haematobium* are found in Ancient Egyptian mummies (Table 5) and *S. japonicum* is only found in mummies from China (Table 6).

Genetic evidence for major zoonotic protozoa from the family trypanosomatids including *Leishmania* sp. and *Trypanosoma cruzi* (Chagas disease) indicate their ancient origins. The earliest identified fossil protozoa from the *Leishmania* genus comes from the gut of a sand fly preserved in amber dating to the early Cretaceous (Poinar, 2007). Current opinion suggests that *Leishmania* originated in the Palaeoarctic and spread to the Americas via the Bering Strait (see Novo et al., 2016 for a review). Even though the specific geographic origins of these diseases are debated, it appears that they evolved to infect mammals in various geographic regions much earlier than the origins of the hominin lineage (Hamilton and Stevens, 2017).

As genomic data for helminths and protozoa continues to grow, the extensive evolutionary history of zoonotic parasites becomes clearer. In many cases, it extends far beyond the origins of the hominin lineage, leaving many opportunities for zoonotic parasites to spread around the globe and develop necessary molecular mechanisms for surviving and thriving in mammal hosts before they were introduced to hominins. Although certain taxa of zoonotic helminths later coevolved with hominins to become host specific, as in the case of *Taenia*, many have remained generalist pathogens. Therefore, it is not surprising that most

zoonotic parasites of humans are classified as re-emerging diseases, those that have increased in prevalence recently or expanded their geographic range.

4. Archaeological Evidence for Zoonotic Parasites

Although many sample types can be studied to find evidence for parasitic infection in the past (including coprolites and latrine sediment), for the purposes of this study we have chosen to only include evidence from human pelvic soil and mummified remains because zoonotic parasites from these contexts can confidently be identified as originating from a human host. For further evidence for parasites from other contexts one could refer to Sianto et al. (2009), Reinhard et al. (2013), and Mitchell (2015).

In the Americas, the majority of parasite evidence has come from coprolites (Araújo et al., 2015). However, six zoonotic species have been identified from human remains (Table 2). *Cryptocotyle lingua*, fish tapeworm (*Diphyllobothrium pacificum*), and *Echinostoma* sp. eggs were identified in feces from mummies. While ancient DNA analysis of skeletal remains have contributed evidence for leishmaniasis (*Leishmania* sp.) and Chagas disease (*Trypanosoma cruzi*). Trichinellosis (*Trichinella spiralis*) was diagnosed through the study of thin sections of mummified muscle tissue using electron microscopy.

Table 2: Zoonotic parasites found in human remains from the Americas.

Parasite	Date	Site	Country	Reference
<i>Cryptocotyle lingua</i>	335–475 CE	St. Lawrence Island	USA	Zimmerman and Smith, 1975
<i>Diphyllobothrium pacificum</i>	3050–2050 BCE	San Miguel de Azapa	Chile	Reinhard and Urban, 2003
	1070–1150 CE	Adak Island	USA	Bouchet et al., 2001
<i>Echinostoma</i> sp.	750–1350 CE	Lapa do Boquete	Brazil	Sianto et al., 2005
<i>Leishmania</i> sp.	950–1450 CE	Coyo Oriente	Chile	Costa et al., 2009
<i>Trichinella spiralis</i>	1450–1500 CE	Cerro El Pomo	Chile	Héctor et al., 2017
<i>Trypanosoma cruzi</i>	7050 BCE–1850 CE	Mummies	Peru and Chile	Aufderheide et al., 2004
	5050–2550 BCE	Abrigo do Malhador	Brazil	Lima et al., 2008
	1350–1430 CE	Peruaçu Valley	Brazil	Fernandes et al., 2008

In Europe, there is substantially more evidence for zoonotic parasites in ancient human remains. Nine different taxa have been found, namely *Capillaria hepatica*, Lancet liver fluke (*Dicrocoelium* sp.), fish tapeworm (*Diphyllobothrium* spp.), hydatidosis (*Echinococcus granulosus*), *Fasciola* sp. liver fluke, giardiasis (*Giardia duodenalis*), visceral leishmaniasis, beef/pork tapeworm (*Taenia* spp.), and trichinellosis (*Trichinella spiralis*) (Table 3). *Dicrocoelium* and *Trichinella* were identified in tissue thin sections from a bog body and mummy, respectively. Evidence for hydatidosis comes from preserved hydatid cysts, one of which also contained eggs from *Capillaria* sp. (Mowlavi et al., 2014). Biomolecular methods contributed evidence for giardiasis using enzyme-linked immunosorbent assay (ELISA) and leishmaniasis based on retrieval of *Leishmania* mitochondrial DNA sequences from bone samples. Other evidence comes from eggs microscopically identified in soil from the pelvis of skeletons.

