

Аглядны артыкул

Археалагічныя сведчанні паразітаў у старажытным Дэлесе ў эліністычны перыяд

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Анотацыя. Гэта даследаванне вывучае сведчанні старажытных паразітарных захворванняў шляхам прымянення мікраскапічнага даследавання і палеагенетычнага аналізу да ўзораў, атрыманых з 59 археалагічных кантэкстаў, у тым ліку з 51 прыбіральні, звязанай з эліністычным паселішчам Дэлес у Кікладах, у Эгейскім моры. З даследаваных кантэкстаў 35 утрымлівалі яйкі страўнікава-кішачных гельмінтаў, у тым ліку прадстаўнікоў груп Ascarididae і Trichocephalida, а таксама некалькі яек тыпу Strongyle і адзін узор трэматоды. Далейшы палеагенетычны аналіз пацвердзіў наяўнасць чалавечых паразітаў, уключаючы *Ascaris* sp., *Trichuris trichiura* і *Enterobius vermicularis*. Гэта даследаванне з'яўляецца адным з найбольш шырокіх вывучэнняў старажытных паразітаў у гарадскім археалагічным асяроддзі, паколькі яно ахоплівае значную частку тэрыторыі паселішча. Вынікі паказваюць, што паразітарныя інфекцыі былі шырока распаўсюджаны сярод насельніцтва, і даюць важную інфармацыю пра гігіену, грамадскае здароўе і паўсядзённыя ўмовы жыцця ў старажытным міжземнаморскім горадзе.

Ключавыя словы: старажытныя паразіты; палеапаразіталагічны аналіз; палеагенетычныя сведчанні; мікраскапічнае даследаванне; гарадская санітарыя; Старажытная Грэцыя.

Review Article

Archaeological Evidence of Parasites in Ancient Delos During the Hellenistic Period

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Abstract. This research investigates evidence of ancient parasitic diseases by applying microscopic examination and paleogenetic testing to samples recovered from 59 archaeological contexts, including 51 latrines linked to the Hellenistic settlement of Delos in the Cyclades, Aegean Sea. Of the contexts studied, 35 contained gastrointestinal helminth eggs, such as those belonging to the Ascarididae and Trichocephalida groups, along with several Strongyle-type eggs and one trematode specimen. Further paleogenetic analysis verified the presence of human parasites, including *Ascaris* sp., *Trichuris trichiura*, and *Enterobius vermicularis*. This study represents one of the broadest investigations of ancient parasites within an urban archaeological setting, as it covers a substantial part of the settlement area. The results demonstrate that parasitic infections were widespread among the population and provide important information about hygiene, public health, and everyday living conditions in an ancient Mediterranean city.

Keywords: ancient parasites; paleoparasitological analysis; paleogenetic evidence; microscopic examination; urban sanitation; ancient Greece

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Introduction

The purpose of this study is to assess the extent of parasitic infections affecting an urban population during the Hellenistic period and to incorporate these findings into a multiproxy framework for reconstructing the sanitary conditions of ancient communities. While previous research has extensively addressed epidemics caused by bacterial and viral agents through historical documentation, archaeological remains, osteological evidence, and funerary contexts, eukaryotic parasites—especially intestinal helminths—have received comparatively limited scholarly attention outside the specialized field of paleoparasitology. As emphasized by Mirko Grmek in *Diseases in the Ancient Greek World* (1991), this lack of attention is noteworthy, considering that endemic parasitic infections likely had substantial long-term consequences for morbidity, mortality, and economic productivity. Large-scale and systematic analyses encompassing extensive archaeological populations, whether from burial assemblages or urban environments, offer valuable opportunities to reconstruct patterns of parasitic prevalence across different chronological and cultural contexts. Such variations can also be associated with changes in behavioral practices and technological developments,

particularly in sanitation and waste disposal systems (Le Bailly et al. 2021). Existing evidence demonstrates that parasites are frequently identified in archaeological materials and were widespread among ancient populations; however, most previous investigations have been limited to a small number of structures. This study takes advantage of the extensive archaeological documentation of latrines across the city of Delos to conduct a broader investigation. The ancient city of Delos, located in the Cyclades archipelago in the Aegean Sea (Fig. 1), was inhabited from the third millennium BCE and reached its peak development during the Hellenistic period (323–30 BCE), particularly under the Second Athenian Domination (167–90 BCE). During this time, Delos became an important center of religious activity and commercial exchange within the Greek world (Bruneau et al. 1996; Hasenorh 2012). Archaeological excavations, primarily conducted by the French School of Athens in the late nineteenth and early twentieth centuries, uncovered approximately 30 hectares of urban remains, providing detailed insight into the organization of a Hellenistic city. These investigations enabled comprehensive examination of waste management infrastructure, including sewage systems and numerous latrines connected to drainage networks (Bouet 2022), representing an unprecedented dataset for this period in the Mediterranean region.

