Microfaunal proxies for the Late Pleistocene climate and environment in Għar il-Fkieren (FIMBank site, Malta)

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Submission noted.

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02.2023

ABSTRACT

This research investigates Għar il-Fkieren, a solution pipe fissure abundant with faunal remains dating to the Late Pleistocene (c. 63 – 53 ka). This study quantifies and analyses the microfauna (such as shrews, rodents and herpetofauna) using taxonomic, taphonomic, and morphometric techniques. This represents the novel use of microfauna as environmental proxies for the Maltese Late Pleistocene, providing a crucial contemporary comparison to the Għar Dalam records. The findings reveal a previously unrecorded colubrid species within local Quaternary features, as well as fossil *Podarcis* cf. *filfolensis*. The results also reveal significant evidence that the Maltese Islands constituted a relatively stable environment during the transition between Marine Isotope Stages (MIS) 4-3, characterised by forested and shrubland habitats with freshwater sources and occasional flooding events. The unique climatic and ecological conditions of the Maltese Islands emphasise the importance of detailed, site-specific palaeoenvironmental studies in island contexts, which is vital for understanding broader patterns of climate change, species survival, and ecosystem stability during periods of global climatic instability. This research advances the field of palaeoecology in Malta and the Mediterranean and has the potential to impact broader discussions on climate change, species adaptation to insular environments and conservation strategies.

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1 INTRODUCTION

1.1 OVERVIEW

The main focus of this study is the microfauna (small mammal, amphibian, and squamates) from Għar il-Fkieren, a Maltese Late Pleistocene solution pipe fissure which contained an abundance of fossil animal remains.

This chapter aims to firstly provide an introduction to the Late Pleistocene within the wider global and Mediterranean context, delving into the major climatic events and ecological shifts which characterised this Epoch (1.1.1), including climatic fluctuations, the consequences of the Late Quaternary extinctions and the transformations in vegetation distribution.

Moreover, this chapter will also shed light on the positioning of Malta and other Mediterranean islands within the broader narrative of the Late Pleistocene (1.1.2), highlighting their unique roles and contributions to the understanding of the global climate dynamics during this period. It will also highlight the significance of microfauna; the small terrestrial mammal, amphibian and reptile vertebrates present in various ecological niches, and describe how they can be utilised as environmental proxies which provide valuable insights into the climate and environment during the Late Pleistocene.

After introducing the pressing questions concerning the implications of climate change and environmental fluctuations during the Late Pleistocene and how these changes affected island biodiversity (1.2), this section will introduce Għar il-Fkieren, the site under study, outline clear research objectives and delineate the overarching goals of the study (1.3), emphasising its potential contributions to the broader fields of palaeoecology and palaeontology within and beyond the context of the Maltese islands (1.4). 1.5 will explore the study's Għar il-Fkieren in further depth, including its discovery, excavation strategy, geomorphology, dates, and a brief overview of the macrofaunal remains.

To conclude, this section will outline the structure of the entire dissertation (1.6), providing a roadmap for the following chapters and sections.

1.1.1 The Late Pleistocene

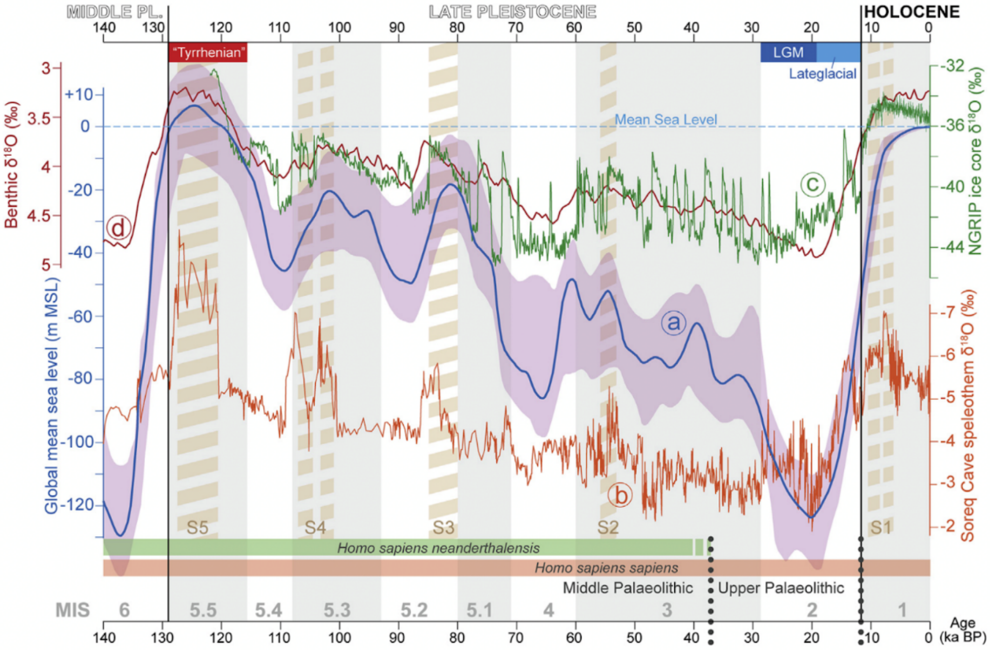


Figure 1: Comparison of past global mean sea level reconstruction with palaeoclimatic, palaeoenvironmental, and archaeological data for the Mediterranean Sea since 140,000 years ago. Benjamin et al. (2017).

The period spanning the Late Pleistocene to the Early Holocene (c. 126 - 11.7 ka) represents a significant Epoch in natural and human history, characterised by dramatic paleoenvironmental and climatic changes happening on a global scale (Figure 1). These climatic changes led to a chain of transformations, including (i) mass extinctions of megafauna, (ii) changes in vegetation, and (iii) substantial shifts in human subsistence strategies (Munro and Atici 2009). Moreover, human communities were rapidly spreading farming across Eurasia (Fernández-López de Pablo *et al*. 2018), experiencing unprecedented population growth and dispersing into previously unoccupied regions, possibly influenced by these shifts in climate (Timmerman and Friedrich 2016).

1.1.1.1 Late Quaternary extinctions

Between c. 50 - 10 ka, a phenomenon known as the Late Quaternary extinction (LQE) began occurring worldwide, mostly in Australia, the Americas, and Eurasia, although more muted in Africa (Doughty *et al*. 2010). Islands also suffered tremendous biodiversity loss, especially following human colonisation. This period involved the extinction of over 97 of 150 genera of megafauna (defined as animals with a mass over 44kg) (Doughty *et al*. 2010). The causes of these extinctions have been hotly debated for decades (Lyons 2004; Koch 2006; Zuo 2013), with explanations varying from climate change, human hunting, or some combinations of the two (Barnosky *et al*. 2004). MacPhee and Marx (1997) also proposed a hyperdisease theory, suggesting that humans spread fatal pathogens to megafauna as they expanded around the globe, although the staggered patterns of extinction observed in Northern Eurasia do not fit with this hypothesis (Stuart 1999). A recent paper by Cooper *et al*. (2015) found a strong association between warming events (i.e., interstadials) and the regional replacement or extinction of megafauna species, suggesting that this may have been further exacerbated by human impact. By settling in resource-rich zones, humans may have interrupted key megafauna metapopulation processes such as subpopulation connectivity, thereby leading to more regional extinction patterns and collapses of ecosystems.

Although much work has been done to see the impact of global climate change and human dispersal on megafauna diversity, there is less research into the impact on island biodiversity and smaller fauna. Pleistocene extinctions also occurred in Europe before 50 ka to about 780 ka, and affected smaller mammals (weighing less than 40 kg). This included species such as the shrews *Beremendia fissidens* and *Sorex savini*, a beaver-like rodent *Trogontherium cuvieri*, and the macaque monkey *Macaca* (Stuart 1999). Notably, *M. sylvanus* experienced regional extinction in Europe, although it remains extant in North Africa. Its current presence in Europe (Gibraltar) is due to recent introduction (Stuart 1999: 262). These "background" extinctions of both large and small mammals were likely driven by the repeated climatic changes during the Pleistocene, marked by several major glaciation episodes. These climatic fluctuations led to a gradual decline in faunal diversity in the European record (Stuart 1993).

This rapid extinction continues to raise many questions for palaeoecologists, conservationists, and archaeologists working on fossil fauna (Koch and Barnosky 2006). Rather than debating the causes of the Late Pleistocene megafauna extinctions, some recent work is increasingly focused on understanding the evolutionary and ecological legacies of these extinctions (Malhi *et al*. 2015). Malhi *et al*. (2015) reviewed the evidence of the megafaunal impacts on the function of ecosystems from the Late Pleistocene to the present day, arguing that understanding the consequences of these extinctions is of enduring relevance to contemporary conservation studies.

1.1.1.2 Vegetation changes

The extinction of many of the Earth's large herbivores had a significant impact on global vegetation. In Alaska and Yukon, for instance, the disappearance of mammoths during the terminal Pleistocene is thought to have caused a drastic increase in *Betula* cover, which in turn resulted in warmer conditions through the decrease in land surface albedo (Doughty *et al*. 2010).

Between 60 – 50 ka, pollen records from Lago di Monticchio (Province of Potenza, Italy) show a consistent presence of wooded taxa but a predominance of steppe taxa (Allen et al. 1999, Figure 2). Following this, between 50 – 40 ka, a climatic amelioration is marked by a significant increase in woody taxa and a decrease in steppe taxa. Watts *et al*. (2000) also provided a high-resolution pollen record from Lago di Monticchio spanning MIS 3 – 4. They identify three interstadial events dated respectively to 37.6 – 40, 43.6 – 50 and 72 -74.6 ka, each of which is characterised by distinct sequences of mesic forest pollen changes, suggesting similar climatic patterns during these periods. The presence of tree pollen, even during interstadials, indicates a mixed landscape of forest and grassland, with tree growth potentially constrained during glacial periods. The interstadials show abrupt beginnings and endings, with rapid climatic shifts that match the GRIP (Summit) Greenland Ice Core profiles.

Combourieu-Nebout *et al*.'s (2015) pollen analysis from southern Italy confirmed the change and alternation between deciduous forest and steppe conditions, suggesting a decline in winter temperatures and precipitation, with drought becoming a recurring feature from the early Pleistocene to the Holocene. This paper provided evidence that the Italian North-South precipitation gradient began during the Early Pleistocene and has been a consistent feature since, with drier conditions in the south.

In Malta, Pleistocene vegetation records are patchy and most analysis has focused on the Holocene onwards (e.g., Carroll *et al*. 2012; French *et al*. 2020). Vegetation is closely linked to climate and fauna, and more studies need to be done to ascertain these relationships of cause and effect. Although out of scope for this study, the study of microfaunal assemblages combined with pollen analysis can offer an opportunity to determine what kind of vegetation conditions were present during the Late Pleistocene in Malta.

1.1.1.3 Subsistence strategies

Researchers have regarded the Late Pleistocene as a period of significant changes in human subsistence and resource exploitation strategies (Munro 2004; Davis 2005; Steele and Klein 2009; Prendergast *et al*. 2016; Mata-González *et al*. 2023). The timing and nature of these changes are of particular importance in the Mediterranean, due to their occurrence between the first anatomically modern humans and the origins of agriculture (Munro and Atici 2009).

The major dietary shifts which appear in the Late Pleistocene faunal records include specialisation, i.e., the reduction of diet to one or two large game species, and diversification, an expansion of diet to include less cost-effective resources (Munro and Atici 2009). The specialisation and diversification of human diets are shown to be connected to demographic growth, technological advances, intensification of subsistence, and occupational intensification of settled sites, all of which are reflected in the archaeological record in the Mediterranean between 50 - 10ka (Munro and Atici 2009). However, traces of human settlement in more isolated regions like Malta and Sicily remain either absent or contested for most of the Late Pleistocene, and it is still unclear how mainland intensification of subsistence and occupation has affected these more marginal environments.

1.1.2 Maltese microfauna within the broader context of the Late Pleistocene climate

All of these events make this epoch a crucial period to understand, due to its relevance to several key research questions in the fields of palaeontology and biogeography. One of the main challenges in this research remains to understand the role of climate change, evolutionary processes and human cultural trajectories in response to these extensive changes taking place (Kintigh *et al*. 2014). The Mediterranean, with its rich biodiversity, vulnerability to climate change and long history of human-environmental interactions therefore offers a unique opportunity to investigate these issues (Fernández-López de Pablo *et al*. 2018).

Paleoenvironmental and climatic records from Marine Isotope Stages (MIS) 4 and 3 provide critical insights into the environmental dynamics during the Late Pleistocene. During MIS 4 (71 – 57 ka), the Mediterranean region experienced significant glaciation and cooler climatic conditions. However, detailed pollen records from Lago Grande di Monticchio, Southern Italy, indicate a diverse climatic pattern within this stage. MIS 4 was preceded by an interstadial event around 72 to 74.6 ka, showing a brief period of warming characterised by the expansion of mesic forests despite the generally cold climate (Watts *et al*. 2000).

Transitioning into MIS 3 (57 – 29 ka), the region witnessed frequent and rapid climate oscillations, known as Dansgaard-Oeschger events. These interstadial periods, marked by rapid shifts between warm and cold conditions, are well-documented in the Mediterranean (Watts *et al*. 2000). Allen *et al*. (1999) highlight that the Southern Mediterranean underwent severe climate fluctuations with rapid transitions between forest and wooded steppe environments occurring approximately every 142 years. Between 60 – 50 ka, pollen records reveal a consistent presence of wooded taxa alongside a predominance of steppe taxa, indicative of cooler conditions. However, from 50 – 40 ka, there was a significant climatic amelioration, with an increase in woody taxa and a decrease in steppe taxa, reflecting warmer and more stable conditions.

Although gaining a deeper understanding of climatic conditions during the Late Pleistocene is crucial for the mainland Mediterranean, it is important to note that the complex climatic patterns of the Central Mediterranean cannot be fully unravelled solely through mainland research. The Sicily/Malta region, situated at the crossroads of the Mediterranean, presents a unique climatic history distinct from both the northern (Italy) and southern (Tunisia) mainland regions (Carroll *et al*. 2012). Understanding the unique climatic history of Mediterranean islands such as Malta is of particular interest due to their pivotal role in fostering the evolution of a high percentage of endemic species and maintaining remarkably low biodiversity during the Pleistocene (Massetti 2009). These unique conditions, characterised by their small geographic area, consistent climate, and limited contact with mainland species, created an environment conducive to investigate the processes of faunal turnover, evolution, and ecology, shedding light on the interactions between species, climate, and the environment (Marra 2004).

Hunt (1997) provided local context by examining Quaternary deposits in the Maltese Islands, which serve as a 'microcosm' of environmental change in Mediterranean. These deposits reveal arid glacial stages and humid interglacial stages preceding the significant agricultural human impact during the Holocene. The sequences described in the Maltese Islands exemplify typical Quaternary lithofacies and provide clear evidence of past environmental changes. During interglacial periods, the landscape was well-vegetated, leading to soil development and limited erosion. In contrast, stadial episodes were characterised by aridity, sparse vegetation, and increased erosion and sedimentation due to occasional extreme rainfall events (Hunt 1997: 108). Hunt's work emphasises the importance of reassessing the Quaternary stratigraphy of Malta using modern methods to better understand the environmental history and the impact of climatic changes.

Other assessments of the Quaternary palaeoenvironment are based on the fossil fauna from Għar Dalam. Storch (1974) suggested that the Pebble (VII) layer, dating to the Early Pleistocene, indicated a Mediterranean climate with large bodies of freshwater and open forests, inferred from the fossil Chiroptera. The Middle Pleistocene fossil avifauna, Fischer and Stephan (1974) noted, suggested an open country, sparse in vegetation, with few trees and freshwater sources. For the Red Earth (IV, V) layers, Hunt (1999: 29) suggested relatively mild conditions, evidenced by the presence of *Emys orbicularis* (European pond terrapin) and woodland/grassland coverage inferred from *Microtus* voles, indicating a predominantly warm climate with possible oscillating conditions for these layers.

Exploring fossil fauna provides a unique opportunity to establish biological events within the expansive Pleistocene timeframe (Marra 2004). While the study of megafauna is crucial for understanding past ecosystem structure and biogeochemistry (Malhi *et al*. 2015), microfauna play distinctive roles as environmental indicators (see Figure 2). Microfauna, encompassing species weighing 1 kg or less (Stahl 1996), constitutes a diverse array of organisms such as reptiles, amphibians, and mammals. Their narrower environmental tolerances compared to larger fauna, coupled with their limited consumption by humans and subsequent restricted movement from their home ranges (Moncunill-Solé *et al*. 2016), make microfauna particularly valuable in reconstructing and interpreting past environmental conditions.

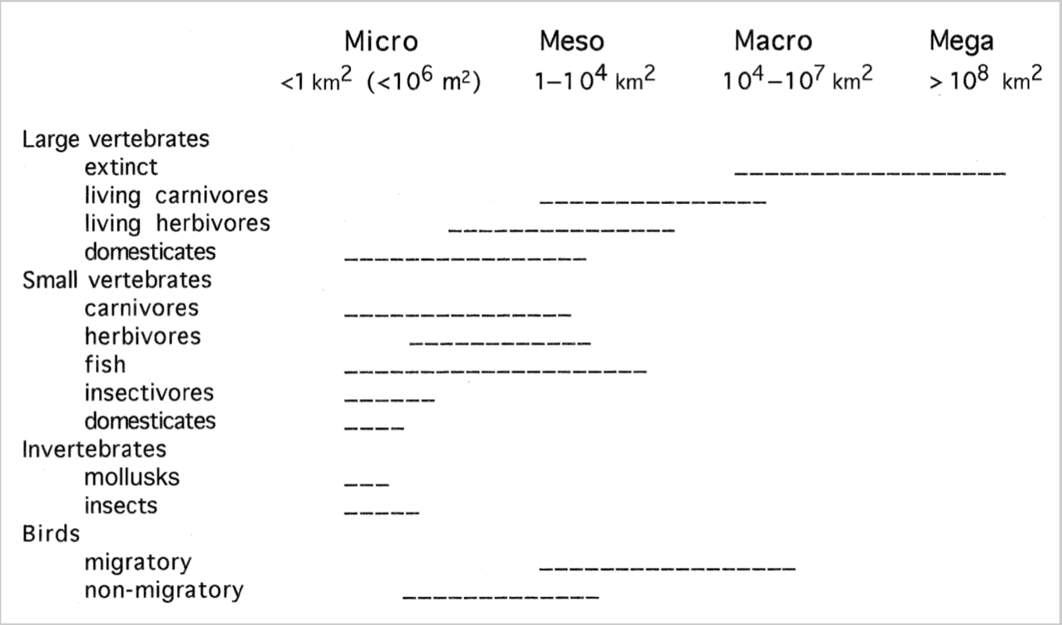


Figure 2: Environmental scaling with fauna, displaying the various fauna data classes used for palaeoenvironmental modelling at different scales. Dincauze (2000).

Although the Late Pleistocene has been researched extensively, especially with regard to larger ungulates and carnivores, microfaunal biogeographic distribution during this period has received much less scholarly attention (Sommer 2020) aside from in the Iberian and Italian Peninsulas, in which there is a long tradition of microfaunal studies (e.g. Cuenca-Bescós *et al*. 2009; Rofes *et al*. 2014; Garcia-Ibaibarriaga *et al*. 2015). Various microfaunal studies have been undertaken in the Mediterranean region in recent decades, the majority of which focus on the Pleistocene (e.g., Masini *et al*. 2008; Bonfiglio *et al*. 2003), while some focus specifically on the Pleistocene/Holocene transition (e.g., Petruso *et al*. 2010; Palombo 2018; Ouahbi *et al*. 2013; Markova *et al*. 2019). Many of these Mediterranean studies concentrate on Sicily, Italy, Iberia and coastal areas, and appear to focus more on the Central and Western Mediterranean regions than the Eastern Mediterranean. Similar studies utilising microfauna as proxies for biochronological or ecological indicators are also increasingly present for North Africa (Geraads 2002; Geraads 2010; Sahnouni *et al*. 2011; Stoetzel *et al*. 2014, Stoetzel *et al*. 2019).

While several studies in the Mediterranean region have emphasised the rich diversity of Pleistocene microfauna and their capacity to serve as indicators of past environments, climates, and human activities (e.g., Spena *et al*. 2021; Kotsakis *et al*. 2020; Salari 2010; Masini *et al*. 2008), research focusing on the Maltese Islands has lagged (Gatt 2015). Despite the Maltese archipelago hosting a diverse faunal complex spanning several thousand years, numerous questions related to the Pleistocene fauna and environment in Malta remain unanswered. These questions will be explored further in the following section.

1.2 RESEARCH QUESTIONS

Fluctuations in climate and environmental conditions played a pivotal role in shaping the composition of the island's animal assemblages and influencing the fate of numerous endemic Pleistocene fossil species. Against the backdrop of past climate change and mass human population dispersal in the Mediterranean, this research aims to understand the interplay between environmental shifts and their cascading effects on the island's ecological balance. The emerging research questions investigate the mechanisms underlying the relationship between climate dynamics and species adaptation.

- What species were present for the duration of the assemblage’s formation, and how abundant were they relative to each other?
- What was the environment like during the Late Pleistocene? Did the local environment exhibit instability, mirroring global climate trends, or was there local stability that promoted long-term species survivability?
- What were the specific climatic patterns and environmental changes that precipitated the extinction of several Maltese endemic Pleistocene fossil species? How did variations in temperature, sea levels, island size and precipitation impact the island's habitats and contribute to the decline of these taxa?
- In the context of shifting climate conditions, what were the primary environmental and physical factors that shaped the taphonomy of the animal fossil assemblages during the Late Pleistocene? How did fluctuations in temperature and habitat suitability influence the distribution and interactions among species? How do these ecological dynamics reflect the broader impacts of past climate change on the island's biodiversity and ecosystem resilience?
- At what stage during the glacial-interglacial cycles recorded for the Late Pleistocene did faunal turnover occur from neighbouring Sicily? How did the microvertebrates from Sicily evolve both when connected to the peninsula and under insular conditions precipitated by higher sea levels?
- What do the species under study reveal about their phylogenetic ancestry and the characteristics of their surrounding habitat? How do their morphological features compare with specimens from different sites and time periods in the Maltese Islands?

1.3 AIMS AND OBJECTIVES

The main aim of this study is to conduct a comprehensive analysis of the microvertebrate fossil assemblage obtained from Għar il-Fkieren, a fossil-rich fissure site excavated in 2010 (1.5). This study will utilise these specimens as key proxies for understanding past climate dynamics and environmental conditions within the vicinity of the site. In pursuit of this overarching goal, the study outlines the following objectives.

Screening of remains: The preliminary step entails the careful screening process of the microfaunal remains. Given the small size of the microvertebrate remains, a specialised flotation technique must be implemented (Stahl 1996). This screening process serves as the foundational gateway to obtaining a collection of microfaunal remains for subsequent analysis and classification.

Taxonomic identification and quantification: Upon successful extraction and isolation of the microfauna fossils from the sediment, the subsequent stage is the taxonomic identification process, which involves identifying the skeletal elements and categorising the specimens into general taxa and species (where possible). After taxonomic identification, the individual elements must be counted, categorised, and entered into a database.

Morphometric analysis: Measurements of selected dental and long bone elements are recorded in order to provide further quantifiable data, which may be used to determine variation in body mass or differentiate between species (Li *et al*. 2021).

Taphonomic analysis: Digestion and breakage patterns are recorded in order to investigate taphonomic processes responsible for the accumulation of the assemblage, elucidating the formation and ecological conditions of the site (Fernández-Jalvo and Andrews 2016; Bisbal-Chinesta *et al*. 2020).

Statistical analysis: The datasets generated by the taxonomic, morphometric and taphonomic analyses serves as the bedrock for a deeper statistical analysis. Based on the research questions (1.2), it is necessary to build a relative abundance profile of the various animals present at the site and subsequently compare these profiles across different strata. This analysis will allow the detection of shifts in animal population dynamics, facilitation a chronological reconstruction of the changing patterns of species abundance throughout the site (Mannino *et al*. 2015). Furthermore, in order to gain a comprehensive understanding of the taphonomy of the site, the quantified data must also be utilised to estimate the percentage of digested skeletal elements. This approach not only helps us to indirectly detect predators by proxy (Andrews 1990), but also provides valuable insights into taphonomic processes which contributed to the formation of the site and its faunal assemblage (Fernández-Jalvo and Andrews 2016).

To effectively visualise the datasets and discern meaningful trends, it is essential to choose appropriate data visualisation techniques (Baxter and Cool 2016). This involves selecting the most suitable plotting method, which can be facilitated through commonly used tools such as Excel for basic plots. However, certain visualisations which demand a higher degree of customisation call for more specialised software, such as R Studio. The utilisation of R Studio provides us with a greater degree of control over the generated graphs, enabling a more nuanced exploration of the data. Baxter and Cool (2016: 20) highlight the significance of R due to its flexibility and robust statistical capabilities.

By leveraging these statistical tools and employing these visualisation techniques, the data is also presented in a more accessible and interpretable format. This approach not only facilitates the identification of underlying patterns but also serves as a means of investigating the relationship between the microfauna and the surrounding environmental dynamics.

Interpretation and comparison: Drawing upon insights from the habitat preferences of known extant and extirpated species in Malta and neighbouring regions, as well as those of extinct species' closest living relatives forms a foundation for interpretation which we can base our understanding of the habitat diversity that existed in the region (Faith and Lyman 2019). These habitat preferences can be quantified using the habitat weighting method and provide valuable insight into the palaeoenvironment. By synthesising and tabulating this ecological knowledge of living species, the study aims to make scientific inferences regarding the environmental conditions and ecological niches proximate to the Għar il-Fkieren site.

An additional interpretive approach involves a comparative analysis with the microfauna of Għar Dalam, Sicily and North Africa. This comparative exploration, based on existing genealogical data, traces the potential evolutionary lineage of species from Għar il-Fkieren and Għar Dalam, shedding light on the divergence points and cross-referencing these with records of sea level rise (Hutterer 1991). Through this, the study discerns when these species separated from the mainland, evolving independently. Special attention is devoted to investigating the effects of insularity versus connectivity with the mainland, exploring potential changes in body size as indicative markers of environmental adaptation (Moncunill-Solé *et al*. 2016).

The amalgamation of these findings provides insights into the climate and environment surrounding the Għar il-Fkieren site. By synthesising these various insights, the study aims to clarify the interplay between ecological variables such as global climate change and sea level rise with faunal dispersal and evolution, while providing a narrative of the site's local formation and evolution over time.

1.4 SIGNIFICANCE OF STUDY

The Maltese Islands offer a dense array of fossiliferous sites containing a rich Quaternary history. This natural history showcases a diverse spectrum of species, each bearing unique environmental adaptations that are of interest to palaeontologists, archaeologists, zoologists and others. This not only serves as a reservoir of biological diversity, but also as a compelling case study for scholars exploring the interplay between environmental factors such as sea level rise and species evolution. Furthermore, the Maltese Islands' climate and environment hold valuable research opportunities for palaeoenvironmental archaeologists and climate scientists. As a ‘living laboratory’ of sorts, the islands’ insularity is ideal for those seeking to understand how past climatic conditions shape island natural and human history, and the impact of changing ecosystems on insular environments.

However, despite its decidedly rich potential, current Quaternary research remains relatively sparse and a comprehensive analysis of the paleoenvironment of the Maltese Islands during the Quaternary period is still lacking (Gatt 2015: 13). Previous works, including Galea Bonavia (1999), Hunt (1997), Hunt and Schembri (1999), Pedley (2011), Savona Ventura and Mifsud (1998, 1999), and van der Geer et al. (2010), provide interpretations of the Maltese Quaternary Period. However, many of these interpretations rely on the century-old stratigraphy of Għar Dalam and a limited number of sites excavated using outdated methods. Only a few of these sites still preserve sediments that can be examined using modern scientific techniques, and the data from these earlier reports cannot be fully verified (Gatt 2015: 19).

