Parasites in ancient Egypt and Nubia: Malaria, schistosomiasis and the pharaohs

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Abstract

The civilizations of ancient Egypt and Nubia played a key role in the cultural development of Africa, the Near East, and the Mediterranean world. This study explores how their location along the River Nile, agricultural practices, the climate, endemic insects and aquatic snails impacted the type of parasites that were most successful in their populations. A meta-analysis approach finds that up to 65% of mummies were positive for schistosomiasis, 40% for headlice, 22% for falciparum malaria, and 10% for visceral leishmaniasis. Such a disease burden must have had major consequences upon the physical stamina and productivity of a large proportion of the workforce. In contrast, the virtual absence of evidence for whipworm and roundworm (so common in adjacent civilizations in the Near East and Europe) may have been a result of the yearly Nile floods fertilising the agricultural land, so that farmers did not have to fertilise their crops with human faeces.

1. Introduction

The great civilizations of Egypt and Nubia have long fascinated those interested in ancient diseases (paleopathology). Restricted to the west by the Libyan Desert, to the east by the barren Red Sea coast, and to the north by the Mediterranean, this arid region could easily have been an unlikely place early civilizations might develop and thrive. However, the River Nile brought large amounts of water from deep within the continent, so that the lack of rain became much less important once people developed ways to use the Nile for agriculture and transport (Bunbury, 2019).

The aim of this paper is to bring together the evidence for parasites in ancient Egypt and Nubia in order to interrogate the data in innovative ways, so improving our understanding of how these infectious diseases impacted such iconic civilizations (Mitchell, 2023, 20-41). We might expect these populations to have been exposed to a considerably larger range of parasites than we find in many past civilizations, due to the variation in habitats found there. Despite the low rainfall in most of the region, the River Nile acted as a conduit for tropical water-born parasites that would not normally be found in arid regions. Insect vectors ranged from mosquitos breeding in the oases and marshlands such as Fayum submerged by the annual Nile floods, to sandflies endemic to the savannah acacia forests of Nubia. As humans evolved in east Africa, a wide range of parasites that previously affected African mammals have had millions of years to themselves evolve to target the people living there (Mitchell, 2013). The Mediterranean coastline led to trade with the other civilizations of the Mediterranean world (Steel, 2007). This could have exposed the Egyptian population to infectious diseases from elsewhere in the Mediterranean region, or acted as a method of transfer of its parasites to other regions. Egypt's military expeditions northeast into the eastern Mediterranean and Levant region (Xekalaki, 2021) would have exposed its citizens to the diseases endemic in the Near East too.

The early societies living along the River Nile included the Badarian culture around 5000 BCE, and then the Naqada culture around 4000 BCE. This time is known as the predynastic period. During the Bronze Age we

see the rise of numerous ruling dynasties in Egypt. The Early Dynastic Period (c.3150–2700 BCE), when the upper and lower Egypt regions were unified, was followed by the Old Kingdom (c.2700-2190 BCE), Middle Kingdom (c.2040–1674 BCE) and the New Kingdom (c.1552–1069 BCE). The phrase 'intermediate period' is used to describe the decades between each of these kingdoms (Lloyd, 2014; Trigger et al., 2012). Egypt reached its greatest extent during the New Kingdom, when its armies conquered Nubia to the south, and much of the eastern Mediterranean coast as far as the Hittite Empire (now Turkey). Alexander the Great led the Macedonian invasion of Egypt in 332 BCE and during the Ptolemaic period (323–30 BCE) Greek influence continued. While Cleopatra was on the throne, Egypt was absorbed into the Roman Empire in 30 BCE, to become one if its provinces. Ancient Egypt is characterised by the pharaohs who used large numbers of slaves to build opulent temples and funerary monuments such as the valley of the kings and the pyramids, the development of hieroglyphic writing, mummification, and for developing irrigation technologies that allowed them to harness the River Nile's waters to grow crops in this arid region (Wilkinson, 2010; Ikram, 2010; Shaw, 2003).

Nubia was the civilization that lay to the south of Egypt, and can be divided into Lower Nubia in the north and Upper Nubia in the south. The Egyptians termed it Kush, and the Greeks referred to it as Ethiopia (Emberling and Williams, 2020). While Nubia was attacked by Egypt many times during the Old Kingdom and Middle Kingdom periods, it was finally conquered by pharaoh Amenhotep I (1514–1493 BCE) (Török, 2009). For the next seven centuries Egypt ruled over Nubia. However, about 800 BCE there arose a new power in Kush, taking back the lands conquered by the Egyptians. By 715 BCE the Nubians had turned the tables and conquered the entirety of Egypt. The Pharaohs of the 22nd, 23rd and 24th dynasties were all Nubians. In time their hold over Egypt faltered and they were driven back south. However, with their capital in Meroe, the Nubians maintained their kingdom until roughly 400 CE (known as the Meroitic period) (Dietrich, 2019). Fig. 1 is a map that shows the locations of the main sites in ancient Egypt and Nubia discussed in this article.

2. Sources of evidence for ancient parasites

Egyptian medical texts written on papyri contain descriptions of diseases and their treatments. While it has been quite a challenge to



Fig. 1 Map showing the location of many of the sites in ancient Egypt and Nubia where parasites have been recovered. Image credit: author. Cover image: Central image of *Taenia* sp. tapeworm egg from the pelvis of a naturally mummified burial at the El-Deir necropolis, Kharga Oasis, Egypt dating to 300–500 CE (image credit: Matthieu Le Bailly), superimposed over the paintings within the tomb of the pharaoh Ramesses V in the Valley of the Kings, Luxor (image credit: Dimitri Zhodzishskii).

determine the meaning of certain hieroglyphic symbols, there are thought to be descriptions of worms and also blood in the urine, which is often found in cases of urogenital schistosomiasis (Bardinet, 1995; Leitz, 1999; Da Silva Veiga, 2009; Eltorai, 2019). Since parasites are associated with a range of tissues on and within the human body, the best sources of evidence will depend upon the life cycle of the parasites in question.

In order to investigate intestinal parasites, we need to identify the remains of human faeces. The toilet was first developed in Mesopotamia in the late 4th millennium BCE, where we find houses with a hole in the floor located over a cylindrical pit with stacked ceramic drain rings (McMahon, 2015). The cesspits and sewer drains associated with toilets typically contain the decomposed faeces of multiple individuals or families and will contain evidence for their diet and intestinal micro-organisms (Smith, 2013). As such, they have the potential to demonstrate the range of species of parasite present in the original population, but the mixed nature of this material means that it is less helpful when assessing the proportion of individuals who might have been infected. While toilets are known from ancient Egypt (Brier and Hobbs, 2008), none have been sampled by the excavating archaeologists in order for parasites to be investigated. Coprolites are pieces of human faeces that may be preserved by desiccation, mineralisation, or being submerged in permanently waterlogged soil which hinders the decomposition process (Bryant and Dean, 2006; Shillito et al., 2020; Yang et al., 2022). These have the potential to demonstrate the parasites present in the particular individual who passed these faeces, in contrast to the mixed origin faeces in cesspits. However, coprolite analysis has not been performed in ancient Egypt or Nubia either. In skeletonised burials, the intestines will decompose and their contents will mix with the soil found in the region of the pelvis and abdomen. Therefore samples of sediment taken from the front of the sacrum may contain the eggs of any parasites that were located in the intestines when the individual was alive, and can demonstrate prevalence (Mitchell et al., 2017a).

The combination of artificial mummification as a burial custom for the wealthy, coupled with natural mummification of even simple burials in the exceptionally dry climate, allows a much more complete assessment of parasite infection in Egypt and Nubia than is possible in many other regions of the world (Mitchell, 2023). The naturally desiccated bodies have their intestines in situ, while the artificially embalmed had their internal organs removed and stored in canopic jars (Taylor, 2010). Both these types of mummies are ideal for studying ectoparasites and when looking for the

biomolecules left by protozoal infection in the soft tissues. When searching for intestinal parasites we can study the in situ intestines in naturally mummified individuals, but in embalmed mummies we must look at canopic jars (Harter et al., 2003). Hair combs can trap headlice between the teeth of the comb and so provide evidence for their presence in past societies (Mumcuoglu and Zias, 1989).

2.1 Early work on mummies and parasites in ancient Egypt and Nubia

Public Egyptian mummy unwrapping events, sometimes referred to as unwrapping parties, became popular social activities for the well to do in Britain the late 1700s and 1800s (Sheppard, 2012). However, the first record we have for the scientific autopsy and attempted medical diagnosis in an Egyptian mummy was by Augustus Granville when he presented to the Royal Society of London in 1825 (Granville, 1825). The mummified individual was a woman named Irtyersenu, who died around 600 BC and was found at the necropolis at Thebes. Recent aDNA analysis shows that she suffered with pulmonary tuberculosis (Donoghue et al., 2010).