Between 2012 and 2016, systematic archaeological research identified and documented 87 latrines and 64 associated drainage conduits, many of which discharged into the urban sewer system. From these, 59 structures were selected for paleoparasitological analysis, although two were later reinterpreted as non-latrines features. This extensive dataset offers a unique opportunity to evaluate parasitic infections across an entire ancient urban landscape rather than isolated locations, which is more typical in paleoparasitological research. The high density and distribution of latrine facilities across the city also provide exceptional sampling potential for investigating gastrointestinal pathogens. Moreover, the widespread presence of such sanitation infrastructure represents a significant development in the history of urban hygiene, as comparable systems from earlier periods remain rare (Bouet 2022). Consequently, documenting these features contributes to a broader understanding of public health, sanitation practices, and disease patterns in ancient populations. Through established paleoparasitological methods, this study aims to reconstruct aspects of hygiene conditions and to provide insight into the circulation of parasitic diseases in the Hellenistic period.

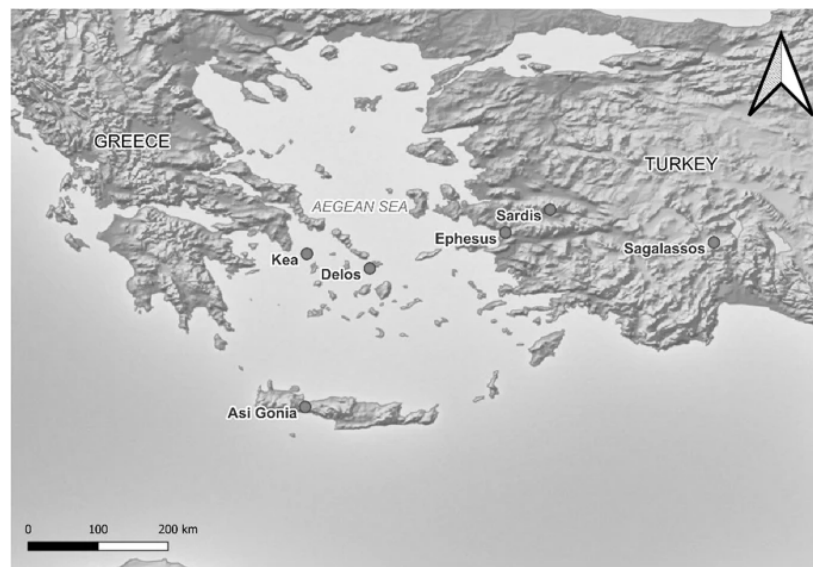


Figure 1. Delos is situated in the Cyclades. Other sites with published paleoparasitological data surrounding the Aegean Sea are also indicated

Materials and Methods

The investigated features primarily consisted of latrine installations from the ancient city of Delos, which had also been examined from an architectural perspective within the same research framework (Bouet 2022). Sampling was systematically conducted in all latrines where residual deposits remained either at the base of the structures or within associated drainage channels, despite prior excavations. Each latrine yielded between one and four samples, resulting in a total of 113 collected specimens, with an average of nearly two samples per structure. A portion of these materials was further selected for paleogenetic examination. Most samples (n=93) consisted of whitish mineralized concretions adhering to the lower surfaces of latrines and sewer conduits. Physical and chemical assessment revealed that these deposits were composed primarily of calcium phosphate overlaying limestone substrates, with clear phosphorus infiltration, likely resulting from prolonged exposure to urine and subsequent recrystallization processes. These residues had remained exposed to environmental conditions since excavations conducted in the late nineteenth and early twentieth centuries. The remaining samples (n=20) comprised sediment extracted from stratified drainage contexts that had not been previously cleared. Control samples were also analyzed and consistently produced negative results under microscopic observation; however, because the site had been excavated and emptied in earlier periods, these controls could not function as fully reliable archaeological comparisons. All sampling procedures were conducted using clean instruments, avoiding contamination from animal activity, and specimens were securely stored in sterile plastic containers.

