Detecting hidden diets and disease: zoonotic parasites and fish consumption in Mesolithic Ireland

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Abstract

Archaeoparasitology is increasingly being used as a tool in archaeological research to investigate relationships between past humans, environments, diets and disease. It can be particularly useful in contexts where parasite eggs preserve, but human and faunal remains do not, including in the identification of disease and/or dietary items otherwise absent from the local archaeological record. We analyzed soil samples from the Late Mesolithic layers of the lake island site of Derragh in County Longford, Ireland. All samples were positive for the presence of *Diphyllobothrium* sp., an intestinal fish tapeworm that infects humans, causing diphyllobothriasis. Though fish are thought to be a staple food in Mesolithic Ireland, evidence for fishing and subsistence from this period is extremely fragmentary. Similarly, there is little available evidence for disease, primarily due to the lack of human remains. This finding represents the earliest known presence of human-derived parasites in Ireland, the earliest known finding of *Diphyllobothrium* sp. in Europe and the only finding of the tapeworm from hunter-gatherer contexts. It suggests parasitic infections, particularly those resulting from undercooked food, may be more common in ancient hunter-gatherer populations than previously suspected. The presence of these zoonotic parasites at hunter-gatherer sites can provide important insight into local environments, health and disease, and culinary practices. In locations like Mesolithic Ireland, the presence of parasites may assist in the identification of subsistence activities, such as fishing, and specific prey.

1. Introduction

Zoonoses, infectious diseases transmitted from animals to humans, are an important part of understanding the origin, evolution, and history of infectious disease and ancient human-animal interactions (Fiennes, 1978; Greenblatt and Spigelman, 2003; Mays, 2005; Bendrey et al., 2008; Bos et al., 2014; Fournié et al., 2017), but they are difficult to trace in the archaeological record. Barrett et al. (1998) proposed a “Paleolithic Age Baseline”, suggesting that infectious agents must have been minimal during times in human prehistory when people lived in small, mobile groups. Since the “Paleolithic Age Baseline”, there have been three epidemiological transitions, all of which have influenced (and are influencing) the presence and frequency of infectious disease across the world. The first was the transition to farming from hunting and foraging, where infections started to increase as a result of living conditions and closer contact with animals. The second was the effect of industrialization on humans which led to a decline in mortality with improved living conditions, the development of antibiotics, and a rise in chronic non-infectious diseases (e.g., heart disease and cancer). The third is the current transition in which the world is seeing the re-emergence of infections and antibiotic resistance.

Discussions of the origin and evolution of infectious disease often focus on the necessity for large, dense human populations and the presence of domesticated livestock, centering on the advent of agricultural subsistence and animal domestication to be present (Wolfe et al., 2007). There has been much paleopathological research on health in past populations at the transition to agriculture that also follows this discussion (e.g. Cohen and Armelagos, 1984; Steckel and Rose, 2002; Cohen and Crane-Kramer, 2007). Reconstruction of health in the past focuses on human remains (bones and teeth, and much less so the eggs of ancient parasites, or indeed animal remains), mainly using macroscopic techniques, less so imaging and histology, but increasingly biomolecular analysis (e.g., ancient DNA analysis). Historical documents and illustrations also play their part in this endeavor, when and where available. However, the macroscopic analysis of skeletons from archaeological sites to explore health at the transitions described remains the majority of the type of research carried out in this domain (see Roberts, 2018). Yet, while high zoonotic disease loads are documented among modern hunter-gatherers (Dunn, 1968; Bennett et al., 1970; Metz et al., 1971; Hill et al. 2007; Jones 2016) the spread of these diseases from wild animals to humans in the archaeological record, specifically via raw or undercooked meat consumption, has received less attention in archaeology.

One area in which the investigation of past zoonotic disease has increasingly developed is archaeoparasitology. A parasite is one that lives on or in a host (e.g., humans and other animals). Helminths (‘worms’), protozoa (e.g., leishmaniasis), and ectoparasites (e.g., head lice) are the three main groups of parasites. Parasitic infection remains a challenge for human populations across the world today. For example, malaria kills more people today than any other parasitic infection and in 2016 affected 216 million people in 91 countries; almost half a million died (World Health Organization, 2017). Archaeoparasitology is the identification of the remains of parasites that infected humans and animals in the past, both externally (e.g., lice, fleas) and internally (e.g., malaria, intestinal worms) (Reinhard, 1992; Reinhard and Araújo, 2008; Dittmar et al., 2012). The identification of intestinal worms, usually through the detection of their preserved eggs in coprolites or sediment, has increasingly been used to investigate the relationships (both social and economic) between humans and animals in the past (Arriaza et al., 2010; Yeh et al., 2014; Mitchell, 2017; Slepchenko et al., 2017).

A main focus of archaeoparasitology, as an interdisciplinary field that seeks to integrate, e.g., culture, climate, and environment, is the pathoecological elements leading to human zoonotic infection (Dittmar, 2013; Reinhard, 2017). Pathoecology is the study of the environmental determinants of disease (Martinson et al., 2003; Reinhard, 2008). Within human paleopathology research this is usually described as (paleo) epidemiology – the distribution and determinants of health (Waldron, 1994). These include human factors (e.g., crowding, sanitation, hygiene), biotic factors (e.g., pathogens, disease reservoirs, intermediate hosts), and physical factors (e.g., climate, soil conditions) (Reinhard and Bryant, 2008). While the pathoecology of post-agricultural environments has been well-documented using parasites (e.g., Mitchell, 2015, 2017; Trigg et al., 2017), ancient hunter-gatherer contexts in the Old World have not been similarly investigated.

2. Old World Prehistoric Archaeoparasitology

Although the beginning of pervasive human parasitic infection likely occurred during the Neolithic period, in association with livestock domestication, permanent settlements and related accumulated human waste (Le Bailly, 2005; Reinhard and Pucu, 2013), we know very little about parasitic infection during earlier prehistoric periods around the world, likely due to the reduced number of identified sites and associated human skeletal remains. Sprent (1969) proposed a division between 'heirloom' and 'souvenir' parasites, with heirloom parasites being those which have co-evolved with humans through time, leading to their being human-specific. This suggests the relationship between some parasites and their human hosts extends deep into human evolutionary history. Souvenir parasites, on the other hand, are parasites that may opportunistically infect a range of host species, including humans. Many of these are zoonotic parasites, spread from animals to humans.