Table 3: Zoonotic parasites found in human remains from Europe.

Parasite	Date	Site	Country	Reference
<i>Capillaria hepatica</i>	400–200 BCE	Amiens	France	Mowlavi et al., 2014
<i>Dicrocoelium</i> sp.	78–233 CE	Zweeloo Woman	Netherlands	Searcey et al., 2013
<i>Diphyllobothrium</i> sp.	7600–7500 BCE	Shillourokambos	Cyprus	Harter, 2003
<i>Diphyllobothrium latum</i>	500 CE	Karwinden Man	Poland	Szidat, 1944
<i>Echinococcus granulosus</i>	400–200 BCE	Amiens	France	Mowlavi et al., 2014
	1–200 CE	Orton Longueville	England	Wells and Dallas, 1976
	Medieval	Not stated	Switzerland	Baud and Kramar, 1991
	1493–1554 CE	Skriouklaustur	Iceland	Kristjánsdóttir and Collins, 2011
<i>Fasciola</i> sp.	8300–7000 BCE	Shillourokambos	Cyprus	Harter-Lailheugue et al., 2005
	7000–6000 BCE	Khirokitia	Cyprus	Harter-Lailheugue et al., 2005
<i>Fasciola hepatica</i>	3000–2000 BCE	Karsdorf	Germany	Dittmar and Teegen, 2003
<i>Giardia duodenalis</i>	600–900 CE	Chevenez	Switzerland	Le Bailly, 2005

<i>Leishmania infantum</i>	1522–1562 CE	Eleonora of Toledo	Italy	Nerlich et al., 2012
<i>Taenia</i> sp.	8300–7000 BCE	Shillourokambos	Cyprus	Harter-Lailheugue et al., 2005
	7000–6000 BCE	Khirokitia	Cyprus	Harter-Lailheugue et al., 2005
<i>Trichinella spiralis</i>	1800–1900 CE	Toledo County	Spain	Bellard and Cortes, 1991

In the Middle East there is very little evidence for parasites in human remains (Table 4). An early case of schistosomiasis was identified from a preserved egg in pelvic soil in an early agricultural community in Syria, and hydatid disease was found in the 1st c. CE in Israel. *Physaloptera* sp. eggs were found in pelvic soil from Bronze Age Iran.

Table 4: Zoonotic parasites found in human remains from the Middle East.

Parasite	Date	Site	Country	Reference
<i>Echinococcus granulosus</i>	1–100 CE	Silwan	Israel	Zias and Mumcuoglu, 1991
<i>Physaloptera</i> sp.	2800–2500 BCE	Shahr-e Sukhteh	Iran	Makki et al., 2017
<i>Schistosoma</i> sp.	4550–4050 BCE	Tell Zeidan	Syria	Anastasiou et al., 2014
<i>Taenia</i> sp.	364–308 BCE	Chehrabad	Iran	Nezamabadi et al., 2013

Evidence for zoonotic parasites in human remains from Africa is larger than other regions due to the fact that mummified remains from Egypt have been studied extensively. Though there is more evidence for zoonotic parasites in Africa compared to other regions this data is very concentrated in Egypt and Sudan, with most of the continent unstudied. Ten taxa of zoonotic parasites have been found associated with human remains in Africa so far (Table 5). These are Lancet liver fluke, fish tapeworm, guinea worm (*Dracunculus medinensis*), hydatidosis, *Fasciola* liver fluke, dwarf tapeworm (*Hymenolepis* sp.), leishmaniasis, schistosomiasis, beef/pork tapeworm, and toxoplasmosis (*Toxoplasma gondii*). Most helminth eggs were identified in pelvic soil or intestinal contents of mummies, except guinea worm which was preserved in the subcutaneous tissue of a mummy. Schistosomiasis was identified using ELISA to test for preserved *Schistosoma* antigen in mummified tissue.

Evidence for leishmaniasis and toxoplasmosis came from sequencing of *Leishmania* and *Toxoplasma* DNA from mummified tissue.

Table 5: Zoonotic parasites found in human remains from Africa.