In 1910 Marc Ruffer published his seminal paper in the British Medical Journal on schistosomiasis in ancient Egyptian mummies (Ruffer, 1910). This was the first ever academic article in the field of paleoparasitology, so while he did not realise it at the time, he was the founder of this scientific discipline (Sandison, 1967). While working in Alexandria as president of The Sanitary, Maritime and Quarantine Council of Egypt, Ruffer became interested in how mummified tissue might be prepared for histological examination (Ruffer, 1909). Elliot Smith, Flinders Petrie and Keatings were archaeologists excavating mummies at the time, and they gave him some organs from mummies dating from the 18th and 20th dynasties. Ruffer examined the kidneys of six mummies, with two of them being positive for parasite eggs. He wrote 'in the kidneys of two mummies of the twentieth dynasty I have demonstrated in microscopic sections a large number of calcified eggs of Bilharzia haematobia, situated, for the most part, among the straight tubules. Although calcified, these eggs are easily recognisable and cannot be mistaken for anything else' (Ruffer, 1910). While no illustrations were included in British Medical Journal notes at that time, the distinctive appearance of Schistosoma haematobium eggs, and their location in the kidneys of mummies from the Nile Valley where the disease was endemic at the time Ruffer was writing, would make it very likely that he had the correct diagnosis.

From the 1970s a more systematic approach to the investigation of disease in Egyptian mummies was developed. A multidisciplinary North American team performed an autopsy of the mummy Nakht ROM 1 which was curated at the Royal Ontario Museum in Canada. A series of papers were published in the same journal issue where different techniques were applied to this mummy, and a range of diseases identified (Hart et al., 1977a,b). The Manchester Egyptian Mummy Research Project was established in 1973 at the University of Manchester, UK, to study the mummies in their museum collection (David, 1979; David and Tapp, 1984). Until the 1990s they focussed on intensively investigating each mummy, but over time they developed a tissue bank that could be used to study infectious diseases at a population level using biomolecular techniques (Lambert-Zazulak et al., 2003). In the following 20 years a number of studies were published by different teams where progressively larger series of mummies from museums across Europe, Egypt and Sudan were analysed for evidence of specific parasites (Hibbs et al., 2011; Rabino Massa et al., 2000; Zink et al., 2006).

3. Methods of detection

While many of the techniques used to identify ancient parasites share similarities with those employed in the clinical analysis of modern parasites, certain adaptations have been found to improve parasite recovery and identification. Light microscopy is a very effective tool for identifying the eggs of intestinal helminths, but in ancient samples that are in dry samples they need to be rehydrated in a solution such as trisodium phosphate before they can be visualised. Unlike fresh modern samples where large numbers of eggs may be present, the taphonomic effects of fungi, bacteria and insects often lead to destruction of many eggs that were originally present. This means that only a minority of the eggs may remain, and they may show signs of surface damage.

Imaging with plain radiographs (x-rays) or CT scans can identify intact desiccated worms in mummies. Guinea worms (*Dracunculus medinensis*) migrate through the soft tissues of the body to find their mate, and then the females go on to move to the lower leg to more easily discharge their offspring into water. When these worms die they may calcify and be detected when the mummy is imaged. Similarly, CT scans may identify parasitic worms or cysts formed by parasites (Isherwood et al., 1984). The presence of soft tissues in mummies allows the application of

biomolecular techniques to detect antigens produced by parasites, and to look for fragments of the ancient DNA of the organisms themselves.

Enzyme-linked immunosorbent assay (ELISA) has been employed to investigate schistosomiasis infection in mummies from both Egypt and Nubia. Circulating Anodic Antigen (CAA) is a proteoglycan released into the host's blood from the syncytium lining the schistosome gut. While its presence cannot distinguish between S. haematobium and S. mansoni, its detection using ELISA would confirm the presence of at least one of these species in the population (Deelder et al., 1990). More recent work has used ELISA to detect the Circulating Cathodic Antigen (CCA), unique to S. mansoni, so allowing determination of the species of schistosome present (Hibbs et al., 2011). While ELISA developed to detect the protozoal parasites that cause diarrhoea and dysentery (such as Giardia duodenalis, Entamoeba histolytica and Cryptosporidium sp.) has been successfully applied to faecal material from early civilizations in the eastern Mediterranean (Le Bailly et al., 2016; Mitchell et al., 2023), it has yet to be applied to material from ancient Egypt or Nubia. In consequence, infection by these parasites among the Nile Valley civilizations remains unclear. Malaria was initially investigated using the immunoenzymatic assay Para-SightTM-F test, which targets the Plasmodium falciparum histidine rich protein-2 antigen (PfHRP-2) (Miller et al., 1994), and a number of studies have employed this since then. One later project applied immunochromatography and indirect immunofluorescence to investigate malaria in a series of mummies (Bianucci et al., 2008). DNA analysis has been used to detect malaria in mummies since 2008 (Nerlich et al., 2008) and a number of other studies have been published. DNA has been used to investigate leishmaniasis in mummies by targeting the kinetoplastid mitochondrial DNA of Leishmania donovani (Zink et al., 2006). Metagenomic aDNA analysis of muscle tissue has also detected a case of toxoplasmosis (Toxoplasma gondii) in a mummy (Khairat et al., 2013).

4. Protozoal parasites in Egypt and Nubia

Malaria has been investigated in Egyptian mummies initially using immunological techniques, and more recently with aDNA analysis (Bianucci et al., 2015). The first study applied the immunoenzymatic assay Para-SightTM-F test, which targets the histidine-rich protein-2 antigen (PfHRP-2) of *Plasmodium falciparum*, to skin biopsies from four naturally desiccated mummies from predynastic Gebelein (c.3200 BCE), a New Kingdom mummy from Gurna (1500–1185 BCE) and also lung tissue from a canopic jar dating from 1304 to 1085 BCE. The test was positive for the canopic jar lung tissue, the New Kingdom mummy, and three of the four predynastic mummies (Miller et al., 1994). The same Para-SightTM-F test was used in a study using samples of skin, muscle and bone from around 80 predynastic mummies from Gebelein (c.3200 BCE). *P. falciparum* was found in 42% of the mummies. The research also assessed the prevalence of the skeletal changes of anaemia (cribra orbitalia and porotic hyperostosis) and found that 61% of the whole series had these changes, compared with 92% of those positive for malaria (Rabino Massa et al., 2000). This highlights the impact of malaria in causing anaemia in ancient Egypt. A study of seven mummies from predynastic and early dynastic Gebelein employed immunochromatography and indirect immunofluorescence of skin and muscle samples for *Plasmodium falciparum*. A child aged 15–18 months, radiocarbon dated to 2820–260 BCE (95.4% probability) was found to be positive, while the other individuals were negative (Bianucci et al., 2008).

Ancient DNA analysis for malaria was first undertaken in mummies from Abydos and Thebes. The study tested bone samples from seven predynastic mummies (3500-15,650 BCE) and 84 mummies from the Middle Kingdom, New Kingdom, and Later period (2050-500 BCE). PCR was used to target the *P. falciparum* chloroquine-resistance transporter gene (pfcrt gene). Two of the 91 (2%) were positive (Nerlich et al., 2008). It is likely that this relatively low prevalence figure was a result of the study design where bone was tested rather than soft tissues, and the lower efficiency in DNA recovery from ancient samples using techniques at that time. Having shown proof of concept, multiple studies have since investigated malaria along the Nile using ancient DNA techniques. From the Valley of the Kings sixteen mummies were analysed for falciparum malaria using PCR and Sanger Sequencing, and four were positive. One of these was the mummy of King Tutankhamun (c.1333-1323 BCE), who was infected by two different strains, as indicated by recovering the alleles MAD20 and RO33 of the MSP1 in their extracts (Hawass et al., 2010). Metagenomic analysis of five Egyptian mummies dating from the 3rd intermediate period to Roman Period (806 BCE-124 CE) found a positive result for P. falciparum in one individual (Khairat et al., 2013).