While many zoonotic parasitic intestinal worms are associated with the Neolithic due to fecal contamination of an environment by domestic animals, tapeworms infect their human hosts primarily via consumption of raw or undercooked flesh or viscera. This culinary pathway indicates tapeworms are likely to have a long-standing association with ancient hunter-gatherers. Indeed, the tapeworms of cows (*Taenia saginata*) and pigs (*Taenia solium, Taenia asiatica*) have evolved to reproduce solely in the human gut (Hoberg et al., 2002). This suggests this genus has likely parasitized *Homo* for a long period of time, probably beginning with the hunting of antelope on the sub-Saharan African savannah during the Late Pliocene (Hoberg et al., 2001; Hoberg, 2006).

Insights offered by archaeoparasitological findings are likely to contribute significantly not only to our understanding of previous prehistoric human-animal interactions, but to the everyday lives of these past populations (Reinhard, 2000), alongside informing research today on these infections. Aside from their use as indicators of ancient human health and disease (e.g., Arriaza et al., 2010; Araujo et al., 2011; Mitchell, 2017), the presence of paleoparasites have been utilized to identify unhygienic sanitation practices likely contributing to the spread of intestinal worms in past groups (Mitchell, 2015), and the presence of certain parasites may be indicative of soil and water polluted with human or animal feces, infecting the population through drinking contaminated water or eating contaminated forage (Bouchet et al., 2003). The presence of parasite microfossils (preserved eggs) across archaeological sites also might suggest contamination of the habitation area with fecal material or the use of feces as hearth fuel. Findings may also point to particular culinary practices. The presence of many zoonotic parasites is associated with the consumption of raw or undercooked flesh or viscera, or processing in another manner that does not kill the parasite (e.g., salting, smoking, pickling) (Adams et al., 1997). Paleoparasites may also identify the consumption of some animals which have not otherwise been identified from faunal remains at the site, but can be documented through their specialized parasites (Sianto et al., 2012).

Archaeoparasitological analysis of early prehistoric sites in the Old World has been more limited than from later time periods, constraining our understanding of the interaction between humans, animals, environment and disease during this period. This is likely due to a combination of factors including fewer identified sites and associated human skeletal remains, poorer preservation, and a lack of attempted analyses owing to a relative absence of common paleoparasite contexts (e.g., coprolites, cesspits, latrines) at early prehistoric sites (Goude et al., 2018). Here, we undertook archaeoparasitological analysis on occupational sediments at the Mesolithic lakeside site of Derragh in the Irish Midlands. There are few findings of paleoparasites during the Mesolithic across the Old World and little is known about the relationship between humans, environments, diets and potential diseases in Mesolithic Ireland given a lack of faunal and human remains from the period. Our focus on this Mesolithic lakeside site offers a point of comparison with later paleoparasite analyses from Neolithic lakeside sites across Europe (Le Bailly et al., 2005; Maicher et al., 2017) and highlights potential ways forward using archaeoparasitology at prehistoric sites, especially those that lack direct human presence in the form of skeletal remains and artifacts.

3. Materials and methods

3.1 Materials: Site background, stratigraphy, and dating

Derragh (Irish: Doire Each; Co. Longford; 53.757221, -7.394755) is a former lake island located in the Irish Midlands. The site is currently on a lake shore, lying at the junction of Lough Kinale, Derragh Lough and the outlet of the River Inny (Figure 1). The site consists of a stone and brushwood platform-like feature with extensive evidence of human habitation, including woodworking, faunal remains and plant food debris. Above ground, these archaeological deposits appear as a waterlogged, low-lying, slightly-rounded mound, c.0.5m in height and 15m in diameter. Although drainage alteration largely emptied the lake in the 1960s, subsequent hydrology modification raised the lake levels and has maintained a high water table on the site. Researchers first noticed the archaeological deposits in the form of characteristic Mesolithic lithics, such as Bann flakes, in the 1970s (O’Sullivan, 1998).