The material under study was retrieved from the Għar il-Fkieren site, a relatively recent discovery of a fossil-rich crevice in Malta unearthed during construction operations in Paceville in 2010 and excavated by the Superintendence of Cultural Heritage. This newly uncovered site provides an abundance of Late Pleistocene faunal material, presenting a distinctive opportunity to examine Quaternary micromammals utilising contemporary screening methods that significantly improve the recovery rates of small animal remains.

The current research represents the first comprehensive study of Maltese Pleistocene microfauna as environmental indicators, signalling a shift in the field of Quaternary research within the region. By leveraging modern scientific techniques and screening methods, the study aims to reconstruct the ecological dynamics and environmental conditions prevalent during the Pleistocene Epoch on the Maltese Islands.

Apart from offering a novel perspective on the trajectory of the region's microfauna, this study also contributes valuable insights into a key area connecting continents. While working with a small, site-specific sample of microfauna from a challenging-to-date location presents certain limitations, the findings still offer a meaningful contribution to understanding pre-Holocene climatic variations and their impact on insular ecosystems. By examining the relationship between animal populations and environmental changes during the Quaternary period, the study provides valuable insights into the adaptive strategies of species in response to climatic fluctuations. These findings could inform policymaking aimed at addressing the current climate crisis, particularly in relation to island ecosystems.

The findings generated from this research also offer a much-needed reference point for future comparative studies, facilitating a more holistic assessment of similar Quaternary species across different geographical regions. By establishing a framework for the systematic analysis of microfaunal remains, this study also contributes to the broader discourse on global biodiversity patterns and the interactive web between climate dynamics and faunal adaptation. Through its pioneering efforts, this study sets a precedent for local Quaternary research, unlocking further insights that may influence future palaeontological and palaeoenvironmental studies and foster a deeper appreciation of the ecological legacies of the Maltese Islands' Quaternary past.

1.5 GĦAR IL-FKIEREN (GĦF)

1.5.1 Site description, discovery and excavation process

The discovery of Għar il-Fkieren, formerly known as Pender Place due to its proximity close to the ‘Pendergardens’ business center, occurred during construction works at Triq Elija Zammit, St Julian’s, Malta in 2010. The site lies on a slope which flows towards the coast of St. George’s Bay (Figure 3). It is a vertical cave shaft approximately 10 m (metres) deep, with a cross-section revealed when digging equipment excavated into it (Figure 4). Unfortunately, the other half of the shaft was seemingly destroyed during this process. Onsite monitors from the Superintendence of Cultural Heritage (SCH) identified bone-rich deposits within the cross-section and initiated a rescue excavation.

The excavation presented challenging conditions, as time was limited, and monitors were given only five days (19-26 April, 2010) to gather and document as much material as possible, therefore leaving scant site documentation available. Sediment from the top 4 m of the shaft was recovered and organised into stratigraphic units (001) - (027), while the next 4.5 m were organised by spit/depth. A further 1.5 m of sediment within the shaft remains unexcavated. Beneath 8.5 m, a concrete slab buffered with polystyrene was used to seal the cave, with the cave beneath remaining unexcavated. Drilling works carried out in 2023 with the aim of investigating whether there was any further deposit did not reveal any more deposit beyond the concrete slab.

Following the discovery of the site, SCH requested an alteration to the original plans to preserve a gap in the building, allowing access for researchers. Currently, the shaft is accessible from the basement levels of the building, providing an opportunity for further investigation and study.

Preliminary geomorphological observations by Prof. Ian Candy (pers. Comm.) suggest that Għar il-Fkieren is likely a solution pipe fissure; karstic landforms which are often formed spontaneously and typically occur in Quaternary calcareous sandstones (Figure 7).

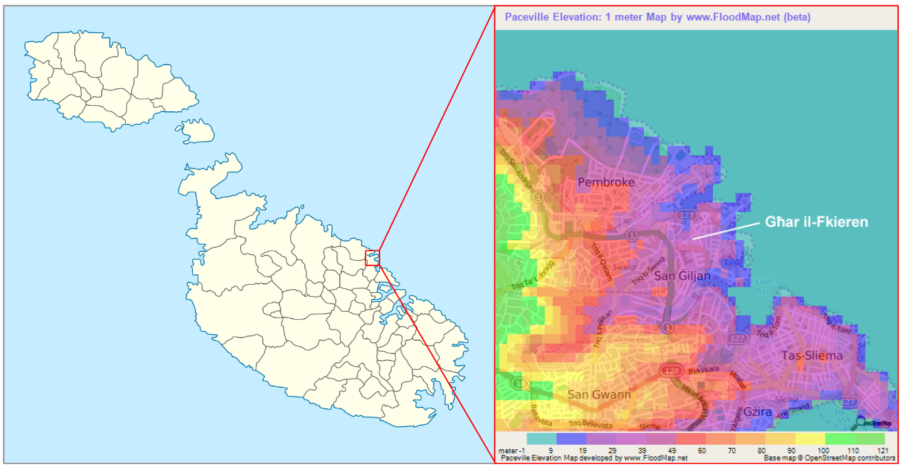
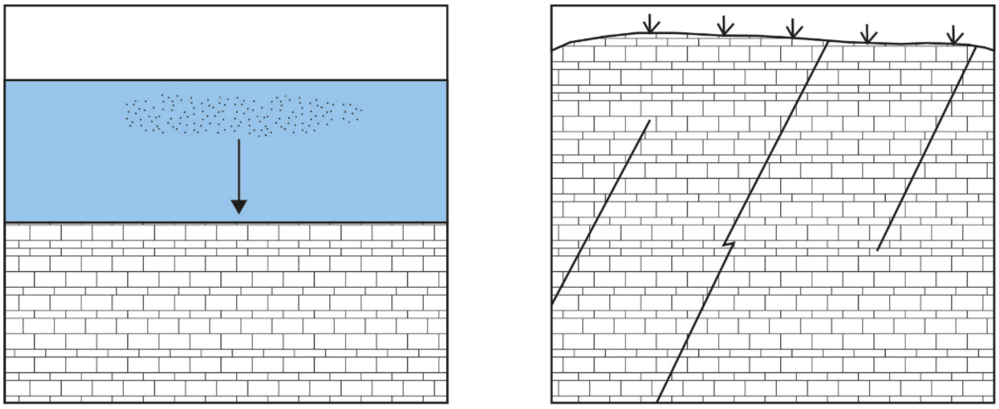


Figure 3: Għar il-Fkieren location relative to the central east coast of Malta, with elevation levels.

Figure 4: Left: Cross section of Għar il-Fkieren after its discovery. Right: Close-up of faunal material in-situ before SCH rescue excavation.

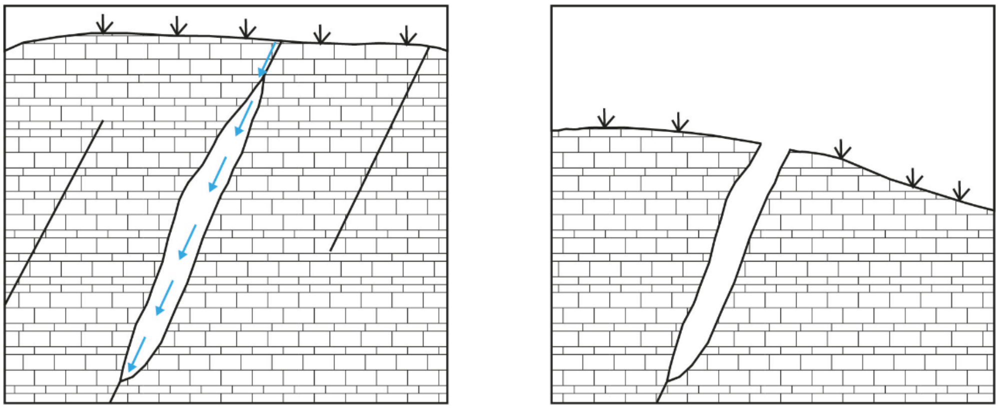
Figure 5: Speleothems at the deeper end of the 8.5 m section.

Figure 6: Sieved, unsorted fauna assemblages from a context in Għar il-Fkieren. Fragmented but otherwise decently preserved. Abundances of bone like this were observed across all contexts.



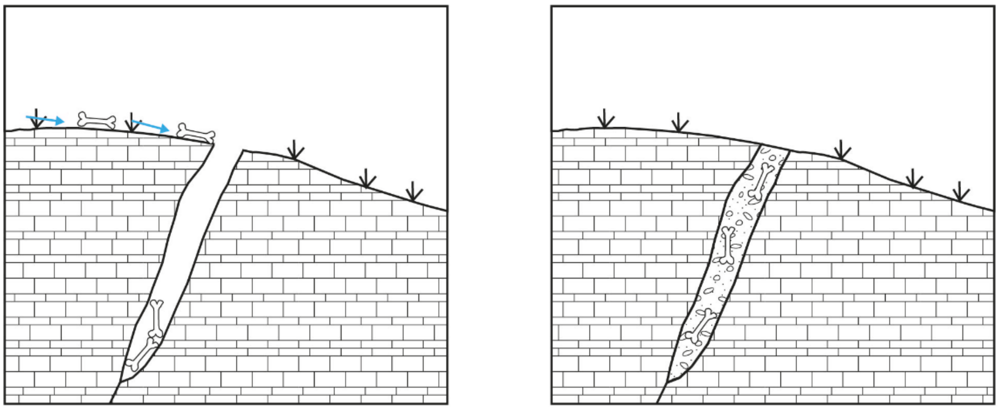
1) The story begins around 10 million years ago when Malta was just part of a shallow sea. Shells of microscopic organisms grew and died in the water column and accumulated on the sea floor as a carbonate rich mud

2) The carbonate rich mud turned into a hard limestone and between 6 and 3 million years ago was uplifted due to Tectonic processes. The island of Malta was formed and the rock, due to the stress and pressure, was cut through by a series of faults



3) Now a fully terrestrial island, water from the rain drains through the soil and down along the faults. The flowing water dissolves the surrounding limestone and forms a cavern/fissure below the land surface

4) Erosion of the landscape causes the mouth of the fissure to be unearthed. There is now a cave entrance exposed at the landscape leading down into the fissure.



5) Storm events wash sediment, and the bones of any animals living on Malta at that time, off the surrounding landscape and into the cave

6) Eventually the fossiliferous sediment completely fills up the cave and sedimentation stops. The bone rich deposit is preserved underground until building work at the bank exposes it for the first time.

Figure 7: Storyboard of Għar il-Fkieren site formation processes. Image credit: Prof. Ian Candy (Royal Holloway).

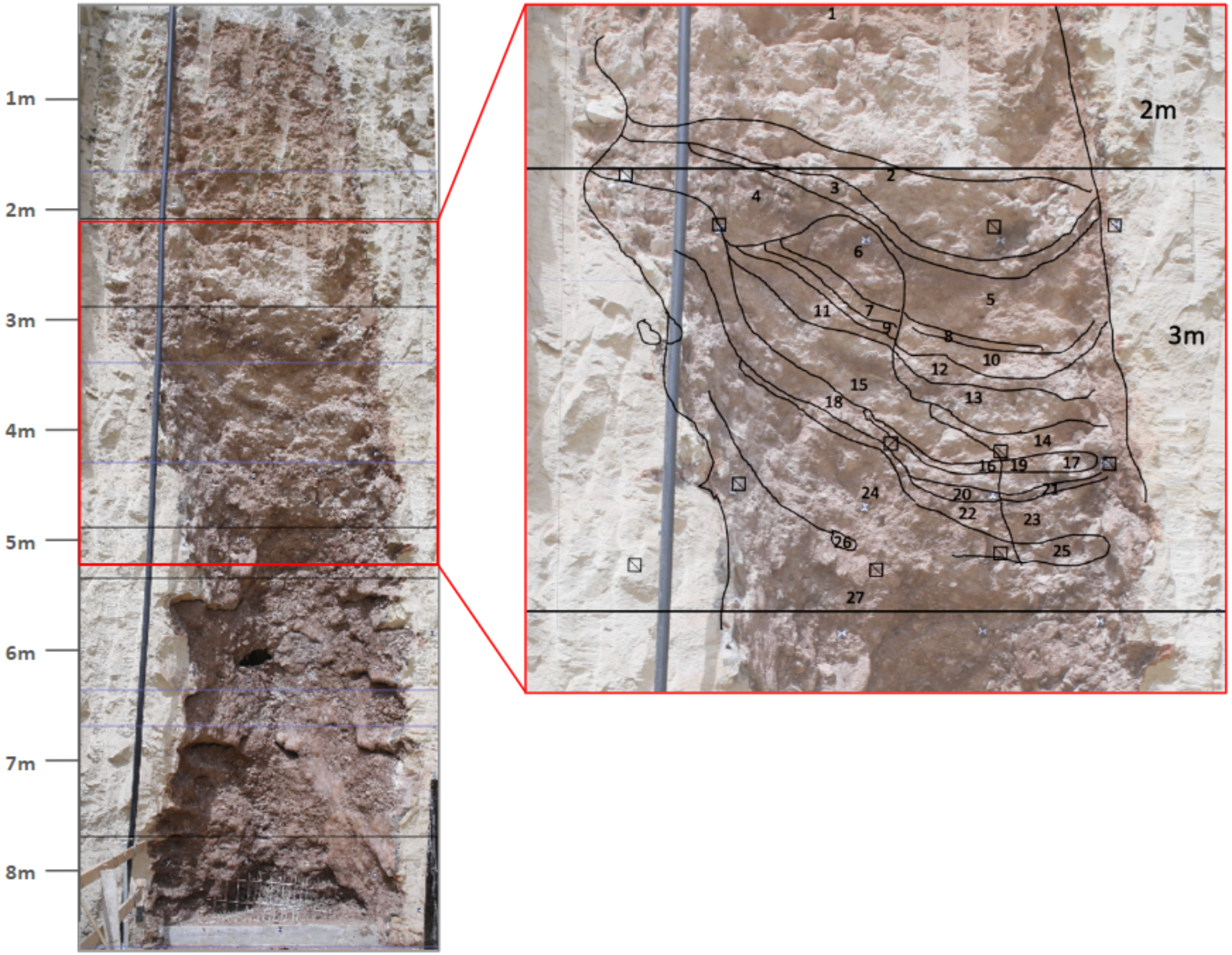


Figure 8: Left: Għar il-Fkieren photogrammetric view, provided by the Superintendence of Cultural Heritage. Right: SU locations overlay reproduced by Prof E. Scerri based on SCH monitor drawings.

1.5.2 Limitations from excavation strategy

A chronological stratigraphic analysis of the whole site was made more complex due to the two different excavation strategies employed during the rescue excavation, owing to developer time pressures. In other words, mainly the division between excavating by stratigraphic units (SUs) followed by spit and depth, as can be seen in Figure 8. These will be further detailed in section 4.2.1.

1.5.3 Dating

Radiocarbon dating yielded three age measurements at different depths within the site: 8.5 m (at the base of the fissure), 4.5 m (in the middle of the fissure), and at 3 m (SU11). These dates exhibited a minor inversion, indicating approximate similarities, with readings of 40 ka at the base, 42 ka at 4.5 m, and two readings from SU11 at 3 m, measuring 43 ka and 45 ka.

However, radiocarbon dating has limitations, particularly when it comes to samples older than ~ 50,000 years. One such issue is the concept of 'infinite ages'; since ^{14}C has a half-life of around 5700 years, it becomes increasingly difficult to measure beyond these dates. The amount of ^{14}C left in the sample is so small by this point that it becomes challenging to distinguish it from background radiation and measurement errors. As a result, radiocarbon dates for such samples can sometimes appear to suggest infinite ages, meaning the ^{14}C levels are so low that they effectively register as being immeasurable (Christie 2018).

To overcome this limitation, Uranium-series dating was carried out to help refine the age estimates of ancient materials. U-series dates from SU-11 (approx. depth 2.5-3m) recorded a date estimate of 53 - 63 ka, showcasing a c. 20,000-year difference from the previous radiocarbon date (Table 1).

To refine the chronology further, future attempts will be made to obtain additional dates. Due to the infinite ages issue of the ^{14}C dates, the dissertation will refer to the U-series dates of c. 63 - 53 ka. These dates should be considered as minimum age estimates.

Context	SU	Depth (m)	Element	Date (ka)
367	11	2.5 - 3	Cervid bone	58 +/- 2
367	11	2.5 - 3	Cervid tooth	59 +/- 3
367	11	2.5 - 3	Cervid tooth	54 +/- 1
368	11	2.5 - 3	Cervid tooth	63 +/- 3
368	11	2.5 - 3	Cervid bone	55 +/- 3
401	11	2.5 - 3	Cervid tooth	53 +/- 1

Table 1: U-series dates on cervid remains retreived from SU 11. Dates should be considered as minimum age estimates. Analysis by Renaud Joannes Boyeau at Southern Cross University, Australia.

1.5.4 Faunal remains

In October 2020, a preliminary evaluation of the palaeontology of the Għar il-Fkieren site was conducted as sediment bags were sieved to separate larger fauna from microfauna in the matrix. Notably, the lower layers of the sediment showcased an abundance of tortoise remains, seemingly intermingling with numerous deer remains. Interestingly, an inverse relationship was observed between the abundance of tortoise and deer remains, suggesting that when one species was abundant, the other tended to be less prevalent.

Moreover, a consistent presence of the same species was observed across all crates, indicating a stable faunal composition within the stratigraphic layers. This included the identification of large avian species that have yet to be classified. Currently, a full report on the deer species is underway and is in preparation, with the tortoise and avian remains also intended to be studied at an indeterminate time.

Aside from abundant macrofauna remains, the site was replete with microfauna - some already well-established from the Għar Dalam Upper Red Earth layers, while others have not yet been recorded in Maltese Pleistocene sites. A full systematic report on the microfauna taxa from Għar il-Fkieren will be included in 5.1.

1.6 STRUCTURE OF THE DISSERTATION

The dissertation is structured as follows: the introductory section (1) lays out the research questions, aims and objectives, and significance of the research. It also provides an overview of the Għar il-Fkieren site, discussing the site's discovery, excavation process, limitations, and the significance of microfauna within its broader local context. This is followed by a comprehensive literature review (2) which includes an analytical framework (2.1) explaining the role of microfauna as environmental indicators, and relevant case studies (2.2) focusing on Late Pleistocene climate studies in the Mediterranean. The main focus will be on Italy and Sicily, the Balearic Islands, Cyprus, Sardinia and Corsica, selected for their insular status and rate of endemic species during the Pleistocene. The review emphasises the significance of focusing on Malta within this context.

The following chapter on the history and review of Pleistocene studies in Malta (3) gives and overview of the Maltese Islands' geological and environmental background (3.1.1) and explores the main sites which have provided our current understanding of the Maltese Pleistocene, mainly Għar Dalam (3.1.2). It also gives an overview of other Pleistocene sites (3.1.3). A brief research history and literature review will be covered in 3.1.4, which sets the stage for exploring current research gaps in the local record (3.2).

The methodology section (4) begins by detailing the research design of the study (4.1), which explains and justifies the chosen research strategies. This is followed by an overview of the main data collection methods (4.2), including site collection of samples (4.2.1), screening strategies to recover microvertebrate specimens (4.2.2), photography (4.2.3) and measurements (4.2.4) of the specimens, and how the main database is structured (4.2.5). The data analysis methods (4.3) are explored in terms of taxonomic identification (4.3.1), quantification (4.3.2), taphonomic analysis (4.3.3), morphometric analysis (4.3.4) and comparative morphometry (4.3.5). Finally, it provides an explanation of the habitat weighting system used to reconstruct the palaeoenvironment (4.3.6).

Section 5 presents the key results derived from the analysis, beginning with a systematic palaeontology section (5.1) describing the taxa identified from Għar il-Fkieren and the relative abundance of species (5.1.1). It then presents the results of the taphonomic (5.2) and morphometric (5.3) analyses, after which it concludes with the results of the habitat weighting (5.4).

The subsequent discussion section (6) synthesises and interprets these findings within the Maltese context and the broader Mediterranean Late Pleistocene framework. It also addresses the limitations of the study, suggests areas for future research. Finally, the conclusion (7) revisits the research questions, examines how the findings clarify them, reiterates the significance of the research in a wider context, providing final thoughts and recommendations.

2 BACKGROUND TO RESEARCH

2.1 ANALYTICAL FRAMEWORK

2.1.1 Introduction to microfauna studies

Microfauna, comprising small mammals, amphibians, reptiles and birds weighing under 1kg (Stahl 1996), are frequently recovered from palaeontological and archaeological sites. However, they cannot be recovered in the same manner as larger vertebrates and instead require sieving and floatation due to their smaller size.

Small vertebrate remains typically accumulate through different processes than those of larger animals. They are most commonly recovered from riverbed clays, fissure fillings, and cave floors, where they generally accumulate through the natural processes of weathering and predation (van den Hoek Ostende 2003). The formation of an archaeological microfaunal assemblage is seldom attributed to human activity unless in commensal contexts, since they were not typically used as food or resources or hold cultural significance in most prehistoric societies. Notable exceptions exist (e.g. Samper Carro *et al*. 2023). However, it is common to find microvertebrate remains (usually commensal species) in settled areas such as dwellings, refuse pits and wells (Andrews 1990). Commensal species, such as house mice (*Mus musculus*) and black rats (*Rattus rattus*), often thrive in human settlements, leading to their frequent discovery in archaeological sites. These species adapt to human environments, exploiting food resources and nesting opportunities. Studies have shown that commensal species can offer insights into human behaviours and settlement patterns (Musser and Carleton 2005; Cucchi *et al*. 2005; Vigne *et al*. 2009).

Although the Għar il-Fkieren assemblage does not represent a typical occupation site, human agency in its formation is likely minimal to nonexistent. Nevertheless, this aspect will be considered within the taphonomic framework of the study. In palaeontological contexts such as Għar il-Fkieren, where human activity is minimal, microfaunal assemblages offer valuable insights into past environments and ecosystems. Their presence and abundance can reveal crucial information about the climatic conditions, vegetation, and other ecological factors that prevailed at the time of deposition. For instance, Piñero *et al*. (2016)'s taphonomic study of small vertebrates in a Spanish Early Pleistocene site revealed mosaic forest environment with rocky areas, forests, and meadows, suggesting a colder and slightly more humid Mediterranean climate than today. Similar studies of rodent and herpetofauna remains from Lazaret cave in Nice, France (López-García et al. 2021) were also used to reconstruct the climate and environment during MIS 6 (185 – 135 ka), revealing a generally cold and humid climate with a landscape dominated by deciduous temperate forests.

The remains of small fossil animals first began to be documented in the 19th century by French and German scientists of that period, including de Blainville (1834), Pomel (1853), Filhol (1876), and Schlosser (1884). During the early 20th century, Martin A. C. Hinton, a pioneering naturalist, released a groundbreaking monograph that detailed vole remains found in Pliocene and Quaternary deposits (Hinton 1926). Concurrently, Dorothea Bate made notable contributions, identifying several Quaternary microfauna species, including those found in Malta (Bate 1920, 1935). While these monographic studies focused on material from fissure fillings or incidental discoveries of microfauna during excavations, this field of study would experience a significant breakthrough in the 1960s, with the development of more sophisticated sieving techniques that could process larger volumes of sediment samples (Struever 1968).

After the development of more sophisticated sampling techniques, the subsequent steps in the evolution of microfauna studies predominantly involved the publication of taxonomic monographs. While this work provided the framework for future studies, taxonomic identification is no longer the sole focus of microfaunal research (van den Hoek 2003).

The link between use of Quaternary vertebrates for reconstructing past climates and environments has long been established (Simpson 1947; Graham and Lundelius Jr. 1984; Andrews 1990; Blois and Hadly 2009). Micromammals may be particularly useful owing to their narrow habitat range, fast life history, small home ranges, abundance throughout stratigraphic sequences and good preservation (Blois *et al*. 2010). A multitude of publications using fossil mammals as environmental proxies are now regularly produced worldwide, with increasing interest also given to reptiles and amphibians (Pinto Llona and Andrews 1999; Blain *et al*. 2008; Stoetzel *et al*. 2012; Blain *et al*. 2019; Bisbal-Chinesta *et al*. 2020; Villa and Delfino 2019; Lev *et al*. 2020; Smith *et al*. 2021).

Small vertebrates, and in particular rodents, also serve as important biostratigraphic indicators (Lowe and Walker 2015). For instance, Cuenca-Bescós *et al*. (2009) conducted a study revealing that the stratigraphic record of the last 1.5 million years in Spain exhibits seven distinct provinces, defined by shifts in the fossil assemblages of small mammals.

Lastly, an intriguing aspect of the Quaternary vertebrate record is the presence of morphological changes in animal populations, particularly those that have become isolated. Prolonged isolation can lead to alterations in size within species, with small mammals undergoing progressive enlargement (gigantism) or larger mammals experiencing a reduction in size (dwarfism). The Quaternary fossil vertebrate record provides numerous examples of such changes, illustrated by the skeletal remains of 'pygmy' hippopotami, elephants, and giant rodents (Millien 2006). There is an observed pattern where the size of large predators diminishes with a decrease in the size or number of available prey, while small animals tend to grow larger when isolated from their natural predators (Raia and Meiri 2006). This is best exemplified on islands, where notable alterations in body mass, reduced species diversity, and accelerated evolution in animal communities are commonly referred to as 'the island rule' (van der Geer *et al.* 2010). The study of the effect of this phenomenon on small mammals can offer valuable insights into these evolutionary aspects.

2.1.2 Microfauna species and their roles as environmental indicators

Due to their distinct ecological niches and sensitivities, understanding the significance of key microvertebrate species is not only crucial for comprehending environmental changes and their impact on biodiversity (Denys *et al*. 1997; Papayiannis 2012; Kligmann 2015; Denys *et al*. 2017) but also the formation of deposits through taphonomic analysis (Denys 1986; Andrews 1990; Fernández-Jalvo *et al*. 2016; Stoetzel *et al*. 2023). This section aims to highlight different microfauna orders and elucidate their unique roles as environmental indicators.

2.1.2.1 Rodentia

Rodents are one of the most widespread and diverse groups of mammals, being present in almost every terrestrial habitat and on every continent, except for Antarctica (Nowak 1999). As small mammals with distinctive habitat preferences and narrow ecological tolerances, rodents play a critical role in understanding past environmental conditions (Marra 2004). Several key characteristics of rodents include small home ranges, low rates of migration, short life histories, fast rates of evolution, and broad distributions. Fossil rodent material is also generally well-preserved and easily identified taxonomically (Moncunill-Solé *et al*. 2016). Due to their large numbers present within site stratigraphies, they are often also key species in understanding chronological changes in the palaeoenvironment (van den Hoek 2003; Kligmann 2015).

Moreover, the significance of rodents as environmental indicators is heightened by the preservation of stable isotopes preserved in tooth enamel. Investigations have established a correlation between the stable oxygen isotope composition of biogenic phosphate in rodent teeth and the oxygen isotope composition of meteoric waters, which in turn is associated with air temperatures at mid and high latitudes (Fernández-García *et al*. 2020). Oxygen isotopes in the tooth enamel of gerbils (*Gerbillus* and *Meriones*) have also been shown to be very responsive to variations in rainfall and relative humidity (Jeffrey *et al*. 2015).

Among the various other ways in which rodents and soricids (shrews) contribute valuable information about past environments is through their interactions with predators such as raptors, canids, and felids. By studying the degrees of digestion, breakage, and abrasion in a bone assemblage, it is possible to identify the (type of) predator responsible for the accumulation of microfauna remains, important information for understanding site formation processes, food webs and past environments (Andrews 1990; Fernández-Jalvo *et al.* 2016; Rhodes *et al.* 2018).

The remains of rodents and soricids have also been instrumental in establishing the stratigraphic ranges for the Quaternary period, including the appearance and extinction dates of various vertebrate species across Europe, the Mediterranean and more (e.g.; Masini *et al*. 2008; Geraads *et al*. 2013; Colombero *et al*. 2014). In the latter study, Colombero *et al*. (2014) conducted taxonomic and morphometric analysis on rodent assemblages found in the sedimentary layers in Moncucco Torinese, Italy. The co-occurrence of taxa from both Turolian and Ruscinian stages of the Miocene suggested a transitional fauna which indicated taxa from Eastern Europe arrived in Italy before dispersing into Western Europe, challenging the prevailing view that there was a sharp faunal change from the Miocene to the Pliocene in the Italian Peninsula. The study thus provided meaningful context for ancent faunal dispersal routes as well as aiding in the stratigraphic interpretation of the site.