Parasite	Date	Site	Country	Reference
<i>Dicrocoelium</i> sp.	2400–1750 BCE	Kerma	Sudan	Harter, 2003
<i>Diphyllbothrium</i> sp.	700–300 BCE	Sai Island	Sudan	Harter, 2003
	400–300 BCE	Deir el-Medineh	Egypt	Harter, 2003
	400–300 BCE	Saqqara	Egypt	Harter, 2003
<i>Dracunculus medinensis</i>	1450 BCE	Valley of the Nobles	Egypt	Horne and Redford, 1955
<i>Echinococcus</i> sp.	750–525 BCE	Thebes	Egypt	Tapp, 1984
<i>Fasciola</i> sp.	2400–1750 BCE	Kerma	Sudan	Harter, 2003
	700–300 BCE	Sai Island	Sudan	Harter, 2003
	400–300 BCE	Saqqara	Egypt	Harter, 2003
	275 BCE–350 CE	Sai Island	Sudan	Harter, 2003
<i>Fasciola hepatica</i>	400–300 BCE	Deir el-Medineh	Egypt	Harter, 2003
<i>Hymenolepis</i> sp.	275 BCE–350 CE	Sai Island	Sudan	Harter, 2003
	1500 CE	Sai Island	Sudan	Harter, 2003
<i>Hymenolepis nana</i>	300–1500 CE	Sedeinga	Sudan	Harter, 2003
<i>Leishmania donovani</i>	2050–1650 BCE	Thebes	Egypt	Zink et al., 2006
	500–1500 CE	Kulubnarti	Sudan	Zink et al., 2006
<i>Schistosoma</i> sp.	3200 BCE	Thebes	Egypt	Deelder et al., 1990
	2700 BCE	Sai Island	Sudan	Harter, 2003
	1200 BCE	Thebes	Egypt	Reyman et al., 1977
	1200–1000 BCE	mummy	Egypt	Ruffer, 1910
	275 BCE–1500 CE	Sai Island	Sudan	Harter, 2003
	300–1500 CE	Sedeinga	Sudan	Harter, 2003

<i>Schistosoma haematobium</i>	2400–1750 BCE	Kerma	Sudan	Harter, 2003
	1198–1150 BCE	Thebes	Egypt	Deelder et al., 1990
	700–300 BCE	Sai Island	Sudan	Harter, 2003
<i>Schistosoma mansoni</i>	2400–1750 BCE	Kerma	Sudan	Harter, 2003
	700–300 BCE	Sai Island	Sudan	Harter, 2003
	350–550 CE	Wadi Halfa	Sudan	Miller et al., 1992
	550–950 CE	Kulubnarti	Sudan	Hibbs et al., 2011
<i>Taenia</i> sp.	2400–1750 BCE	Kerma	Sudan	Harter, 2003
	1200 BCE	Thebes	Egypt	Reyman et al., 1977
	700–300 BCE	Sai Island	Sudan	Harter, 2003
	275 BCE–1500 CE	Sai Island	Sudan	Harter, 2003
	300–500 CE	El-Deir	Egypt	Le Bailly et al., 2010
<i>Taenia solium</i>	200–1 BCE	Not stated	Egypt	Bruschi et al., 2006
<i>Toxoplasma gondii</i>	806 BCE–124 CE	Not stated	Egypt	Khairat et al., 2013

Parasite studies have more recently been undertaken at archaeological sites in Russia. So far there is evidence for zoonotic species in human remains including fish tapeworm, *Opisthorchis felinus* (cat liver fluke), and beef/pork tapeworms. All evidence comes from the 12th c. CE onwards from analysis of soil from the pelvis of skeletons (Table 6).

Due to work on mummified remains, there is good evidence for zoonotic parasites in humans from China and Korea from the 5th c. CE onwards. Nine taxa of zoonotic parasites have been found, namely Chinese liver fluke (*Clonorchis sinensis*), fish tapeworm, *Fasciolopsis buski* liver fluke, *Gymnophalloides seoi*, *Metagonimus yokogawai*, *Paragonimus westermani*, schistosomiasis (*S. japonicum*), *Taenia* tapeworms, and *Trichostrongylus* sp. (Table 6). This evidence comes from eggs found in feces collected from the intestines of mummies or soil from the pelvis of skeletons.

Table 6: Zoonotic parasites found in human remains from Asia.