The sampled structures were located across various sectors of the excavated city, predominantly in residential zones. Concentrations were particularly notable in the Theatre and Inopos districts in the southern area (29 structures), the northern or Lake district (16 structures), and the central plain near the Sanctuary of Apollo (nine structures). Additional latrines were identified in the Stadium district, the sanctuary of the Syrian goddess on Mount Cynthus, and the Fourni bay area. In certain cases, samples were obtained from associated waste pits or nearby features rather than directly from latrine conduits when no residue remained. Chronological attribution indicates that most of these installations date to the late second and early first centuries BCE, corresponding to the Hellenistic period and especially the era of the Second Athenian Domination, when Delos experienced significant urban and economic growth. Although some deposits may have been affected by later activity, most structures were abandoned during the transition to the Imperial period, supporting their attribution to the Hellenistic context (Bouet 2022).

Laboratory procedures focused on identifying microscopic remains of gastrointestinal helminths. The Rehydration-Homogenization-Microsieving (RHM) protocol was applied to isolate parasite eggs (Dufour and Le Bailly 2013). Identification was conducted using light microscopy, relying on morphological characteristics and established parasitological reference standards (Garcia 2007; Taylor et al. 2016; Zajac et al. 2021). Egg measurements were obtained using a Leica DM2000 LED microscope with LAS V4 analytical software. Additionally, molecular analysis was performed on selected sediment samples containing preserved archaeological layers. DNA extraction was conducted using the DNeasy PowerMax Soil kit (Roche et al. 2021), followed by targeted simplex PCR amplification using primers specific to human and animal gastrointestinal parasites (Côté et al. 2016). The resulting genetic sequences were compared with reference data available in the NCBI database through BlastN analysis.

Table 1. aDNA targets

Primers	Species	Target	Amplicon size (bp)
Asc2	<i>Ascaris lumbricoides</i> / <i>Ascaris suum</i>	Cytochrome b (cytb)	74
Trich4	<i>Trichuris trichiura</i>	Large ribosomal subunit (LSU)	91
Fas3	<i>Fasciola hepatica</i> / <i>Fasciola gigantica</i>	rRNA 18S	85
Entero4	<i>Enterobius vermicularis</i>	Cytochrome oxidase I (cox1)	53

Results

Light Microscopy

Microscopic examination revealed that 44 out of 113 analyzed samples (39%) contained at least one type or morphologically identifiable group of gastrointestinal helminth eggs (SI1). These positive findings were associated with 35 archaeological structures, including four vertical drainage pipes, one structure later excluded after reclassification as a non-latrine, and 30 confirmed latrines. This corresponds to a positivity rate of 57% across all examined structures and 59% when considering only latrines (Fig. 2). Positive samples were identified throughout all investigated sectors of the city, including both densely populated districts, such as the Theatre and Lake areas, and less intensively urbanized zones like the House of Fourni. Among the identified remains, Ascarididae eggs were the most abundant, totaling 1,169 specimens (96%), and were present in 30 structures. Trichocephalida eggs were detected in eight structures (n=25, 2%), while Strongyle-type eggs were found in 11 structures (n=20, >2%). Additionally, a single Trematode egg was observed in one latrine. Preservation quality was generally poor, with many eggs lacking distinct morphological features (Fig. 2). Ascarididae eggs exhibited an oval form with thick shells and measured on average $61.6 \pm 3.49 \mu\text{m}$ by $45.5 \pm 2 \mu\text{m}$, based on 190 measured specimens. Trichocephalida eggs displayed the typical lemon-like morphology with polar plugs, although only two measurable specimens were recorded. Strongyle-type eggs were characterized by thin shells containing larval forms and measured approximately $79.7 \pm 24.2 \mu\text{m}$ by $41.6 \pm 11 \mu\text{m}$. The single Trematode egg showed a thin, operculated shell and measured $113 \times 77 \mu\text{m}$ (Fig. 3).