The Fayum Depression was a region of natural wetlands flooded each year by the Nile, making it a fertile region for farming. Analysis of muscle biopsies from 16 mummies dating from the 3rd Intermediate Period (1064–525 BCE) to the Roman Period (30 BC–195 CE) tested for the *P. falciparum* AMA1 gene and the MSP1 gene, and six were positive (Lalremruata et al., 2013). In Nubia, malaria has been investigated in tissue samples taken from eleven naturally mummified burials from North Argin, dating to 350–500 CE. Employing the Para SightTM-F immunoenzymatic assay, one of the individuals was positive for falciparum malaria (Miller et al., 1994). A later study of ten burials from Sayala, dating to the 3rd to 6th century CE, employed both DNA analysis with shotgun sequencing and also the immunological antigen tests Pv/Pf DiaSys and Pan/Pf DIASys. This indicates either *P. falciparum* or *P. vivax*, but cannot differentiate the two. These were not randomly selected individuals, but were chose for analysis as their bones showed lesions suggestive of chronic anaemia (cribra orbitalia). Four of the ten individuals were positive on both DNA and immunological antigen tests, and a further two were positive on either aDNA or antigen test (Loufouma-Mbouaka et al., 2020, 2021).

Toxoplasmosis (*Toxoplasma gondii*) was identified in an Egyptian mummy dating from the 3rd intermediate period to the Roman period (806 BCE-124 CE). Metagenomic analysis of muscle tissue samples from five mummies recovered the aDNA sequence of *Toxoplasma* in one of the individuals (Khairat et al., 2013). As toxoplasmosis can be caught by humans when they are in close contact with cats, it is possible that the disease occurred due to the role of cats as cult animals which were often mummified and used as religious offerings in ancient Egypt (Ikram, 2005).

Leishmaniasis (*Leishmania donovani*) has been investigated using bone and tissue samples from 91 mummies. PCR targeted the kinetoplastid mitochondrial DNA. The mummies originated in Abydos (dating to the Predynastic to Early Dynastic periods, 3500–2800 BCE), and Thebes (Middle Kingdom, New Kingdom, and Late Period, 2050–500 BCE). While the Predynastic, Early Dynastic, New Kingdom and Late Period samples were negative, four of the 42 Middle Kingdom samples were positive (9.5%). The authors suggest that since Egypt does not appear to have had Acacia-Balanites woodland preferred by the sandfly, while there was plenty of such woodland in Nubia, these individual may have become infected while travelling in Nubia for trade or during military activity (Zink et al., 2006).

5. Helminths

5.1 Blood helminths

The two species of schistosome endemic in the region in both recent and ancient times are *S. haematobium* and *S. mansoni* (Contis and David, 1996; Di Bella et al., 2018). We have read above how over a century ago Marc

Ruffer found the eggs of S. haematobium in the kidneys of two out of three 20th Dynasty mummies from Egypt (Ruffer, 1910). The mummy of Nakht from 1200 BCE Thebes was noted to have an enlarged spleen and histological examination showed schistosomal cirrhosis of the liver. Microscopy of tissue from his intestines, liver and kidneys demonstrated that these contained schistosome eggs (Hart et al., 1977b). As S. haematobium infects the blood vessels of the urinary tract and S. mansoni infects the blood vessels of the intestines, this would indicate that he was infected by both species. Nakht was later analysed further, together with the late predynastic mummy of an adolescent (3200 BCE), using a biomolecular approach. Tissue from the colon, skin and cheek was tested using ELISA targeting schistosomal circulating anodic antigen (CAA). As CAA is produced by both S. haematobium and S. mansoni, its use demonstrates that schistosomiasis is present but cannot determine the species. Both mummies were found to be positive for the CAA antigen (Deelder et al., 1990). The 12th Dynasty (c.1900 BCE) mummies of Khnum-Nakht and Nekht-Ankh from Rifeh underwent ancient DNA analysis for schistosomes using PCR. Both S. haematobium and S. mansoni were detected in Khnum-Nakht, while S. mansoni alone was detected in Nekht-Ankh (Matheson et al., 2014).

In Nubia, tissue biopsies from 23 naturally mummified individuals from Wadi Halfa, dating to 350–550 CE, were tested for CAA using ELISA. Sixteen (65%) were positive for this schistosomal antigen, indicating either *S. mansoni* or *S. haematobium* infection, or both (Miller et al., 1992). A later study of 46 individuals from the same site used ELISA with IgM monoclonal antibody to the CCA produced by *S. mansoni*. They found an infection rate of 26%, and there was an increasing prevalence with advancing age (Hibbs et al., 2011). Comparison was made with 191 naturally mummified burials dating from 550 to 950 CE at Kulubnarti. CCA was positive on ELISA in 9.4% of individuals, indicating *S. mansoni* infection (Hibbs et al., 2011). Again, no test specifically looking for *S. haematobium* was undertaken.

5.2 Intestinal helminths

Taenia tapeworms have been found causing both intestinal parasitism and cysticercosis. The mummy of Nakht, a weaver connected with the royal funerary chapel at Thebes, has been dated to around 1200 BCE. The intestines were found to contain the eggs of *Taenia* sp. in the faeces (Hart et al., 1977b). A canopic jar from Akhthepep's mastaba at Saqqara, containing the eviscerated organs of a mummy dating to the 25th Dynasty (715–656 BCE),

was found to contain the eggs of both Taenia sp. and one possible egg of roundworm (Ascaris sp.) (Harter et al., 2003). A cemetery dating to 300-500 CE at El-Deir at the Kharga oasis contained naturally mummified individuals. Twelve burials underwent parasite analysis of the pelvic sediment, and one adult was found to contain Taenia eggs (Le Bailly et al., 2010). These all indicate intestinal infection by adult tapeworms, but it is unclear from egg microscopy alone if they represent pork tapeworm, beef tapeworm or Asiatic tapeworm. In contrast, a Ptolemaic period mummy from Egypt, dating from 200 to 100 BCE, was noted to have a cystic lesion in the stomach wall. Histology employing indirect immunofluorescence (using serum from a person infected by Taenia solium), showed that this was a case of cysticercosis, from infection by the intermediate stage of pork tapeworm (Bruschi et al., 2006). Cysticercosis is often asymptomatic if located in the abdomen or chest, but can cause seizures, hydrocephalus and raised intracranial pressure if cysts are located in the brain (Garcia et al., 2003). In Nubia, Taenia sp. tapeworm eggs were also recovered from dry faeces taken from the pelvic region of a naturally mummified burial from Sai Island dating from 700 to 300 BCE (Harter, 2003).

Fish tapeworm (*Dibothriocephalus* sp.) has been found in intestinal samples from two mummies from Saqqara in Egypt, dating from 400 to 300 BCE (Harter, 2003). In Nubia, fish tapeworm eggs were also found in faeces preserved in the pelvic region of a naturally mummified burial from Sai Island, dating to 700–300 BCE (Harter, 2003). It would seem highly likely that fresh water fish caught in the River Nile had been eaten without thorough cooking, so leading to infection of these individuals. Infection may be asymptomatic, or contribute to anaemia.

Pinworm (*Enterobius vermicularis*) appears to have been endemic in the population of the Dakhla Oasis around 395 BCE-30 CE (Ptolemaic and Roman Periods). Faecal samples were taken from eight naturally preserved mummies, and two were positive for pinworm eggs (Horne, 2002). Infection typically causes intense night-time peri-anal itching, so interrupting sleep.

Threadworm (*Strongyloides stercoralis*) was diagnosed in the mummy of Asru, a chantress of Amun in the Temple of Karnack at Luxor. Asru lived during the 25th dynasty (600 BCE). Histological examination of samples from her intestinal wall found structures compatible with threadworm (Tapp, 1984). However, in the absence of eggs in the faeces, it would be reassuring to have aDNA confirmation of such a diagnosis. Infection may cause abdominal pain, diarrhoea and skin rashes.

5.3 Tissue helminths

Trichinosis (*Trichinella spiralis*) has been found in the intercostal muscles of the chest in the mummy of Nakht (known as ROM I), which was interred in Thebes around 1200 BCE (Hart et al., 1977b). *Trichinella* is a nematode contracted by eating raw or undercooked pork meat, and the immature larvae migrate through the body to striated muscle where they encyst. Symptoms include initial abdominal pain and diarrhoea, with later muscle pains, and death may occur if cardiac muscle or respiratory muscles are involved (Garcia, 2016).

Hydatid worm (*Echinococcus granulosus*) was identified in the head of Mummy 2240 curated at the Manchester Museum, UK. Histological analysis demonstrated the hydatid cyst within the brain tissue. The date of the mummy, and its origin within Egypt, remains unknown (Tapp, 1984). Any expansile cyst in the brain has the potential to cause neurological symptoms such as seizures or neurological deficit, depending upon the anatomical location.