Aside from this, rodents can also be effectively used to demonstrate the activity of humans, such as their economic behaviour and their impact on island ecology. The phenomenon of commensalism can be described as the relationship between a passive host and active commensal, with the commensal benefitting from the host’s activities for nutrition and safety. The host is unharmed by the process (Tchernov 1984). Papayiannis (2012) highlights this relationship in the study of Bronze Age Crete, showing how introduction of new commensal micromammal species by humans competed with established endemics, leading to their extinction. Cucchi (2008) had carried out analyses of the mouse mandible retrieved from the Uluburun shipwreck, providing clues of the boat’s last journey.

Papayiannis (2012) builds upon Cucchi (2008)’s work by suggesting that almost two millennia before the Late Bronze Age shipwreck of the Uluburun, Cretan boats were transporting goods and other animals.

Recent studies have further advanced our knowledge of paleoenvironmental reconstruction using rodent remains. Notable research includes that of Sese and Villa (2008), Demirel *et al*. (2011), Lopez-García *et al*. (2011, 2020), and Erdal *et al*. (2018) who demonstrate the utility of rodent remains in deciphering climatic conditions, habitat changes, and human-animal interactions in various regions and periods.

2.1.2.2 Soricidae

Shrews, primarily terrestrial creatures, actively forage for a varied diet, including insects, worms, seeds, and nuts, often in the leaf litter and dense undergrowth. Some species, however, have adapted to specialised lifestyles, such as arboreal, fossorial, subnivean, and even aquatic foraging behaviours, showcasing their ecological versatility (Barnard 1984). Morphologically distinct from rodents, shrews are characterised by their sharp, spike-like dentition, contrasting the gnawing incisors found in rodents.

Among the smallest of mammals, shrews are notable for the abundance of their dental remains in palaeontological and archaeological records. Carbon isotope analysis of shrew teeth has been employed to gain insights into past environmental conditions. These analyses are promising due to the shrews' limited home ranges and generalist feeding habits, making their diets reflective of local ecological conditions, past temperatures and vegetation in their habitats (Leichliter *et al*. 2016).

Recent studies of shrew population dynamics also revealed that shrews can respond differently than rodents to climatic changes. Their small size and high metabolic rate make them sensitive to snow cover duration, which makes them less abundant during long winter seasons, possibly due to lessened prey abundance (Dokulilová *et al*. 2023).

However, shrews have been relatively understudied in certain aspects. While they share several characteristics with rodents, such as elucidating aspects of the palaeoenvironment and having good preservation in fossil records, there is a gap in research concerning their body mass estimations and life history. This gap indicates potential areas for future research that could provide a deeper understanding of their ecological roles and evolutionary history in various environments (Moncunill-Solé *et al*. 2016).

2.1.2.3 Chiroptera

Bats are excellent indicators for studying hypogean microclimates due to their unique roosting habits and sensitivity to climatic and environmental changes (Festa *et al*. 2023). This sensitivity to climatic change means that their remains can provide data on past temperatures, precipitation patterns, and even the presence of water bodies in the vicinity of their habitats (Amorim *et al*. 2018).

Unlike other micromammals, bats have distinct accumulation processes. Thus, they may provide independent and valuable insights into past paleoenvironments (Salari *et al*. 2015). Their specific roosting behaviours, such as in caves or tree hollows, are particularly informative for reconstructing past forest covers and vegetation types (Altringham 2011).

The presence and diversity of bat remains in archaeological sites are indicative of historical changes in both vegetation and climate. For instance, a high abundance of bat remains can reflect dense forest cover, while a decline may indicate deforestation or climate shifts (Salari *et al*. 2015; Galan *et al*. 2016). Moreover, the accumulation of bat remains in cave sediments can be a marker for human activity. A significant presence of bats might suggest minimal human disturbance, whereas a lack of bat remains could imply frequent human presence or activities that disrupted their natural roosting sites (Salari *et al*. 2015).

Finally, an emerging method to study palaeoclimates is the study of bat guano deposits in caves, which offers insights into past diets and ecological conditions (Tsalickis and Walker 2021).

2.1.2.4 Anura

Adult frogs and toads exhibit a versatile habitat range, residing in both freshwater and terrestrial environments. Some species of Anura have adapted to life underground or in trees. Typically, frogs deposit their eggs in water. While adult frogs mainly consume small invertebrates, there are omnivorous species, and a few even include plant matter in their diet. Frogs play a crucial role in the food web dynamics of various ecosystems, serving as a significant food source for predators. Since their semi-permeable skin renders them susceptible to dehydration, frogs either inhabit moist environments or have developed special adaptations to thrive in dry habitats (Duellman and Trueb 1986).

While amphibians are frequently discovered in archaeological and palaeontological sites, they remain among the less examined fossils in the Quaternary record when compared to small mammals, possibly due to a lack of specialised attention (Bisbal-Chinesta *et al*. 2020). Despite the well-established role of mammals in providing paleoenvironmental information, amphibians offer a distinct advantage: their dependence on temporary or permanent water sources for reproduction and shelter makes them valuable indicators of freshwater availability in the surrounding site (Bailon and Rage 1992; Rage 2002).

Anura present a further unique aspect as they are occasionally found in accumulations formed entirely by a single species (e.g., Bailon 1997; Blain and Villa 2006). Kyselý (2008) has suggested that such accumulations may result from factors such as mortality during hibernation/aestivation, ritual human activity, animal predation, human consumption, or natural traps. Additionally, Cochard (2004) has documented instances of catastrophic mortality attributed to floods.

2.1.2.5 Squamata

Squamata, the largest order of reptiles, includes scaled lizards and snakes. As ectothermic animals with limited dispersal abilities, these reptiles heavily rely on their environment, especially climatic conditions, for thermoregulation and tend to respond negatively in relation to their reproduction patterns when thermal and precipitation alterations occur (Lourenço-de-Moraes *et al*. 2019).

Due to these characteristics, over the past decade, amphibian and reptile assemblages have gained significant prominence as proxies for palaeoclimatic and paleoenvironmental studies (Bailon and Rage 1992; Rage 2002; Blain 2009; Cruz *et al*. 2016; Blain *et al*. 2018, 2019; Villa *et al*. 2018a, 2018b). The utilisation of these assemblages in research has thus contributed to a more nuanced and balanced understanding of past climate conditions.

2.2 LATE PLEISTOCENE CLIMATE AND MICROFAUNA STUDIES IN THE MEDITERRANEAN

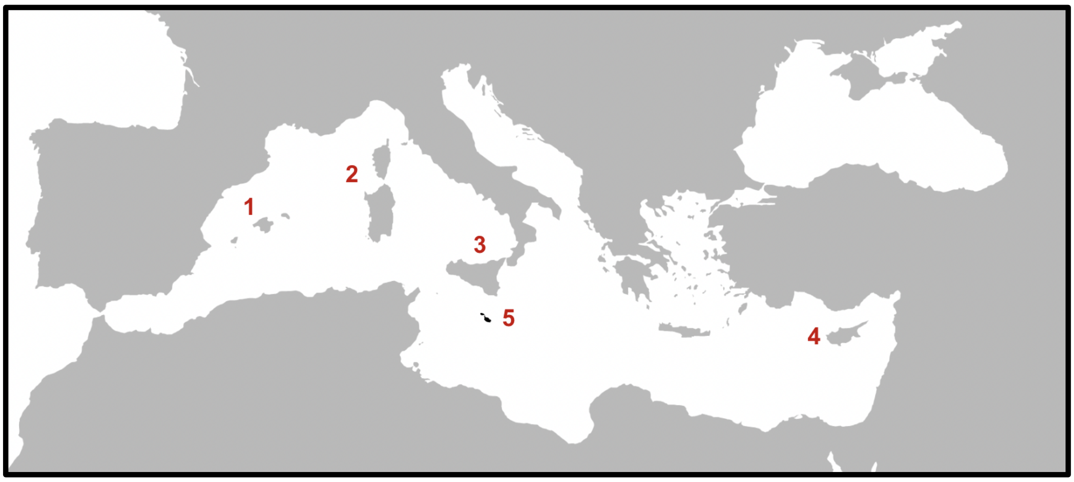


Figure 9: Islands within the Mediterranean basin discussed in this section: (1) the Balearic Islands, (2) Sardinia and Corsica, (3) Sicily, (4) Cyprus, (5) the Maltese Islands.

The Mediterranean, known for its biodiversity and complex ecosystems, is home to one of the largest insular groups worldwide, boasting approximately 5,000 islands - a number that ascends to about 11,879 when considering the myriad of smaller islets (Blondel *et al*. 2010). This region's islands and archipelagos have played host to several unique species of endemic flora and fauna which have long attracted ecologists, biologists, and palaeontologists interested in the processes of biogeography and climate change (Pasta 2008; Minelli 2012). This is due to the fact that Mediterranean islands serve as natural ‘laboratories’ for studying the effects of insularity on fauna - their limited size, geographical isolation, and temperate climate facilitate the study of evolution and ecology over vast periods.

The unique environmental conditions and selective pressures present on the islands which led to adaptations and evolution of distinct endemic species highlights their role in fostering biodiversity (Zunino and Zullini 1995). Factors such as the distance from the mainland, island size, and elevation above sea level have collectively contributed to the high rates of endemism observed during the Pleistocene (ANPA 2001). Fossil records from these islands thus provide a window into these past biological events, despite the inevitable gaps in the data for taxa that have not been preserved (Marra 2005).

Aside from endemic species and evolutionary adaptations, analysis of fossil records can also provide much needed information on the local environment and past climates, which may help to reconstruct broader climatic trends. However, the Mediterranean's varied topography and maritime influences present challenges in correlating local and regional climatic events (Carrión 2002). Its location, bordered by three continents and featuring a complex landscape, gives rise to diverse microclimates. This complexity necessitates detailed and localised multidisciplinary studies to provide a comprehensive understanding of regional climatic patterns and evolutionary trends.

The study of microfauna, though often overlooked in favour of larger vertebrates, has been instrumental in understanding the complex localised palaeoclimatic patterns of the Mediterranean, especially on islands. These studies shed light on the region's climate evolution, particularly the effects of the gradual increase in aridity from the Pliocene to the present (Tzedakis 2007). However, despite there being a wide range of Pleistocene fauna studies, the biogeographic distribution of microfauna during this period has been relatively underexplored (Sommer 2020), limiting our understanding of past ecosystems and interspecies interactions. Recent microfaunal studies in the Mediterranean have begun to fill these gaps, especially concerning the Late Pleistocene and the Pleistocene/Holocene transition (e.g., Masini *et al*. 2008; Bonfiglio *et al*. 2003; Petruso *et al*. 2010; Palombo 2018; Ouahbi *et al*. 2013; Markova *et al*. 2019; Stoetzel *et al*. 2019). This section aims to systematically explore palaeoclimatic and microfaunal research within the Mediterranean region, with emphasis on islands selected for their rate of endemic species. These regions include Italy and Sicily (2.2.1), the Balearic Islands (2.2.2), Cyprus (2.2.3) and Sardinia and Corsica (2.2.4), ending in a summary and discussion (2.2.5).

2.2.1 Italy and Sicily

The Italian Peninsula and Sicily, characterised by their diverse landscapes ranging from alpine mountains in the north to Mediterranean coastlines in the south, were subject to various sea-level fluctuations during the Quaternary due to alternating sedimentation and erosional processes (DiStefano *et al*. 2021), driven by global glacial/interglacial cycles. This resulted in Sicily's intermittent connection with the mainland, making the region a prime candidate for studying sea-level influences on island biogeography, due to the opening and closing of the marine filter barrier influencing the spread of terrestrial mammals (Marra 2013).

2.2.1.1 Palaeoclimate

During the cold stages of the Pleistocene, large ice caps and glaciers dominated the Italian Apennines and the Alps (Carraro and Giardino 2004). The Italian Apennines are home to some of the most accurately dated Pleistocene glacial sequences on the peninsula, with six documented glacial advances linked to Marine Isotope Stages (MIS) 14, 10, 6, 4, 3, and 2 (Giraudi 1998; Giraudi *et al*. 2011). The most recent significant ice advance in the Italian Alps was dated using cosmogenic methods to between 30 – 18 ka (Monegato *et al*. 2007). This timeline aligns with findings from Greece and other parts of the Mediterranean, indicating an early local Last Glacial Maximum (LGM) (Lewin *et al*. 1991; Woodward *et al*. 2008). However, it differs from certain regions of the Iberian Peninsula, where the oldest glacial evidence corresponds to MIS 8 (Lewis *et al*. 2009). Such findings highlight the differences in regional Mediterranean glaciation patterns.

Dates from marine cores, however, align closely with the Greenland records (Grootes *et al*. 1993; Dansgaard *et al*. 1993), indicating significant climatic variability. Allen et al. (1999)'s pollen records from Lago di Monticchio in southern

Italy demonstrated that vegetation in the Mediterranean could change in less than 200 years, highlighting the region's sensitivity to climatic shifts. Over the past 65 ka, the Southern Mediterranean has experienced particularly rapid climate fluctuations, with transitions between forest and wooded steppe environments occurring on average every 142 years. These quick changes suggest a highly dynamic ecosystem that responds swiftly to climatic improvements and deteriorations.

Research into the environmental and climatic changes in Italy during the Pleistocene offers crucial evidence of how these climatic shifts impacted local ecosystems. For instance, by studying Late Pleistocene pollen records from Italy, Comborieau-Nebout *et al*. (2015) found a trend of increasing drought intensity, duration, and recurrence since Marine Isotope Stage 11 (MIS 11). This period witnessed alternations between deciduous forests and steppe/semi-desert environments across northern and southern Italy. During warm interglacials, typical Mediterranean taxa were abundant, whereas during the last glacial period, their presence was severely limited.

Sicily during the LGM (approx. 26 - 20 ka) saw a substantial drop in temperature with estimates suggesting temperatures around 7-8°C lower than today. Sea surface temperatures also dropped, with variations across different regions. Evidence suggests a strengthened atmospheric circulation during this period, with increased wind activity (Incarbonara *et al*. 2010). The vegetation pattern indicated a steppe or semi-steppe environment, with some pockets of forested areas acting as refugia. Sicily experienced low precipitation levels, supported by oxygen isotopic data. Overall, southern Europe saw a substantial decrease in precipitation, with temperate grasslands dominating the vegetation (Incarbonara *et al*. 2010). Lower sea levels which resulted in connecting Sicily to the mainland and Malta also facilitated the dispersal of continental fauna, leading to turnover in faunal assemblages. The endemic large mammals such as elephants, fallow deer and large predators subsequently died out, being replaced by species such as

Cervus elaphus (red deer), *Sus scrofa* (boar) and *Equus* (equids) (Masini et al. 2008).

Faunal assemblages and sedimentary records have also provided insights into the climatic conditions of Late Pleistocene Italy and Sicily, highlighting a diverse range of environments influenced by both glacial and interglacial climates (Bonfiglio *et al*. 2000; Marra 2015).

2.2.1.2 Microfauna

Up until 1985, knowledge of the Southern Italian/Sicilian palaeoenvironment was quite limited (Bonfiglio *et al*. 2003). However, the ensuing synthesis of studies on Quaternary aminostratigraphy, stratigraphy, and taphonomy provided a more comprehensive picture of the Pleistocene vertebrate record and distribution in Sicily, allowing for correlation with marine deposits and therefore major palaeogeographic events (Agnesi *et al*. 1997; Bonfiglio *et al*. 2000).

Bonfiglio *et al*. (2000) noted that prior to 2000 research in the region remained focused on the taxonomic-evolutionary aspects of the microfauna. Since, there has been a considerable increase in utilising microfauna as proxies for the environment (e.g., Spena *et al*. 2021), biochronological markers (e.g., Bonfiglio *et al*. 2013; Kotsakis *et al*. 2020), indicators of human activity (e.g., Salari 2010) and indications of dispersal and exchange (e.g., Masini *et al*. 2008).

Marra (2013) notes that in addition to dispersal of taxa and biochronology, the interactions between species and faunal complexes should also be considered. There are six established faunal complexes for Sicily, five Pleistocene followed by one Holocene complex (Bonfiglio *et al*. 2001). Marra (2013)'s table illustrating the faunal complexes compared with marine isotopes, dispersal routes and bioevents gives an overview of the major biological and climatic events occurring during the Pleistocene (Figure 10) which facilitates analysis of the relationships between the Pleistocene faunal complexes.

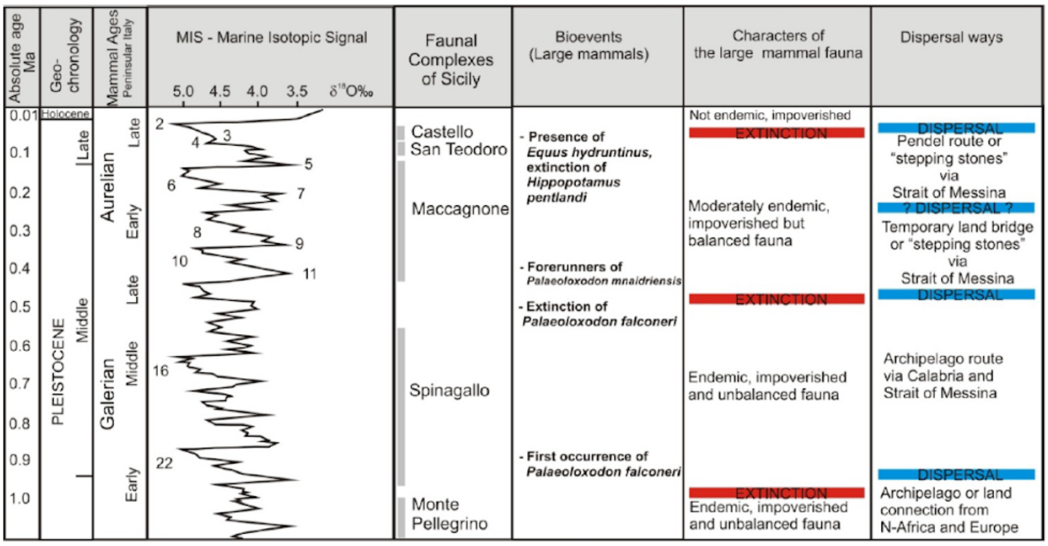
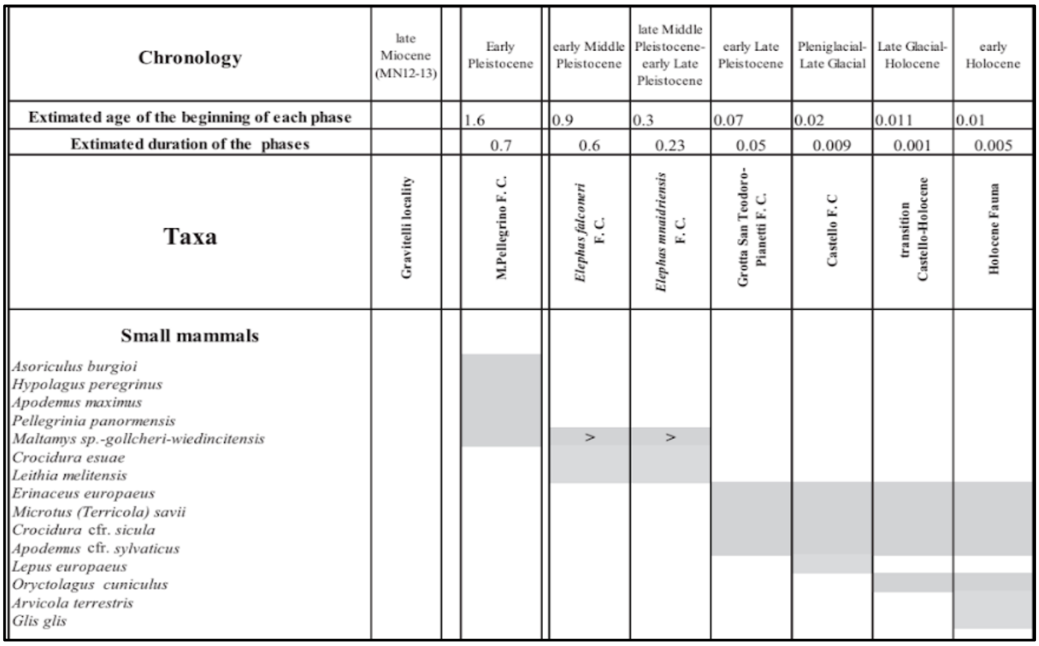


Figure 10: Quaternary mammals of Sicily: bioevents, endemic characters, times and dispersal ways. From Marra (2013: 134).

As illustrated in Figure 10, Sicily was also affected by the Late Quaternary extinctions, despite its relative insularity and land size. Masini *et al*. (2008) studied this phenomenon in three insular regions: the Sardinia-Maritime Tuscany, the Gargano paleo-archipelago, and the Sicilian insular complex during the Late Miocene and Quaternary. The observed biodiversity changes throughout the different periods led to inferences of faunal origination and extinction patterns. Masini *et al*. (2008) outline the geographical histories of each of the three regions, discussing the possible mechanisms which drove the faunal species to arrive, disperse, and eventually go extinct in each of them. An important factor to consider when discussing these dispersal and extinction patterns is the body size of mammals. Body sizes influence dispersal ability and therefore small mammals have different likelihoods of crossing filters and barriers, and different degrees of resistance to environmental disturbances. By comparing Sardinia and Sicily's faunal complexes through time and creating a histogram illustrating large vs small mammal survivorship, Masini and colleagues (2008) showed that the dispersal and extinction of large and small mammals do not necessarily coincide, and indeed small mammals tend to survive longer than their larger counterparts.

Possible explanations for micromammal survivorship include, (i) the equilibrium that micromammals establish with predators such as raptors and reptiles, (ii) the smaller body size requiring less food, and (iii) the prolific reproduction of small mammal species (Masini *et al*. 2008). Finally, Masini *et al*. (2008) consider the possible influence of Pleistocene climatic changes on the regions' biodiversity. By comparing and reconstructing the faunal histories of the three regions with known climatic events (Figure 11), the study shows that the intense Pleistocene climate change had a very clear influence on island communities connected to their mainland counterparts. However, without these exchanges with the continent, islands remain quite stable refugia which are not drastically affected by environmental changes (Masini *et al.* 2008).

The Italy-Sicily-Malta geographical region has also been shown to be ideal for the study of the dynamics of biological exchanges, which can help elucidate the relationships and dynamics between insular and mainland fauna. In one such study by Petruso *et al*. (2011), morphometric and morphological variability of the Savi's pine vole (*Microtus Terricola savii*) was studied in order to understand the phylogenetic history of the vole during the mid-Pleistocene to Early Holocene, and to reconstruct the relationships between the insular and continental voles. Using measurements and morphological indexes, analysis was carried out by using bivariate diagrams. This allowed for the identification of two morphotypes of vole, and morphological separations between the Sicilian and peninsular *Microtus (Terricola*) (Petruso *et al*. 2011). Petruso *et al*. (2011) attribute the small size of the Sicilian *savii* vole to human impact negating the enlarging effects of geographic isolation. It was also noted that the morphology of the Sicilian *savii* vole was very close to that of the Southern Italian populations from MIS 3 (Marine Isotope Stage 3), c. 60 - 27 ka to the early Holocene. However, size variations between the vole populations of Sicily were also observed and attributed to varying degrees of isolation. A proposed explanation for this is that the *savii* group dispersed from the mainland and developed endemic features (Petruso *et al*. 2011). Two further dispersal events are also identified. The Sicilian voles from Isolidda 3, dated to MIS 6 (195 - 123 ka), revealed to differ from the post-MIS 4 (71-59 ka) voles and appear closer to the Tyrrhenian side of the region, suggesting that this population descends from an earlier dispersal, enabled by the lowered sea levels of MIS 6. Finally, the isolated features of the *M. melitensis* sample examined from Għar Dalam (Malta) indicated that it did not derive from the Late Pleistocene Sicilian Savi's vole but from a potentially much older dispersal event (Petruso *et al*. 2011). The results support the conclusion made by Masini *et al*. (2008) that climate change does not have a drastic direct effect on size and morphology of small mammals; rather, the connection to the mainland is the most major cause of changes in island microfaunal biodiversity.



Chronology	late Miocene (MN12-13)	Early Pleistocene	early Middle Pleistocene	late Middle Pleistocene-early Late Pleistocene	early Late Pleistocene	Pleniglacial-Late Glacial	Late Glacial-Holocene	early Holocene
Extimated age of the beginning of each phase		1.6	0.9	0.3	0.07	0.02	0.011	0.01
Extimated duration of the phases		0.7	0.6	0.23	0.05	0.009	0.001	0.005
Taxa	**Gravitelli locality**	**M.Pellegrino F. C.**	***Elephas falconeri* F. C.**	***Elephas mnaidriensis* F. C.**	**Grotta San Teodoro-Pianetti F. C.**	**Castello F. C**	**transition Castello-Holocene**	**Holocene Fauna**
Small mammals								
Asoriculus burgioi		▨						
Hypolagus peregrinus		▨						
Apodemus maximus		▨						
Pellegrinia panormensis		▨						
Maltamys sp.-gollcheri-wiedincitensis		▨	▨ >	▨ >				
Crocidura esuae			▨	▨				
Leithia melitensis			▨	▨				
Erinaceus europaeus					▨	▨	▨	▨
Microtus (Terricola) savii					▨	▨	▨	▨
Crocidura cfr. *sicula*					▨	▨	▨	▨
Apodemus cfr. *sylvaticus*					▨	▨	▨	▨
Lepus europaeus						▨		
Oryctolagus cuniculus							▨	▨
Arvicola terrestris								▨
Glis glis								▨

Figure 11: Range chart and chronology for the Pleistocene–Holocene of Sicily. From Masini et al. (2008: 69).

Bonfiglio *et al*. (2000) describe the Sicilian faunal complexes and dispersal routes. The Late Glacial Stage (c. 115 - 11.7 ka) is characterised by a substantial decrease in diversity, especially of large mammals. Bonfiglio *et al*. (2000) attribute this to climatic changes rather than human influence or faunal disequilibrium, since human occupation of Sicily is not confirmed before the terminal stages of the Pleistocene. This was a favourable time for faunal exchange between Calabria and Sicily-Malta due to the eustatic drop in sea levels (Bonfiglio *et al*. 2000). The prevalent appearance of the *savii* vole in the fossil assemblages for this period, among others, suggest a rising aridification in the Mediterranean, a phenomenon also observed contemporaneously in North Africa (Petit-Maire 1993). By the Early

Holocene, gradual reforestation and increase in humidity is suggested to take place by the emergence of *Arvicola* cf. *amphibius* (European water vole) among larger ungulates like horses (Bonfiglio *et al*. 2000).

One study conducted recently by Kotsakis *et al*. (2020) demonstrates this by documenting and analysing the microfauna from a fossiliferous cavity in La Grave, southern Italy. Comparing the known specimens in the La Grave assemblage to those in other sites allowed researchers to date the remains to extend from the Late Pleistocene, between MIS5e (124-119 ka) and MIS3 (60-25 ka) (Kotsakis *et al*. 2020: 1). It was concluded that the area around the site was coastal plain with marshes, with rocky coastal areas and forested areas nearby, supporting earlier findings based on microfauna from the same site Petronio *et al*. (2007).

A large number of prehistoric cave sites in Italy and Sicily have preserved an abundance of bat fossils in the Pleistocene and Holocene layers. The utility of bat remains is exemplified in Salari's (2010) analysis of the bat remains in Arene Candide cave (Northern Italy), an important multi-period site in Italian prehistory with remains spanning from the Pleistocene to the Byzantine periods. The methodology included osteological comparisons with other collections and morphological and morphometrical observation using a stereoscopic microscope. Dentition, crania, and humeri were chosen elements as they were more numerous and accurately identifiable to species level (Salari 2010). The quantification of these metrics was key to extrapolate bat populations, which allows for a considerably detailed reconstruction of the climate and environment around the cave. In addition, Salari (2010) notes that the richness of bat layers and lack of juvenile bats in the assemblage indicate that humans periodically abandoned the cave or made seasonal use of it during the summers.