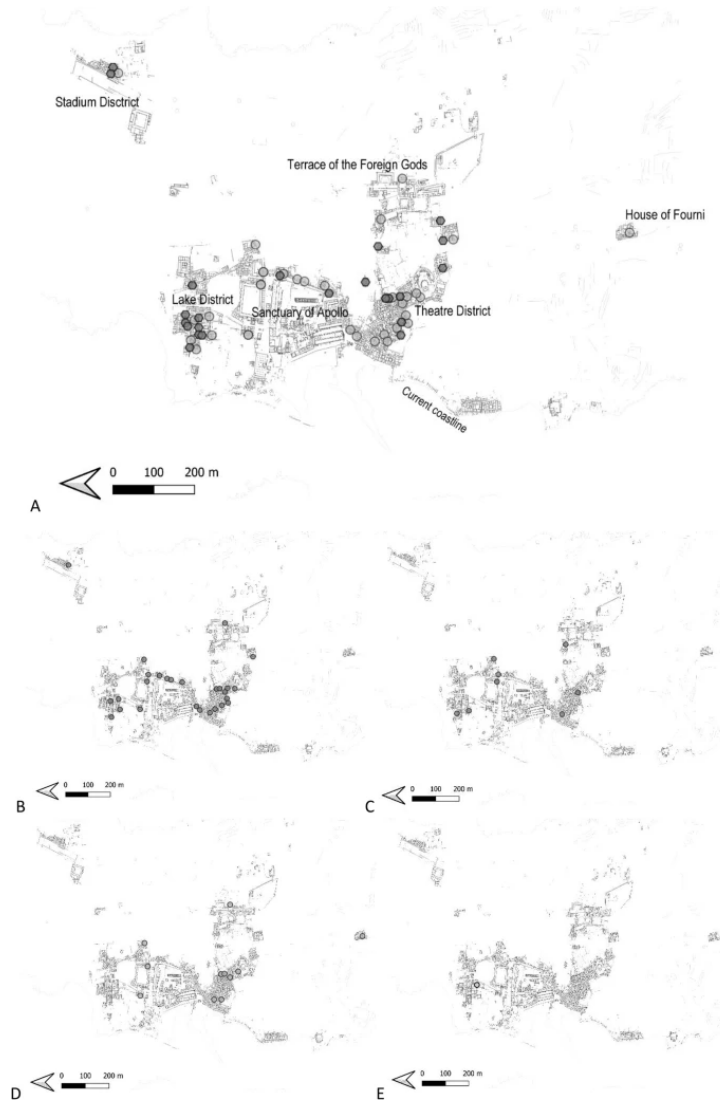


Figure 2. (A) Positive and Negative structures in Delos; (B) Ascarididae eggs distribution; (C) Trichocephalidae eggs distribution; (D) Strongyle-type eggs distribution; (E) Fasciola sp. egg distribution