Filariasis (likely *Wuchereria bancrofti*) has been noted on histological examination of groin tissue from the mummy of Natsef-Amun. He was a temple priest at Karnack, who died around 1200 BCE (Tapp and Wildsmith, 1992). Filarial worms are spread by the bite of mosquitos and live in the lymphatic system, causing filariasis with fevers, swollen lymph glands, and later lymphedema with swollen limbs (Garcia, 2016).

Guinea Worm (*Dracunculus medinensis*) was also present in ancient Egypt. The mummy 1770 dates from 1000 to 770 BCE, and is curated in the Manchester Museum (UK). Plain radiographs (x-rays) have shown calcified serpiginous structure in the abdominal wall of the mummy, compatible with the calcification of the guinea worm after it died (Isherwood et al., 1984). A further mummy from the tomb of Parennefer in the Valley of the Nobles on the west bank of the Nile dates from about 1450 BCE. Multiple serpentine lesions were identified in the skin over both legs, and histological examination showed a section of a gravid nematode containing large numbers of rhabditoid larvae, compatible with the female Guinea worm (Horne and Redford, 1995). Symptoms of dracunculiasis include intense itching and burning pain at the location where the worm erupts through the skin and releases its larvae into water sources.

6. Ectoparasites

Head lice (*Pediculus humanus capitis*) were found in a wooden comb at Antinoë in Egypt. Recovered from a rubbish mound, the comb dates from

400 to 600 CE. There are broadly spaced teeth on one side for removing tangles in the hair, and finely spaced teeth on the other side for stripping away lice from the hair. Microscopy of debris from the finely spaced side showed both male and female lice, together with an embryonated egg (nit) and some nymphs (Palma, 1991). A study of individuals from Wadi Halfa in Nubia, dating from 350 to 550 CE, investigated the hair remaining on 218 mummies. It was found that 40% had head lice (Armelagos, 1969). A summary of all the parasite evidence discussed here can be found in Tables 1 and 2.

7. Parasite prevalence

If we bring together the various studies discussed above, we can start to create large enough datasets to roughly estimate how widespread infections by certain types of parasite may have been (Mitchell, 2023, 35–38). We need to be careful to only include individuals that had no risk factor that resulted in their being pre-selected for a study. For example, some studies only included individuals with skeletal signs of anaemia, while excluding those without such skeletal lesions. In this group, we might expect a higher proportion of have been infected by parasites that cause anaemia than we would find in the whole population.

The one study assessing head lice prevalence at a population level found the 40% of mummies from Nubia dating from 350 to 550 CE were infected (Armelagos, 1969). While research from other regions and time periods would increase our confidence in how common head lice were, this sounds a plausible figure when we compare with studies in ancient mummies from other regions of the world (Reinhard and Buikstra, 2003; Arriaza et al., 2013).

Visceral leishmaniasis was identified in 12.9% of mummies from Kulubnarti in Nubia dating from 550 to 1500 CE. It was also found in 9.5% of mummies from a Middle Kingdom series of mummies from Thebes West in Egypt (2050–1650 BCE), a time when Egyptians travelled to Nubia for trade in gold and slaves, but not in other time periods in Egypt (Zink et al., 2006). Such studies might indicate that leishmaniasis was endemic in ancient Nubia and could also affect Egyptians who spent time in Nubia. If representative of the larger picture, perhaps around 10% of ancient Nubians might have been affected by visceral leishmaniasis.

Table 1Parasites in ancierParasite	nt Egypt. Date	Site	References
Ectoparasites			
Head Lice (Pediculus humanus capitis)	400–600 CE	Antinoë	Palma (1991)
Protozoa			
Leishmaniasis (Leishmania donovanî)	2050–1650 BCE	Thebes	Zink et al. (2006)
Malaria (Plasmodium	3200 BCE	Gebelein	Miller et al. (1994)
jalcıparum)	3200 BCE	Gebelein	Rabino Massa et al. (2000)
	2820–2630 BCE	Gebelein	Bianucci et al. (2008)
	1550–1324 BCE	Thebes	Hawass et al. (2010)
	1500–1085 BCE	Gurna	Miller et al. (1994)
	1500–500 BCE	Thebes	Nerlich et al. (2008)
	1304–1085 BCE	Unknown	Miller et al. (1994)
	806 BC-124 CE	Unknown	Khairat et al. (2013)
	801–777 BCE	Fayum	Lalremruata et al. (2013)
Toxoplasmosis (Toxoplasma gondii)	806 BC-124 CE	Unknown	Khairat et al. (2013)
Helminths			
Filarial worm (Wuchereria bancrofti?)	1200 BCE	Karnack	Tapp and Wildsmith (1992)
Fish Tapeworm (Diphyllobothrium sp.)	400-300 BCE	Unknown	Harter (2003)
Guinea worm (Dracunculus medinensis)	1450 BCE	Thebes	Horne and Redford (1995)
	1000–770 BCE	Unknown	Isherwood et al. (1984)

Table 1 Parasites	in	ancient	Egy
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(continued)

Parasite	Date	Site	References	
Hydatid worm (Echinococcus granulosus)	unknown	Unknown	Tapp (1984)	
Liver Fluke (Fasciola sp.)	2400-1750 BCE	Unknown	Harter (2003)	
	400-300 BCE	Unknown	Harter (2003)	
	300–275 BCE	Unknown	Harter (2003)	
Pinworm (Enterobius vermicularis)	395 BCE-30	CE Dakhla Oasis	Horne (2002)	
Pork tapeworm (<i>Taenia solium</i>)	200-100 BCE	Unknown	Bruschi et al. (2006)	
Roundworm (possible)	715–656 BCE	Saqqara	Harter et al. (2003)	
(Ascaris lumbricoides)	c.170 BCE	Unknown	Cockburn et al. (1975)	
Schistosomiasis	3200 BCE	Unknown	Deelder et al. (1990)	
(Schistosoma haematobium and	1900 BCE	Rifeh	Matheson et al. (2014)	
S. mansoní)	1250–1000 BCE	Unknown	Ruffer (1910)	
	1200 BCE	Thebes	Hart et al. (1977b)	
	1198–1150 BCE	Thebes	Deelder et al. (1990)	
Taenia sp. Tapeworm	300–500 CE	El-Deir	Le Bailly et al. (2010)	
(species uncertain)	1200 BCE	Thebes	Hart et al. (1977b)	
Threadworm (Strongyloides stercoralis)	600 BCE	Thebes	Tapp (1984)	
Trichina worm (<i>Trichinella spiralis</i>)	1200 BCE	Thebes	Hart et al. (1977b)	

Table 1 Parasites in ancient Egypt. (cont'd)

Falciparum malaria has been repeatedly found in ancient Egypt and Nubia by multiple studies. When we bring together the data for all 221 mummies analysed using either aDNA or immunological tests, 49 (22%) were positive for malaria. As such, we would expect malaria to have had a major impact upon child deaths and debilitating anaemia in all ancient populations along the Nile. The nature of the way the data is present in publications means that we cannot assess for any change in prevalence over

Parasite	Date	Site	References	
Ectoparasites				
Head Lice (Pediculus humanus capitis) Protozoa	350–550 CE	Wadi Halfa	Armelagos (1969)	
Leishmaniasis (Leishmania donovani)	550–1500 CE	Kulubnarti	Zink et al. (2006)	
Malaria (<i>Plasmodium</i>	350–500 CE	North Argin	Miller et al. (1994)	
falcıparum)	3rd–6th cent. CE	Sayala	Loufouma-Mbouaka et al. (2021)	
Helminths				
Fish Tapeworm (Dibothriocephalus sp.)	700–300 BCE	Sai Island	Harter (2003)	
Liver Fluke (Fasciola sp.)	700–300 BCE	Sai Island	Harter (2003)	
Schistosomiasis (species unknown)	350–550 CE	Wadi Halfa	Miller et al. (1992)	
Schistosomiasis	350–550 CE	Wadi Halfa	Hibbs et al. (2011)	
(Schistosoma mansoni)	550–950 CE	Kulubnarti	Hibbs et al. (2011)	
<i>Taenia</i> tapeworm (species uncertain)	700–300 BCE	Sai Island	Harter (2003)	

Table	2	Parasites	in	ancient	Nubia
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time, or determine if malaria was absent in the oldest samples and only found in the region after a certain date. Malaria is thought to have originated in gorillas in Africa and underwent host switching to humans somewhere between 112,000 and 1 million years ago (Baron et al., 2011). However, it seems the significant majority of mutations in the haemoglobin gene that give some resistance against malaria have developed within the last 6000 years (Hedrick, 2012). This indicates greater selection pressure upon human survival in cases of malaria in Africa and the Mediterranean region at just the time when ancient Egypt and Nubia developed and flourished.