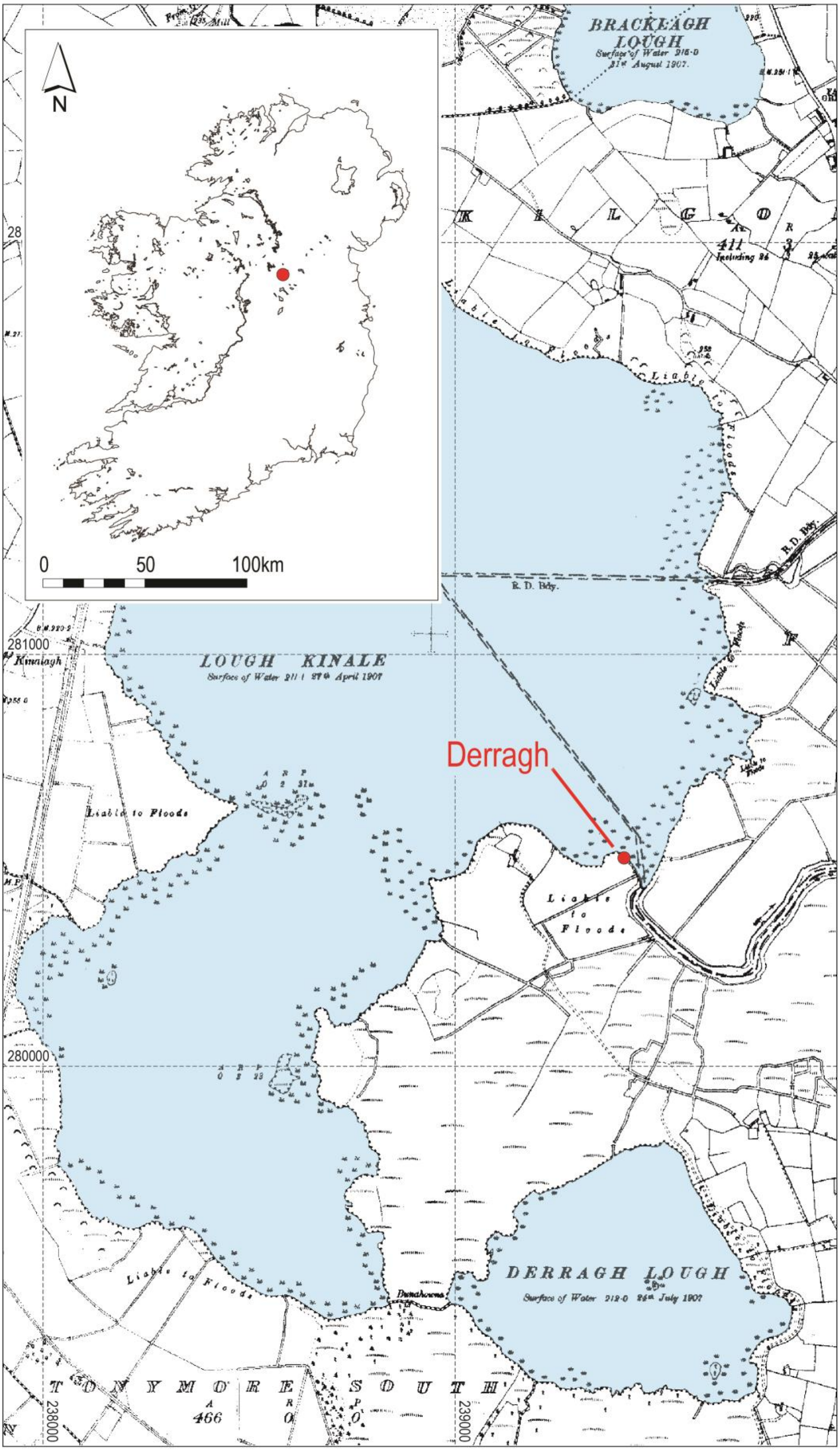

Figure 1. Map of Derragh site location.

The Discovery Programme, an all-Ireland public center of archaeological research supported by the Heritage Council, surveyed the site in 2002 and excavation followed in the summers from 2003 –2005 as part of the Lake Settlement Project (Fredengren, 2009, 2007, 2002). Excavation revealed multiple phases of human occupation at the low-lying lakeshore mound, a possible platform crannog (Fredengren 2007). The earliest evidence of occupation comprised a stake structure, a hollow, three hearths and associated charcoal, ash and hazelnut spreads. The later phase of activity is represented by the construction of a stone and gravel floor over a compressed peat layer, sealing the hearths. Although there are traces of the early Mesolithic, the overwhelming majority of artifacts suggest a period of intermittent but intensive use from the Late Mesolithic into the earliest part of the Neolithic.

One of the distinctive features of the site is the hollow (c. 1.5m x 1.3m; Figure 2, C197), which is part of the sterile brushwood-rich peat layer (C210). The hollow would have been below the water table during occupation and likely used as a place to dump habitation debris from the lakeshore edge. It contained stones, lithic debris, hazelnuts, butchered and burned faunal remains, and charcoal and was likely deliberately filled in with the considerable woodworking waste that was generated on site. Overlying the hollow are two oak planks (C172), a peat layer (C78), a layer of hazelnuts (some charred; C79) and a brushwood floor (C22). The brushwood floor is approximately contemporaneous to a stone layer which covers the entire knoll, including the perimeter of the hollow. Above the brushwood floor is a redeposited topsoil with evidence of Mesolithic, Neolithic and early modern activity (Figure 2).

The hollow occupation phase dates to 7424–7020 cal BP based on bone and a burnt pine taper found within it (Table 1). Given that the pine taper was burnt and that pine wood was not available within several kilometers from the site, it must have been introduced to the site by human inhabitants. The artifacts from the hollow suggest no post-Mesolithic activity during this phase. Two oak planks (C172) overlie the hollow, one of which was dated to 6630–6360 cal BP. The context above the planks, a spread of hazelnuts (C79), dates to 6883–6645 cal BP. The date of the planks indicates they sunk into the earlier hazelnut deposit. Above the spread of hazelnuts lies a phase of brushwood accumulation situated in peat with 175 artifacts and dated to 6633–6323 cal BP.

Above these layers there is a platform-like stone layer, covered on its western edge with a second brushwood layer, some of which is worked, dating to 6228–5971 cal BP. This layer is archaeologically rich, yielding 9,000 artifacts and bones from suids, bear, otter, domestic cattle and a single human tooth directly dated to 6244–6006 cal BP. The vast bulk of lithic artifacts typologically indicate the Later Mesolithic, although there are a number of tools, and the presence of domestic cattle, that date from the Neolithic, as well as the Early Mesolithic. Tools associated with the stone layer display a high amount of weathering suggesting that they were exposed for some time.

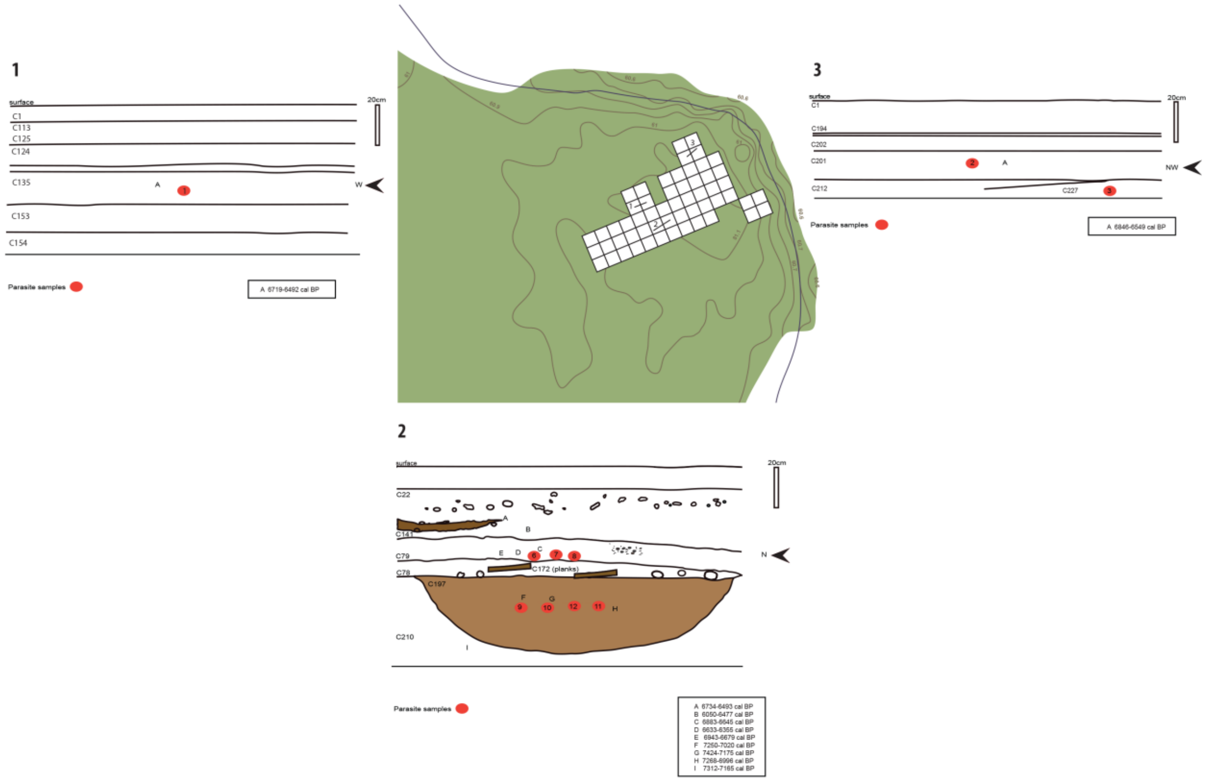

Figure 2. Outline of excavated profiles at Derragh with associated contexts (C), parasite sample locations and dating.