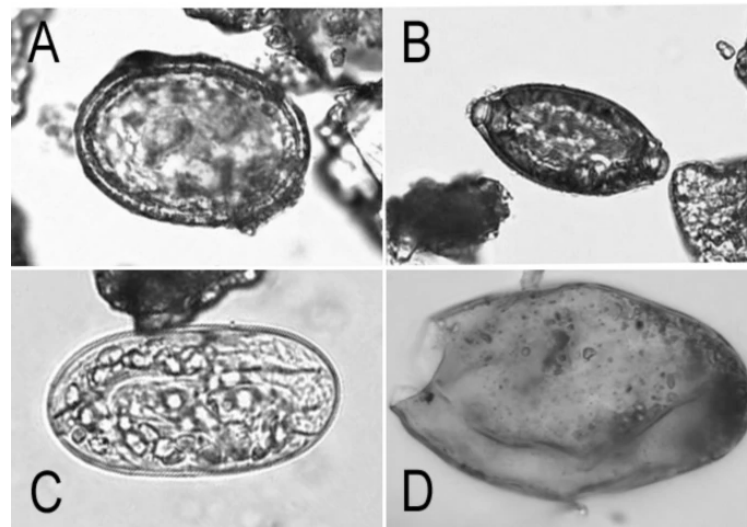


Figure 3. (A) Ascarid-type egg showing remains of its outer shell, $63.5 \times 45.5 \mu\text{m}$ ($\times 200$). (B) Well-preserved *Trichuris* sp. egg, $54.7 \times 27.2 \mu\text{m}$ ($\times 200$) with visible polar plugs and shell wall. Most *Trichuris* sp. eggs partly lost these features, leading to highly inaccurate measurements. (C) Strongyle-type egg with clearly visible larva filling its inner volume, $80 \times 40.2 \mu\text{m}$ ($\times 200$). (D) Trematode egg, possibly *Fasciola* sp., $113 \times 77 \mu\text{m}$ ($\times 200$). The operculum (now open), a characteristic feature of Trematodes, is clearly visible on the left side

Paleogenetics

Molecular analysis conducted on four selected sediment samples produced amplifiable DNA corresponding to at least one parasitic species in each tested structure (Table 2). These samples originated from the Theatre district and the area surrounding the Sanctuary of Apollo. Sediment samples, rather than mineralized concretions, were chosen for genetic analysis, and each underwent duplicate DNA extraction. Of the 150 PCR reactions performed, 28 (18%) yielded detectable amplification products. The highest amplification success was observed with primers targeting *Ascaris* sp. (19/24), followed by *Trichuris trichiura* (8/24) and *Enterobius vermicularis* (1/24). Amplification products associated with *Ascaris* sp. were obtained from all four analyzed structures, while *T. trichiura* was identified in two structures, and *E. vermicularis* was detected in only one. Cloning and sequencing of the amplified DNA fragments were performed using the Sanger method, and sequence alignment through BlastN analysis confirmed their correspondence with known genetic sequences of *Ascaris* sp., *T. trichiura*, and *E. vermicularis* (Table 3).

Table 2. Comparative results of aDNA and microscopy-based detections

Structure	aDNA			Eggs (microscopy)		
	<i>Ascaris</i> sp.	<i>T. trichiura</i>	<i>E. vermicularis</i>	Ascarididae	Trichocephalid a	Strongyle-type
[R8]	Yes	–	–	Yes	–	–
[L50]	Yes	–	–	Yes	–	–

Structure	aDNA			Eggs (microscopy)		
[L57]	Yes	Yes	–	Yes	–	Yes
[L22]	Yes	Yes	Yes	Yes	Yes	–

Table 3. Obtained sequences after BlastN queries

Species	Target	Obtained sequence	Sequence size (bp)	Identity (%)	E-value
<i>Ascaris</i> sp.	Cytochrome b (cyt b)	TGGTACTTTTTTTGGCTTTT TATTATTCTAATGATGGTGCTT TGGC	45	100.0	2e-13
<i>T. trichiura</i>	Large ribosomal subunit (LSU)	GGTTTAAACTCAAATCACGTA ATGTCTATCGTCGAACAGACGA GAATAAAATTCT TCTGCCAAACTATATATACAAAT GATTC AACATCGA	92	97.8	2e-33
<i>E. vermicularis</i>	Cytochrome oxidase I (cox1)	TCCCCCTATCAAAGT CAACAACCAGTTAAAAATCTTTA CCCCAGTCGGCACAG	53	94.34	9e-13

Discussion

Microscopy-based observations indicate that the spatial distribution of parasite-positive structures in Delos may partly reflect sampling variation caused by differences in material availability rather than true epidemiological patterns. Statistical testing revealed no significant associations when comparing sample types collectively or concretions alone (Fisher's Exact Test; concretion + sediment: $p = 0.07$; concretions only: $p = 0.5$). Although most analyzed samples were recovered from archaeological contexts excavated decades ago and exposed to weathering and bioturbation, several lines of evidence support the authenticity of the paleoparasitological record. In particular, the detection of parasites known to infect humans, including Trichocephalida eggs, *Trichuris trichiura* DNA fragments, and *Enterobius vermicularis* DNA sequences, confirms anthropogenic contamination patterns consistent with human waste disposal practices.

The reconstructed ecological network of host–parasite interactions demonstrate the central role of humans in sustaining parasitic transmission cycles within the urban environment of Delos. This network structure highlights the interconnected relationships between humans, domestic animals, and parasite species, indicating continuous biological exchange within anthropogenic settings (Fig. 4). In particular, the detection of Ascarididae eggs and corresponding *Ascaris* sp. DNA strongly suggests infection by human-associated species, most likely *Ascaris lumbricoides*, given the predominantly human context of sampled latrines. Although morphological differentiation between *Ascaris lumbricoides* and *Ascaris suum* remains impossible based solely on egg morphology or molecular fragments, the urban and sanitary context strongly favors a human origin.