Schistosomiasis was caused by both *S. haematobium* and *S. mansoni* in Egypt and Nubia. Some studies were able to identify that schistosomiasis

was present but not distinguish which species, while others studies were able to assess infection at species level. Of the 266 mummies tested for any form of schistosomiasis, 46 individuals (17%) had been infected. However, the largest two studies (with 237 mummies) only tested for *S. mansoni* (using CCA), so would miss cases of *S. haematobium* that may have been present. The one study that tested for both *S. mansoni* and *S. haematobium* (looking for CAA) found a prevalence of 65% (Miller et al., 1992). This would suggest that the prevalence of infection by all forms of schistosomiasis would certainly have been higher than 17%, and was potentially up to 65%.

8. Parasites and anaemia

In cases of infection by many parasites, it may not be the direct effects of the parasite itself that causes the greatest morbidity, but instead the consequence that the parasite causes anaemia. Anaemia can be defined as a reduction in the number of red blood cells, or in the amount of haemoglobin they contain, which results in a decrease in the capacity of the blood to carry oxygen. This can result in stunted growth in children, and reduced exercise capacity, tiredness, and shortness of breath in any age group (Ngui et al., 2012; Oliveira et al., 2015). Depending upon the parasite responsible, anaemia may result from parasite absorption of nutrients from the diet, inflammation in the lining of the intestines impairing nutrient absorption, blood loss from the intestines, kidneys or bladder (e.g. schistosomiasis), or shortened life span of red blood cells when infected by protozoal parasites (e.g. malaria) (Ghosh and Ghosh, 2007; Koukounari et al., 2008).

Cribra orbitalia is the term that describes a lesion of the orbital roof of the skull, with pitting in the cortical bone due to inflammation and blood vessel formation. Research suggests that the most common cause is anaemia in childhood (especially in lesions whether there is expansion of the underlying bone marrow layer in the orbital roof), but that it can also be caused by scurvy and rickets. It is thought that this lesion can result from anaemia in childhood, rather than in adulthood, as red bone marrow is only found in the orbital roofs in childhood, and it disappears before adulthood (Brickley, 2018; Oxenham and Cavill, 2010; Walker et al., 2009). A study in rats showed that cribra orbitalia can be caused by iron deficiency or magnesium deficiency in the diet (Polo-Cerdá et al., 2000). Such evidence suggests that while the prevalence of cribra orbitalia does not directly equate to the prevalence of anaemia, variations in cribra orbitalia may broadly reflect variations in anaemia if there are no other lesions indicating scurvy or rickets in the skeletal remains.

A large study brought together the data published on cribra orbitalia in 4760 skeletons from 29 Nile Valley locations. The results showed that 42.8% of people in these populations had cribra orbitalia. When they compared the prevalence in different time periods from the pre-dynastic to Christian periods, there was no significant change. The study author felt the most likely explanation for the consistently high prevalence of cribra orbitalia was infection by malaria (Smith-Guzmán, 2015). While is clear that malaria commonly causes anaemia in children (Ghosh and Ghosh, 2007), we have shown that about 22% of mummies were positive when tested for malaria, which is only around half the prevalence of cribra orbitalia. Therefore we must also consider whether the many other parasite species found in ancient Egypt could also have contributed to this pattern. The parasites that most commonly cause anaemia are malaria, schistomoiasis, and hookworm (Koukounari et al., 2008). As hookworm has yet to be identified in ancient Egypt, we should focus on the effects of schistosomiasis. Here we have shown that a minimum of 17%, and in one study 65%, of mummies were positive for schistosomiasis. Therefore, together with the various other causes of anaemia such as nutritional deficiencies, it is likely that both malaria and schistosomiasis were major contributors to the high prevalence of anaemia noted in ancient Egypt and Nubia.

9. The role of the River Nile

The civilizations of ancient Egypt and Nubia could not have existed were it not for the waters of the River Nile. However, it was this very river that acted as the key driver of parasitism in the populations who lived there. The waters enabled mosquitos to breed and spread malaria and filariasis (Lalremruata et al., 2013; Tapp and Wildsmith, 1992). Agricultural techniques with irrigation using the Nile waters put farmers at risk of infection by schistosomiasis as they waded in the fresh water (Matheson et al., 2014). Those drinking the water without boiling it first could have caught dracunculiasis (Horne and Redford, 1995). Fish caught from the Nile led to infection by fish tapeworm if eaten raw or undercooked (Harter, 2003). Water plants eaten fresh by the population would have put them at risk of *Fasciola* liver fluke (Harter, 2003), even if the main hosts of this parasite would have been farm animals such as cattle and goats. In contrast to the success of parasites spread by poor sanitation in many other ancient civilizations, in ancient Egypt and Nubia we see the dominance of zoonotic parasites (Ledger and Mitchell, 2022; Wang and Mitchell, 2022). It seems likely that the Nile acted as a conduit for the movement of these parasites from central Africa to the arid northeast of the continent, but also provided sufficient water levels to maintain these parasites in the region year round, despite the extremely low rainfall.

> 10. Spread of disease from ancient Egypt

We have seen that malaria was present in ancient Egypt at least as early as the predynastic period c.3200 BCE (Miller et al., 1994). Since malaria is thought to have originated in Africa and spread to humans from other primates (Baron et al., 2011; Liu et al., 2010; Rayner et al., 2011), there is potential for malaria to have gone on to spread from ancient Egypt to other cultures around the Mediterranean through trade and shipping. Early written texts suggest that malaria was introduced into Italy around 700 BCE, based on descriptive records of periodic fevers (Sallares, 2002; Sallares et al., 2004). Genetic studies of Roman period human skeletal remains from Italy have confirmed cases of both malaria (Marciniak et al., 2016; Sallares and Gomzi, 2001) and the haemoglobin mutations that protect children against death from malaria (Sallares and Gomzi, 2001; Viganó et al., 2017). Together, these textual descriptions, pathogen DNA and human DNA evidence suggests that malaria resulted in major health consequences to the populations of Italy during the Etruscan and Roman periods (Mitchell, 2017b). As the Mediterranean civilization with the earliest evidence for malaria, it seems the most likely source for malaria in ancient Italy and Greece would have been Egypt.

11. Limitations of the study

When comparing the evidence for parasites in ancient Egypt and Nubia with those from other regions of the world, we need to bear in mind the differences in the nature of the samples available. In the regions neighbouring Egypt and Nubia, such as the rest of Africa, the Near East, and Europe, the bulk of parasite evidence comes from latrines, coprolites and the pelvic sediment of burials. This gives plenty of opportunity to detect intestinal helminths and the protozoa that cause diarrhoea and dysentery, but limited chance of detecting ectoparasites or parasites that live outside the intestines or urinary tract. While some analysis of the pelvic sediment of some naturally partially mummified burials has been undertaken in ancient Egypt (Le Bailly et al., 2010), the bulk of the research has focussed on artificially preserved mummies and organs preserved in canopic jars. The lack of analysis of sediment from toilets in Egypt and Nubia limits the opportunity to detect intestinal helminths and the protozoa that cause diarrhoea and dysentery and compare with evidence from Europe and the Near East. However, in Egypt and Nubia there has been plenty of research investigating parasites in soft tissues that are not available in regions of the world where mummies just do not survive. A consequence of this is that we cannot determine whether malaria was more or less common in Egypt than the rest of the Mediterranean world, or if schistosomiasis was more or less common in the Nile cultures than those living along the Tigris and Euphrates rivers in Mesopotamia, because these regions do not have surviving mummies to analyse and allow a meaningful comparison.

As with all studies of ancient diseases, there may be a reporting bias that affects the published data. Articles only tend to be submitted to journals when the authors find positive results, as most journal editors are not interested in publishing negative findings from unsuccessful projects. When these positive papers are brought together in a review such as this, we remain ignorant of other unpublished studies that might have taken place where no positive results were found. This could inappropriately increase the perceived prevalence of disease in past societies as all the positive cases are published, but not all the negative cases will be.