AMS Nr.	Sample	Context	% Coll	d $^{13}C/^{12}C$	d $^{15}N/^{14}N$	%C	%N	C:N	^{14}C Age	1s Err	cal BP
Ua34064	pine taper	197	–	-26.3	–	–	–	–	6375	60	7424–7175
Ua34065	wood	226	–	-29.3	–	–	–	–	6235	55	7268–6996
MAMS-34675; R-EVA 2129	suid	197	12.1	-21.53	4.1	43.9	15.8	3.2	6229	27	7250–7020
MAMS-34689; R-EVA 2125	suid	78	15	-21.11	4	45.3	16.3	3.2	6200	21	7174–7006
UBA23758	twig	28	–		–	–	–	–	6086	41	7156–6800
MAMS-	suid	192	4.1	-21.3	4.6	41.7	14.6	3.3	6065	21	7155–6786

34690; R-EVA 2128											
UBA22335	wood	135	–	–	–	–	–	–	5801	42	6719–6492
Ua 34027	hazelnut	79	–	-25.9	–	–	–	–	5980	50	6943–6679
Ua 34028	hazelnut	79	–	-26.1	–	–	–	–	5920	50	6883–6645
UBA22333	hazelnut	201	–	-26.3	–	–	–	–	5876	54	6846–6549
Ua32380	alder root	40	–	-29.5	–	–	–	–	5810	50	6734–6493
MAMS-34674; R-EVA 2122	suid	95	17	-21.12	4.1	44.4	16.2	3.2	5708	27	6600–6410
Ua35483	oak plank	172	–	-27	–	–	–	–	5690	45	6633–6355
MAMS-34688; R-EVA 2120	suid	71	17.2	-21.12	4.3	46.6	16.8	3.2	5635	22	6480–6323
Ua42649	human tooth	115	0.6	-17	–	–	–	–	5308	34	6193–5955

Table 1. Radiocarbon dates, isotopic values, % of collagen and C:N ratios of Derragh site. The isotopic values, C:N ratios, amount of collagen extracted (%Coll, >30 kDa fraction) were performed at Max Planck for Evolutionary Anthropology, Leipzig, Germany (Code R-EVA). δ^{13}C values are reported relative to the vPDB standard and δ15N values are reported relative to the AIR standard. All radiocarbon dates are calibrated at the 2-sigma confidence using OxCal v 4.3 (Bronk Ramsey, 2009) with the IntCal13 curve (Reimer et al., 2013).

Twelve occupational sediment samples from Derragh were analyzed for paleoparasites in the paleoparasite lab at the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany). Four samples (DL9-12) come from within the hollow, one sample (DL8) is from sediment on the oak planks above the hollow, and four (DL4-7) are from the hazelnut layer directly above the oak planks (Figure 2). The other three samples come from other parts of the site (Figure 2). Sample DL1 comes from a compacted peat layer (C135) about 3m to the north of the hollow which is dated to 6720 –6490 cal BP. Samples DL2 and DL3 come from peat layers (C201, C227) about 5m to the northwest of the hollow dated to 6850 –6550 cal BP.

3.2 Methods

The standard RHM protocol (Rehydration-Homogenization-Microsieving) was employed to extract paleoparasite eggs from this material (Bouchet et al., 2001; Le Bailly, 2011; Dufour and Le Bailly, 2013; see Supplemental Material).

Bone collagen from samples (MAMS-34675, MAMS-34689, MAMS-34690, MAMS-34674, MAMS-34688) was extracted at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA; Leipzig, Germany) for the new radiocarbon dating, using pretreatment methodology based on Talamo and Richards (2011) (see Supplemental Material).

4. Results

All twelve sediment samples tested were positive for the presence of paleoparasite eggs (Table 2). Some samples were richer in eggs than others, with samples DL2, DL3, and DL8 containing the most eggs. Operculated eggs (52–63 x 38–49 µm), some with open and others with closed opercula (Figure 3), corresponding to the cestode (tapeworm) genus *Diphyllobothrium* (Cobbold, 1858), were identified in all samples. *Diphyllobothrium* sp.is a common tapeworm infecting animals, including humans, who consume raw or undercooked infected fish. *Diphyllobothrium* sp. eggs are characteristically ovoid, operculated, thick-shelled, and measure on average 58 –75 µm long and 40 –50 µm wide (Ash and Orihel, 1980). Given the difficulty in distinguishing between the different species of *Diphyllobothrium* (Le Bailly et al., 2005; Le Bailly and Bouchet, 2013) we only identify the eggs to the genus level, but the eggs mostly likely represent *D. latum* and/or *D. dendriticum*.

In addition to *Diphyllobothrium* sp., sample DL8 and DL10 also contained a few eggs which appear to be from the trematode (fluke) genus *Fasciola* sp. (130–150 x 60–90 µm average egg size) or *Echinostoma* sp. (80–135 x 55–80 µm average egg size) (Figure 4). One egg is badly preserved, but measures approximately 132 x 88 µm, is amber-colored and ovoid with a wide, open operculum. The others are also amber or straw-colored with wide, open opercula, but have varying ovoid shapes and vary in size (85–150 x 55–87 µm).

Sample	Context	Associated context	Associated date (cal BP)	Result	Parasite	Number of *Diphyllobothrium* eggs	Other
DL1	135	compacted peat layer	6720–6490	positive	*Diphyllobothrium* sp.	6	
DL2	201	sandy peat layer	6846–6549	positive	*Diphyllobothrium* sp.	57	
DL3	227	bark-rich peat layer	_	positive	*Diphyllobothrium* sp.	44	
DL4	79	hazelnut layer	6943–6645	positive	*Diphyllobothrium* sp.	5	
DL5	79	hazelnut layer	6943–6645	positive	*Diphyllobothrium* sp.	4	
DL6	79	hazelnut layer	6943–6645	positive	*Diphyllobothrium* sp.	15	
DL7	79	hazelnut layer	6943–6645	positive	*Diphyllobothrium* sp.	11	
DL8	172	oak planks	6633–6355	positive	*Diphyllobothrium* sp.	33	Trematode egg?