Salari *et al*. (2019) also illustrate how bats can shed light on human activity. At the Grotta dei Pipistrelli in Sicily, another key palaeontological site, it is concluded that the climate during the Pleistocene remained relatively warm compared to the rest of Europe, and with the arrival of the Holocene there was a gradual increase in open spaces which may be connected to human activity and deforestation (Salari *et al*. 2019). These finds were further corroborated by a later study of the remaining microfaunal assemblage at the same site, using the same method Spena *et al.* (2021).

2.2.2 Balearic Islands

The Balearic Islands, situated in the Western Mediterranean Sea, offer an excellent opportunity to investigate island biogeography processes due to their status as some of the most isolated in the region when compared to their continental counterparts. Their history of fluctuating sea levels in the Quaternary also facilitates investigation into the influence of marine filtering barriers and insularity on the biodiversity of islands (Ginés *et al*. 2012).

The islands are also a key site to understand climatic interactions between North Africa and Northern Europe/the North Atlantic, additionally serving as a crucial climatic boundary between the cooler Gulf of Lions and warmer Algerian Basin. This location between the two different water and land masses makes this area very sensitive to changes in atmospheric and oceanic circulations. This results in the development of dunes during the influence of northern winds, while warmer stages brought by southern winds induce soil development (Bardají *et al*. 2022).

2.2.2.1 Palaeoclimate

Mallorca's Pleistocene sedimentary deposits have provided an impressive record of sea level, atmospheric circulation patterns and glacial/interglacial climate which has benefitted from ample research over the past decades, starting from the second half of the twentieth century (Butzer and Cuerda 1962). This has cemented Mallorca as one of the classic regions for Pleistocene marine studies in the Western Mediterranean (Bardají *et al*. 2009). The Balearic Islands' very stable and minor tectonic activity also makes this Pleistocene record much easier to interpret since this does not interfere with sea level changes (Fornós *et al*. 2009).

At the turn of the millennium, data collected over the years began to be synthesised in works such as Gómez-Pujol and Pons (2007), who collected various

Pleistocene studies of eolianites, palaeosols and alluvial fans, along with various radiometric, luminescence and magnetostratigraphic dates. The entire sedimentary record (spanning from MIS 11 to 1) revealed aeolian activity associated with arid/windy climatic episodes related to sea level drops during stadials, while the terrestrial deposits correspond to less wind influence and more humidity during interstadials. Dating and characterisation of Quaternary mollusca also provided a more thorough chronology of the Mallorcan Quaternary. Phreatic speleothems have also been used as a method to reconstruct sea-level curves, providing insight into previously sparsely known low sea stands in the Western Mediterranean (Gómez-Pujol and Pons 2007).

While the island of Mallorca has been the subject of numerous studies on the Upper Pleistocene deposits (Ginés *et al*. 2021), these have been very limited for the smaller Formentera Island. This has recently begun to be remedied by Bardají *et al*. (2022) who conducted a detailed study of its southeastern coast during the last glacial period. The research provided insights into the environmental changes between MIS 5e and MIS 2, indicating a range of climatic fluctuations. During MIS 2, a brief period of humid/warm climate was recorded which contrasts with records from the rest of the western Mediterranean during the Last Glacial Maximum (LGM) (Bardají *et al*. 2022), highlighting the complexity and variability of Mediterranean island palaeoclimatology and the need for detailed and localised studies on individual islands.

2.2.2.2 Microfauna

The Quaternary fauna of Mallorca can be traced back to the Messinian Salinity Crisis, a major Miocene desiccation event which occurred approximately 5.6 to 5.32 million years ago (Ma) (Clauzon *et al*. 1996; Krijgsman *et al*. 1999). This major desiccation led to lowered sea levels and the formation of land bridges connecting the Balearic Islands with the mainland. With the subsequent reflooding of the Mediterranean basin, Mallorca and its neighbouring islands were once again isolated, leaving microfauna free from carnivore predation. The stranded fauna underwent evolutionary processes for an additional five million years in completely insular conditions (Ginés *et al*. 2012), resulting in the islands evolving entirely separate faunal complexes and each having unique ecologies by the time of human arrival (Bover *et al*. 2008). Five million years of evolution in this insular and predator-free environment led to a number of morphological adaptations in many of the endemic species, with smaller mammals like the soricid shrew and glirid rodents exhibiting a significantly increased size, and larger herbivores decreasing in size (Bover *et al.* 2010).

During the Pliocene, the fauna of Mallorca included *Myotragus* (goat-antelope), *Hypnomys* (Balearic giant dormouse) and *Nesiotites* (large red-toothed shrew), whereas Menorca was home to a distinctly different set of species, such as *Nuralagus rex* (giant rabbit) and *Titanochelon gymnesica* (Balearic giant tortoise) (Bover *et al*. 2007). The Pityusic islands were characterised by the presence of indeterminate caprids, bovids, glirids, soricids, rabbits, birds and reptiles (*Antilopini*, *Bovidae*, *Gerbillinae*, *Eliomys*, *Leporidae*, *Soricidae*, *Testudinae*, *Podarcis* and *Puffinus)* until a significant faunal change took place in the Late Pliocene/Early Pleistocene (Moyà-Solà *et al*. 1984). This shift saw the fauna from Mallorca spread to Menorca, replacing the indigenous giant rabbit. Concurrently, in the Pityusics, all mammalian species and the tortoise became extinct prior to the Late Pleistocene, leaving only birds and the lizard as the surviving vertebrates (Bover *et al*. 2007).

The cause of this widespread extinction remains unknown (Bover *et al*. 2007). However, successive research on the Balearic microfauna has shed some light on the potential origin and extinction causes of these endemic species. Bover and Alcover (2008) presented the first radiocarbon dating of bone collagen from the extinct giant dormouse (*Eliomys morpheus*) and Balearic shrew (*Asoriculus hidalgoi*), providing evidence that these endemics were absent in the earliest Mallorcan sites. In combination with cultural associations, the direct dates established a chronology for faunal change on Mallorca, facilitating a comparison with climate records and dates of human arrival. Apart from proposing a tentative schedule of ecological changes in the Mallorcan Islands based on observed shifts in keystone species, the study was also able to hypothesise the likely causes for the endemic extinctions. Interestingly, although transformation of insular ecosystems is frequently attributed to human activity, in this case disease emerged as the most likely explanation (Bover and Alcover 2008), which highlights the unique circumstances and factors involved in the formation of island ecologies.

Recent research demonstrates the utility of molecular phylogenetics in uncovering the genetic lineage and origins of ancient fauna. In a study by Bover *et al*. (2018), the application of this approach revealed that *Nesiotites hidalgo*, a species of shrew found in the Balearic Islands from the Late Pleistocene to Early Holocene, diverged from its closest extant relative around 6.44 Ma. This timing supports the hypothesis that nectogaline shrews colonised the Balearic Islands during the Messinian Salinity Crisis. Moreover, the study highlights the feasibility of extracting preserved genetic data from extinct small mammals, even those from environments typically challenging for DNA preservation. This not only sheds light on the species' origins but also opens avenues for exploring genetic information from ancient, marginal environments (Bover *et al*. 2018).

Recent ancient mitochondrial DNA analyses are also playing a pivotal role in elucidating the origins of island fauna and resolving ambiguities regarding the relationships between extinct and modern species. In this vein, Bover *et al*. (2020) explored the genetic lineage of the Balearic giant dormouse (*Hypnomys morpheus*), a species that existed on the Balearic Islands during the Late Pleistocene. The study's molecular dating indicates that *Hypnomys* diverged from its sister genus *Eliomys* around 13.67 million years ago, suggesting that the Balearic giant dormouse originated from a continental glirid species during the Middle-Late Miocene period (Bover *et al*. 2020).

2.2.3 Cyprus

Cyprus is the third largest island in the Mediterranean and one of its few oceanic islands. It has never been connected to the mainland and has experienced prolonged isolation since the Miocene (Davis 2003). Cyprus' Pleistocene fossil mammalian fauna is unique for being extremely impoverished, consisting almost exsluviely of *Palaeoloxodon cypriotes* (Cypriot dwarf elephant) and *Hippopotamus minor* (pygmy hippo) (Hadjisterkotis *et al*. 2000). This faunal stasis remained unchanged until the onset of the Holocene, which heralded the end of the Pleistocene fauna (van der Geer *et al*. 2010). Cyprus thus offers an invaluable case study for examining the effects of extended isolation on species evolution in oceanic islands throughout the Quaternary period.

2.2.3.1 Palaeoclimate

Extrapolating from Eastern Mediterranean and Levantine sequences, tentative extrapolations regarding the Pleistocene climate of Cyprus suggest cold, dry conditions with freshwater flow and low sea levels during glacial episodes, succeeded by hot temperatures, humidity, freshwater flow and rainfall along with sea level rise during interglacial episodes (Moutsiou 2021).

Despite these insights gleaned from neighbouring regions, there remains a significant research gap in Cyprus' local Pleistocene climate record (Moutsiou 2021). Given the island's unique geographical and ecological characteristics, further investigations tailored to Cyprus are warranted. Such focused studies could provide a more nuanced understanding of the Pleistocene climate dynamics on the island, potentially uncovering localised climatic variations and their impact on the island's flora, fauna, and landscape evolution.

2.2.3.2 Microfauna

The island of Cyprus is often referred to by palaeontologists as a 'true island', due to the characteristics of its endemic fauna. Fossil remains found at numerous Quaternary open-air and cave sites suggest that the endemic fauna of Cyprus included dwarfed large mammals such as hippos and at least one species of elephant (van der Geer *et al*. 2010, Moutsiou 2020). Despite the abundance of mammalian fossils, species diversity remains consistently low and impoverished throughout its history, showcasing an exceptional example of stasis in an endemic island fauna. This enduring stasis and limited faunal variety have been attributed to the island’s oceanic origins and considerable distance from the mainland (van der Geer *et al*. 2010).

According to Hadjisterk *et al*. (2000), a genet (*Genetta plesictoides*), murid rodents (*Mus* sp., *Mus cypriacus*), and a soricid (*Crocidura suaveolens*) were discovered in association with cultural remains and the pygmy Hippopotamus fossils at the Akrotiri-Aetokremnos site, suggesting that these smaller mammals were introduced by humans and the decline of the pygmy elephants and hippos could be attributed to human hunting activity (Simmons 1988). However, uncertainties persist regarding the stratigraphic positioning of certain species such as *G. plesictoides*, *C. suaveolens*, and *Mus* sp., as noted by Reese (1995). Among the fauna, only two survivors from the Pleistocene epoch have persisted into the present day (*Crocidura cypria* and *M. cypriacus*). The causes of this extinction remain the focal point of ongoing research and debate.

The first human settlements on Cyprus and their potential interactions with endemic fauna have been a significant focus of research. Vigne *et al*. (2000) and Davis (2003) proposed that the extinction of the island's fauna likely occurred either just before or shortly after human arrival. Evidence now suggests that humans began settling Cyprus during the Epi-Palaeolithic (c. 14 ka) (Bradshaw *et al*. 2014). Radiocarbon dating of pygmy hippopotamus bones shows that the accumulation was natural and occurred sometime during the Younger Dryas. Bone modifications indicate anthropogenic burning that occurred long after their death, likely for use as fuel (Zazzo et al. 2015).

However, there have not been many studies of microfauna or their role as environmental indicators. In addition, the role of species like the Levantine viper (*Macrovipera lebetina)*, in the island's ecology warrants further investigation. Integrating such studies could yet offer valuable insights into the dynamics of Cyprus's ancient ecosystems and shed light on the possible interactions between humans and endemic fauna.

2.2.4 Sardinia and Corsica

Sardinia and Corsica present unique case studies for understanding insular faunal evolution due to their dynamic geological and climatic histories. During the Eocene, Sardinia and Corsica were part of a microplate connected to southern France, hosting continental faunas reflective of their connection to the European mainland (van der Geer *et al*. 2010). As the Miocene commenced, the microplate's isolation led to the development of unique insular faunas, with the Late Miocene witnessing a land bridge to Tuscany that facilitated faunal exchanges (van der Geer *et al*. 2010). This land bridge was lost until the archipelago was once again reconnected to Europe and North Africa during the Messinian Salinity Crisis (5.96-5.33 Ma). The islands have since been intermittently connected as a result of sea level changes during Pleistocene glacial periods, with the last bridge occurring during the LGM (Rodríguez *et al*. 2017).

2.2.4.1 Palaeoclimate

Recent research in Sardinia has made use of advanced dating methods to investigate its geological history over the past 200 ka (Coltorti *et al*. 2010; Thiel *et al*. 2010; Orrù *et al*. 2011; Tuccimei *et al*. 2012).

In 2014, researchers identified eight distinct periods by analysing changes in soil characteristics within coastal sedimentary layers (Pascucci *et al*. 2014). During warmer intervals, such as MIS 5e and 5c, sea levels were notably higher, resulting in the formation of gravel beaches and intertidal bioherms. Conversely, cooler periods, including MIS 5b and 4, witnessed different beach formations and an increase in rainfall-induced debris flows. Throughout MIS 3, characterised by fluctuating climate conditions, sedimentation patterns reflected alternating phases of erosion and deposition, likely influenced by shifts in precipitation and sea level dynamics.

2.2.4.2 Microfauna

Palombo *et al*. (2004) identify three main faunal complexes in the Plio-Pleistocene of Sardinia. The earliest, dating to the Pliocene-Early Pleistocene, was marked by low endemism and included diverse taxa such as artiodactyls, micromammals, and the top predator *Chasmaporthetes lunensis*. This period's faunal turnover is attributed to climatic changes leading to sea-level fluctuations (Sondaar and Van der Geer 2003).

The subsequent faunal complex, spanning the Early Pleistocene to the Middle Pleistocene, witnessed the arrival of new species, such as arvicolids and cervids. The changes in the biodiversity of this era, including the extinction of previous faunas, have been suggested to be linked to human migrations during the early Middle Pleistocene (Sondaar *et al*. 1986). However, Palombo *et al*. (2017)'s palaeogeographical reconstructions and analysis of the chronology of Late Pleistocene faunal assemblages do not support this hypothesis, concluding that any human presence in Sardinia preceding the Holocene was at best sporadic. Phoca-Cosmetatou and Rabett (2014) also argue against this proposal, based on the contentious nature of the Palaeolithic archaeology and the unfavourable temperatures and insularity likely to predominate during the Late Pleistocene.

During most of the Middle and Late Pleistocene, no new dispersals appear to have occurred and Sardinia and Corsica were mainly composed of endemic species, including the mammoth *Mammuthus lamarmorai* (van der Geer *et al*. 2010). This indicates that the island was isolated during this period, leading to the phyletic evolution of the endemic taxa. These endemic species last appear in the Holocene (Masini *et al*. 2008).

Corsica's Pleistocene fauna shares notable similarities with Sardinia, including the presence of endemic species such as *Cervus elaphus rossii* and *Cyrnolutra castiglionis.* The debate over the presence of *Cuoninae* highlights the ongoing discussions about these islands' faunal connections and separations (Pereira and Salotti 2002). The distinct evolutionary trajectories of Sardinia and Corsica may stem from their separation or the unique environmental conditions each island experienced (Marra 2005).

Current research seems to focus on tracing genetic lineages to past geological events, such as the Miocene split, as is the case with the study on the evolutionary history of *Podarcis tiliguerta* (Rodríguez *et al*. 2017). Nevertheless, micromammals remain underutilised in paleoenvironmental reconstruction efforts within the Sardinia-Corsica archipelago. Historically, most research efforts have been directed towards understanding the combined geological and human influences on the islands' biogeography.

2.2.5 Summary and discussion

The ongoing research into the Pleistocene Mediterranean Islands reveals how the unique conditions of insularity, such as geographical isolation, limited size, and distinct ecosystems, have driven the evolution and adaptation of endemic species and the formation of localised climatic trends against the backdrop of the broader climate events spanning the Late Pleistocene.

Research in Italy and Sicily in particular, underscores the critical role of microfauna in reconstructing past environmental conditions and climate changes (e.g., Kotsakis et al. 2020; Spena *et al*. 2021). This approach has also been utilised in the Balearic Islands (e.g., Bover and Alcover 2008), and highlights how microfauna can indicate broader climatic trends, such as increasing aridity from the Pliocene to the present and the impact of sea-level fluctuations on island biogeography (Marra 2013). These findings offer a window into the complex interplay between climate change, sea level rise, faunal adaptation, and extinction events.

While the focus is predominantly on natural processes, there is also acknowledgment of the potential impact of early human activity on microfaunal distributions and diversity. This aspect underscores the potential for paleoenvironmental data to provide an understanding of past ecosystems and human activity (Lebreton *et al.* 2021), however it also highlights the need for further strands of archaeological evidence to conclusively identify traces of hominins in Mediterranean islands prior the Holocene. The use of palaeontological markers as indications of Palaeolithic human island occupation is most focused in

Cyprus (Simmons 1988; Davis 2003; Vigne *et al*. 2000) and in Sardinia (Sondaar *et al*. 1986, Sondaar 2000).

Comparative analyses across different Mediterranean regions also provide a panoramic view of the diverse ecological settings and faunal assemblages, highlighting regional variations in climate and environmental conditions during the Late Pleistocene (Masini *et al*. 2008).

These islands, with their unique geological and ecological contexts, have provided valuable insights into the past climatic conditions of the Mediterranean, faunal evolution, and the impacts of human activity. While Sicily leads in employing microfauna as environmental proxies, further research is needed to understand the distinctive conditions of each island and the geological and anthropogenic influences on microfaunal evolution and dispersal. Investigating each island will contribute to a more nuanced understanding of these aspects and facilitate a comprehensive grasp of climate change in the Pleistocene Mediterranean.

3 THE LATE PLEISTOCENE IN MALTA

The Late Pleistocene in Malta (129 – 11.7 ka) is characterised by significant biogeographical processes influencing faunal turnover and environmental conditions. Such processes include global glacial-interglacial cycles leading to climatic and sea level fluctuations, which alternately connected or isolated the Maltese Islands with Sicily, and later mainland Italy (c. 25 – 17 ka) (Antonioli *et al*. 2014). These processes impacted species evolution and composition on the islands in various ways (Thake 1985), however, current understanding of these local dynamics remains rudimentary.

Among the various factors influencing island biogeography and faunal turnover, human activities have also played a major role in animal dispersals in the Mediterranean during the Late Pleistocene (Zeder 2008). However, there is currently no local documented evidence of human occupation of Malta during this period. French *et al*. (2020: 68) place the current earliest arrival of humans on Malta at around 7 - 7.5 ka, based on evidence of agriculture including wheat, barley and ruderal flora which indicate livestock grazing activity. Alongside understanding the impacts of global climate dynamics and the isolation of island populations, interpreting the faunal record can also provide insights and set a baseline for understanding later human impacts on the islands.

This chapter aims to explore what is currently known about the Late Pleistocene in Malta, encompassing its climatological, archaeological, and palaeontological data. The chapter is structured to first examine the historical palaeontology and archaeology of the Late Pleistocene (Error! Reference source not found.). This will be followed by an exploration of gaps in current research (3.2).

3.1 QUATERNARY RESEARCH IN MALTA

This section will examine the geological and environmental data for the Late

Pleistocene in Malta (3.1.1), providing the context for a review of Għar Dalam: the primary fossiliferous site critical to our current understanding of Quaternary Malta (3.1.2). Additional sites of significance will be reviewed in 3.1.3, followed by a concise overview of Quaternary research history in 3.1.4.

3.1.1 Geological and environmental background

The stratigraphy of the Maltese Islands is composed of five marine sedimentary rocks - limestone and clays formed during uplifts in the interval between the Oligocene to Miocene epochs. Fossil fauna can be observed from the Tertiary, consisting mainly of mollusca and some marine vertebrate species. During times of marine regression, periodic influxes of vertebrate fauna can be observed based on remains recovered from the Pleistocene fissure infills and deposits found over the islands (Galea Bonavia 1999).

The first known major marine regression event is dubbed the Messinian Salinity Crisis (MSC), which occurred during the Miocene epoch. This geological event profoundly impacted Europe and the Mediterranean basin, leading to the emergence of narrow land bridges in the Sicily-Malta region. Fossil evidence suggests that this facilitated the migration of paleoendemic species to the Maltese Islands, originating from both southern Europe and North Africa (Hunt and Schembri 1999). At least two endemic species are shown to have phylogenetic links to North Africa: *Crocidura sicula* (Maddalena *et al*. 2004; Vogel *et al*. 2004; Dubey *et al*. 2007) and *Podarcis filfolensis* (Psonis *et al*. 2017)

Pedley (2011)'s study of Plio-Quaternary marine deposits confirms that the Maltese region was isolated from both Sicily and North Africa for at least 4 Ma after the Messinian crisis. Following this prolonged period of isolation in the Pliocene, continental links were then re-established with Sicily at around 780 ka, during the Middle Pleistocene (Pedley 2011). While Pedley (2011) and Hunt and Schembri (1999) hypothesise that the arrival of *Palaeoloxodon falconeri* is linked to the marine lowstand recorded at MIS 16 (c. 676 ka) (Figure 12), there has not been any secure dating evidence published to confirm this.

Hunt (1999) further proposes possible further influxes during the marine regressions of MIS 12 (490 ka) and/or MIS 8 (c. 300 ka), resulting in the first Maltese fossil faunal complex (*'Maltamys/Gliridae'*) dated to before 165 ka (Table 5). The Maltese assemblage had a more reduced number of species compared to the Sicilian complex, leading Hunt (1999: 33) to suggest reduced land carrying capacity compared to Sicily.

Meanwhile, carnivores such as *Ursus arctos* and endemic herbivores such as *P. mnaidriensis* and *H. pentlandi* disappear from the Għar Dalam fossil record by c. 116 ka. This may be linked to MIS 5a, when sea levels again rose the highest since MIS 9e, reducing land carrying capacity. Further extreme lowstands are linked to MIS 6, with a Penultimate Glacial Maximum (PGM) occurring around 140 ka, and MIS 2 during the Late Glacial Maximum (LGM).

The isolated periods between glaciation events played a crucial role in shaping Malta's distinct biota and facilitating the evolution of endemic species. However, further research is needed to fully understand the link between sea level rise, climate change, and the biogeography of the Malta-Sicily region during the Late Pleistocene. The research gaps regarding the Pleistocene climate and environment will be further explored in section 3.2.2.

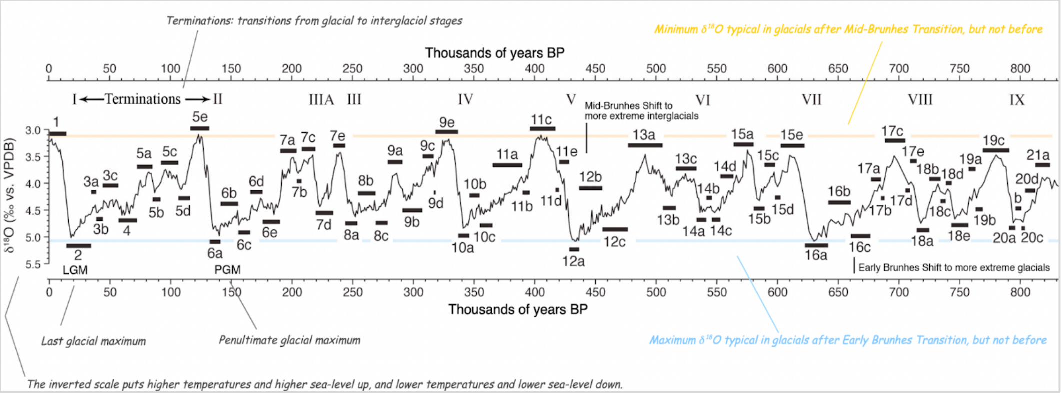


Figure 12: Marine isotope stages and substages. From Railsback et al. (2015).

3.1.2 Għar Dalam (GħD) cave and fossil record

Għar Dalam cave (Għar Dalam) currently stands as the most renowned Pleistocene site in the Maltese Islands, distinguished by its vast abundance of fossil fauna spanning from the Middle Pleistocene to the Holocene. Notably, some of its fossil specimens exhibit size variations that align with the 'Island Rule', showcasing both giant and pygmy forms of various species. Among these examples are the giant dormouse *Leithia melitensis,* and pygmy hippopotamus *Hippopotamus melitensis*, which have captured both academic and public imaginations.

First explored by Arturo Issel in 1865, Għar Dalam is a phreatic tube or solution tunnel that formed beneath a stream bed previously coursing through Wied Dalam (Hunt and Schembri 1999). While Zammit Maempel (1989a) has suggested that the deposits were funnelled into the cave through a collapsed tunnel ceiling, forming a doline, the precise geomorphic processes responsible for the cave's stratigraphy remain unclear (Hunt and Schembri 1999). Given that Għar Dalam stands as the sole site known to contain such an uninterrupted sequence of fossiliferous deposits, its significance in the study of Maltese palaeontology is immense.

Since its exploration in 1865, Għar Dalam cave has been the focus of numerous excavations conducted by various teams, beginning with J. H. Cooke in 1892 and concluding with G. Zammit-Maempel in 1996 (Savona Ventura and Mifsud 1998). Recent dating (Standish *et al*. in prep) and palaeontological work has also been undertaken by the University of Bristol and Natural History Museum (London), aiming to understand the biochronology of the cave and the evolution and origins of the elephant (Herridge 2010) and cervid (D'Souza 2019) fossil fauna. In 2023, scholars from the Max Planck Institute of Geoanthropology in Germany in collaboration with the National Museum of National History in Malta also conducted surface area cleaning of bones in the central cave area in preparation for works on the scaffolding holding up the central stalagmite, sending various stratigraphically in-context specimens for collagen dating.

While the earlier excavations have provided invaluable insights into the cave's stratigraphy and fossil fauna, the majority of the site has now been excavated, leaving only a small section of the entire stratigraphy preserved. Due to the diverse and sometimes outdated excavation methodologies employed over the years, interpreting the cave's stratigraphy also remains challenging. This is further compounded by the various stratigraphic schemes devised by authors such as Vaufrey (1929), Trenchmann (1938), Storch (1974) and Zammit Maempel (1985, 1989a) (Table 2).

These fossil remains were mostly studied from the late 19th - early 20th centuries (Zammit Maempel 1989a, Savona Ventura and Mifsud 1998). In the late 20th century, more studies were conducted by Boessneck and Kuver (1970), who assessed the upper domestic fauna layers, Fischer and Stephan (1974), who studied the avian remains, and Storch (1970) who utilised the micromammalian fauna to produce a stratigraphic system applicable to other Pleistocene deposits on the Maltese Islands.

Syntheses of recovered fauna from all Għar Dalam contexts can be found in Hunt and Schembri (1999, Table 4) and Marra (2005, Figure 4). However, as Herridge (2010: 75-77) notes, such correlation of Sicilian vs Maltese taxa is not so simple due to the absence of absolute dates for Maltese sites and the complexities of biostratigraphical data. While biostratigraphical correlations based on published faunal lists suggest some similarities, these must be treated cautiously due to potential synonymy issues.

Despite the taxa repeatedly listed for Għar Dalam across various publications, the pygmy elephant *Paleoloxodon falconeri* and possibly giant swan *Cygnus falconeri*, among other taxa come from Żebbuġ Cave, Mnajdra Gap and Bengħisa Gap. These unique faunal associations are not seen in Sicilian complexes, which questions the validity of applying Sicilian faunal complexes to Malta. Additionally, the typical association between *Hippopotamus* and *P. mnaidriensis* observed in Sicily is not found in most Maltese sites, raising further questions about biostratigraphic and biogeographic correlations. Despite geographic proximity suggesting potential biogeographic connections, Herridge (2010: 75 - 77) notes that geographic evidence for a contiguous Sicilian-Maltese environment during sea-level low-stands is insufficient without further absolute dating and biogeographic reasoning.