Parasite	Date	Site	Country	Reference
<i>Clonorchis sinensis</i>	500–221 BCE	Jiangling, Hubei Province	China	Yeh and Mitchell, 2016
	475–221 BCE	Guo-Jia-Gang	China	Wu et al., 1996
	475–221 BCE	Mazhuan Tomb	China	Yang et al., 1984
	167 BCE	Phoenix Hill, Hubei Province	China	Wei et al., 1981
	960–1644 CE	Canton	China	Wei et al., 1981
	960–1279 CE	Hengyang, Hunan Province	China	Yeh and Mitchell, 2016
	1368–1644 CE	Fuqing, Fujian Province	China	Yeh and Mitchell, 2016
	1368–1644 CE	Fuzhou, Fujian Province	China	Yeh and Mitchell, 2016
	1368–1644 CE	Guangzhou, Guangdong Province	China	Yeh and Mitchell, 2016
	Medieval	Yangju Child	Korea	Seo et al., 2007
	1600–1700 CE	Hadong	Korea	Seo et al., 2008
	Medieval	Waegwan	Korea	Seo et al., 2010
<i>Diphyllbothrium latum</i>	1600–1900 CE	Kikkii-Akki	Russia	Slepchenko and Ivanov, 2015
	1800–1900 CE	Vesakoyakha	Russia	Slepchenko et al., 2016
<i>Fasciolopsis buski</i>	960–1644 CE	Canton	China	Wei et al., 1981
	1368–1644 CE	Fuqing, Fujian Province	China	Yeh and Mitchell, 2016
	1368–1644 CE	Guangzhou, Guangdong Province	China	Yeh and Mitchell, 2016
<i>Gymnophalloides seoi</i>	1600–1700 CE	Hadong	Korea	Seo et al., 2008
<i>Metagonimus yokogawai</i>	1600–1700 CE	Hadong	Korea	Seo et al., 2008
<i>Opisthorchis felinus</i>	1100–1300 CE	Zeleniy Yar	Russia	Slepchenko et al., 2015
<i>Paragonimus westermani</i>	1600–1800 CE	Gongju	Korea	Shin et al., 2009
	Medieval	HY HM (Yongin)	Korea	Seo et al., 2010
<i>Schistosoma japonicum</i>	202 BCE–220 CE	Mawangtui Tomb	China	Wei et al., 1981
	167 BCE	Phoenix Hill, Hubei Province	China	Wei et al., 1981

<i>Taenia</i> sp.	2000–1000 BCE	Neftprovod	Russia	Slepchenko et al., 2017
	167 BCE	Phoenix Hill, Hubei Province	China	Wei et al., 1981
	1800–1900 CE	Vesakoyakha	Russia	Slepchenko et al., 2016
<i>Trichostrongylus</i> sp.	1600–1800 CE	Gongju	Korea	Shin et al., 2009

One consideration to be taken is the zoonotic potential of *Ascaris* spp. (roundworm) and *Trichuris* spp. (whipworm). Recent work is bringing to light the zoonotic role of these parasites (Liu et al., 2012; Nejsun et al., 2012), which may have played a role in ancient transmission as well. These are two of the most common intestinal parasites found worldwide in the past, with evidence from the Paleolithic through to modern day (Mitchell, 2015). We have not included them in the tables reviewing zoonotic parasites as they are commonly considered direct fecal-oral parasites that have infected humans throughout our evolution, and do not need an alternative animal host besides humans to complete their life cycles (Mitchell, 2013; Garcia, 2016). However, in the case of *Ascaris* spp. (roundworm) recent studies of the mitochondrial genomes have shown an inability to genetically distinguish pig roundworm (*Ascaris suum*) from human roundworm (*Ascaris lumbricoides*), and experimental and clinical cases have shown that humans can be infected with pig roundworm (Nejsun et al., 2012; Betson, 2014). Similarly, clinical trials focused on helminth therapy for autoimmune disease have shown that *Trichuris suis* (pig whipworm) can establish itself in humans for a short period of time (Beer, 1971; Beer, 1976). However, the reproductive potential of pig infecting species in the human host has been questioned and recent evidence seems to show that though these worms can be established and persist for a time they may not reproduce (in the case of *T. suis*) or if they do they may produce far fewer eggs (Søe et al., 2016). Though close interactions between humans and pigs in past communities may have resulted in some cases of zoonotic infections it is unclear to what extent these eggs may be recovered in paleofeces and if they represent true infections or merely passing of ingested eggs through the intestines unchanged.