DL9	197	hollow	7424–7020	positive	*Diphyllobothrium* sp.	3	
DL10	197	hollow	7424–7020	positive	*Diphyllobothrium* sp.	2	Trematode egg?
DL11	197	hollow	7424–7020	positive	*Diphyllobothrium* sp.	12	
DL12	197	hollow	7424–7020	positive	*Diphyllobothrium* sp.	11	

Table 2. Paleoparasite results from Derragh.

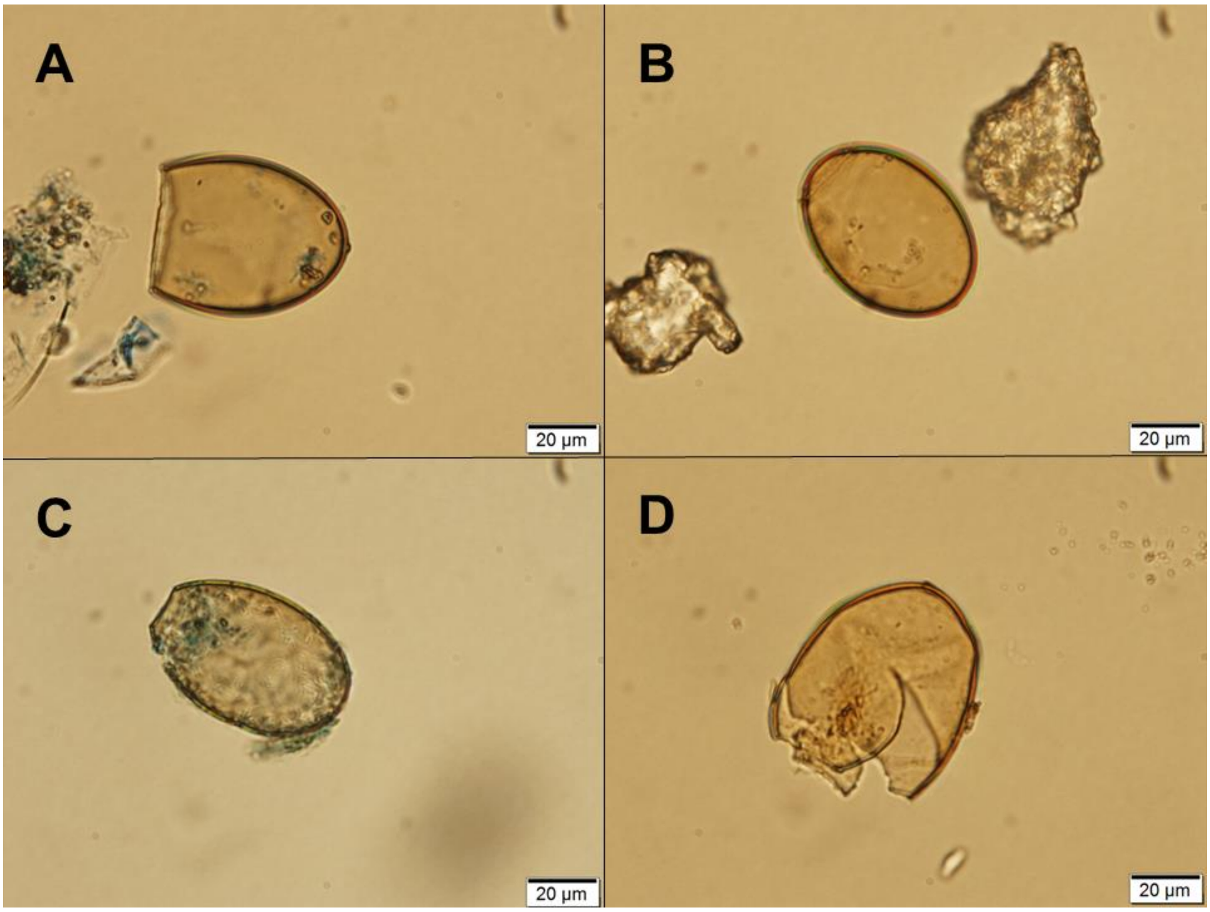

Figure 3. *Diphyllobothrium* sp. eggs from Derragh. (A) Hatched egg from DL5; (B) egg with intact operculum from DL12; (C) distorted egg from DL1; (D) broken egg from DL9.