There have been several attempts to date the stratigraphic layers at Għar Dalam (Table 2); which will be dealt with systematically below.

<u>i) **I-III** (Holocene):</u> Storch (1974) identified 2 different divisions of the uppermost Holocene layers based on the micromammals. Layer III was based on the presence of the murid *Apodemus sylvaticus* and dated from the 'Għar Dalam' phase to the Bronze Age (7.2 ka to 2.7 ka). Layer II and I, the *Rattus* stage, dated from Phoenician to modern times (2.7 ka - present), based on the presence of human remains and cultural artefacts such as pottery, lithics, and ornaments (Evans 1971) However, it is widely known that there was significant disturbance in these uppermost layers (Despott 1923: 25; Caton Thompson 1925: 3-4; Savona-Ventura and Mifsud 1998, Gatt 2015: 219), making a precise interpretation difficult.

<u>ii) **IV-V** (Upper and Lower Red Earth)</u>: According to Zammit Maempel 1989a, deer remains from these levels are dated to 18 ka. Savonta Ventura and Mifsud (1998) first proposed the split between Upper and Lower divisions due to the presence of carnivores in the lower, but not upper red earth layers. Although human artefacts were also discovered from these layers (Despott 1918), their presence at this earlier stage is disputed due to the above-mentioned disturbances.

<u>iv) **VI** (Pebbles):</u> A sterile or fossil-free pebble/rock layer, estimated by Zammit Maempel (1989a) to be Late Pleistocene in age.

<u>v) **VII** (Bone Breccia):</u> The earliest fossiliferous deposit was first dated by J. L. Ma in 1988 using Electron Spin Resonance (ESR), establishing a date of 180 ka (± 10%) based on a *Hippopotamus pentlandi* molar recovered from this deposit. However, the authors subsequently subjected this molar to additional Thorium and Uranium dating, revising the date to 115 ka (± 10,000) (Bouchez *et al*. unpublished). The remains dated from this layer have therefore been placed at the end of the Middle Pleistocene to the beginning of the Late Pleistocene, but the accuracy of this dating is difficult to determine as the Bouchez *et al*. manuscript remains unpublished (Hunt and Schembri 1999: 12; D'Souza 2019: 25).

<u>vi) **VIII** (Clay):</u> Sterile bottom clay layer.

A more recent assessment of the cave stratigraphy was carried out by Dr. Chris Standish (University of Southampton; formerly University of Bristol) and Dr. David Richards (University of Bristol). Speleothem-associated material in relation to fossiliferous deposits was chosen for Uranium/Thorium (U-Th) dating. Two zones were chosen; Zone 1 which is the area around the large stalagmite 35m from the cave entrance, and Zone 2 which is the area around a second large stalagmite 42m from the cave entrance. Forty-four U-Th dates were produced, enabling a more thorough reconstruction of the sedimentation processes of the cave. These dates will be used in this dissertation; however, this paper is still in preparation (Standish *et al*. in prep.; D'Souza 2019).

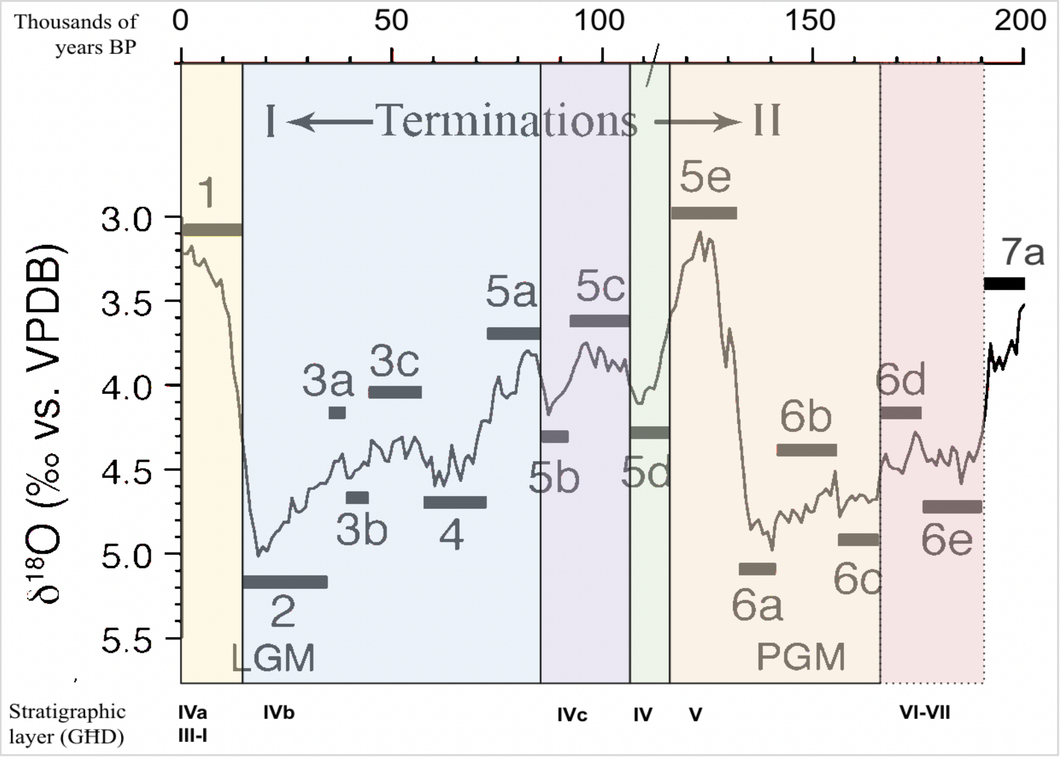
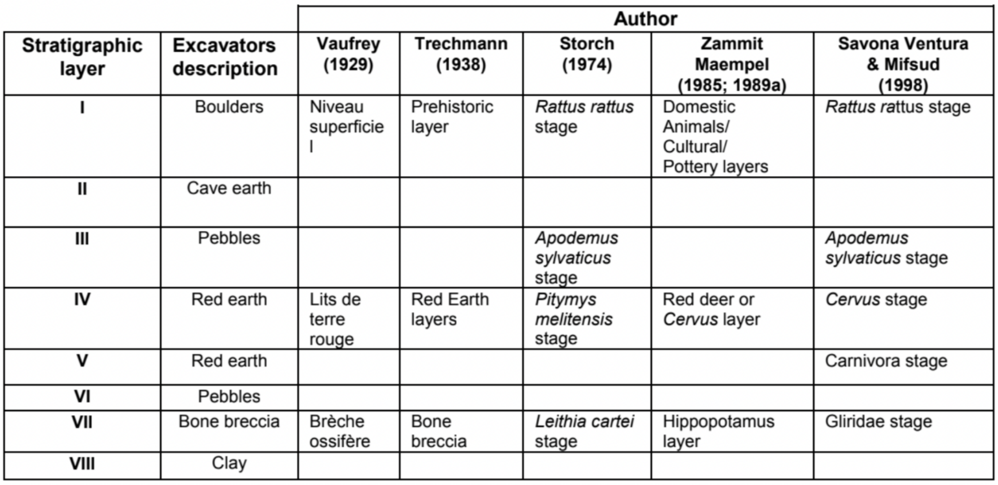
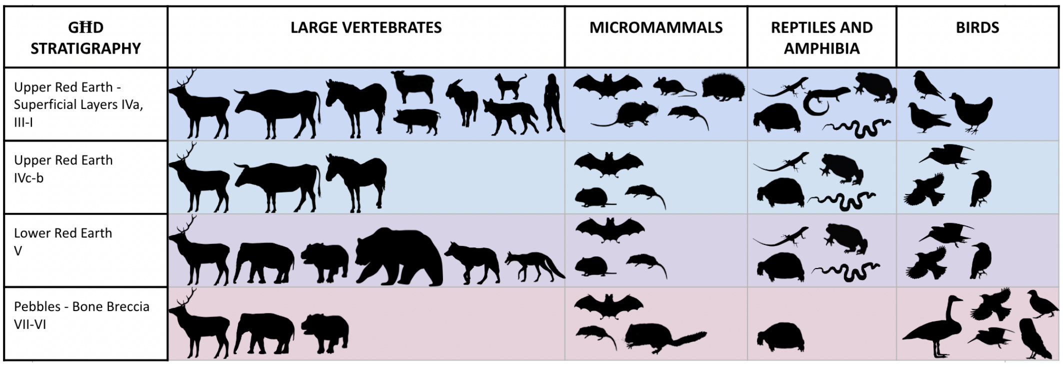


Figure 13: MIS stages. LGM: Late Glacial Maximum. PGM: Penultimate Glacial Maximum. Terminations: Transitions from glacial to interglacial stages. Adapted from Railsback et al. (2015).



Stratigraphic layer	Excavators description	Author Vaufrey (1929)	Trechmann (1938)	Storch (1974)	Zammit Maempel (1985; 1989a)	Savona Ventura & Mifsud (1998)
I	Boulders	Niveau superficie I	Prehistoric layer	*Rattus rattus* stage	Domestic Animals/ Cultural/ Pottery layers	*Rattus rattus* stage
II	Cave earth					
III	Pebbles			*Apodemus sylvaticus* stage		*Apodemus sylvaticus* stage
IV	Red earth	Lits de terre rouge	Red Earth layers	*Pitymys melitensis* stage	Red deer or *Cervus* layer	*Cervus* stage
V	Red earth					Carnivora stage
VI	Pebbles					
VII	Bone breccia	Brèche ossifère	Bone breccia	*Leithia cartei* stage	Hippopotamus layer	Gliridae stage
VIII	Clay					

Table 2: Għar Dalam stratigraphic sequence with descriptions for different faunal stages and layers from various authors. From Hunt and Schembri (1999).



GĦD STRATIGRAPHY	LARGE VERTEBRATES	MICROMAMMALS	REPTILES AND AMPHIBIA	BIRDS
Upper Red Earth - Superficial Layers IVa, III-I				
Upper Red Earth IVc-b				
Lower Red Earth V				
Pebbles - Bone Breccia VII-VI				

Table 3: Stratigraphy of Għar Dalam (GĦD) and representative taxa from Għar Dalam and Għar il-Fkieren. For a full list of species, see Table 5.

Stratigraphic layer (Savona-Ventura and Mifsud 1998)	**Description**	**U-series disequilibria derived deposition dates** (D'Souza 2019)	**Previous dates** (Storch 1974; Ma 1988; Zammit Maempel 1989a)	**Marine Isotope Stage (MIS)** (Railsback *et al.* 2015)
IVa, III, II, I	Domestic animals/ pottery layers (I-III); Upper Red Earth (IVa)	After c. 20-15 ka	I-III: 7.2-2.7 ka	1
IVb	Upper Red Earth	Between 80.1 ka and c. 23/20 ka	IV, IVa-c: 18 ka	5a-2
IVc	Upper Red Earth	Before 80.1 ka		5c-5a
IV	Upper Red Earth	After 116.3 ka and/or 103.8 ka		5d or later
V	Lower Red Earth	Between 167.3 ka - 151.2 ka	Late Pleistocene	6c or 6b
VI-VII	Pebble Layer - Bone Breccia	Before 165.9 ka	Mid-Pleistocene - Late Pleistocene	6d or older

Table 4: U-series dates. Adapted from D'Souza (2019).

Island	SICILY	SICILY	SICILY	MALTA	SICILY	MALTA	MALTA	SICILY	MALTA	SICILY
Faunal Complex or Stage	**“Monte Pellegrino”**	***“Palaeoloxodon falconeri”***	***“Elephas mnaidriensis”***	***Maltamys/* Gliridae**	**“Grotta San Teodoro Pianetti”**	***Pitymys melitensis***		**“Castello”**	***Apodemus sylvaticus / Rattus rattus***	**Holocene**
						Carnivora	***Cervus***			
Stage (ICS)	Late Pliocene-Early Pleistocene	Early Middle Pleistocene	Late Middle Pleistocene – Late Pleistocene	Late Middle Pleistocene – Late Pleistocene	Late Pleistocene	Late Pleistocene	Late Pleistocene	Late Pleistocene (‘Late Glacial’)	Late Pleistocene - Holocene	Holocene
GDM stratigraphy	NA	NA	NA	**VII – VI**	NA	**V**	**IVc-b**	NA	**IVa, III - I**	NA
***Approximate dates**	c. 1.6 ma	From c. 900 ka	a) 200 ± 40 ka / b) 146.8 ± 28.7 to 88.2 ± 19.5 ka	Before 165.9 ka	Between c. 70 ka and c. 32 ka	Between 167.3 ka and 151.2 ka	Between 80.1 and c. 23/20 ka	Either c. 20 ka or c. 14-11 ka	After c. 20 – 15 ka	After c. 10 ka
CARNIVORES	*Pannonictis arzilla*	*Vulpes* sp. (?) *Nesolutra trinacriae*	*Panthera leo* *Canis lupus* *Ursus* cf. *arctos* *Crocuta crocuta* cf. *spelaea* *Nesolutra trinacriae*	*Mustela nivalis (?)*	*Vulpes vulpes* *Canis lupus* *Ursus* cf. *arctos* *Crocuta crocuta* cf. *spelaea*	*Vulpes vulpes* *Canis lupus* *Ursus* cf. *arctos*		*Vulpes vulpes* *Canis lupus*	*Felis catus*	*Vulpes vulpes* *Canis lupus* *Felis silvestres* *Ursus* sp. *Mustela* cf. *nivalis* *Martes* sp. *Monachus monachus*
‘LARGE’ HERBIVORES		*Palaeoloxodon falconeri*	*Palaeoloxodon mnaidriensis* *Hippopotamus pentlandi* *Bos primigenius siciliae* *Bison priscus siciliae* *Cervus elaphus siciliae* *Dama carburangelensis* *Sus scrofa*	*Palaeoloxodon mnaidriensis* *P. melitensis* (?) *P. falconeri* (?) *H. pentlandi* (?) *H. melitensis* *Cervus* sp. (?) *Equus* sp. (?)	*Palaeoloxodon mnaidriensis* *Sus scrofa* *Bos primigenius siciliae* *Equus hydruntinus* *Cervus elaphus siciliae*	*P. mnaidriensis(?)* *H. pentlandi* (?) *Cervus* cf. *elaphus* *Cervus* cf. *barbarus*	*Bos* sp. *Equus* sp. *Cervus* cf. *barbarus* (?) *Dama* sp.	*Sus scrofa* *Equus hydruntinus* *Equus caballus* *Cervus elaphus*	*Bos taurus* *Capra hircus* *Ovis aries* *Cervus* sp. (?) *Sus scrofa domesticus* *Equus* sp.	*Sus scrofa* *Bos primigenius* *Cervus* sp.

Island	SICILY	SICILY	SICILY	MALTA	SICILY	MALTA	MALTA	SICILY	MALTA	SICILY
‘SMALL’ MAMMALS	*Asoriculus burgioi* *Apodemus maximus* *Leithia* sp. *Maltamys* cf. *gollcheri* *Pellegrinia panormensis* *Hypolagus* sp.	*Crocidura esuae* *Leithia cartei* *Leithia melitensis* *Maltamys gollicheri* Chiroptera (several species)	*Erinaceus europaeus* *Crocidura* aff. *esuae* *Leithia* cf. *melitensis* *Maltamys* cf. wiendincitensis	*Eliomys (Maltamys) gollcheri* *Eliomys (Maltamys)* wiendincitensis *Crocidura* cf. sicula (?) *Leithia cartei* Chiroptera (10 species)	*Erinaceus* cf. *europaeus* *Crocidura* cf. *sicula* *Apodemus* cf. *silvaticus* *Microtus* (*Terricola*) ex. gr. *savii* Chiroptera	*Pitymys melitensis* *Pitymys pauli* *Crocidura* sp. (?) Chiroptera (5 species)	*Pitymys melitensis* *Crocidura* sp. (?) Chiroptera (5 species)	*Erinaceus europaeus* *Crocidura* cf. *sicula* *Apodemus* sp. *Microtus* (*Terricola*) ex. gr. *savii* *Lepus europaeus* Chiroptera indet.	*Apodemus sylvaticus* *Crocidura russula* *Rattus rattus* *Mus musculus* *Oryctolagus cuniculus* Chiroptera (5 species)	*Erinaceus europaeus* *Crocidura sp.* *Apodemus* sp. *Microtus* (*Terricola*) cf. *savii* *Arvicola terrestris* *Mioxus glis* Chiroptera indet.
‘REPTILES” and AMPHIBIA	*Testudo graeca*	*Emys orbicularis* *Testudo hermanni* *Geochelone* sp. *Lacerta siculomelitensis* *Lacerta* sp. *Lacerta viridis* *Coluber* cf. *viridiflavus* *Natrix* sp. *Discoglossus* cf. *pictus* *Bufo* cf. *viridis* *Hyla* sp.	*Emys orbicularis* *Testudo hermanni* *Lacerta siculomelitensis* *Discoglossus* cf. *pictus*		*Podarcis* sp. Gekkonidae *Testudo* sp. *Anura* *Rana* sp. *Bufo viridis* *Hyla* gr. *H. arborea*	*Emys orbicularis* *Bufo* sp.	*Emys orbicularis* *Bufo viridis* *Podarcis* cf. filfolensis *Colubrinae* sp.		*Testudo* sp. *Discoglossus pictus* *Chalcides ocellatus tiligugu* *Bufo viridis*	Turtle indet. *Emys orbicularis* *Lacerta viridis* *Bufo bufo* *Bufo* cf. *viridis*
OTHER TAXA		Aves: 60+ species	Aves: 50+ species, incl. *Cygnus falconeri*	Aves: 12 species, incl. *C. falconeri*	Aves: 14 species	Aves: 3 species	Aves: 3 species *Homo* sp.(?)	Aves: 30+ species *Homo* sp.(?).	Aves: 3 species *H. sapiens*	Aves Fish Osteichthyes

Table 5: Comparison of Sicilian faunal complexes (Bonfiglio et al. 2002) and Maltese faunal stages (Storch 1970; 1974) with representative taxa excavated from Għar Dalam and Għar il-Fkieren. Adapted from D’Souza (2019). For comparisons with other Maltese sites and discussion of uncertain association of taxa, see Herridge (2010: 76).

3.1.3 Other sites

Numerous fissures and caves across the Maltese Islands have yielded Pleistocene fossils, with some sites showcasing different fossil content compared to Għar Dalam, as documented by Hunt and Schembri (1999, Table 4.1). However, detailed records of excavations and stratigraphies for these sites were not adequately maintained, posing challenges in correlating them with Għar Dalam's stratigraphy. While some fauna correlations can be made, the absence of systematic dating and the degradation or destruction of these sites over time have diminished many research possibilities (Hunt and Schembri 1999).

Moreover, many of the specimens recovered from these sites were not fully preserved in museum collections, and some may have ended up in private ownership or in museums abroad. However, if these specimens can be located, there is still potential to explore the feasibility of dating the bone material directly. Alternatively, if chronometric dating is not possible, these specimens may still hold value as reference and/or display material, contributing to an understanding of the Pleistocene fauna of the Maltese Islands. The recorded taxa and associated literature has been compiled in Table 6.

Site	Location	Approx. date	Vertebrate fauna	Source
Wied il-Ħesri / Żebbuġ Cave (Spratt)	Siġġiewi	MP	*Elephas* sp. *Palaeoloxodon melitensis* *Palaeoloxodon falconeri* *Cygnus* sp. *Cygnus cygnus* *Cygnus falconeri* *Anas / Branta* sp. *Aves* sp. *Gyps melitensis* *Grus melitensis* *Mustela nivalis vulgaris* *Leithia melitensis* *Chelonia* sp. *Testudo* sp.	Adams (1863, 1866a, 1870) Busk (1867) Spratt (1867) Lydekker (1890, 1891) Lambrecht (1933)
Bengħisa Gap	Birzebbuġa	MP	*Palaeoloxodon falconeri* *Palaeoloxodon melitensis* *Palaeoloxodon mnaidriensis* *Geochelone robusta* *Chelonia* sp. *Lacertilia* sp. *Leithia melitensis* *Cygnus falconeri*	Adams (1864, 1867, 1870, 1877)

Site	Location	Approx. date	Vertebrate fauna	Source
			Cygnus equitum *Cygnus* sp. *Branta leucopsis* *Gyps melitensis* *Textrax tetrax*	
Magħlaq Cave	Qrendi	MP	*Hippopotamus pentlandi* *Hippopotamus melitensis* *Hippopotamus* sp. *Leithia* sp. *Leithia melitensis* *Leithia cartei* *Aves* sp. *Pinnipedia* sp.	Adams (1863, 1865, 1866, 1870, 1874) Spratt (1867) Falconer (1868b, 1868c)
Mnajdra Gap	Qrendi	MP	*Chiroptera* sp. *Leithia melitensis* *Leithia cartei* *Maltamys gollcheri* *Palaeoloxodon falconeri* *Palaeoloxodon mnaidriensis* *Grus grus* *Grus melitensis* *Cygnus falconeri* *Cygnus equitum* *Aves* sp.	Adams (1865, 1866, 1870) Spratt (1867) Cooke (1892)
Żebbuġ fissure	Żebbuġ	MP	*Elephas antiquus* *Cygnus falconeri*	Tagliaferro (1915)
Tal-Ġnien Fissure	Imqabba outskirts	MP (?)	*Palaeoloxodon mnaidriensis* *Leithia melitensis* *Maltamys gollcheri* *Geochelone robusta* *Geochelone spratti* *Geochelone robustissima* *Lacerta* sp. *Crocidura* cf. *russula* *Lutra euxena* *Anura* sp. *Aves* sp. *Cygnus falconeri*	Baldacchino (1935) Bate (1935) Böhme and Zammit-Maempel (1982)
Middle Cave	Qrendi	MP- LMP (?)	*Hippopotamus pentlandi* *Palaeoloxodon* sp. *Arvicola* sp. *Rodentia* sp.(?) *Leithia melitensis* *Aves* sp. *Anseres* sp. *Cygnus falconeri*(?) *Anura* sp. *Lacerta* sp. *Carcharocles megalodon* Fish sp.	Adams (1864, 1865, 1866, 1870)
Ħal Resqun	Quarry between Gudja and Luqa	MP- LMP (?)	*Palaeoloxodon mnaidriensis* *Hippopotamus* sp.	Despott (1931, 1932)
Ta' Vneżja	Mosta	MP- LMP (?)	*Palaeoloxodon falconeri* *Palaeoloxodon melitensis* *Hippopotamus pentlandi*	Rizzo (1936) Baldacchino (1936)

Site	**Location**	**Approx. date**	**Vertebrate fauna**	**Source**
Unknown Qrendi site	Qrendi	MP- LMP (?)	*Proboscidea* sp. *Hippopotamus* sp.	Adams (1863)
Mellieħa Cave	Mellieħa	MP- LMP (?)	*Elephas* sp. *Hippopotamus pentlandi*	Spratt (1867) Adams (1870) Zammit Maempel (1989) Savona-Ventura *et al*. (1999)
Unknown Żabbar fissure	Żabbar	MP- LMP (?)	*Elephas* sp.	Adams (1870)
Buqana	Attard	MP- LMP (?)	*Elephas* sp.	Despott (1928)
Ta' Kandja/Gandja fissure	Mqabba	MP- LMP (?)	*Elephas* sp. *Lacertilia* sp.(?)	Adams (1865, 1866) Zammit Maempel (1994)
Wied Inċita fissure	Attard	MP- LMP (?)	*Paleoloxodon* sp. *Hippopotamus* sp. *Rhinolophus* sp. *Ursus arctos* *Cervus* sp. *Eliomys melitensis* *Leithia melitensis* *Aves* sp. *Lacerta siculimelitensis*	Zammit-Maempel (1982) Böhme and Zammit-Maempel (1982)
Ħal Bidni	Marsascala	LMP	*Elephas* sp. *Ursus* sp.(?)	Zammit (1906) Tagliaferro (1915)
Capt. Formosa Fissure	Mrieħel	LMP	*Elephas* sp. *Hippopotamus* sp. *Ursus* sp.	Zammit (1962)
Valletta Dock fissure	Valletta	LMP	*Dama dama*(?) *Equus* sp. *Vulpes vulpes*	Adams (1874a)
George Sinclair's unknown fissure	Unknown	LMP-LP	*Equus asinus* *Cervus elaphus* var. *barbarus* *Vulpes vulpes* *Testudo graeca*(?) *Aves* sp.	Despott (1925)

Table 6: Summary of other fossiliferous Pleistocene sites discovered in Malta with associated taxa. Approximate dates based on vertebrate remains and Standish et al. (in prep) U-Th series for GHD depositional events (see D'Souza 2019). Abbreviations: ***MP*** *(Middle Pleistocene [before 165.9 ka]);* ***LMP*** *(Late Middle Pleistocene [c. 167 - 129 ka]);* ***LP*** *(Late Pleistocene [c. 129 – 11.7 ka]).*

3.1.4 A brief history of Pleistocene studies

While remains of terrestrial fauna began to be catalogued as early as the 17th century (Abela 1647), the first sophisticated attempts at scientific research began to be undertaken during the mid-19th century (e.g., Spratt 1867; Adams 1863-1877; Cooke 1891-1896). However, while able to shed some light on this relatively obscure period, most 19th century research focused on describing the fossiliferous contents and discoveries of particular sites.

The first half of the 20th century was characterised by several new discoveries of fossiliferous sites and species, many of which were excavated under the direction of Themistocles Zammit (1906, 1912, 1922, 1924) and Napoleon Tagliaferro (1911a, 1911b, 1913, 1915). Excavations also continued to be undertaken at Għar Dalam, under the direction of scholars such as Thomas Ashby (1916) and Giuseppe Despott (1917; 1918; 1923).

In the second half of the 20th century, Dr. Trevor Shaw published observations of cave morphology and geological features of Għar Dalam and other cave sites (Shaw 1951). More discoveries of fossiliferous Pleistocene deposits were made, such as the Mrieħel Capt. Formosa fissure deposit (Zammit 1962) and the deposit found during construction works of the St. Theresa College at Mrieħel (Zammit Maempel 1965). The latter site was studied and given a full and detailed analysis on the sediment and animal remains (Zammit Maempel 1981). Zammit Maempel continued to produce several publications on Maltese palaeontology (1989; 2007; 2009) and was the author of several new species, including the dormouse *Maltamys wiedincicitensis* from the Wied Incita Fissure deposit (Zammit Maempel and De Bruijn 1982). Gerhard Storch, a specialist in micromammals, produced papers on Pleistocene micromammals, identifying several bat species including *Rhinolophus mehelyi birzebbugensis* and *Myotis Ghardalamensis*, as well as identifying three faunal stages at Għar Dalam (Storch 1974). This early work in cataloguing and recording fauna, while not executed with modern scientific standards, was still an important step in recognising the value of Pleistocene Malta and encouraging public interest in its unique biological history.

Systematic studies of Quaternary deposits with the aim of reconstructing the environment would not be attempted until 1997. Hunt (1997) reinterpreted the Quaternary deposits, showing arid glacial and humid interglacial stages by correlating Maltese lithofacies with their climatic signals. This much-needed modern assessment of Quaternary environmental change was followed up with Hunt and Schembri 1999, which aimed to critically reassess early Quaternary research and describe the development of Maltese fauna correlated with

Quaternary environmental changes. Utilising a modern theoretical background based on new stratigraphic methods aided understanding of geological, environmental and evolutionary processes affecting the islands at the time. However, since this work was based on the stratigraphy of Għar Dalam and with the absence of a solid dating scheme, the whole picture still remains incomplete.

Most works during this period rely on the stratigraphy of Għar Dalam and a limited number of sites (e.g., Galea Bonavia 1999; Pedley 2011; Savona Ventura and Mifsud 1998, 1999; and van der Geer *et al*. 2010). Unfortunately, previously excavated sites do not retain sufficient sediments which can be reassessed using modern techniques, and as such the interpretations gathered from the previous excavators cannot be ascertained (Gatt 2015).