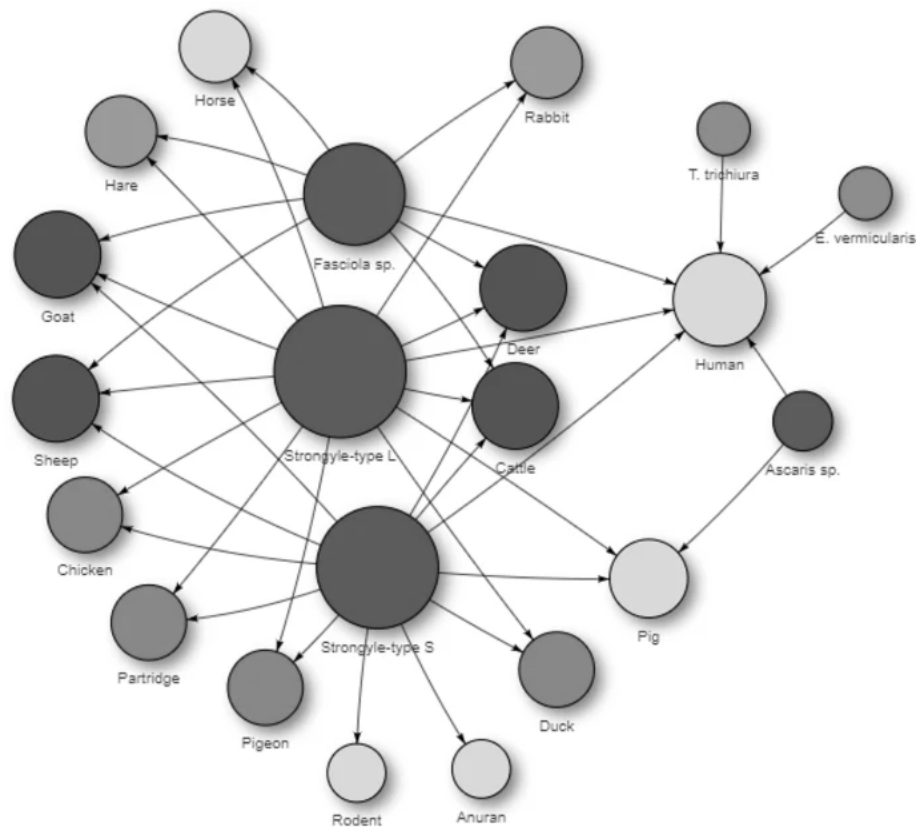


Figure 4. Reconstructed network of host-parasite relationships in Delos based on paleoparasitological and archaeozoological data (considering the detected Trematode as *Fasciola* sp.). Brown: animal and or/human parasites; orange: human parasites; dark green: ruminants; light green: lagomorphs; blue: birds; flesh: others. Nodes size relates to Eigenvector centrality in the network. Arrows go from parasites to hosts taxa

The preservation state of parasite remains reflects typical taphonomic conditions observed in Mediterranean archaeological environments (Roche et al. 2019; Anastasiou et al. 2018). Egg morphology frequently showed fragmentation, loss of diagnostic features, and deformation, complicating precise identification. Nevertheless, size measurements of Ascarididae eggs form a consistent cluster within expected morphological ranges for *Ascaris* sp., supporting taxonomic attribution (Fig. 5). Strongyle-type eggs exhibited substantial size variability, indicating the presence of multiple morphotypes likely originating from various host species, including ruminants and possibly humans. In contrast, *Enterobius vermicularis* was identified exclusively through molecular analysis, reflecting the fragility of its eggs and limited preservation potential (Côté and Le Bailly 2018).