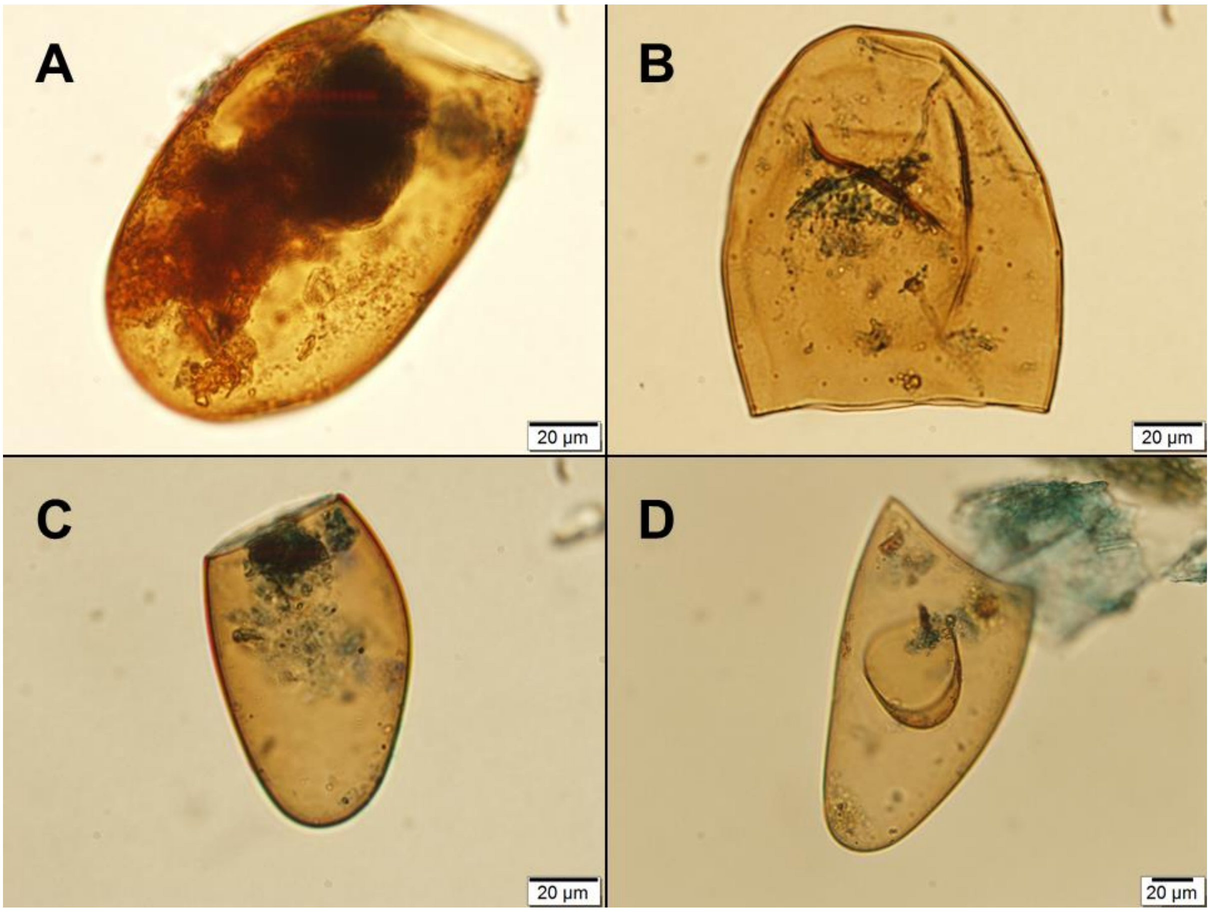

Figure 4. (A) Distorted egg from DL8; (B) hatched egg from DL8; (C) hatched egg from DL10; (D) hatched egg from DL10

5. Discussion

5.1 Paleoparasites at Derragh

Archaeoparasitological analyses have not been common at Irish archaeological sites. The previous earliest finding came from a Bronze Age site at Chancellorsland and may have originated from a human, pig, or dog coprolite (Collins and Reinhard, 2008). Later evidence includes intestinal parasites, probably originating from domestic animals, reported from an Early Christian rath in Co. Antrim, N. Ireland (Allison et al., 1999). Three reports of hydatid cysts, the results of the tapeworm *Echinococcus granulosus*, are also reported from Medieval and 18th–19th century burials in Counties Cork, Tipperary, and Kerry (Power, 1997, 2010). These are likely the result of close human contact with infected farm dogs.

The positive results from Derragh are the earliest reported parasites and the first unambiguously human-associated prehistoric parasites from Ireland. The finding of *Diphyllobothrium* sp. eggs from all the Derragh samples suggests infection with the parasite and environmental contamination with human feces may have been widespread at the site. Given the presence of paleoparasite eggs up to 100 cm below the surface of the site in three different areas and in association with dates spanning 7424–6355 cal BP, we are confident our findings represent parasitic infection in Late Mesolithic hunter-gatherers at Derragh. All stratigraphic contexts in which paleoparasites were found were in secure, undisturbed layers and there is no evidence of bioturbation or other significant sediment movement, although we cannot control for potential percolation of parasite eggs between layers (Morrow et al., 2016).

Aside from humans, other possible fish tapeworm hosts identified from the Mesolithic layers include bear, otter, and some water fowl, though evidence of the presence of these animals at the site is minimal and the continuous human occupation of the site makes this unlikely. There is no evidence of domestic dogs from the Mesolithic layers. Given the recurrent use of the site for human habitation and the presence of positive samples within human-derived hearth, ash, charcoal, hazelnut and peat layers, it is doubtful that the tapeworm eggs result from anything other than human feces.

5.2 Paleoepidemiology

The earliest evidence for human infection with *Diphyllobothrium* sp. comes from Peru, dating to around 8000 BC (Reinhard, 1992). Similar findings are fairly common in the analysis of coprolites from the pre-colonial periods in coastal Peru and Chile, usually associated with the infection of marine fish with *Diphyllobothrium pacificum* (Patrucco et al., 1983; Reinhard and Aufderheide, 1990; Reinhard and Urban, 2003). Le Bailly and Bouchet (2013) reported the earliest finding of the parasite in the Old World from an early Neolithic site in Cyprus dating to 7600–7500 BC. Other early findings of *Diphyllobothrium* sp. in the Old World have been associated with Neolithic lacustrine sites in France (Dommelier et al., 1998), Germany (Le Bailly et al., 2005), Spain (Maicher et al., 2017), and Switzerland (Le Bailly et al. 2005). The parasite-associated dates for Derragh represent the earliest reported finding in Europe and the first identification of *Diphyllobothrium* sp. from a Mesolithic hunter-gatherer site. Later findings of *Diphyllobothrium* sp. through the Roman and Medieval periods are more common, though they decrease from the 16th century onward (Le Bailly and Bouchet, 2013).

The life cycle of *Diphyllobothrium* sp. is complex and can include up to three intermediate hosts. The first intermediate host, a crustacean such as a copepod, is not infective to humans. These copepods are consumed by smaller fish, such as minnows, into the flesh of which the larvae then encyst. At this point the larvae are infective to humans and other fish-eating animals. The consumption of these smaller fish by larger predatory fish (e.g., salmonids, eel), which the larvae also infect, is the most common source of human infection with the tapeworm (Scholz et al., 2009). To be infected an individual must consume fish flesh or viscera which is raw or undercooked. Smoking does not kill the parasite, nor does salting or freezing if not under −10°C for 24 hours (Scholz et al., 2009). Once infected, an individual tapeworm may live in the body for over 25 years, producing up to one million eggs per day (von Bonsdorff, 1977). This extraordinary level of egg production means that rates of contamination in unsanitary conditions, such as at a temporary hunter-gatherer camp, may have been particularly high.