The evidence found in ancient Egypt can only reflect the techniques employed in each study. If methods are employed that target falciparum malaria but not other species, then we get the impression that all malaria in ancient Egypt was due to *P. falciparum*. Very few papers have explored whether other types of malaria were present, and nor do they explain why they all focus on falciparum. It could reflect the testing methods available at the time they undertook their study, or the fact that falciparum malaria might have been of more interest to researchers than other forms of malaria due to its greater lethality. The same applies to schistosomiasis, where there has been considerably more work testing for *S. mansoni* than has been the case testing for *S. haematobium*. It is likely that with increasing use of metagenomics which recovers all the available DNA and identifies the source using pathogen DNA sequence databases, then hopefully in the future we should get a more accurate picture of the species of malaria and schistosomes present in the region.

We should also consider the effects of survival of aDNA, antigens and parasite eggs. All biological materials degrade over time, destroyed by the effects of bacteria, fungi, insects and other agents, and the hot temperatures in Egypt may accelerate this process (Marota et al., 2002). Over thousands of years it would not be surprising to find that individuals who were once infected by parasites may lose that evidence, so that when analysed by scientists they may become a false negative (Morrow et al., 2016; Reinhard et al., 2019). While the degree to which this occurs will vary depending upon the environmental conditions in which they originated, it could be argued that this effect may broadly counteract much of the publication bias discussed above.

12. Conclusion

The evidence brought together here shows that parasite infection in ancient Egypt and Nubia was quite distinct from that found in many other civilizations of the ancient world. Species spread by ineffective sanitation were rare, possibly due to the role of the annual Nile floods fertilizing the fields so that the population did not need to use their faeces to do so. It was zoonotic parasites that dominated. In view of this, there is great potential for future research to undertake parasite analysis of mummified animals, which at present is lacking. The role of the Nile has been highlighted for enabling mosquitoes to breed and spread malaria, providing the freshwater fish that spread fish tapeworm, water plants which spread Fasciola liver fluke, and drinking water that led to dracunculiasis. Agricultural technologies developed to harness the Nile waters put farmers at risk of schistosomiasis. The role of cats as a cult status animal in the religion of ancient Egypt would have increased the likelihood of contracting toxoplasmosis. The effects of malaria and schistosomiasis, potentially exacerbated by nutritional deficiencies, would have resulted in widespread anaemia. When the effects of visceral leishmaniasis are also factored in, it does appear that a large proportion of the ancient populations living along the Nile would have suffered with chronic debilitating illness due to their parasites.

References

- Armelagos, G.J., 1969. Disease in ancient Nubia: changes in disease patterns from 350 B.C. to A.D. 1400 demonstrate the interaction of biology and culture. Science 163 (3864), 255–259. https://doi.org/10.1126/science.163.3864.25.
- Arriaza, B., Standen, V., Reinhard, K., Araújo, A., Heukelbach, J., Dittmar, K., 2013. On head lice and social interaction in archaic Andean coastal populations. Int. J. Paleopathol. 3, 257–268. https://doi.org/10.1016/j.ijpp.2013.10.001.
- Bardinet, T., 1995. Les Papyrus Médicaux de l'Égypt Pharaonique: Traduction Intégrale et Commentaire. Fayard, Paris.
- Baron, J.M., Higgins, J.M., Dzik, W.H., 2011. A revised timeline for the origin of *Plasmodium falciparum* as a human pathogen. J. Mol. Evol. 73, 297–304. https://doi.org/ 10.1007/s00239-011-9476-x.
- Bianucci, R., Araujo, A., Pusch, C.M., Nerlich, A.G., 2015. The identification of malaria in paleopathology—an in-depth assessment of the strategies to detect malaria in ancient remains. Acta Tropica 152, 176–180. https://doi.org/10.1016/j.actatropica.2015.09.002.
- Bianucci, R., Mattutino, G., Lallo, R., Charlier, P., Jouin-Spriet, H., Peluso, A., et al., 2008. Immunological evidence of *Plasmodium falciparum* infection in a child mummy from the Early Dynastic Period. J. Archaeol. Sci. 35, 1880–1885. https://doi.org/10. 1016/j.jas.2007.11.019.
- Brickley, M., 2018. Cribra orbitalia and porotic hyperostosis: a biological approach to diagnosis. Am. J. Phys. Anthropol. 167, 896–902. https://doi.org/10.1002/ajpa.23701.
- Brier, B.M., Hobbs, H., 2008. Daily Life of the Ancient Egyptians. Greenwood, Westport.
- Bruschi, F., Masetti, M., Locci, M.T., Ciranni, R., Fornaciari, G., 2006. Cystercercosis in an Egyptian mummy of the late Ptolemaic Period. Am. J. Trop. Med. Hyg. 74, 598–599. https://doi.org/10.4269/ajtmh.2006.74.598.
- Bryant, V.M., Dean, G.W., 2006. Archaeological coprolite science: the legacy of Eric O. Callen (1912–1970). Palaeogeogr. Palaeoclimatol. Palaeoecol. 237, 51–66. https://doi. org/10.1016/j.palaeo.2005.11.032.
- Bunbury, J., 2019. The Nile and Ancient Egypt: Changing Land and Waterscapes, from the Neolithic to the Roman Era. Cambridge University Press, Cambridge.
- Cockburn, A., Barraco, R.A., Reyman, T.A., Peck, W.H., 1975. Autopsy of an Egyptian mummy: a mummy can be a scientific treasure; to unlock its secrets, a multidisciplinary approach is needed. Science 187 (4182), 1155–1160. https://doi.org/10.1126/science. 187.4182.1155.
- Contis, G., David, A.R., 1996. The epidemiology of Bilharzia in ancient Egypt: 5000 years of schistosomiasis. Parasitol. Today 12 (7), 253–255.
- Da Silva Veiga, O.A., 2009. Health and Medicine in Ancient Egypt: Magic and Science. Archaeopress, Oxford.
- David, A.R. (Ed.), 1979. Manchester Museum Mummy Project: Multidisciplinary Research on Ancient Egyptian Mummifies Remains. Manchester Museum, Manchester.
- David, A.R., Tapp, Es (Eds.), 1984. Evidence Embalmed: Modern Medicine and the Mummies of Ancient Egypt. Manchester University Press, Manchester.
- Deelder, A.M., Miller, R.L., de Jonge, N., Krijger, F.W., 1990. Detection of schistosome antigen in mummies. Lancet 335, 724–725. https://doi.org/10.1016/0140-6736(90)90838-v.
- Di Bella, S., Riccardi, N., Giacobbe, D.R., Luzzati, R., 2018. History of schistosomiasis (bilharziasis) in humans: from Egyptian medical papyri to molecular biology on mummies. Pathog. Global Health 112, 268–273. https://doi.org/10.1080/20477724.2018.1495357.
- Dietrich, R. (Ed.), 2019. Handbook of Ancient Nubia, vol. 2 Walter de Gruyter, Boston, MA.
- Donoghue, H.D., Lee, O.Y.-C., Minnikin, D.E., Besra, G.S., Taylor, J.H., Spigelman, M., 2010. Tuberculosis in Dr Granville's mummy: a molecular re-examination of the earliest known Egyptian mummy to be scientifically examined and given a medical diagnosis. *Proc. R. Soc.* B 277, 51–56. https://doi.org/10.1098/rspb.2009.1484.

- Eltorai, I.M., 2019. A Spotlight on the History of Ancient Egyptian Medicine. CRC Press, Boca Raton, FL.
- Emberling, G., Williams, B.B. (Eds.), 2020. The Oxford Handbook of Ancient Nubia. Oxford University Press, New York.
- Garcia, H.H., Gonzalez, A.E., Evans, C.A.W., Gilman, R.H., 2003. Taenia solium cysticercosis. Lancet 362 (9383), 547–556. https://doi.org/10.1016/S0140-6736(03) 14117-7.

Garcia, L.S., 2016. Diagnostic Medical Parasitology, sixth ed. ASM Press, Washington, DC.