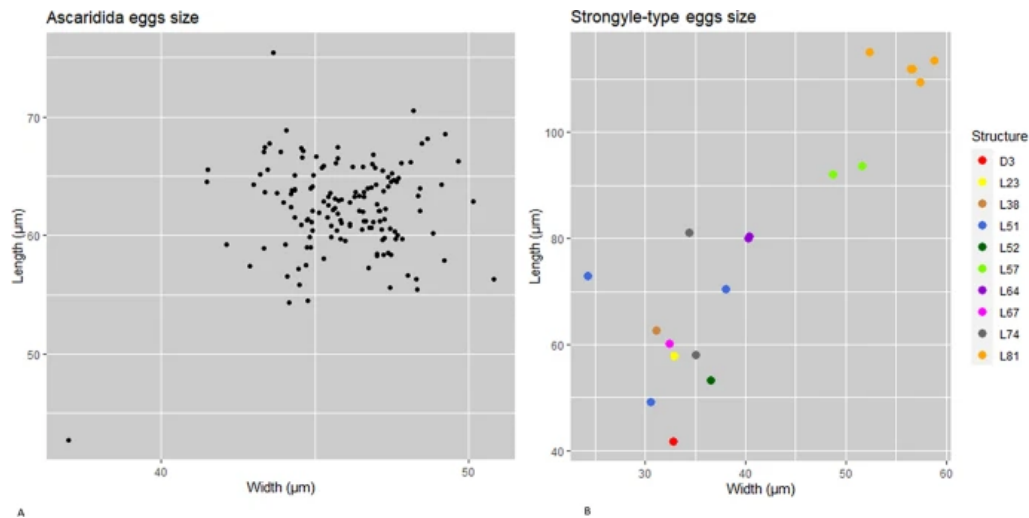


Figure 5. (A) *Ascaridida* eggs form a cluster consistent with *Ascaris* sp. typical measurements; (B) Strongyle-type eggs show a wide size variation encompassing certainly 2 morphotypes at least, with possible clusters depending upon archaeological structures, as seen in L81 corresponding to the *Bothros* situated in the House of Fourni

Zooarchaeological and environmental evidence further supports the persistence of parasitic transmission cycles on the island. Faunal remains recovered from latrines demonstrate the presence of domesticated animals, particularly sheep, cattle, and pigs, which likely served as parasite reservoirs (Rodet-Belarbi 2022; Ephrem 2019). Palynological data indicate the presence of humid grazing environments favorable to parasite survival and transmission (Argant 2022). These environmental and ecological conditions created a stable framework for sustained host–parasite interactions, particularly within agricultural and urban settings. The host–parasite network reconstruction confirms that both domestic and wild animals contributed to maintaining parasitic circulation, facilitating repeated transmission between animals and humans (Fig. 4).

Transmission pathways identified in this study include fecal–oral transmission, airborne transmission, oral ingestion, and possible transcutaneous infection routes, reflecting diverse mechanisms of parasite dissemination. Species such as *Trichuris trichiura*, *Enterobius vermicularis*, and *Ascaris* sp. are primarily transmitted through fecal contamination, highlighting the widespread presence of fecal pollution in the urban environment. Trematode parasites, likely associated with *Fasciola* sp., indicate additional transmission through contaminated food or intermediate hosts. These findings demonstrate that sanitation infrastructure in Delos, although architecturally developed, was insufficient to prevent parasitic transmission.

Historical and epigraphic sources corroborate these paleoparasitological findings. Ancient texts mention waste accumulation and sanitation concerns, including references to waste disposal restrictions near sacred sites (Bruneau 1973). Classical authors such as Hippocrates and Aristotle described parasitic infections consistent with *Ascaris* sp. and *Enterobius vermicularis*, demonstrating awareness of intestinal parasites in antiquity (Dufour 2015; Trompoukis et al. 2007). These written records align with the biological evidence presented here, confirming the widespread presence of parasitic infections in ancient Greek urban populations.

Urbanization and sanitation infrastructure did not eliminate parasite transmission. Despite the presence of latrines and sewer systems, inadequate waste management and structural inefficiencies likely facilitated continued environmental contamination (Bouet and Fournié 2022). Similar patterns have been observed in other ancient urban environments, including Roman cities and Mediterranean settlements, where sanitation systems improved comfort but did not effectively control infectious diseases (Taylor 2015; Scheidel 2009). The persistence of parasite transmission

despite sanitation development reflects a broader phenomenon known as the “urban penalty,” in which densely populated urban environments experienced increased disease burdens compared to rural populations (Meinzer et al. 2018; Nikita et al. 2016; Lewis 2010; Lagia 2014, 2015; Redfern and DeWitte 2011).