3.2 RESEARCH GAPS

Despite the wealth of information gathered from surrounding regions, Malta remains a significant gap in Mediterranean Pleistocene microfauna studies. Given Malta's centrality within the Mediterranean and its unique palaeontology, geological history and climate, Malta’s Pleistocene record has the potential to offer crucial insights into migration patterns, species adaptation, and ecological dynamics in the Central Mediterranean. Furthermore, it could provide valuable information on local island climate variations against the backdrop of global climate change patterns.

Currently, Quaternary research on the islands is gradually increasing but remains relatively scarce, making a comprehensive analysis of the paleoenvironment of the Maltese Islands during the Quaternary period elusive (Gatt 2015). In contrast, contemporary studies of the Quaternary fauna and paleoenvironment in Sicily have been relatively extensive (e.g., Incarbona *et al.* 2010; Marra 2013; Palombo 2018; Salari *et al*. 2019; Spena *et al*. 2021), indicating that Malta is being excluded from pan-Mediterranean advances in Pleistocene studies.

The newly discovered faunal assemblages from Għar il-Fkieren therefore offer an exciting opportunity to redress several key questions which remain unresolved, mainly the extinction of endemic species (3.2.1), climate and environment (3.2.2), the Island Rule (3.2.3), phylogenetic relationships between species (3.2.4), and the current faunal complexes (3.2.5). This section aims to systematically review these identified gaps.

3.2.1 Extinction of endemic species

One of the main questions that has not yet been sufficiently addressed is why several Maltese species went extinct by the Late Pleistocene - Early Holocene. The Quaternary mass extinctions were not restricted to larger mammals such as hippopotami and elephants, but also invertebrates (e.g., land snails) and smaller vertebrates (e.g., dormice) (Thake 1985). Thake (1985) attributes the extinction of deer to hunting pressure and increased modification of the environment for farming, but this does not wholly explain the disappearance of several species before the Holocene. Thake (1985) acknowledges the possibility that these pre-human arrival endemics did not adapt to new competitors arriving from Sicily during times of low sea level, or to the climatic fluctuations of the Late Pleistocene. As Hunt and Schembri (1999) note, although the broad outline of Maltese biogeography is clear, the details remain obscure.

3.2.2 Climate and environment

Quaternary records of the Maltese climate remain patchy and inconsistent, possibly since the majority of research conducted thus far has focused on the Holocene era onwards, primarily with the objective of reconstructing the environment and human impact from the Neolithic period (e.g., Marriner *et al.* 2012; French *et al.* 2020).

Meanwhile, the investigation of previously glaciated landscapes advanced rapidly in Northern Europe, due to the relatively straight-forward availability of bog peats and lake muds which allowed easy identification of plant and animal fossils (French *et al.* 2020). The development of pollen analysis allowed a much better understanding of climate change and the role of humans in altering landscapes. However, Quaternary research into non-glaciated European and Mediterranean countries did not pick up pollen analysis until the 1950s due to the lack of glacial features and difficult application of analysis to oxidised deposits (French et al. 2020). Pollen studies on a small island also present unique limitations, in that it may easily be blown in from the mainland. However, pollen anthers, seeds, phytoliths and macrocharcoal beyond a certain size may indicate local signals.

Speleothem (e.g., Lechleitner *et al*. 2018), geomorphological (e.g, DiMaggio *et al.* 2017) and isotopic (e.g., Jeffrey *et al*. 2015) studies highlight the wealth of palaeoenvironmental methods and studies elsewhere, but such studies have been lacking for the Maltese Islands.

Consequently, much of the early research attention was on the archaeology of early humans and cave deposits containing animal and human remains. As a result, climate models were often extrapolated from models developed in Northern Europe (French *et al*. 2020) and are only applicable to the Maltese Islands to a certain extent.

Until the above types of palaeoenvironmental analyses can be successfully carried out on Quaternary deposits in Malta, analysis of the fossil fauna remains a valuable avenue for gaining insights into the Maltese climate and environment preceding the Holocene. By studying the composition, diversity, and distribution of fossil fauna, researchers can discern patterns of species adaptation, migration, and extinction, shedding light on the environmental dynamics of the Maltese Islands throughout the Quaternary period. This information is crucial for understanding the long-term environmental history of Malta and its responses to global climate changes over geological timescales.

3.2.3 The 'Island Rule'

The 'island rule' was first described by Foster (1964) who observed that certain small mammals tend to increase in size on islands (gigantism). This pattern was later established as a rule by Van Valen (1973), who also noted opposing instances of dwarfism in larger species of insular mammals. Despite the rule having exceptions, it continues to be a key topic in island biogeography (Palombo and Rozzi 2013), since the special characteristics of island environments make them ideal to study the forces influencing diversification and evolution. Such forces include time and magnitude of isolation, available resources, biological diversity, and intensity of ecological interactions (Palombo and Rozzi 2013). Amori and Massetti (1996) additionally studied the co-occurrence between large micromammals and predators and revealed that micromammal size increase does not appear to be directly related to the co-occurence of predators. Rather, it is possible that reduction of food supply, competition between species and endothermic adaptations have caused the size difference.

The two main issues include the loss of biodiversity and evolutionary changes in island settlers, chiefly body size. The body-size of organisms plays a key role in the ontogeny and biology of species, affecting the fitness of individuals and showing a significant correlation with life-history and physiological parameters (Moncunill-Solé *et al*. 2016). Therefore, one of the key processes in the study of palaeontological remains involves morphometric analysis of crania and post-cranial elements. This can allow archaeologists and palaeontologists to study the underlying mechanisms governing processes such as gigantism and dwarfism.

Malta's isolation led to several well-known examples of Middle Pleistocene giant and dwarf species such as *Leithia melitensis* (giant dormouse) and *Palaeoloxodon falconeri* (pygmy elephant). However, a focused study of the morphology of the Maltese Late Pleistocene microfauna has yet to be undertaken, although Petruso *et al*. (2011) and Locatelli (2010) published intriguing analyses of *Microtus* and *Crocidura* remains from Malta and Sicily. In addition, Moncunill- Solé *et al*. (2016) analysed a large sample of soricids from Mediterranean islands including Sicily, suggesting that *Crocidura* does not tend towards gigantism or larger body size. It remains to be confirmed whether Maltese fossil specimens of *C. sicula* exhibit the same morphological 'stasis'.

Environmental data coupled with phylogenetic and morphometric studies could help to clarify when Malta underwent a period of isolation and endemic species evolved, providing an opportunity to investigate certain assumptions about the island rule and the evolution of species in isolated or insular environments.

3.2.4 Phylogenetic relations to Sicilian and North African fauna

As demonstrated by Thake (1985), the Pleistocene fossils of the Maltese Islands exhibit the closest affinities to the Sicilian faunal complexes, suggesting the existence of a Pleistocene land connection between the islands. However, certain aspects of biogeography and phylogeographical relationships between species require clarification, and a more detailed reconstruction of the colonisation history of the Maltese Islands is warranted.

Phylogenetic analysis focusing on *Crocidura sicula* fossils have provided valuable insights, building upon the work of Hutterer (1990), who analysed the temporal and geographical variation of Pleistocene shrews in the Sicilian-Maltese region. These studies indicate that the endemic species *Crocidura sicula* descended from *Crocidura esuae*, whose phylogenetic origins can be traced to North Africa (Dubey *et al*. 2008)

Similarly, the study into the genetic origins and relationships of *Microtus melitensis* by Petruso *et al*. (2011) revealed its close affinity to the Italian *M. savii* vole. However, the relationship between *M. melitensis* and the enigmatic *Pitymys pauli* retrieved from the Lower Red Earth layers from Għar Dalam, first recorded by Bate, remains unclear.

Genetic and microsatellite studies by Rodríguez and colleagues (2014) also suggest North African origin for the endemic *Podarcis filfolensis*, indicating the ancient form of this species arrived in the Maltese Islands during the Messinian Salinity Crisis and became isolated when the Mediterranean basin re-flooded approximately 5.33 Ma. The diversification of current *Podarcis* subspecies and their dispersal to other Maltese Islands may have been facilitated by shallower sea levels during glacial periods. This highlights the potential of phylogenetic studies to elucidate aspects of island connectivity and climatic changes.

Further exploration of these phylogenetic relationships has the potential to shed light on dispersal events in the Mediterranean region, offering valuable insights into the links between evolutionary history of Maltese fauna and the climatic and geological history of the Late Pleistocene Mediterranean.

3.2.5 Current faunal complex scheme

Secure data on the palaeoclimate and environment, when combined with a comprehensive faunal complex scheme, can greatly aid in the interpretation of dispersal routes and biogeographical origins of different species. While many Pleistocene taxa are well-studied and understood, the current faunal complex scheme for Malta primarily relies on Għar Dalam layers, some of which have been heavily disturbed. Consequently, there is a pressing need for a systematic explanation of phylogenetic relationships, along with the creation of maps and visual data depicting species distributions. Additionally, more dates from secure layers in both Sicily and Malta are essential for refining our understanding of the timing of faunal turnover and environmental changes.

The excavation of Għar il-Fkieren and other potential Pleistocene sites holds promise in addressing these issues by providing new and independent data to complement existing research. By analysing the faunal assemblages from Għar il-Fkieren and comparing them with those from Għar Dalam, it is hoped that we can gain a more comprehensive understanding of Malta's Pleistocene faunal complex and how it relates to its broader geographical context. This comparative approach will facilitate the identification of species distributions, phylogenetic relationships, and potential dispersal routes, thereby advancing our knowledge of the biogeographical history of the Maltese Islands.

4 METHODOLOGY

4.1 RESEARCH DESIGN

The research design for the study at Għar il-Fkieren aimed to provide a comprehensive analysis of all recovered specimens from selected samples representing each stratigraphic layer of the site. This approach enables various chronological analyses, crucial for understanding ecological dynamics, biodiversity, and environmental changes over time.

The primary objectives of this study were:

- To investigate the ecological dynamics and biodiversity changes at Għar il-Fkieren;
- To reconstruct past environmental conditions and their through-time changes;
- To examine morphological variations between species from Għar il-Fkieren and Għar Dalam in order to elucidate aspects of island evolution; and
- To conduct taphonomic analyses to determine site formation processes.

Hypotheses included:

- Expectations of potential ecological shifts throughout the stratigraphic layers.
- Taphonomic signatures indicative of both predator-prey interactions and flooding events which washed the majority of the assemblage into the fissure.

- The Late Pleistocene fauna represent a separate dispersal event from Sicily, distinct from the Middle Pleistocene faunal complexes.
- The extinction or extirpation of certain species in the assemblage is due to environmental pressures associated with abrupt climatic shifts and/or to competition with later Holocene faunal arrivals.

In order to achieve the aim of understanding environmental changes over time through stratigraphic analysis, a representative sampling strategy had to be carried out. Out of the total 118 boxes of bone-rich sediments recovered from the site, thirty-five were chosen for analysis (Table 7), chosen from each context and depth of the site.

The chosen sediment samples were screened systematically. First, dry sieving was used to separate the bone from the sediment. This was followed by flotation, which utilised a fine mesh to screen the sediment and separate small microfaunal material, achieving high recovery rates.

One of the most important steps involved the taxonomic identification and quantification of the individual microfauna bone elements from each context. The proper recording and identification of the specimens was essential since it enabled all further quantitative analysis, including NISP and MNI for relative abundance, and taphonomic analysis from each layer.

To estimate body sizes and compare the morphology of specimens from Għar il-Fkieren and Għar Dalam, measurements of select elements were also recorded, primarily dentition and the most numerous postcranial elements. These measurements facilitated the comparison of size variations in the same taxa between the two sites.

Taphonomy was a critical component of the research. Variables recorded for taphonomic analysis included digestion marks and breakage patterns of select elements, chosen for their abundance throughout all layers to ensure a satisfactory sample size. This analysis helped determine the factors involved in site formation and assemblage accumulation by examining bone surface modifications.

The final objective was to infer past environmental conditions using the habitat weighting technique. This method provided insights into the ecology of the area around Għar il-Fkieren during the time these species lived, allowing for a reconstruction of past habitats based on the distribution of extant species.

The research design for the study at Għar il-Fkieren integrated systematic sampling, detailed screening, taxonomic identification, taphonomic and morphometric analyses, and habitat weighting to achieve a comprehensive understanding of ecological dynamics, biodiversity, and environmental changes over time. This multifaceted approach ensured the collection of representative data to facilitate meaningful interpretations of the site's paleoecology.

The following sections will describe the methods in depth for the steps described, including sampling and screening (4.2.2), taxonomic identification (4.3.1), taxonomic quantification (4.3.2), taphonomic (4.3.3) and morphometric (4.3.4) analyses, and habitat weighting for paleoenvironmental reconstruction (4.3.6).

4.2 DATA COLLECTION

4.2.1 Site collection strategy

During the 2010 excavation at Għar il-Fkieren, the goal of the archaeological monitors was to systematically recover as much of the bone-rich matrix from the site as possible. Initially, this material was organised into large tubs based on assigned stratigraphic units (SUs) within the top four metres of the site. However, onsite monitors observed that the SUs were too similar to warrant objective discrimination, prompting a change in excavation strategy early on. Time constraints imposed by developers further necessitated this adjustment. Consequently, excavators of the 4.5 metres incorporated a mix of both horizontal layers (spits) and depth. A total of 118 boxes from 8.5m of the fissure were recovered.

4.2.2 Screening strategy

In October 2020, the Malta Quaternary Palaeoecology Project team, together with student volunteers from the University of Malta, undertook dry sieving of the total 118 boxes of the bone-rich matrix from Għar il-Fkieren. The bone material was separated from the sediments, with sediments being later put aside for soil sampling and floatation.

The sieved material was then sorted into labelled bags of sediment, bone, and shell. Out of these, thirty-five bags were selected for further analysis. This sampling strategy aimed to provide a relatively even representation across the stratigraphy, allowing for a general estimate of the entire fissure (Table 7).

Site code	Depth	Depth (converted)	Spit	SU	Box No.
PEN2010	6.5-6.75m	n/a	6	n/a	403
PEN2010	n/a	3-3.5m	n/a	13	381
PEN2010	n/a	2.5-3m	n/a	7	379
PEN2010	n/a	2.5-3m	n/a	7	373
PEN2010	n/a	3.5-4m	n/a	25	371
PEN2010	n/a	2.5-3m	n/a	9	366
PEN2010	n/a	2-2.5m	n/a	3	362
PEN2010	n/a	2-2.5m	n/a	4	361
PEN2010	n/a	2.5-3m	n/a	7	360
PEN2010	n/a	2.5-3m	n/a	11	358
PEN2010	n/a	3-3.5m	n/a	18	357
PEN2010	n/a	3.5-4m	n/a	16	356
PEN2010	n/a	3.5-4m	n/a	22	355
PEN2010	n/a	3.5-4m	n/a	22	354
PEN2010	n/a	3.5-4m	n/a	20	353
PEN2010	n/a	4-4.5m	n/a	27	352
PEN2010	n/a	3-3.5m	n/a	14	351
PEN2010	n/a	3.5-4m	n/a	22	350
PEN2010	n/a	3-3.5m	n/a	13	349
PEN2010	4.5-5m	n/a	n/a	n/a	348
PEN2010	4.5-5m	n/a	n/a	n/a	347
PEN2010	4.5-5m	n/a	n/a	n/a	346
PEN2010	4-4.5m	n/a	n/a	n/a	345
PEN2010	4.5-5m	n/a	n/a	n/a	344
PEN2010	5.5-6m	n/a	2	n/a	342
PEN2010	5.5-6m	n/a	1	n/a	334
PEN2010	5-5.5m	n/a	n/a	n/a	330

Site code	Depth	Depth (converted)	Spit	SU	Box No.
PEN2010	5.75-6m	n/a	n/a	n/a	329
PEN2010	6-6.25m	n/a	n/a	n/a	322
PEN2010	6.25-6.5m	n/a	n/a	n/a	321
PEN2010	6-6.5m	n/a	4	n/a	311
PEN2010	6.5-7m	n/a	n/a	n/a	310
PEN2010	7.5m - end	n/a	n/a	n/a	305
PEN2010	7-7.25m	n/a	8	n/a	303
PEN2010	7-7.5m	n/a	n/a	n/a	301

Table 7: List of sediment bags sampled for microfauna from Għar il-Fkieren processed for the study.

The labelled bags of sediment required further screening, owing to the very small size of the microfaunal material. Using bucket flotation (described below), the small fauna was separated from the remaining sediment. Flotation is a relatively simple technique of recovering small animal bones, seeds, and cultural remains which may otherwise be lost in the normal screening of sediments during excavation and sieving (Stahl 1996).

First, around 20% of the sediment from each bag was extracted for environmental sampling, in order to retain a portion for any future analyses. The remaining material was poured into buckets up to one third of the way, filled with water, and stirred. The stirring causes the light fraction of the sediments to rise to the surface, along with charcoal, plant remains (such as seeds), and small animal remains (such as shells and bones). After waiting a few minutes for the light fraction (or float) to rise, the buckets were then poured carefully into a bottomless jug fitted with a 250µ mesh bag, which catches the light fraction. This process is repeated until no more material floats on the surface. The mesh bags full of floated material were then hung to dry and the remaining sediment in the buckets were then poured into a standard 0.5 mm hand sieve. Any remaining shell and bone missed by the floatation which could be identified were then hand-picked out of the hand sieve, left to dry, and packed according to material type (shell, microfauna, etc.). The material bags were labelled by context and the microfauna were set aside for further study.

This bucket flotation technique is relatively simple and inexpensive, and allows the processing of large volumes of sediment. Without this procedure, there would be a sizable bias on inferences about the prehistoric environment, since any quantification of the remains would otherwise be skewed towards larger animals (Struever 1968).

4.2.3 Photography

Colour photographs of postcranial specimens measuring over 1 cm were captured using a Canon EOS 10D Digital Camera fitted with a Canon Ultrasonic 100mm macro lens. The images were saved in .CRW format, and white balance corrected using Camera Raw 13.0 in Adobe Photoshop 2021. Adjustments, such as rotation and brightness reduction, were applied where necessary.

Dental elements were photographed using a Keyence VHX-6000 microscope. Multiple photos at varying depths were taken and automatically stitched together using the microscope's software to produce an in-focus composite image. For specimens with dental elements, occlusal views were prioritised as the shape of the chewing surface of the molar is highly diagnostic for species identification. Additional views, such as dorsal and ventral, were taken for elements like postcranial bones or mandibles.

A systematic coding scheme was employed for all specimens: Context Number / Bag Number / Specimen Number. For example, "30311_1" refers to context number 303, bag number 11, and specimen number 1.

All photographs referenced in the text were imported into Adobe Photoshop for post-processing. White balance correction was performed, and the background was removed using the pen tool. Scale bars were generated by measuring the pixels corresponding to the scale in the photo and then using these measurements to create an accurate scale bar.

Għar Dalam femora in the Senckenberg collection [1890, 1891], as well as a few more complete specimens from the Għar il-Fkieren [1897, 1898] were scanned with a scanner, while *Colubridae* sp. vertebrae (Figure 27) were photographed with an AmScope SM-4 Series.

All photographs are included in the appendix and cross-referenced in the main database for easy reference.

4.2.4 Measurements

Morphometric data offer a range of uses in the study of fossil species, including the study of size variation, body-size estimation, tracing phylogeny, and determination of species or sub-species (O'Connor 2000). In the case of this study, the morphometric data was recorded with the aim of (i) comparing body size of arvicolids present in the same time period from Għar il-Fkieren and Għar Dalam; and (ii) identifying size variations in amphibian postcrania to detect any difference in species or subspecies.

Bufotes viridis and *Microtus melitensis* were chosen for further measurements, as other identified species lacked elements that were numerous enough for statistical significance or comparison.

In Arvicolids, only the first lower is diagnostic, and its length is particularly useful for estimating body mass (Locatelli 2010; Petruso *et al*. 2011). Given the size of the dentition, the Keyence VHX-6000 microscope was used both for photographing and measuring these specimens due to its built-in measuring feature. By plotting two points on the photo, the software accurately measures the distance between them. This digital method allows for precise measurements of the tiny dental specimens, which would be too small and fragile to handle with digital callipers. Dentition of *M. melitensis* from Għar Dalam was also measured using ImageJ software, based on the scale of the microscopy photos previously taken by Dr. Daria Petruso.

For *M. melitensis* specimens from Għar il-Fkieren, femora were also measured due to their well-preserved state and abundance in the assemblage. Similarly, *M. melitensis* femora from the Għar Dalam collection were measured. Although these elements were not identifiable with absolute certainty to species level, due to their similarity with *Mus*, the *M. melitensis* species was inferred due to the co-occurrence of large amounts of *M. melitensis* postcrania and concurrent absence of *Mus* postcrania. The metrics recorded included shaft width and thickness, proximal and distal epiphysis width and thickness, and total length in millimetres (mm) for complete specimens. The same measurement process was applied to *B. viridis* remains, where humeri were the most numerically significant and well-preserved elements. All postcranial element measurements were taken using digital callipers with a USB interface, which allowed for more precise measurement and direct input into the database. A separate spreadsheet was compiled for these measurements to facilitate data analysis.

According to Gifford-Gonzalez (2018: 106), the basic requirement of metrical data collection is that it be 'accurate, replicable, and made at commonly agreed-upon locations on an element'. The measurement locations have therefore been illustrated in Figure 14.

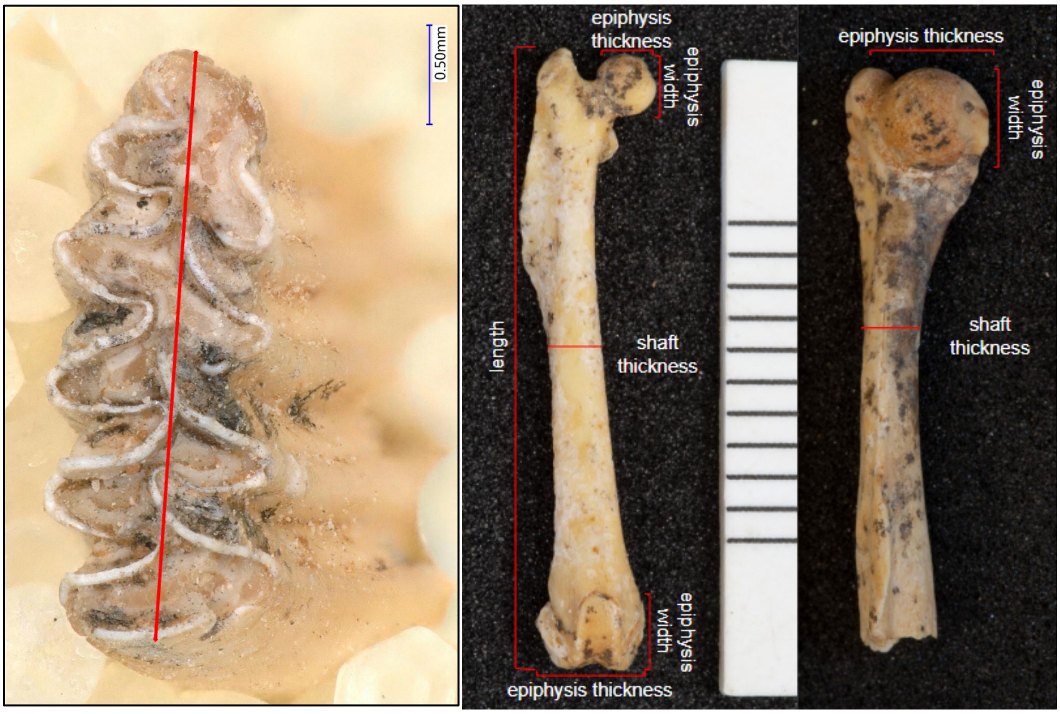


Figure 14: Left: Measurement location of width of M. melitensis m1 molars. Centre: Measurement locations of M. melitensis femora. Right: Measurement locations in B. viridis humeri; locations follow the same scheme. Proximal epiphysis and length measurements omitted due to specimen not being complete. Scale = 1 cm.

4.2.5 Database

The main data on the specimens studied from the 35 sample contexts were recorded in a Google Docs spreadsheet. Each key header provides specific information to facilitate the identification, classification, and analysis of the materials. These headers are explained in Table 8.

Photo ID	This identifier links each specimen to the corresponding photograph in the appendix photo database. It consists of the bag number followed by the individual specimen number.
Box No.	Indicates the original crate or box number where the specimen was stored.
Depth	Specifies the depth (in meters) at which the specimen was found within the fissure.
Spit	Refers to the arbitrary vertical subdivision of the stratigraphic layer from which the specimen was excavated.
SU	Denotes the stratigraphic unit, providing context on the geological layer where the specimen was located.
Bag No.	The number assigned to a bag of sorted specimens, formatted as the box number followed by the bag number.
Taxa	Provides the common name of the taxonomic group to which the specimen belongs.
Species	The scientific name of the species to which the specimen is identified.
Element	Describes the specific bone or skeletal element (e.g., femur, humerus).
Portion	Identifies the part of the bone fragment (e.g., distal, proximal, midshaft).
Count	The total number of the same specimens for each entry.
Side	Indicates whether the bone is from the left or right side of the body.
Fragmentation	Describes the condition of the specimen, noting whether it is complete or fragmented.
Age	Specifies whether the specimen is from an adult or juvenile individual.
Comments	Includes any additional observations or relevant notes about the specimen.

Table 8: Microfauna main database header information.

4.3 METHODS OF DATA ANALYSIS

4.3.1 Taxonomic identification

Specimens from each context bag were first carefully poured into a tray and sorted by class (e.g., mammal, amphibian, bird) using plastic tweezers. Non-study bones, such as bird remains, were packed and labelled for future specialist study. The mammal group, for instance, was analysed further by sorting into family (e.g., vole, shrew) and then by skeletal element (e.g., femur, humerus). Each element was counted, categorised by fragmentation type, and entered into a database under the relevant genus name (e.g., 2 left proximal femur, 3 right distal femur). Finally, elements were packed into labelled bags (e.g., vole femur). This process was repeated for all postcranial elements, and generally follows the systematic protocol outlined by Beisaw (2013: 10). Bones were not cleaned, as they would be in the case of larger faunal remains, due to their size and fragility.

Although identifying the family and even genus of the animal is usually straightforward, identification of species is often more difficult. For this reason, cranial bones and dentition were separated from postcrania. The dentition could be further identified to species by using a microscope at 40x magnification. Taxonomic identification was aided by comparisons with comparative material, as well as bone atlases and online catalogues. Hillson (2005) was consulted as a general guide to identifying the genus and labelling the individual molars of the mammals in the assemblage, which were narrowed to species using comparative reference material and publications (Bate 1920; 1935; Locatelli 2010). For colubrids, specialist publications were considered due to lack of available local reference material (Carmona *et al.* 2010; Racca *et al*. 2020). For amphibians, comparative collections were used, as well as Blain *et al*. 2020. For *Podarcis* cf. *filfolensis*; no comparative was available, therefore references were consulted (Böhme and Zammit-Maempel 1982; Čerňanský & Syromyatnikova 2019).

Aside from visual reference material, it was also essential to be familiar with the Late Pleistocene fauna from different sites on the Maltese Islands in order to make accurate analogies and estimations of species (Hunt and Schembri 1999; Gatt 2006). A working knowledge of extant species was also key to determining the potential species of fossil fauna which were not mentioned in Quaternary literature. The limitations of the use of analogy in species identification is covered in 6.4.

4.3.2 Taxonomic quantification

In order to analyse relative abundance and patterns over time, it was necessary to quantify the remains. There are several methods for doing so, the most popular in zooarchaeology and palaeontology being NISP (Number of Individual Specimens) and MNI (Minimum Number of Individuals).

The definitions of NISP and MNI according to Gifford-Gonzalez (2018):

i) **NISP**: 'the total count of specimens that are taxonomically identifiable' (Gifford-Gonzalez 2018: 287).

ii) **MNI**: 'an estimate based on NISP of the lowest number of individual animals necessary to have provided the single most abundant element of each taxon in a sample, derived by finding the most abundant element for each taxon' (Gifford-Gonzalez 2018: 188).