In living populations today, the majority of individuals with diphyllobothriasis (the infection caused by *Diphyllobothrium* sp.) are asymptomatic (Dick, 2007). In about one out of five infections individuals experience diarrhea and abdominal pain or discomfort and may also experience other symptoms such as headaches, fatigue, constipation and pernicious anemia (Garcia and Bruckner, 1993; Scholz et al., 2009). A prolonged or heavy infection may lead to megaloblastic anemia resulting from the depletion of vitamin B_{12} by the parasite. In populations today about 40% of infected individuals show low vitamin B_{12} levels, but only <2% develop clinical anemia (Garcia and Bruckner, 1993). It is unclear how pervasive anemia may have been in prehistoric Irish populations infected with parasites, but some coastal prehistoric populations in Peru had high rates of anemia, documented via the pathological bone condition cribra orbitalia (CO: in the eye sockets) and porotic hyperostosis (PH: on the cranium), particularly in children in whom the bone lesions originally develop (Blom et al., 2005). This anemia was likely associated with the consumption of aquatic resources because they experienced high rates of parasitic infection, including *Diphyllobothrium pacificum*. Porotic hyperostosis identified in Californian skeletons has also been suggested as the result of consuming marine resources, leading to parasitic infection (Walker 1986). While the aetiology of CO and PH continues to be debated in paleopathology circles (e.g., Walker et al 2009, Wapler et al 2004, Oxenham and Cavill 2010, McIlvaine 2015), purported anemia-related cribra orbitalia and porotic hyperostosis associated with likely parasitic infection have also been documented at many Old World sites from various periods (Carlson et al., 1974, Facchini et al., 2004, Keenleyside and Panayotova, 2006, Djuric et al., 2008).

The finding of potential trematode eggs from the *Fasciola* or *Echinostoma* genera is curious. Both are present in Europe and the earliest finding of *Fasciola* sp. dates to 3600 BC (Dommelier and Espejo, 2001). We could not find any archaeoparasitological reports of *Echinostoma* sp. from the Old World. *Fasciola* sp. most commonly parasitizes domestic sheep and cattle, but sometimes infects humans and wild ruminants as well. This is most often associated with the consumption of contaminated water plants. Given the lack of domestic livestock or wild ruminants in Mesolithic Irish archaeological sites (Carden et al., 2012; Woodman, 2015), the presence of *Fasciola* sp. is unlikely. *Echinostoma* sp., on the other hand, parasitizes a variety of animals, including humans (as definitive hosts). Humans are most commonly infected while consuming raw or undercooked snails, fish or frogs (Roberts and Janovy, 2000). The presence of *Echinostoma* sp. eggs may also be the result of false infection (the presence of eggs in the stool resulting not from an actual infection but from recent ingestion of infected hosts carrying eggs) due to human consumption of infected whole, bite-sized fish (e.g., minnows) (Sianto et al., 2005). Given the difficulty in identifying these few eggs, we cannot confirm the presence of trematodes at the site.

5.3 Paleopathoecology

Diphyllobothrium sp. is considered an indicator of fecal water pollution in freshwater systems (von Bonsdorff, 1977). The continuation of the *Diphyllobothrium* life cycle requires the release of eggs into the water system by definitive hosts. Temperatures in early Holocene Ireland suggest *D. dendriticum* eggs likely hatched between mid-August and late October, but even given colder temperatures eggs can survive, embryonate, and hatch years after they are shed (Wright and Curtis, 2000). At Derragh, contamination could be the result of direct human defecation or feces disposal in the lake (as evidenced by egg presence in the underwater hollow) and/or defecation into the lake by other host animals, particularly migratory birds, which are common definitive hosts of *D. dendriticum*. *Diphyllobothrium* sp. has been identified in modern pike from Lough Sheelin, just a few kilometers from Derragh (Kane, 1966), and in brown trout, char, perch, and stickleback from lake sites across modern Ireland (Holland and Kennedy, 1997).

5.4 Fishing in Mesolithic Ireland

A small assemblage of fish remains was recovered from the excavations at Derragh (Supplemental Table 1). All of this material is burnt, most of it to high-temperature calcination, as indicated by white and bluish coloring (Nicholson, 2017; Supplemental Figure 1). A majority of the remains are from eel (*Anguilla anguilla*) of subadult age ("yellow eels"). As eels tend to withdraw to the bottom of water bodies during winter it is probable that these were caught in the summer and autumn months. In a few cases the larger vertebrae have been crushed laterally (Supplemental Figure 2); this is not a result of burning but is likely to indicate human chewing (Jones 1986), although it seems likely that these particular vertebrae were not swallowed but spat out and disposed. A few remains are of a different taxon, a salmonid. These could not be precisely identified to salmon or trout but are of very small individuals.

Paradoxically, fish remains are rare or absent on similar Mesolithic lake islands in the Irish Midlands, such as Moynagh and Clonava Island (Little, 2014, 2009; McCormick, 2004). This has raised the question of whether fish were even present in the area by 7000 years ago (Woodman, 2015). Due to the separation of Ireland from continental Europe about 16,000 years ago when the climate was still intensely cold, contemporary Irish freshwater fauna is depauperate compared to the rest of Europe (Edwards and Brooks, 2008). Species that lingered after the last glaciation may have been wiped out by the Nahanagan cold phase (11,000–10,500 BP). Yet, the survival of relic populations of Arctic fish in a number of Irish lakes until the present day (Table 3), shows that at least these species have been present since the last glaciation, and must have been available to Mesolithic foragers (Woodman, 2015).

Actual evidence of Irish Mesolithic fishing and subsistence is extremely fragmentary and no evidence survives of the use of these relic species (e.g., Arctic char, shad, cisco). Salt-tolerant sticklebacks certainly colonized the waterways by this time but are too small to have been a major food resource. However, Mesolithic faunal assemblages verify that a variety of useful euryhaline temperate fish taxa recolonized Irish rivers and lakes by the early postglacial (Table 3). The few available Mesolithic faunal assemblages from coastal and inland sites indicate that fishing was at least locally present (Woodman, 1985; Woodman et al., 1999), particularly given the lack of other terrestrial food sources staple in continental Europe. Irish Mesolithic foragers lacked many of the mammal quarry favored by other Mesolithic populations, including deer (Cervidae), elk (*Alces alces*), and auroch (*Bos primigenius*), with only the wild boar (*Sus scrofa*) occurring and even this potentially having been introduced by Mesolithic people (Edwards and Brooks, 2008; Woodman et al., 1997; Woodman, 1986).

Crucially, fish assemblages from the early Mesolithic Midland site at Lough Boora, 65 km from Derragh, shows waterways deep inland contained salmonids and eel species by this time period (Table 3) (Woodman, 2015), similarly to Derragh. Although there is little other evidence for inland use of fish, it seems unlikely that fish were absent from forager subsistence strategies in the Midlands or across Ireland. Fish, mostly salmonids (salmon and trout) compromise 81% of the burnt bone assemblage at coastal Mount Sandel, which is the earliest sizable Mesolithic assemblage found so far. Eel and trout bones are also dominant at the inland site of Lough Boora (Wijngaarden-Bakker, 1989). Lack of fish remains at lake sites may relate to lake islands being specialized seasonal camps unrelated to fishing, but this is unlikely given their location. Early postglacial lakes were considerably greater in area than present day lakes and they covered a high proportion of the Midlands (Mitchell and Ryan, 2001). Thus, whether due to abundance or necessity, freshwater fish probably were a resource that Mesolithic settlers used across the island.