5. Discussion

The modern genetic evidence for the origins and spread of some key zoonotic parasites in humans shows very ancient origins for these pathogens, allowing them time to spread around the globe with early mammal migrations. Whether they originated in Africa or

spread there from Eurasia, many were present in animals in Africa before the divergence of the hominin lineage. For some species it is possible that humans picked up zoonotic parasites in Africa and then spread them around the world with migrations, but in others it is likely humans were first exposed in Africa and then continually re-exposed as they moved to other regions where the parasites had already been spread by animal migrations in the past. Certainly this appears to be the case for schistosomiasis and *Fasciola*, and possibly others such as *Trichinella* and fish tapeworm. The exception is geographically restricted parasites (e.g. *D. pacificum*, *T. cruzi*, *S. japonicum*, *C. sinensis*) which can only exist in certain parts of the world due to geographically restricted intermediate hosts. In consequence, these zoonoses would have only emerged as human diseases when humans migrated to their endemic region. In the past, human movement to new regions of the world had a large role to play in emergence of these zoonotic parasites as human diseases. As humans have now colonized all continents except Antarctica, the emergence of new species to infect humans simply as a result of moving to new regions would be expected to be lower. Instead, increased movement of individuals, and long distance trade of animal products that can be infective, may be contributing to the re-emergence of foodborne parasites.

The risk for zoonoses is often considered to increase with domestication of animals for food sources and as companion animals (Wolfe et al., 2007; Reinhard et al., 2013). Domestication of animals occurred at various times and localities in human history, with the earliest domesticated animal believed to be dogs about 16,000 ya (Perri et al., 2019). It has been shown that the number of parasites shared between humans and domesticates increases with the time since domestication (Morand et al., 2014). Humans share the highest percentage of their parasites with carnivores, followed by ruminants and pigs, and then rodents (Perrin et al., 2010). Within carnivores, the highest percentage of parasites are shared by dogs and cats, also the earliest animals to be domesticated. The domestication of dogs and the resulting close association between humans and their canines likely increased the risk for hydatid disease, caused by the zoonotic parasite *Echinococcus granulosus*. The earliest archaeological cases of hydatid disease come from the 8th c. BCE in Egypt and 4th c. BCE in Europe, and in Europe persists through the medieval period (Table 3 and Table 5). The transmission of parasites between humans and animals is not unidirectional, and humans would have also acted as long term reservoirs for parasites infecting domesticated animals. This is an important factor to consider when we look at the resurgence of zoonotic parasites today. This has been exemplified with setbacks to the eradication of guinea worm due to increasing prevalence in dogs, a previously underrecognized host for the worm, that can

transmit it back to humans in areas where it was thought to be eradicated (Galán-Puchades, 2017). The nature and outcome of interactions between humans and their domesticated animals varies through time and settlement type (e.g. rural vs urban) but the impact of these interactions can frequently be seen in the presence of zoonotic diseases in the past.

It was not uncommon for people to live with their animals in past societies. As populations of humans and animals grew in more urban environments, waste disposal would become more challenging. In particular, dumping of fecal material into bodies of water and the use of human excrement as fertilizer, known to occur in many communities in the past (Jones, 2012), would create ideal conditions for animals or humans to consume parasite eggs and maintain the life cycles of many species. Historical texts from the Roman Period mention dogs being used to clean up human excrement within cities (Scobie, 1986), other animals kept within the city such as pigs and cattle would also be able to ingest human fecal material from open street sewers. These are all practices that could increase the prevalence or maintain the life cycles of many zoonotic parasites. Aside from interactions revolving around shared living spaces and waste disposal that exposes animals to human excrement, a major interaction between humans and animals comes from reliance on them as a source of food.

Many zoonotic parasites found throughout human history are transmitted by the ingestion of fish and other seafood. In Asia we do not have any archaeological evidence for zoonotic parasites prior to the 5th c. BCE, making it difficult to detect long term changes. However, in East Asia starting in the 13th c. CE we begin to see unique taxa not seen in other regions or earlier, such as *Gymnophalloides seoi* and *Metagonimus yokogawai*. Both of these species can infect many fish eating mammals, and infect humans when they eat raw or undercooked oysters (*G. seoi*) or freshwater fish (*M. yokogawai*). In Russia, we have evidence for *Opisthorchis felineus* (cat liver fluke), found in the 12th–14th c. CE. This parasite can infect any fish eating mammal when poorly cooked fish is eaten. Today it is often found in Russia and Siberia. These foodborne zoonotic parasites that are acquired from ingestion of fish or other seafood are found commonly in the past, though many of these are geographically restricted due to intermediate hosts. For example, Chinese liver fluke is found quite consistently in China but it is limited to the region by its snail intermediate host. Evidence for these species in combination with fish tapeworm, *Echinostoma*, and *Cryptocotyle* found in Europe and the Americas, suggest that dietary reliance on fish appears to be a consistent and major contributor to zoonotic parasite infection in past communities. Modern epidemiological studies have also suggested that dispersal of cultural tastes for raw

fish, coupled with the widescale trade of fish, may in part be responsible for an increase in cases of fish tapeworm infection in some communities today (Scholz et al., 2009).