Therefore, NISP values are a count of tangible specimens representing primary quantitative data (Gifford-Gonzalez 2018: 189), whereas MNI presents a secondary abstraction; it is an analytical unit derived from the primary NISP count (Gifford-Gonzalez 2018: 190). However, bias still occurs in NISP due to post-mortem processes affecting the assemblage, as well as the intrinsic properties of vertebrate skeletons. For instance; (i) not all species have the same number of skeletal elements, meaning some will be over or under-represented in the relative abundance; (ii) taphonomic processes affect bones of varying densities and shapes differently; and (iii) field and post-excavation collection biases (Gifford-Gonzalez 2018).

Although MNI has been the preferred quantitative method in paleoecology for the past century or so (Lyman 2016, 2018), there are several limitations to the MNI method (Lyman 2018). Firstly, it can be challenging to identify which skeletal elements belong to the same individual, particularly in large assemblages. Using MNI can sometimes also lead to incorrect interpretations of abundance, especially when dealing with taxa which have different numbers of identifiable skeletal elements per individual. For instance, many of the bones in a snake's skeleton are not easily identifiable to a specific position within the skeleton (e.g., distinguishing between different vertebrae). This lack of diagnostic elements can hinder the accurate calculation of MNI, as it is harder to ascertain the minimum number of individuals represented. Snakes also have numerous small and similar vertebrae, making it challenging to distinguish between individual snakes based on these bones alone. Unlike mammals, which have distinct and varied skeletal elements, snakes' vertebrae can be very uniform, complicating the aggregation process.

Although there has been much discussion over which quantitative method is ‘best’ and both quantitative measures have limitations (Marshall and Pilgram 1993, Lyman 2018), it is increasingly popular in the field of zooarchaeology since the 1970s to include both methods in order to compensate for each method’s biases (Lyman 2018). Therefore, both NISP and MNI were chosen as quantitative methods to measure the taxonomic abundance of Għar il-Fkieren, since NISP presents primary quantitative data and MNI corrects for the biases present in NISP.

4.3.3 Taphonomic analysis

Taphonomy is the study of all the processes that affect animal remains from the moment of death until its discovery as a fossil in the palaeontological/zooarchaeological record. The taphonomic history of individual specimens or fossil assemblages of animals or plants begins when living organisms die and undergo modifications through decay, exposure, burial, and subsequent diagenetic effects. The observed effects (modifications) on the remains of organisms form the basis for interpreting the processes that have influenced the assemblages. The evidence of these processes is then combined to elucidate aspects of the fossil association (Fernández-Jalvo and Andrews 2016: 2).

Modifications may result from:

- **Burial**: How remains are interred below surface and encased by sediment, as well as altered by sub-surface taphonomic processes (Behrensmeyer *et al.* 1989).
- **Decay**: The breakdown of soft tissue and decomposition, influenced by factors like temperature, moisture and microbial activity (Lyman 1994).
- **Preservation**: The conditions which contribute to the preservation of the remains, such as mineralisation or creation of anoxic environments which slow decay (Lyman 1994).
- **Weathering**: The physical and chemical breakdown of bones and other hard tissues due to exposure to environmental elements such as water, wind, and temperature fluctuation (Behrensmeyer 1978).
- **Predation and scavenging**: The impact of animals consuming, digesting and regurgitating prey, as pellets or scat, which can result in partial or complete destruction of the carcass; as well as the impact of animals or insects which consume or modify the dead animal remains as a food source, which can include gnawing, trampling and other forms of bioturbation. It is often not possible to distinguish between predation and scavenging modifications (Fernández-Jalvo and Andrews 2016: 2).
- **Transport**: The movement of remains from the original site of death to the final location through physical action, such as carnivores, water flow, gravity or wind (Behrensmeyer and Badgley 1989).

According to Lyman (1994), a ‘process’ can be defined as the action of a taphonomic agent, which is the immediate cause of modifications. The process is identified in the fossil record by the effects it has on fossils, which include physical, chemical, and biological modifications. These modifications are identified and interpreted by comparing them with processes observed under experimental conditions or through naturalistic monitoring projects where agents and processes are known (Fernández-Jalvo and Andrews 2016: 2). Modifications recorded on fossil bones, resulting from organic or inorganic agents that may not fossilise, while destructive, are valuable sources of information (Fernández-López 1991).

By building on the modifications and processes observed on individual fossils within an assemblage, we can reconstruct the extent of alterations in prehistoric bone assemblages. This includes determining the mode of accumulation, the time taken for accumulation, and fossilisation or diagenetic processes. Accurate identification of taphonomic processes thus relies on precise observations of these traces (Fernández-Jalvo and Andrews 2016: 2).

The two most abundant species, *M. melitensis* and *B. viridis*, were selected as the primary subjects for the taphonomic analysis. It is noted that the findings will be biased, due to the taphonomic analysis being restricted to two species, however these were chosen to ensure a sufficient sample size, since they were both consistently present throughout the stratigraphy. Arvicolids and amphibians also potentially served as prey for raptor birds and small carnivores. The impact of predation on small mammals has been extensively studied by researchers such as Andrews (1990) and Fernández-Jalvo *et al*. (2016). Additionally, anuran and reptile assemblages are increasingly becoming subjects of taphonomic studies, as demonstrated by Bisbal-Chinesta *et al*. (2020). This existing body of research provides a foundation for interpreting the Għar il-Fkieren assemblage.

4.3.3.1 Digestion and corrosion

Predation is an ecological process based on predator-prey relationships, in which the predator animal consumes the prey, and it is one of the main factors influencing small mammal accumulation in fossil deposits (Andrews 1990). It may be recognised by the presence of digestion marks, caused by the acidic saliva of avian predator species which causes the bone tissue to corrode, as well as breakage patterns and fauna representation (Fernández-Jalvo *et al*. 2016).

Two types of modifications may result from digestive processes of predators; surface modifications, and chemical alteration to the internal structure. These result from the stomach acidity and digestive enzymes of the predators. The acidic conditions tend to etch on the bone surface, while digestive enzymes break down the organic components of the internal structure. However, the extent of the modifications depends on the digestive tract acidity and the duration of the exposure to the digestive system (Fernández-Jalvo and Andrews 2016: 238).

The degree of modification also depends on how the prey is ingested. For instance, whereas mammalian carnivores chew their prey, nocturnal raptors ingest prey whole, while diurnal raptors tear the prey apart with claws and beaks, with each leaving their own distinct taphonomic signature (Fernández-Jalvo and Andrews 2018: 238). Breakage occurring before digestion also increases the exposure of bones to digestive acids, allowing the effects to penetrate more bone surface area. A hungry predator may also retain food in its stomach longer, leading to more advanced degrees of digestion and complete loss of more easily digestible skeletal elements (Fernández-Jalvo and Andrews 2018: 238). Avian predators often regurgitate indigestible parts of vertebrate prey, such as fur, feather and bone, leaving pellets in which bones are partially preserved. In contrast, mammalian carnivores, reptiles, and some birds like ospreys rarely or never regurgitate, causing their ingested prey to pass entirely through their digestive systems (Andrews and Evans 1983; Andrews 1990).

Thus, by quantifying the degrees of digestion one can identify the predator signatures and infer the predator responsible for the modifications (Fernández-Jalvo *et al*. 2016). However, the process of identifying digestion signatures can be complicated by the presence of chemical corrosion.

Corrosion refers to surface modifications resulting from chemical attacks due to either biological or geochemical actions. Unlike weathering, corrosion requires bones to be exposed to moist, chemically reactive conditions, often removed from direct air contact. This can occur through burial in soil, coverage by dense vegetation, or long-term immersion in still or stagnant water, which can degrade bone surfaces biologically (e.g., algae) or chemically (e.g., water acidity) (Fernández-Jalvo and Andrews 2018: 235). Both inorganic and organic processes contribute to corrosion, leading to unsystematic tissue loss. Specific environments like caves can create unique taphonomic conditions. One aspect is surface degradation and corrosion caused by presence of bat guano, while other factors include high humidity and protection from subaerial conditions, which produce corrosive conditions similar to burial in active soils and prevent weathering (Fernández-Jalvo and Andrews 2016: 235).

For *M. melitensis,* isolated and in-situ molars and incisors were chosen as the basis for inference, both due to their taxonomic utility in assigning species and because digestion patterns are the easiest to distinguish in arvicoline molars (Fernández-Jalvo *et al*. 2016). These were assessed for digestion patterns with a microscope at x20 magnification, following the typology devised by Stoetzel *et al*. (2009) and modified by Fernández-Jalvo *et al*. (2016) (Figure 15).

For *B. viridis*, specimens were analysed based on the scheme proposed by Bisbal-Chinesta et al. (2020). Modifications observed include: (i) rounding based on gastric acid action; (ii) cracking due to longitudinal fractures; (iii) thinning; (iv) flaking; and (v) digestive corrosion, which causes bone loss in the articular surfaces.

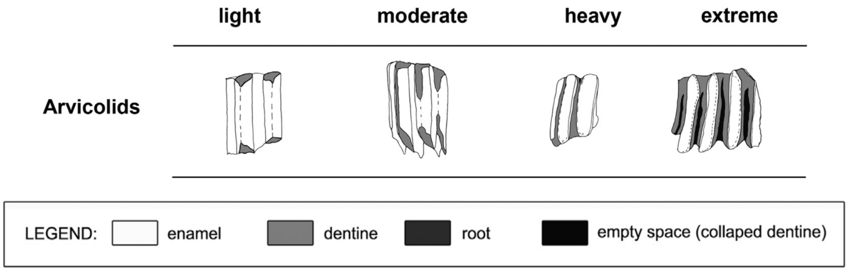


Figure 15: Light, moderate, heavy and extreme digestion in arvicolin molars from the same predator's pellet or scat (Fernández-Jalvo et al. 2016).

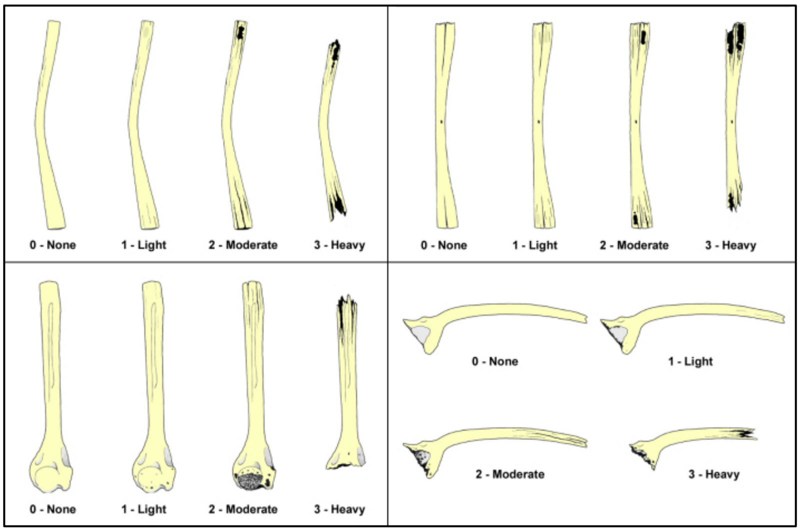


Figure 16: Anuran digestion typology. Digestion grades represent main digestive marks (splitting, thinning, bone collapse and corrosion). Chinesta-Bisbal et al. (2020).

4.3.3.2 Breakage

Breakage can be defined as fragmentation or fracturing of the skeletal element. Breakage can occur in different stages: (i) prior to burial and often resulting from predation, scavenging, trampling and/or rock fall in caves; (ii) during burial, by compression or sediment action; and (iii) post-burial, occurring after the skeleton has been preserved in sediment (diagenesis) (Fernández-Jalvo and Andrews 2016). Present-day exposure during collection or screening can also be potentially destructive and cause breakage, although these fractures will appear fresher than those occurring before field collection.

The characteristics of broken bones depend on several factors, including the developmental age of the bone (immature or adult), the condition of the bone (fresh/green or old/dry), and the shape of the element; with small, compact bones and teeth typically being more resilient to destructive taphonomic processes (Darwent and Lyman 2002).

While patterns of breakage are often not diagnostic, the greatest distinction is between post-depositional breakage resulting from sediment pressure or impact, occurring when bones have lost much of their organic matter and have dried out, and other agents affecting bones when they are still green or fresh (Fernández-Jalvo and Andrews 2016). Analysing these breakage patterns helps distinguish types of natural modifications and provides insights into the paleoecological conditions at the time of deposition. Different animals also cause different degrees of breakage (Andrews 1990), facilitating the identification of predators by proxy.

Since *M. melitensis* and *B. viridis* have different skeletal element counts and shapes, two different schemas were used when analysing breakage patterns. *M. melitensis* had a higher rate of surviving mandibles, so these were used in the scheme. *B. viridis* had no surviving mandibles, so four types of postcranial element were analysed; the humerus, radio-ulna, femur and ilium. These were the same elements used for the digestion analysis, allowing for a consistent sample size to compare breakage and digestion rates. The same references were also used to assess breakage degrees, with *M. melitensis* using the scheme proposed by Fernández-Jalvo *et al*. (2016: 141-142) and *B. viridis* using the scheme by Bisbal-Chinesta *et al*. (2020) (Figures 18-19).

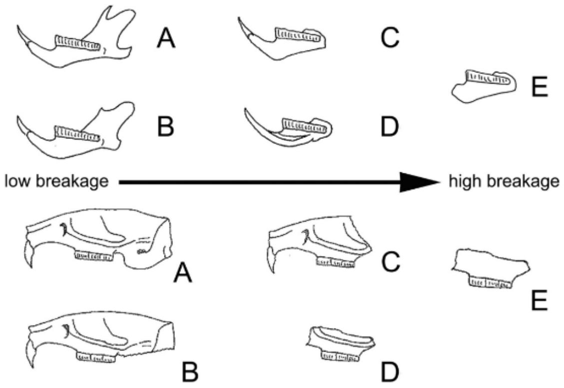


Figure 17: Breakage in mandibles (top) and maxillae (bottom) from low breakage (A and B) to the highest level of breakage indicated by E (Fernández-Jalvo et al. 2016, after Andrews 1990).

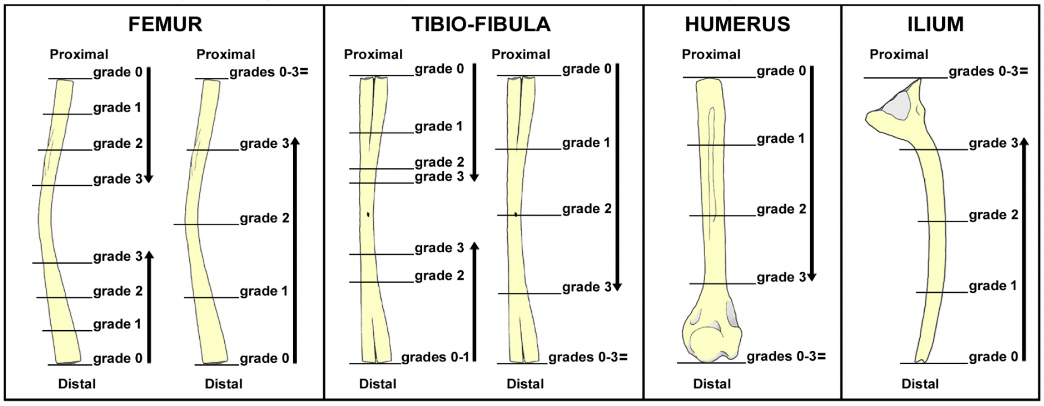


Figure 18: Breakage grades in anuran postcrania. Arrows indicate increasing breakage degrees from one or both proximal or distal parts. Bisbal-Chinesta et al. (2020). Humeri have been recorded as per diagram, although the distal ends appear to have been inverted by the authors.

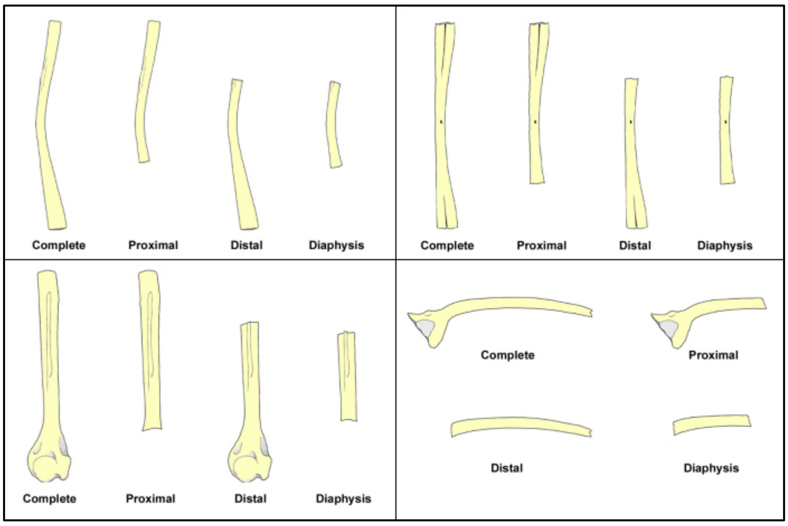


Figure 19: Breakage typologies in anuran postcrania. Digestion grades represent main digestive marks (splitting, thinning, bone collapse and corrosion). Bisbal-Chinesta et al. (2020). Humeri have been recorded as per diagram, although the distal ends appear to have been inverted by the authors.

4.3.4 Morphometic analysis

4.3.5 Comparative morphometry

A sample of 47 *M. melitensis* m1 molar specimens from Għar Dalam were observed and measured for m1 length. This allowed an estimation of body mass for each m1 of *M. melitensis* from both sites, in order to see if there was any statistically significant difference in body size across the two habitats.

4.3.5.1 Boxplot

A box plot (or 'box and whisker' plot) is method of displaying batches of data. It typically represents five values from the dataset: the maximum values, the upper and lower hinges (quartiles) and the median, along with any outliers (McGill *et al*. 1978). The box is a representation of interquartile (IQR) range (the middle 50% of the dataset), while the hinges (quartiles) represent the smallest and largest values 1.5 times the IQR range from the quartiles. Outliers are any values going beyond the quartiles, and are typically separately plotted as points outside of them.

In this study, the data from the Għar il-Fkieren (GhF) and Għar Dalam (GhD) datasets were prepared by focusing on the left and right m1 molar measurements for *M. melitensis*. The separate left and right m1 measurements were combined into a single variable, and missing values were handled by replacing zeros with NA.

To effectively compare the m1 sizes, normal distributions with the same mean and standard deviation as the measured data were generated for both datasets.

A box plot was then created to visualise the size comparisons between the GhF and GhD datasets and their corresponding normal distributions. The box plot was customised with specific colors, borders, horizontal orientation, and notches for clarity. This visualisation provided a clear representation of the morphological variations in *M. melitensis* m1 sizes, facilitating a straightforward comparison of the two datasets. The box plot's ability to show the central tendency, variability, and potential outliers made it an ideal tool for this analysis.

4.3.5.2 PCA, K-Means clustering and ANOVA

Principal Component Analysis (PCA) is one of the most fundamental forms of multivariate analysis. Its primary goal is to summarise the main aspects of variation within a dataset. PCA achieves this by reducing a set of variables into combinations that produce uncorrelated indices, ranked by their importance, to explain the data's variation. It is particularly effective when the original variables are highly correlated, either positively or negatively.

Traditionally, PCA has been applied to identify distinct groups of morphotypes, indicative of species and morphological variations. Phenetic taxonomy relies on examining numerous unweighted characteristics. Given the vast number of variables that can be evaluated for a plant or animal species, a mathematical method is required to organize them into units that correspond to taxa. Principal Component Analysis (PCA) helps researchers decrease the number of potential groupings. This is important because there is often redundancy among the variables, meaning that some variables are correlated with each other since they measure the same attribute (Kucharczyk *et al*. 2012).

The colour gradient on the PCA plots represents the $\cos^2$ values, indicating the quality of representation for each point. The principal components, Dim1 and Dim2, represent the axes of maximum variance in the data, allowing the identification of potential clusters or groups within the dataset. Points closer to each other on the plot are more similar in terms of the variables used in the PCA.

K-means clustering is a widely-used method for partitioning datasets. The algorithm aims to classify data points into clusters (K clusters), so that each data point belongs to the cluster with the nearest mean. It randomly selects points from the dataset (centroids), representing the centres of the K clusters. Each value in the dataset is then assigned to its nearest centroid. Once all values have been assigned, the mean of all the values is recalculated and the new centroid becomes the mean. This is repeated until the centroid values no longer change. At this stage, the data is finally grouped into K clusters which are representative of the final centroid. This method is particularly useful for grouping similar data points based on specific characteristics (Jain 2010). In this study, K-means clustering was applied to the PCA scores to classify the data into three clusters. The clusters were visualised using ggplot2, highlighting the grouping based on principal components.

Analysis of Variance (ANOVA) is a statistical method used to compare means among different groups and determine if any of those means are significantly different from each other. In this study, ANOVA was conducted on the original measurements, such as shaft width, shaft thickness, epiphysis width, epiphysis thickness, and length, to further understand the differences between the clusters identified by K-means clustering. ANOVA helps in identifying significant differences in the morphological traits among the clusters.

In summary, the morphological variations in the humeri of *B. viridis* and the femora of *M. melitensis* were analysed using PCA and K-means clustering. Measurements of humerus and femur shaft width, shaft thickness, epiphysis width, epiphysis thickness, and length were collected and cleaned by removing rows with missing values. PCA was conducted to reduce dimensionality and identify key components explaining the variance in the data. The data was standardised, and the PCA results were visualised through a scree plot and a biplot, displaying the relationships between variables and observations. K-means clustering was then applied to the PCA scores to classify the data into three clusters, which were visualised using ggplot2. To further understand the differences between clusters, ANOVA was conducted on the original measurements, testing for significant differences in the measured traits. This comprehensive approach, combining PCA and K-means clustering, allowed for an effective analysis of morphological variations and the identification of significant differences among the clusters.

4.3.6 Habitat weighting and palaeoenvironmental reconstruction

The habitat weighting method is a way to determine the habitat preferences of the species of past environments and quantify them to show how these habitats were distributed. This method, also known as the taxonomic habitat index, relies on the current distribution of each taxon in its modern habitats to reconstruct past environments (Evans *et al*. 1981; Andrews, 2006; modified by Blain *et al*. 2008; López-García *et al*. 2011).

The assumption underlying this approach is that the ecological requirements of the fauna found in Għar il-Fkieren are equivalent to those of their present-day relatives. Given that the Late Pleistocene species identified are still extant today and only one extinct fossil species is present in the assemblage, this assumption seems reasonable. The method is adapted to the study area, differentiating between various habitat types:

Forest (**Fo**): Large areas covered with trees.
Shrubland (**Sh**): Vegetation dominated by shrubs.
Grassland (**Gr**): Open areas covered with grass.
Desert (**De**): Areas with minimal precipitation and no vegetation cover.
Wetland (**We**): Areas where water covers the soil.
Steppe (**St**): Dry grassy plains.
Rocky (**Ro**): Substrates characterised by rocks or stones.

Each species was assigned a score of 1.00, which was then divided among the habitats where the species is currently found. The distribution ranges of all species were obtained from the IUCN Red List of Threatened Species spatial data (https://www.iucnredlist.org/resources/spatial-data-download). This method allowed inference of the likely habitats present in the past based on the ecological preferences of the extant fauna found in the study area.

The habitat weighting method was based on the R script first published in Berto *et al*. (2022). The process began by loading habitat weighting data from the habitat weighting dataset (Table 9) and the MNI or NISP percentages datasets. Species names in both datasets were standardised by trimming whitespace, converting to lowercase, and replacing spaces with underscores to ensure consistency. The two datasets were joined on the species column, creating a unified dataset containing only species present at the site. The joined table and MNI/NISP data were then converted into matrices necessary for subsequent calculations. Raw habitat weightings were calculated using matrix multiplication of the transposed joined data and the MNI/NISP matrix. The raw values were normalized to percentages by dividing by the row sums and multiplying by 100. These percentages were then rounded to two decimal places for clarity. The final habitat weighting percentages and the joined species-habitat data were then saved into separate Excel files for further analysis and record-keeping.

Species	**Fo**	**Sh**	**Gr**	**De**	**We**	**Ro**
Microtus melitensis	0.50	0.50	0.00	0.00	0.00	0.00
Crocidura sicula	0.00	1.00	0.00	0.00	0.00	0.00
Bufotes viridis	0.33	0.33	0.33	0.00	0.00	0.00
Podarcis cf. *filfolensis*	0.00	0.50	0.00	0.00	0.00	0.50

Table 9: Assigned values for habitat preferences. 1.00 distributed between preferred habitats.

5 RESULTS

This chapter is organised into four main sections, each addressing a specific aspect of the research findings: taxonomic identifications and systematic palaeontology (5.1), taphonomic analysis (5.2), morphometric data (5.3), and habitat weighting (5.4).

5.1 details the taxonomic identifications of the specimens analysed in this study, starting with a systematic review of the species identified from Għar il-Fkieren. Detail on the material studied, as well as the taxonomic process of identification is given in order to increase the scientific rigour of the study. The species habitat and research background are also given for each species in order to provide context for each species.

Section 5.1.1 outlines the Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI), providing foundational data on the diversity and abundance of species present in the sample.

Following this, the taphonomic analysis (5.2) examines the post-mortem processes affecting the specimens. This is divided into sub-sections covering digestion and soil corrosion (5.2.1) and breakage (5.2.2). Each subsection details the effects of these modifications on both *Microtus melitensis* and *Bufotes viridis* specimens.

Subsequently, the results of the morphometric analysis are presented (5.3), including Principal Component Analysis (PCA) (5.3.1) and a comparative morphometric analysis (5.3.2). These analyses provide insights into the morphological variation of the species under study.

The final section of this chapter, Habitat Weighting (5.4), explores the ecological contexts of the identified species. By assessing the habitat preferences and ecological niches, the environmental conditions at the time the specimens were deposited can be quantified and inferred.

5.1 SYSTEMATIC PALAEONTOLOGY

A total of 1697 number of specimens were taxonomically identified across all layers of the site. The following is a systematic review of the recovered species, including the material recovered and used as a basis for identification, a description of the identification process, research context for the species in the Maltese Islands and Sicily, and the known habitats of each species based on the IUCN red list (2023).

Order Rodentia Bowdich, 1821
Family Cricetidae Fisher, 1817
Subfamily Arvicolinae Gray, 1821
Genus *Microtus* Schrank, 1798
Microtus (Terricola) melitensis syn. *Pitymys melitensis* Bate, 1920

Material: 2-2.5m: 21 isolated teeth: nine lower incisors, five upper incisors, two left lower m1, two right lower m2, three right upper m1. **2.5-3m**: 54 isolated teeth: forty-one lower incisors, twenty-eight upper incisors, two left lower m1, 1 lower m2, two left and one right upper m1; 6 in-situ teeth: three lower right m1, two right lower m2, one right upper m3. **3-3.5m:** 277 isolated teeth: 137 lower incisors, 100 upper incisors, thirteen left and seven right lower m1, three left and two right lower m2, one left and one right lower m3, four left and six right upper m1, two left and one right upper m2. 43 In-situ teeth: eleven left and eleven right lower m1, ten left and ten right lower m2, one right lower m3. **3.5-4m**: 208 isolated teeth: 81 lower incisors, 83 upper incisors, fourteen left and eight right lower m1, five left and three right lower m2, one left lower m3, seven left and three right upper m1, two right upper m2, one left upper m3; 14 in-situ teeth: four left and two right lower m1, four left and three right lower m2, one left upper m3. **4-5m**: 97 isolated teeth: 29 lower incisors, 11 upper incisors, eleven left and ten right lower m1, ten left and seven right lower m2, four left and one right lower m3, five left and five right upper m1, one left and one right upper m2, two left upper m3;

65 in-situ teeth: fourteen left and eighteen right lower m1, thirteen left and fourteen right one right lower m2, four left upper m1, one right upper m3. **5-5.5m**: 34 isolated teeth: 17 lower incisors, 16 upper incisors, one left lower m1. 2 in-situ teeth: one right lower m1, one left lower m2. **5.5-6m**: 75 isolated teeth: 38 lower incisors, 27 upper incisors, four left and 3 right lower m1, one left and 2 right lower m2. **6-6.5m**: 108 isolated teeth: 41 lower incisors, 37 upper incisors, six left and six right lower m1, four left and three right lower m2, two left and one right lower m3, one left and three right upper m1, one left and three right upper m3; 42 in-situ teeth: twelve left and nine lower m1, six left and seven right lower m2, three left and four right lower m3, one right upper m3. **6.5-7m**: 54 isolated teeth: 26 lower incisors, 21 upper incisors, two right lower m1, one left lower m2, two left and one right upper m1, one upper m2. 1 in-situ tooth: one left lower m1. 7-7.5m: 59 isolated teeth: 23 lower incisors, 25 upper incisors, one right lower m1, two lower m1, three lower m2, one lower m3, one upper m1, three upper m2. 2 in-situ teeth: one right lower m1, one right lower m2. **7.5m-end**: 18 isolated teeth: 5 lower incisors, 7 upper incisors, one left and one right lower m1, one right lower m2, one left lower m3, one left and one right upper m1. 7 in-situ teeth: one left and two right lower m1, three left lower m2, one right upper m3.