- Ghosh, K., Ghosh, K., 2007. Pathogenesis of anemia in malaria: a concise review. Parasitol. Res. 101, 1463–1469. https://doi.org/10.1007/s00436-007-0742-1.
- Granville, A.B., 1825. An essay on Egyptian mummies; with observations on the art of embalming among the ancient Egyptians. Proc. R. Soc. Lond. 115, 269–316. https:// doi.org/10.1098/rstl.1825.0015.
- Hart, G.D., Cockburn, A., Millet, N.B., Scott, J.W., 1977a. Lessons learned from the autopsy of an Egyptian mummy. Can. Med. Assoc. J. 117, 415–416.
- Hart, G.D., Horne, P.D., Lewin, P.K., Millet, N.B., Rideout, D.F., Scott, J.W., et al., 1977b. Autopsy of an Egyptian mummy (Nakht – ROM I). Can. Med. Assoc. J. 117, 461–476.
- Harter, S., 2003. Implication de la Paléoparasitologie dans l'Etude des Populations Anciennes de la Vallée du Nil et du Proche-Orient: Etudes de Cas (PhD thesis). Universite de Reims Champagne-Ardenne.
- Harter, S., Le Bailly, M., Janot, F., Bouchet, F., 2003. First paleoparasitological study of embalming rejects jar found in Saqqara, Egypt. Mem. do Inst. Oswaldo Cruz 98 (Suppl. 1), 119–121. https://doi.org/10.1590/s0074-02762003000900017.
- Hawass, Z., Gad, Y., Ismail, S., Khairat, R., Fathalla, D., Hasan, N., et al., 2010. Ancestry and pathology in King Tuthankhamun's family. J. Am. Med. Assoc. (JAMA) 303, 638–647. https://doi.org/10.1001/jama.2010.121.
- Hedrick, P.W., 2012. Resistance to malaria in humans: the impact of strong, recent selection. Malar. J. 11, 349. https://doi.org/10.1186/1475-2875-11-349.
- Hibbs, A.C., Secor, W.E., Van Gerven, D., Armelagos, G., 2011. Irrigation and infection: the immunoepidemiology of schistosomiasis in Ancient Nubia. Am. J. Phys. Anthropol. 145, 290–298. https://doi.org/10.1002/ajpa.21493.
- Horne, P., Redford, S., 1995. Aspergillosis and dracunculiasis in mummies from the tomb of Parennefer. Paleopathol. Newsl. 92, 10–12.
- Horne, P.D., 2002. First evidence of Enterobiasis in ancient Egypt. J. Parasitol. 88, 1019–1021. https://doi.org/10.2307/3285550.
- Ikram, S., 2005. Divine Creatures: Animal Mummies in Ancient Egypt. American University of Cairo, Cairo.
- Ikram, S., 2010. Ancient Egypt: An Introduction. Cambridge University Press, Cambridge.
- Isherwood, I., Jarvis, H., Fawcitt, R.A., 1984. Radiology of the Manchester mummies. In: David, A.R., Tapp, E. (Eds.), Evidence Embalmed: Modern Medicine and the Mummies of Ancient Egypt. Manchester University Press, Manchester, pp. 25–64.
- Khairat, R., Ball, M., Chang, C.-C.H., Bianucci, R., Nerlich, A.G., Trautmann, M., et al., 2013. First insights into the metagenome of Egyptian mummies using next-generation sequencing. J. Appl. Genet. 54, 309–325. https://doi.org/10.1007/s13353-013-0145-1.
- Koukounari, A., Estambale, B.B.A., Njagi, J.K., Cundill, B., Ajanga, A., Crudder, C., et al., 2008. Relationship between anaemia and parasitic infections in Kenyan schoolchildren: a Bayesian hierarchical modelling approach. Int. J. Parasitol. 38, 1663–1671. https:// doi.org/10.1016/j.ijpara.2008.05.013.
- Lalremruata, A., Ball, M., Bianucci, R., Welte, B., Nerlich, A.G., Kun, J.F.J., et al., 2013. Molecular identification of falciparum malaria and human tuberculosis co-infections in mummies from the Fayum depression (Lower Egypt). PLoS One 8 (4), e60307. https:// doi.org/10.1371/journal.pone.0060307.

- Lambert-Zazulak, P.I., Rutherford, P., David, A.R., 2003. The international ancient Egyptian mummy tissue bank at the Manchester Museum as a resource for the paleoepidemiological study of schistosomiasis. World Archaeol. 35, 223–240. https:// doi.org/10.1080/0043824032000111399.
- Le Bailly, M., Maicher, C., Dufour, B., 2016. Archaeological occurrences and historical review of the human amoeba *Entamoeba histolytica* over the past 6000 years. *Infect. Genet. Evol.* 42, 34–40. https://doi.org/10.1016/j.meegid.2016.04.030.
- Le Bailly, M., Mouze, S., Rocha, G.C.D., Heim, J.-L., Lichtenberg, R., Dunand, F., et al., 2010. Identification of *Taenia* sp. in a mummy from a Christian necropolis in El-Deir, oasis of Kharga, ancient Egypt. J. Parasitol. 96, 213–215. https://doi.org/10.1645/GE-2076.1.
- Ledger, M.L., Mitchell, P.D., 2022. Tracing zoonotic parasite infections throughout human evolution. Int. J. Osteoarchaeol. 32 (3), 553–564. https://doi.org/10.1002/oa.2786.
- Leitz, C., 1999. Magical and Medical Papyri of the New Kingdom. British Museum, London.
- Liu, W., Li, V., Learn, G.H., Rudicell, R.S., Robertson, J.D., Keele, B.F., et al., 2010. Origin of the human malaria parasite *Plasmodium falciparum* in gorillas. Nature 467, 420–425. https://doi.org/10.1038/nature09442.
- Lloyd, A.B. (Ed.), 2014. A Companion to Ancient Egypt. Wiley Blackwell, Chichester.
- Loufouma-Mbouaka, A., Binder, M., Noedl, H., Gamble, M., 2020. Evaluation of rapid diagnostic tests and Enzyme Linked Immunoassay in the detection of malaria in ancient human remains. J. Archaeol. Sci. 116, 105118. https://doi.org/10.1016/j.jas.2020.105118.
- Loufouma-Mbouaka, A., Gamble, M., Wurst, C., Jäger, H.Y., Maixner, F., Zink, A., et al., 2021. The elusive parasite: comparing macroscopic, immunological, and genomic approaches to identifying malaria in human skeletal remains from Sayala, Egypt (third to sixth centuries AD). Archaeol. Anthropol. Sci. 13, 115. https://doi.org/10.1007/ s12520-021-01350-z.
- Marciniak, S., Prowse, T.L., Herring, D.A., Klunk, J., Kuch, M., Duggan, A.T., et al., 2016. *Plasmodium falciparum* malaria in 1st-2nd century CE southern Italy. Curr. Biol. 26 (23), R1205–R1225. https://doi.org/10.1016/j.cub.2016.10.016.
- Marota, I., Basile, C., Ubaldi, M., Rollo, F., 2002. DNA decay rate in papyri and human remains from Egyptian archaeological sites. Am. J. Phys. Anthropol. 117, 310–318. https://doi.org/10.1002/ajpa.10045.
- Matheson, C.D., David, R., Spigelman, M., Donoghue, H.D., 2014. Molecular confirmation of Schistosoma and familial relationship in two ancient Egyptian mummies. Yearb. Mummy Stud. 2, 39–47.
- McMahon, A., 2015. Waste management in early urban southern Mesopotamia. In: Mitchell, P.D. (Ed.), Sanitation, Latrines and Intestinal Parasites in Past Populations. Ashgate, Farnham, pp. 19–39.
- Miller, R.L., Armelagos, G.J., Ikram, S., Jonge, D.N., Krijger, F.W., Deelder, A.M., 1992. Paleoepidemiology of Schistosoma infection in mummies. BMJ 304, 555–556. https:// doi.org/10.1136/bmj.304.6826.555.
- Miller, R.L., Ikram, S., Armelagos, G.J., Walker, R., Harer, W.B., Schiff, C.J., et al., 1994. Diagnosis of *Plasmodium falciparum* infection in mummies using the rapid manual ParaSight-F test. Trans. R. Soc. Trop. Med. Hyg. 88, 31–32. https://doi.org/10.1016/ 0035-9203(94)90484-7.
- Mitchell, P.D., 2013. The origins of human parasites: exploring the evidence for endoparasitism throughout human evolution. Int. J. Paleopathol. 3, 191–198. https://doi. org/10.1016/j.ijpp.2013.08.003.
- Mitchell, P.D., 2017a. Sampling human remains for evidence of intestinal parasites. In: Mitchell, P.D., Brickley, M. (Eds.), Updated Guidelines to the Standards for Recording Human Remains. Chartered Institute for Archaeologists/British Association for Biological Anthropology and Osteoarchaeology, Reading, pp. 54–56.