Technological developments have also impacted human-animal interactions in unexpected ways. Early technological developments in the Middle East and Egypt, such as building irrigation channels to water crops (Helbaek, 1972), may well explain the early evidence for schistosomiasis and guinea worm in these regions. Irrigation technology would create standing water that could harbour populations of snails that serve as intermediate hosts of schistosomes or larval forms of guinea worm, in which humans would then wade as they tended their crops. Alongside technological developments comes risk factors associated with urbanization. *Hymenolepis* (dwarf tapeworm) is found in the Sudan beginning just before the Roman Period through to the 16th c. CE. It was not found in human remains in any other region, though has been found in coprolites in the Americas (Reinhard et al., 2013). *Hymenolepis* sp. are typically parasites of humans and rodents, and their intermediate hosts are insects including grain beetles. It has been proposed that there was a rise in *Hymenolepis* in past populations after the agricultural revolution, when humans began to store grain (Reinhard et al., 2013). It is possible that with increased urbanization in the Sudan during the Roman Period, grain storage increased the prevalence of *Hymenolepis*.

Although zoonotic parasites are recognized as major contributors to disease in humans today (Mackey et al., 2014), the archaeological and genetic evidence reviewed here suggests that they have contributed to human disease for millennia (Robinson and Dalton, 2009; Sianto et al., 2009). It appears that a diverse range of species is well suited to infect humans, whether as their sole obligate hosts or one of many potential mammalian hosts. Environmental conditions and sociocultural factors have a large role to play in the success of these organisms as human pathogens at any given time.

Various factors are thought to have contributed to the re-emergence of zoonotic parasites today. One group of factors that we have noted in the past but remain important today in zoonotic parasite re-emergence are dietary habits. Consumption of raw or undercooked fish and meat is necessary for the transmission of many zoonotic parasites that are major causes of disease in humans. With urbanization and altering of landscapes we also see ecological shifts that can allow for alignment of parasites, intermediate hosts, and definitive hosts in the same ecological niche, thus allowing for transmission of zoonotic parasites. Climate change is predicted to further exacerbate this process, allowing expansion of endemic regions for many parasites and their hosts. With expanding population sizes we see growing populations of domestic animals as a food source, which can serve as a reservoir

for parasites and a link between disease in humans and wildlife (Webster et al., 2016; Wells et al., 2018).

6. Conclusions

Zoonotic parasites are found consistently in prehistoric human populations around the world, particularly from the Neolithic Period onwards. Risk factors for zoonotic parasite infection in the past include human movement to new regions, dietary habits (especially eating uncooked foods), urbanization, poor waste disposal, growing population sizes, and increased proximity to animals. These overlap with many identified causes for the emergence and re-emergence of zoonotic diseases today.

The genetic evidence presented highlights the ancient origins of many zoonotic parasites and their ubiquity throughout much of human evolution. While it is easy to identify human actions that have resulted in emergence or re-emergence of diseases, the millions of years that these parasites have been coevolving with hominins makes us consider that they likely have very specialized interactions at a biological or immunological level with us.

There are limitations to our understanding of zoonotic diseases in past populations, and as further archaeological and genetic evidence is gathered these hypotheses are expected to evolve. Some of the major limitations are that paleoparasitological studies have been very regionally and temporally focused. Indeed, many regions and time periods have not been studied at all. This should be a focus of future work in paleoparasitology. As we fill in the regional and temporal gaps in the history of zoonotic parasites we will be better equipped to contribute to the discussion of risk factors for re-emergence of these diseases. Molecular studies on the DNA of ancient parasites themselves will also be a fruitful area of work allowing us to refine phylogenies and help us understand how these pathogens are evolving. As evidence for human parasitic infection in the past and genetic data grows, there are many intricacies of human-animal relationships that we can begin to explore.

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