Comparative evidence from other archaeological sites across the Aegean region confirms the widespread and persistent nature of parasitic infections throughout antiquity. Previous paleoparasitological studies have documented the presence of *Ascaris* sp. and *Trichuris* sp. in multiple Mediterranean urban contexts, including Kea Island, Ephesus, and Roman Italy (Anastasiou et al. 2018; Ledger et al. 2018; Ledger et al. 2021; Williams et al. 2017). These findings demonstrate the long-term stability of parasite transmission in urbanized environments, despite variations in geography and chronology. A synthesis of regional paleoparasitological evidence highlights the broader epidemiological context of parasitic infections in the ancient Aegean world (Table 4).

Table 4. Paleoparasitological detections around the Aegean Sea

Location	Period	Archaeological context / sample	Detected species	Reference
Sardis, Turkey	6th–7th c. CE	Late Roman drains / sediment	<i>Ascaris</i> sp.	Ledger et al., 2020
Sagalassos, Turkey	2nd–5th c. CE	Roman baths / sediment	<i>Ascaris</i> sp., <i>Dicrocoelium</i> sp., <i>Giardia duodenalis</i>	Williams et al., 2017
Ephesus, Turkey	1st c. BCE–6th c. CE	Roman latrines and canals / sediment and mineralised material	<i>Ascaris</i> sp., <i>Trichuris</i> sp.	Ledger et al., 2018
Kea Island, Greece	Neolithic–Roman period	Burials / sediment	<i>Ascaris</i> sp., <i>Trichuris</i> sp.	Anastasiou et al., 2018
Crete, Greece	1st c. BCE–20th c. CE	Peat bog / sediment	<i>Ascaris</i> sp., <i>Trichuris</i> spp., <i>Capillaria</i> spp., strongyle-type, <i>Fasciola</i> sp., <i>Paramphistomum</i> sp., <i>Macracanthorhynchus</i> sp.	Roche et al., 2020
Kouphovouno, Greece	5000–2000 BCE	Burials / sediment	<i>Entamoeba histolytica</i>	Le Bailly & Bouchet, 2006

Overall, the paleoparasitological evidence from Delos demonstrates that intestinal parasites were widespread and persistent within the Hellenistic urban environment. Although taphonomic limitations and preservation biases prevent precise quantification of infection intensity, the consistent detection of human-associated parasites confirms the presence of chronic parasitic burden among the inhabitants. These findings contribute significantly to understanding health conditions, sanitation effectiveness, and environmental contamination in ancient urban societies, while also providing important insights into the long-term relationship between human populations, urbanization, and infectious disease transmission.

Conclusions

This comprehensive paleoparasitological investigation conducted in Delos represents a significant contribution to the study of parasitic infections in the ancient Greek world, where such large-scale analyses remain uncommon. By examining numerous archaeological samples using both light microscopy and paleogenetic techniques, this study provides a detailed reconstruction of the parasitic burden affecting the urban population during the Hellenistic period. The integration of paleoparasitological evidence with archaeological, bioarchaeological, and historical data offers a multidimensional perspective on sanitation conditions and confirms the widespread presence of fecal contamination across the city. Furthermore, the findings demonstrate that previously excavated archaeological contexts continue to hold valuable bioarchaeological information, highlighting their ongoing scientific relevance despite earlier disturbances.

Although parasite remains were detected throughout the urban landscape, their preservation was generally poor and their distribution sparse, reflecting the challenging preservation conditions typical of Mediterranean environments, except in humid or waterlogged contexts. Importantly, the inclusion of paleogenetic analysis significantly enhanced diagnostic precision and expanded the range of identifiable parasite species beyond what microscopy alone could achieve. These results emphasize the importance of combining traditional and molecular methods in paleoparasitological research. Future studies incorporating broader molecular approaches and comparative analyses across diverse environmental settings will further improve understanding of parasitic diversity, transmission dynamics, and the health consequences of parasitic infections in ancient populations. Ultimately, such research contributes to reconstructing the long-term interactions between humans, parasites, and environmental changes, particularly in relation to urbanization, sanitation development, and evolving human activities.

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