Isotopic data from the human burial at Stoney Island shows tentative evidence of freshwater fish use (Kador et al., 2014), but dating ambiguity undermines the Mesolithic classification of this burial. On the other hand, isotopic analysis of human remains from Rockmarshall and Killuragh Cave shows a terrestrial signal despite Rockmarshall's coastal location (Woodman et al. 1997, 1999). Caution is needed in interpreting isotopic results as some inland foods, such as sea trout and salmon, possess a marine signal (Darimont and Reimchen, 2002). Little is known about fish exploitation techniques, and concrete examples of Mesolithic fishing technology are limited to the identification of wicker basket fish traps at a lake shore Clowanstown and in a estuarine setting Spencer Dock (McQuade and O'Donnell, 2007).

Taxa	**Evidence type**	**Arrival in Ireland**	**Citation**
Salmon (*Salmo salar*)	Bones	By 9900– 9500 cal. BP	(Woodman, 1985)
Eel (*Anguilla anguilla*)	Bones	By 9900– 9500 cal. BP	(Woodman, 1985)
Trout (*Salmo trutta)*	Bones	By 9900– 9000 cal. BP	(Woodman, 1985)
Three-spined stickleback (*Gasterosteus aculeatus*)	Genetic	Last glaciation or early postglacial	(Ravinet et al., 2014)
Nine-spined stickleback (*Pungitius pungitius*)	Genetic	Last glaciation or early postglacial	(Ravinet et al., 2014)
Brook lamprey (*Lampetra planeri*)	None	Likely early postglacial	(Woodman, 2015)
River lamprey (*Lampetra fluviatilis*)	None	Likely early postglacial	(Woodman, 2015)
Arctic char (*Salvelinus alpinus*)	Relic populations	Last glaciation	(Carlsson et al., 2014)
Shad (*Alosa* sp.)	Relic populations	Since last glaciation and early postglacial	(Carlsson et al., 2014)
Cisco/Pollan (*Coregonus* sp.)	Relic populations	Last glaciation	(Carlsson et al., 2014)
Pike (*Esox lucius*)	Genetic	Possibly mid Holocene	(Carlsson et al., 2014)

Table 3: Fish species present during the Irish Mesolithic and their origins

6. Conclusions

Discussions of parasites in the Old World often focus on the introduction of agriculture and domestic animals as the primary vectors for parasitic infection due to larger human populations, increased environmental fecal contamination, and human interaction with livestock. Though these factors undoubtedly increased human infection with many intestinal parasites, others were likely an omnipresent part of past hunter-gatherer lives. These include tapeworms, some of which have evolved to reproduce solely in the human gut, highlighting the antiquity of our interaction with them.

The finding of the fish tapeworm *Diphyllobothrium* sp. eggs at the Derragh site provides several insights into the pathoecology and daily lives of hunter-gatherers in Mesolithic Ireland. Their presence suggests the living environment and local water supply were contaminated with human feces. The contamination of nearby water sources, such as Lough Kinale and Derragh Lough, with the feces of infected individuals would contribute to continuing the cycle of the parasite within local lacustrine communities. Given the presence of *Diphyllobothrium* sp. eggs in the subsurface layers of the Derragh hollow this type of contamination was undoubtedly occurring.

The presence of fish tapeworm at Derragh also alludes to the culinary practices undertaken by inhabitants of the site. Since the tapeworm is passed to humans via the ingestion of larvae encysted in fish flesh, the residents of Derragh must have been consuming fish raw, undercooked, or processed by some other method that failed to kill the parasite (e.g., smoking, salting, curing). The regular consumption of infected fish may have led to heavy parasitic loads within the human population, potentially leading to serious health problems including vitamin B_{12} deficiency and anemia. Though often associated with periods of dietary stress in people who relied on farming and increased parasitic loads in the past (see papers in Cohen and Armelagos 1984 and Cohen and Crane-Kraner 2007), skeletal indicators of anemia, such as porotic hyperostosis and cribra orbitalia, are more likely to indicate heavy parasitic loads in pre-agricultural individuals as these populations are unlikely to have suffered anemia related to iron deficiency given the typically meat-rich diet of past hunter-gatherers.

Due to the rarity of Mesolithic human remains in Ireland, insights into health during this period have been limited. Aside from the single tooth found at Derragh (Co. Longford) the only known remains consist of a cremation burial at Hermitage (Co. Limerick), a scatter of teeth and limb fragments from Ferriter's Cove (Co. Kerry), an ulna from Rockmarshall (Co. Louth) and a reworked bone from the Lower Bann in Northern Ireland (Woodman, 2015). While the presence of tapeworms at Derragh indicates Mesolithic foragers in Ireland may have suffered from the deleterious effects of parasitic infectious disease, the lack of human remains from this period, particularly cranial remains, leaves this possibility unclear for now.

Nevertheless, the occurrence of *Diphyllobothrium* sp. at Derragh is an important indicator of the use of fish as a food item for inland Irish Late Mesolithic communities, which has been a long-standing question. Given the lack of fish remains in the region during this period, especially from lake island sites, the presence of fish parasites may provide a critical way forward in the indirect identification of prehistoric fish consumption in Mesolithic Ireland and beyond.

Our findings at the Derragh site provide important insight into the local environments, diets, living conditions and culinary practices of Mesolithic Ireland, highlighting the use of archaeoparasitology as a critical development within archaeology and human paleoecology. This work also emphasizes the value of extending the use of archaeoparasitological analysis as another major tool in bioarchaeology for exploring zoonotic disease in the past, particularly in contexts where environmental conditions enable parasite eggs to preserve, but where human remains do not. Additionally, as seen at Derragh, the use of archaeoparasitology can assist in the identification of dietary resources which may not otherwise be identified in the faunal assemblage. As archaeoparasitology becomes more widespread in interdisciplinary archaeological research future applications, particularly in the case of prehistoric sites and/or sites with limited preservation of human and faunal remains, will increasingly contribute to our understanding of the relationship between humans, local environments, diets and disease in the past.

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