- Mitchell, P.D., 2017b. Human parasites in the Roman world: health consequences of conquering an empire. Parasitology 144, 48–58. https://doi.org/10.1017/S0031182015001651.
- Mitchell, P.D., 2023. Parasites in Past Civilizations and Their Impact Upon Health. Cambridge University Press, Cambridge.
- Mitchell, P.D., Wang, T., Billig, Y., Gadot, Y., Wanrnock, P., Langgut, D., 2023. Giardia duodenalis and dysentery in Iron Age Jerusalem (7th–6th centuries BCE). Parasitology 150, 693–699. https://doi.org/10.1017/S0031182023000410.
- Morrow, J.J., Newby, J., Piombino-Mascali, D., Reinhard, K.J., 2016. Taphonomic considerations for the analysis of parasites in archaeological materials. Int. J. Paleopathol. 13, 56–64. https://doi.org/10.1016/j.ijpp.2016.01.005.
- Mumcuoglu, K.Y., Zias, J., 1989. How the ancients de-loused themselves. Biblcal Archaeol. Rev. 15, 66–69.
- Nerlich, A.G., Schraut, B., Dittrich, S., Jelinek, T., Zink, A.R., 2008. Plasmodium falciparum in ancient Egypt. Emerg. Infect. Dis. 14 (8), 1317–1319. https://doi.org/10.3201/ eid1408.080235.
- Ngui, R., Lim, Y.A.L., Chong Kin, L., Sek Chuen, C., Jaffar, S., 2012. Association between anaemia, iron deficiency anaemia, neglected parasitic infections and socioeconomic factors in rural children of West Malaysia. PLoS Negl. Trop. Dis. 6 (3), e1550. https://doi.org/10.1371/journal.pntd.0001550.
- Oliveira, D., Ferreira, F.S., Atouguia, J., Fortes, F., Guerra, A., Centeno-Lima, S., 2015. Infection by intestinal parasites, stunting and anaemia in school-aged children from southern Angola. PLoS One 10 (9), e0137327. https://doi.org/10.1371/journal.pone. 0137327.
- Oxenham, M., Cavill, I., 2010. Porotic hyperostosis and cribra orbitalia: the erythropoietic response to iron-deficiency anaemia. Anthropol. Sci. 118 (3), 199–200. https://doi. org/10.1002/ajpa.21031.
- Palma, R.L., 1991. Ancient head lice on a wooden comb from Antinoe, Egypt. J. Egypt. Archaeol. 77, 194. https://doi.org/10.1177/030751339107700124.
- Polo-Cerdá, M., Miquel-Feucht, M., Villalaín-Blanco, J.D., 2000. Experimental cribra orbitalia in wistar rats: an etiopathogenic model of porotic hyperostosis and other porotic phenomena. In: La Verghetta, M., Capasso, L. (Eds.), Proceedings of the XIIIth European Meeting of the Paleopathology Association, Chieti, Italy. Edigrafital S.p.A, Teramo, pp. 253–259.
- Rabino Massa, E., Cerutti, N., Savoia, A.M.D., 2000. Malaria in ancient Egypt: paleoimmunological investigations in predynastic mummified remains. Chungara 32, 7–9. https://doi.org/10.4067/S0717-7356200000100003.
- Rayner, J.C., Liu, W., Peeters, M., Sharp, P.M., Hahn, B.H., 2011. A plethora of Plasmodium species in wild apes: a source of human infection? Trends Parasitol. 27, 222–229. https://doi.org/10.1016/j.pt.2011.01.006.
- Reinhard, K., Buikstra, J., 2003. Louse infestation of the Chiribaya culture, southern Peru: variation in prevalence by age and sex. *Mem. do Inst. Oswaldo Cruz* 98 (Suppl. 1), 173–179. https://doi.org/10.1590/s0074-02762003000900026.
- Reinhard, K., Camacho, M., Geyer, B., Hayek, S., Horn, C., Otterson, K., et al., 2019. Imaging coprolite taphonomy and preservation. Archaeol. Anthropol. Sci. 11, 6017–6035. https://doi.org/10.1007/s12520-019-00946-w.
- Ruffer, M.A., 1909. Preliminary note on the histology of Egyptian mummies. BMJ 1 (2521), 1005. https://doi.org/10.1136/bmj.1.2521.1005.
- Ruffer, M.A., 1910. Note on the presence of "Bilharzia haematobia" in Egyptian mummies of the twentieth dynasty [1250–1000 BC]. BMJ 1 (2557), 16. https://doi.org/10.1136/ bmj.1.2557.16-a.
- Sallares, R., 2002. Malaria and Rome: A History of Malaria in Ancient Italy. Oxford University Press, Oxford.

- Sallares, R., Bouwman, A., Anderung, C., 2004. The spread of malaria to southern Europe in antiquity: New approaches to old problems. Med. History 48, 311–328. https://doi. org/10.1017/s0025727300007651.
- Sallares, R., Gomzi, S., 2001. Biomolecular archaeology of malaria. Anc. Biomol. 3, 195–213.
- Sandison, A.T., 1967. Sir Marc Armand Ruffer (1859–1917) pioneer of palaeopathology. Med. History 11, 150–156. https://doi.org/10.1017/S002572730001200X.
- Shaw, I., 2003. Exploring Ancient Egypt. Oxford University Press, Oxford.
- Sheppard, K.L., 2012. Between spectacle and science: Margaret Murray and the tomb of the two brothers. Sci. Context. 25, 525–549. https://doi.org/10.1017/S0269889712000221.
- Shillito, L.-M., Blong, J.V.C., Green, E.V.J., Van Asperen, E., 2020. The what, how and why of archaeological coprolite analysis. Earth-Science Rev. 207, 103196. https://doi. org/10.1016/j.earscirev.2020.103196.
- Smith, D.N., 2013. Defining an indicator package to allow identification of 'cesspits' in the archaeological record. J. Archaeol. Sci. 40, 526–543. https://doi.org/10.1016/j.jas. 2012.06.014.
- Smith-Guzmán, N.E., 2015. Cribra orbitalia in the ancient Nile valley and its connection to malaria. Int. J. Paleopathol. 10, 1–12. https://doi.org/10.1016/j.ijpp.2015.03.001.
- Steel, L., 2007. Egypt and the Mediterranean world. In: Wilkinson, R. (Ed.), The Egyptian World. Routledge, London, pp. 459–475.
- Tapp, E., 1984. Disease in the Manchester mummies. In: David, A.R., Tapp, E. (Eds.), Evidence Embalmed: Modern Medicine and the Mummies of Ancient Egypt. Manchester University Press, Manchester, pp. 95–102.
- Tapp, E., Wildsmith, K., 1992. The autopsy and endoscopy of the Leeds mummy. In: David, A.R., Tapp, E. (Eds.), The Mummy's Tale: The Scientific and Medical Investigation of Natsef-Amun, Priest in the Temple at Karnack. Michael O'Mara, London, pp. 132–153.
- Taylor, J.H., 2010. Egyptian Mummies. British Museum, London.
- Török, B.L., 2009. Between Two Worlds: The Frontier Region Between Ancient Nubia and Egypt, 3700 BC–AD 500. Brill, Leiden.
- Trigger, B.G., Kemp, B.J., O'Connor, D., Lloyd, A.B., 2012. Ancient Egypt: A Social History. Cambridge University Press, Cambridge.
- Viganó, C., Haas, C., Rühli, F.J., Bouwman, A., 2017. 2,000 year old β-thalassaemia case in Sardinia suggest malaria was endemic by the Roman period. Am. J. Phys. Anthropol. 164 (2), 362–370. https://doi.org/10.1002/ajpa.23278.
- Walker, P.L., Bathurst, R.R., Richman, R., Gjerdrum, T., Andrushko, V.A., 2009. The causes of porotic hyperostosis and cribra orbitalia: a reappraisal of the iron-deficiencyanemia hypothesis. Am. J. Phys. Anthropol. 139, 109–125. https://doi.org/10.1002/ ajpa.21031.
- Wang, T., Mitchell, P.D., 2022. Liver fluke infection throughout human evolution. Gastro Hep Adv. 1 (4), 500–507. https://doi.org/10.1016/j.gastha.2022.02.027.
- Wilkinson, T., 2010. The Rise and Fall of Ancient Egypt: The History of a Civilisation from 3000 BC to Cleopatra. Bloomsbury, London.
- Xekalaki, G., 2021. On borders and expansion: Egyptian imperialism in the Levant during the Ramesside Period. Heritage 4, 3938–3948. https://doi.org/10.3390/heritage4040216.
- Yang, L., Zhang, X., Zhao, X., Xiang, H., 2022. The technological advance and application of coprolite analysis. Front. Ecol. Evol. 9, 797370. https://doi.org/10.3389/ fevo.2021.797370.
- Zink, A., Spigelman, M., Schraut, B., Greenblatt, C.L., Nerlich, A.G., Donoghue, H.D., 2006. Leishmaniasis in ancient Egypt and upper Nubia. Emerg. Infect. Dis. 12, 1616–1617. https://doi.org/10.3201/eid1210.060169.