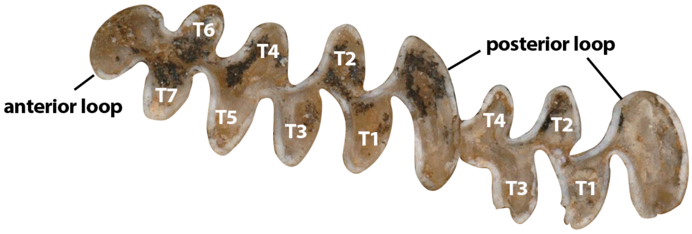


Figure 20: Microtus melitensis lower right m1 + m2 from Għar il-Fkieren, occlusal surface, with labels. T = triangle.

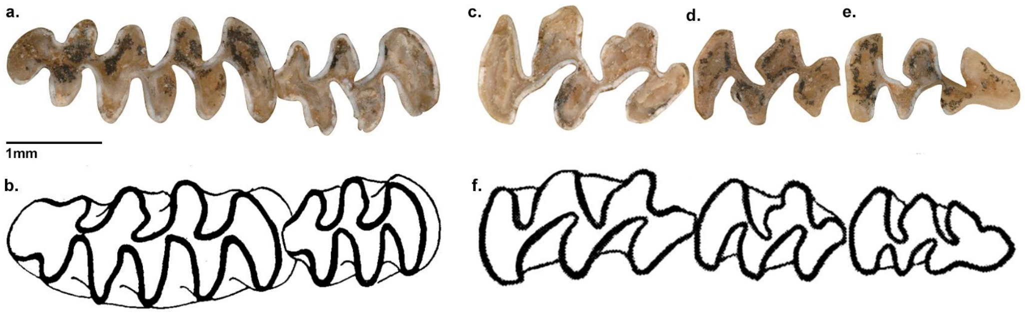


Figure 21: Microtus melitensis molars, occlusal surfaces. a: Lower m1 + m2 from Għar il-Fkieren. b: Lower m1 + m2 from Għar Dalam, Bate (1920). c-e: Upper molars (m1, m2, m3) from Għar il-Fkieren. f: Upper molars (m1, m2, m3) from Għar Dalam, Bate (1935).

Description: *Microtus (Terricola) melitensis* can be differentiated by its close relative *Microtus (Terricola) savii* by its subterraneomorph features, including a wide construction between the T6 and T7 and the anterior loop (Locatelli 2010). Observations include the irregularity of the T4 cusp on the lower first molar (m1), which presents as a pinched triangle. This shape deviates significantly from the more symmetrical or predictable forms seen in related species. The T2 cusp of the lower second molar (m2) and T3 cusp on the upper third molar (m3) display a similar pinched triangular shape, a morphological feature which appears unique to *M. melitensis*.

Background: The initial documentation of this species dates back to Adams (1866), who reported the presence of *Arvicola* remains in the Middle Cave and Mnajdra Cave, alongside frog remains within reddish soil layers. Adams (1877) additionally documented *Arvicola amphibius*, commonly known as the water vole. Bate (1920) officially designated the specimens recovered from the Upper Red Earth layers of Għar Dalam as *Pitymys melitensis*, based on the morphology of distinct cusps discernible on the first and second molars. Furthermore, Bate (1925) introduced a novel species named *Pitymys pauli*. The precise stratigraphic positioning of these two species remains ambiguous; however, it is apparent that both originated from the Red Earth layers. *Pitymys pauli* appears to represent an earlier species, traced to the Lower Red Earth layers of Għar Dalam, and is notably absent from the Għar il-Fkieren assemblage.

Microtus melitensis appears to have gone extinct sometime between the Late Pleistocene and the beginning of the Holocene; the reasons for this extinction have not yet been explored. Chaline *et al*. (1999) suggest that *M. melitensis*' closest living relative is the Italian endemic *Microtus (Terricola) savii* (common pine vole). Both *M. savii* and *M. pyrenaicus* are characterised by a 'simplex type' third upper molar (M3) (Chaline 1972). This same M3 morphotype in *M. melitensis* and *M. tarentina* of Apulia suggests the common ancestry which *M. savii* shares with these species (Chaline et al. 1999). Brunet-Lecomte and Chaline (1991) place *M. tarentina* and *M. savii* in the 'Mediterranean' group with the fossil species *M.*

henseli and *M. melitensis* based on their morphological characteristics and geographic distribution.

Locatelli (2010) suggests that due to its larger size than current *M*. *savii* voles, *M. melitensis* is the result of a dispersal of primitive *M*. *savii* voles from Isolidda 3 sometime during a period of glacial marine highstands during MIS 6. *Microtus melitensis* then underwent genetic drift, resulting from living in isolated conditions for a long time.

Habitat and distribution: Since *M. melitensis* are an extinct fossil species, its habitat and distribution are inferred from its closest relative, *M. savii*. *Microtus savii* is endemic to Europe, where it is found throughout most of Italy (excluding the far north-east), Sicily, the borders of southern Switzerland and southeast France. It occurs from sea level to 2,000 m above sea level, preferring most terrestrial habitat types except for high altitudes, dense woodlands or very wet, sandy or rocky areas (IUCN 2023).

Order Soricomopha Gregory, 1910
Family Soricidae Fischer von Waldheim, 1917
Genus *Crocidura* Wagler, 1832
Crocidura sicula Miller, 1900

Material: 2-2.5m: one left and two right mandibles with teeth. **2.5-3m**: one left and one right mandible with teeth. **3-3.5m**: two left and one right mandible with teeth. **3.5-4m**: two right mandibles with teeth. **4-5m**: one right mandible with teeth. **5-5.5m**: two left mandibles with teeth. **5.5-6m**: one left and one right mandible with teeth. **6-6.5m**: five left and two right mandibles with teeth. **6.5-7m**: one femur and two tibiae. **7-7.5m**: four left and four right mandibles with teeth. **7.5m-end**: four left and one right mandibles with teeth.

Description: The recovered soricid material consisted primarily of dentition, which enabled identification of the species *Crocidura sicula*. The length and height of the mandibular body, the size and shape of the ramus matched both those of Sicilian extant (Figure 24) and fossil *C. sicula* (Locatelli 2010: 58, Plate 4). The internal temporal fossa, the pterygoid spicule, as well as the angular process when present,

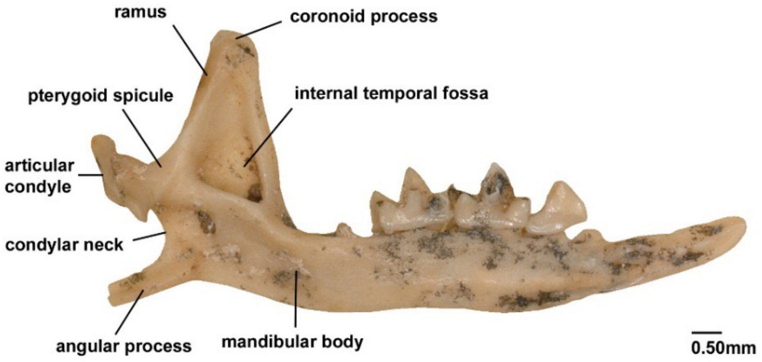


Figure 22: Crocidura sicula left mandible from Għar il-Fkieren [35112_2], medial view, labeled.

Figure 23: Crocidura sicula left mandible from Għar il-Fkieren [33041_1]: Occlusal, lingual and labial views.

Figure 24: Crocidura sicula right mandible from Sicily in medial view. Scale bar = 5mm. Siracusa et al. (2022).

are also morphologically similar (see Figure 22). Vogel *et al*. (1989) have also published taxonomic comparisons of *Crocidura* species; however, these are based on the upper unicuspid teeth, of which not enough specimens were available for comparison. Comparative analysis was also conducted with extant *Suncus etruscus* from Sicily (Kouvari *et al*. 2021; Siracusa *et al*. 2022) but not assigned to this species since: (i) *S. etruscus* are significantly smaller; (ii) the ventralmost point of the condylar neck is indented further in *C. sicula*. The specimens were also not assigned to *Crocidura esuae*, the more ancient form of *C. sicula* on account of: (i) the more robust ramus, and (ii) the coronoid process, which does not angle backwards (Locatelli 2010).

Background: Remains of *Crocidura* are mentioned from two Pleistocene sites; Għar Dalam and tal-Ġnien fissure in Imqabba. The first remains of *Crocidura* were recovered by Caton Thompson in Għar Dalam in disturbed layers (1925) and observed to have similarities to the species *Crocidura leucodon* by Bate (1925). Storch, during his assessments of the micromammalian fauna of the cave (1970, 1974), uncovered *Crocidura* remains from virtually every stratigraphic layer in the cave. Although these *Crocidura* specimens were attributed to many subspecies (*C. leucodon, C. russula, C. suavolens*), it was Hutterer (1990, 1991) who ultimately classified all these specimens under *Crocidura sicula esuae*. This subspecies appears to have been endemic to the islands since the Middle Pleistocene, while a more recent species (*Suncus etruscus*) recovered from the Għar Dalam superficial '*Rattus rattus*' layer was most likely introduced by humans (Storch 1974).

According to Masini *et al*. (2008), *C. sicula* is considered to be a descendant of a Late Pleistocene newcomer. However, Kotsakis (1986), Esu *et al*. (1986) and Sarà (1995) consider *C. esuae* to be an ancestor of *C. sicula*. Further morphological, genetic and DNA studies (Maddalena *et al*. 2004; Vogel *et al*. 2004; Dubey *et al*. 2007) strongly indicates that *C. sicula*, and by extension *C. esuae*, descended from the African shrew *Crocidura tarfayaensis* due to its strong genetic affinity to living African forms, with the split occurring sometime between African and Sicily during the Messinian, thus raising the possibility that these ancestral species of *C. sicula* had arrived from North Africa sometime during the Late Miocene (Marra 2013). Fossil remains of *C. esuae* have been present in Sicily since the Early Middle Pleistocene, first recorded at Spinagallo cave (Locatelli 2010: 67, Marra 2013: 117). *Crocidura* have not been recorded at Monte Pellegrino, the oldest Quaternary

Sicilian type site (likely Early Pleistocene age), however, this does not necessarily exclude the possibility of a Late Miocene origin (Marra 2013).

Habitat and distribution: *C. sicula* is an endemic species which currently inhabits Gozo, Sicily, Ustica and the Egadi Islands (IUCN 2023). In Malta, it may be extinct as it is only found as fossil remains (Vogel 1999), although Aloise *et al*. (2011) have discovered possible specimens from *Asio otus* owl pellets on Comino Island. According to owl pellet analysis, its preferred habitats are open shrub and suburban areas such as gardens (Vogel 1999). Amori *et al*. (2008) also note that it is widespread in all environments from sea level up to 1600m above sea level, although it prefers less arid environments.

Order Anura Duméril, 1806
Family Bufonidae Gray, 1825
Genus *Bufotes* Laurenti, 1768
Bufotes viridis syn. *Bufo viridis* Laurenti, 1768

Material: 2-2.5m: one astragalus, three humeri, two radio-ulnae, one tibio-fibula, one vertebra. **2.5-3m**: three left humeri, three ilia, five phalanges, three radio-ulnae, two urostyles. **3-3.5m**: two astragali, one coracoid, one left and three right humeri, two ilia, two radio-ulnae, one scapula, one talus, six tibio-fibulae, four ulnae, three urostyles, two vertebrae. **3.5-4m**: seven astragali, two left and eleven right humeri, five ilia, two phalanges, one quadratojugal, two radio-ulnae, two scapulae, eighteen tibio-fibulae, one urostyle, nineteen vertebrae. **4-5m**: one femur, one left humerus, two ilia, three phalanges, two radio-ulnae, one tibio-fibula. **5-5.5m**: four astragali, one right humerus, two ilia, seven indeterminate long-bones, two tibio-fibulae, one urostyle. **5.5-6m**: three left and two right humeri, one hyoid, one quadratojugal, two radio-ulnae, two tarsals, one tibio-fibula, one urostyle, two vertebrae. **6-6.5m**: one astragalus, one coracoid, two femurs, nine humeri, four hyoids, ten ilia, nineteen phalanges, ten radio-ulnae, four scapulae, fifteen tibio-fibulae, forty-one vertebrae. **6.5-7m**: one coracoid, six humeri, three ilia, one radio-ulna, one tibio-fibula, one urostyle, two vertebrae. **7-7.5m**: one coracoid, three humeri, four ilia, one phalanx, two radio-ulnae, one scapula, five tibio-fibulae, three urostyles. **7.5m-end**: one astragalus, one humerus, nine radio-ulnae, one scapula, one tibio-fibula, one urostyle, four vertebrae.

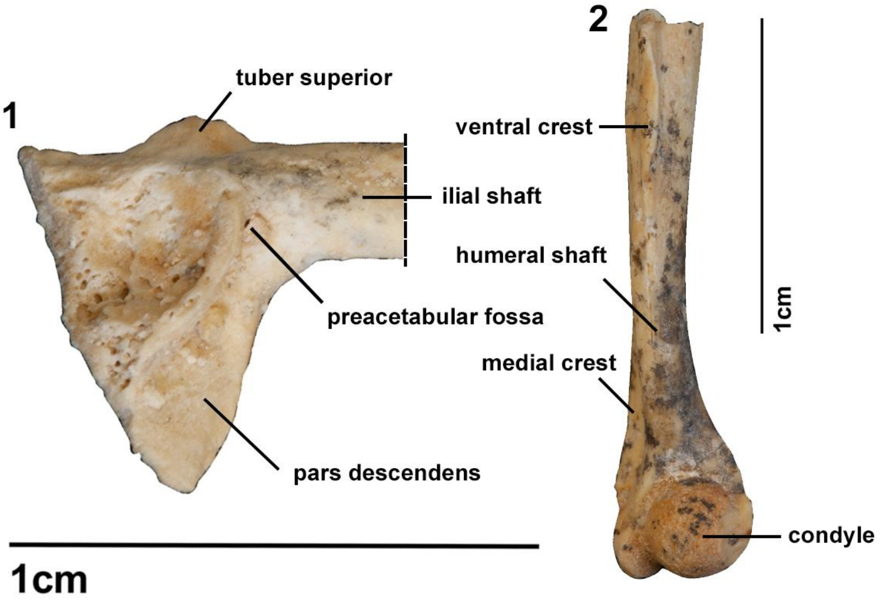


Figure 25: Bufotes viridis from Għar il-Fkieren, labelled. 1. Right ilium, lateral view; 2. Left humerus, ventral view.

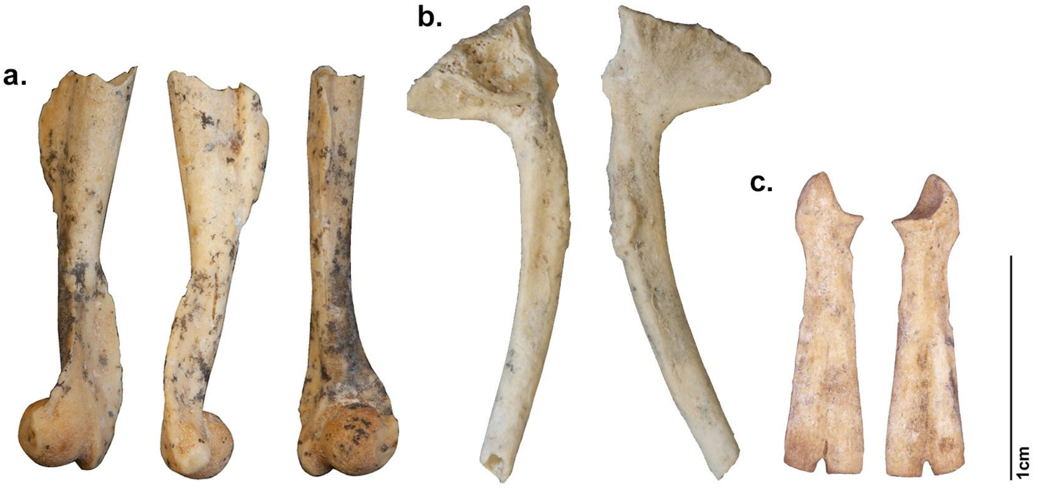


Figure 26: Bufotes viridis from Għar il-Fkieren. a. Humerus; b. Ilium c. Radio-ulna in lateral and medial view.

Description: Recovered specimens consisted entirely of postcranial elements (Figure 26), which were compared to visual references both for *Discoglossus pictus* (Martínez-Navarro *et al*. 2014) and *Bufotes viridis* (Blain *et al*. 2010). The specimens were assigned to the *Bufotes* genus, based on the absence of the dorsal wing on the ilial shaft which is present in *Discoglossus*, as well as the laterally displaced condyle present on the *B. viridis* humerus (Blain *et al*. 2010), which in *Discoglossus* is more central. The humerus has a slightly curved and thick shaft.

Diaphysis of the humerus is also longer and less curved and robust, and according to Hossini (2002: 242) the ventral crest is slightly shorter than other *Bufotes* species. On the ilium, there is an absence of a calamital ridge on the ilial shaft, and the outline of the *pars descendens* is less markedly convex (Blain *et al*. 2010). Based on these characteristics and the fact that there is only one recorded *Bufotes* fossil species, the specimens were assigned to *B. viridis*.

Background: The earliest reference to the *Bufotes* genus of toads in the Maltese Islands can be attributed to G. A. Boulanger, who identified a *Bufo* species from Għar Dalam (Despott 1923: 9). Despott (1923) also noted the abundance of *Bufo* remains from the second Red Earth layer, aligning with the date and associated fauna of Għar il-Fkieren. Parker, in Bate (1935), was the first to identify *Bufo viridis*, distinguishing it from *Bufo bufo* based on the morphology of the remains found, implying that earlier records may have been misattributed. Despite this, subsequent studies continued to mention *Bufo bufo* alongside *Bufo viridis* (Savona Ventura 1984; Hunt and Schembri 1999; Baldacchino and Schembri 2002).

Bufo cf. *viridis* is linked to Sicily's Spinagallo faunal complex and has been documented at Monte Pellegrino, Sicily, a site dating back to the early Middle Pleistocene (Guglielmo and Marra 2011; Marra 2013). It is plausible that, akin to its associated fauna *Leithia*, *Bufo* cf. *viridis* dispersed to Sicily, and possibly Malta, prior to the early Middle Pleistocene through natural rafting (Marra 2013).

Habitat and distribution: *B. viridis* thrive in forest, forest steppe, scrub, grass and alpine type habitats. Their reproduction and larval development require the presence of temporary or permanent water bodies, such as lakes, pools, streams or rivers (IUCN 2023). *B. viridis* is extirpated and no longer inhabits the Maltese Islands; this species is now distributed across the western Palearctic region, from North Italy to West Russia (IUCN 2023).

Order Squamata Oppel, 1811
Suborder Serpentes Linnaeus, 1758
Superfamily Colubroidea Oppel, 1811
Family Colubridae Oppel, 1811
Colubridae sp.

Material: 2.5-3m: two vertebrae. **3-3.5m**: nine vertebrae. **3.5-4m**: seventeen vertebrae. **4-5m**: three vertebrae. **5-5.5m**: eight vertebrae. **5.5-6m**: twenty-five vertebrae, one left dentary with teeth. **6-6.5m**: twenty-three vertebrae. **6.5-7m**: fourteen vertebrae. **7-7.5m**: eight vertebrae.

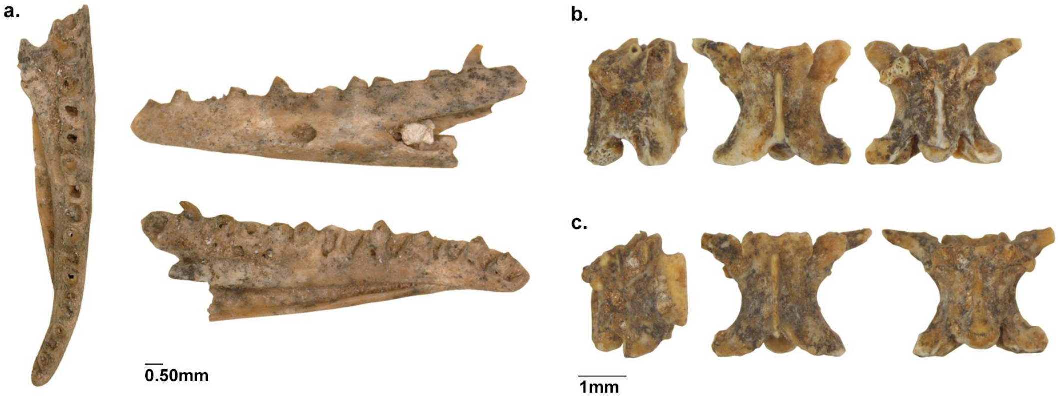


Figure 27: Colubridae sp. from Għar il-Fkieren. a: Left dentary [33414_1]. b-c: Trunk vertebrae [3441_1, 33474_1].

Description: The vertebrae recovered from the site averaged 4 mm in size and were determined to belong to small-sized colubrids based on the absence of hypapophyses, a characteristic used to differentiate specific subfamilies (Carmona *et al*. 2010). *Natricinae* and *Elapidae* were excluded as potential subfamilies since hypapophyses are present on all vertebrae in these groups. *Hierophis viridiflavus* was also ruled out as a potential identification based on several key morphological features of the dentary: (i) the ventralmost point of the dentary is more robust and curved; (ii) the Meckel’s canal opens further posteroventrally; (iii) the dorsomedial process is less robust (Racca et al. 2020: 17). The specimens closely resemble those of *Telescopus fallax* and *Zamenis situla* (see Szyndlar (1991). There is also a possibility that the specimens belong to *Hemorrhois algirus*; however, this species is generally much larger in size, and no comparative reference was available for confirmation.

Background: Serpentae are notably absent from documentation of other known Quaternary sites. Presently, four colubrid snake species inhabit the Maltese Islands: the cat snake (*Telescopus fallax fallax*), leopard snake (*Zamenis situla*), green whip snake (*Hierophis viridiflavus*), and Algerian whip snake (*Hemorrhois algirus*). Borg (1939) proposed that the Algerian whip snake and the cat snake were introduced to Malta during the First World War via shipments of firewood. However, the fossil material at Għar il-Fkieren confirms the presence of at least one colubrid species on Malta since the Late Pleistocene and indicates its status as a local species.

In Sicily, a *Coluber* cf. *viridiflavus* along with indeterminate *Natrix* sp. are associated with the early Middle Pleistocene Spinagallo faunal complex (Kotsakis 1977, Guglielmo and Marra 2011). Material from Monte Pellegrino (De Gregorio 1887) and Castellana (De Gregorio 1925) originally referred to as rodents actually pertains to snakes, likely colubrids (Delfino 2002; Georgalis 2019: 289). If the Sicilian taxonomic attributions are correct, it appears that the Għar il-Fkieren specimens did not descend from these species. However, much further studies and comparisons are needed to confirm the taxonomy, phylogeny and origins of this newly uncovered colubrid species.

Habitat and distribution: While the species has not been determined yet, all surviving Maltese colubrids which most closely resemble the specimens prefer shrub Mediterranean type habitats with or without vegetation cover. *Telescopus fallax* inhabits Malta, Eastern Europe and the Middle East, and can be found in shrubby landscapes or open and degraded woodland; in some cases, it can be found on sandy beaches with vegetation cover. It is the most adapted to temperate forest type habitat from the three species (IUCN 2023). *Zamenis situla* populations extend from Croatia to Eastern Turkey as well as Malta. This species prefers Mediterranean-type shrubby vegetation and may be found in macchia, karst habitats, marshes, stream edges, and in agricultural or rural areas. *Hemorrhois algirus* is the species most adapted to arid, hot landscapes with sparse vegetation; it inhabits most of North Africa and the Sahara and can be found in open scrub, semi-desert, steppe and rural areas (IUCN 2023).

Family Lacertidae Oppel, 1811
Genus *Podarcis* Wagler, 1830
Podarcis cf. *filfolensis* Bedriaga, 1876

Material: 2-2.5m: one left lower dentary with teeth. **2.5-3m**: one left lower dentary with teeth. **7.5-end**: one left lower dentary with teeth.

Figure 28: Podarcis cf. filfolensis left dentary from Għar il-Fkieren [3052_1].

Description: The recovered remains (three dentaries) are very small, measuring an average of 6-7mm. These specimens were identified as Lacertidae based on the characteristics of the dentition. Due to the lack of comparative material and the fact that Maltese herpetofauna has not yet been osteologically characterised, the specimens could not be physically compared to any comparative material. However, based on the size of the specimens and the fact that there is only one species of small Lacertid present in the Maltese Islands (*Podarcis filfolensis*), the specimens were assigned as *Podarcis* cf. *filfolensis* to increase the robustness of the habitat weighting method.

Background: The earliest reference to lizard remains from Pleistocene sites can be traced back to Adams (1865), who later described these as *Lacerta* (1866) remains from Ta' Gandja fissure; however, these specimens were not locatable (Böhme and Zammit-Maempel 1982). Adams associated these remains with those of elephants and hippos, some of which he identified as 'small lizards,' while others were likened to a chameleon in size (Adams, 1865, 1866). Possibly the most well-known lizard specimen in the Maltese Islands is *Lacerta siculimelitensis*, a giant species of lacertid originally designated as *Lacerta melitensis* by Giovanni Gulia (1912). Mertens (1942) also described this Pleistocene species with the same name, and notes the co-existence of giant and dwarf lizards as a common occurrence on islands.

Böhme and Zammit-Maempel (1982) further elucidated this giant species based on findings from the Wied Incita fissure, discovered in 1973. The fossils were associated with *Leithia*, *Ursus*, *Paleoloxodon*, *Hippopotamus* and *Cervus*, placing its existence tentatively in the early stages of the Late Pleistocene (167.3 - 151.2 ka) based on the present fossil fauna. The absence of this species at Għar il-Fkieren indicates that by the Late Pleistocene (80.1 - c. 20-23 ka), this giant species seemingly did not coexist with the small lacertid species present in the vicinity of the site. This raises intriguing questions regarding the reasons behind its absence during this period, although with so little remains of *L. siculimelitensis,* it is difficult to comment on their contemporaneity with other species.

Lacerta sp., *Lacerta viridis* and *Lacerta siculimelitensis* were also discovered at Monte Pellegrino in Sicily, in layers dated to approximately 900 ka. These lacertids were associated with other fauna discovered in the Middle Pleistocene of the Maltese Islands, including *Leithia melitensis*, *Maltamys gollcheri* and *Palaeoloxodon falconeri* (Bonfiglio et al. 2001).

Rodríguez and colleagues’ (2014) genetic and microsatellite analysis suggest that ancient forms of *Podarcis* arrived in the Maltese Islands during the Messinian Salinity Crisis and became isolated when the Mediterranean basin re-flooded around 5.33 Ma. A divergence of the two founding lineages which shared a common ancestor sometime between 869 - 105 ka indicates a mid-late Pleistocene divergence (Rodríguez *et al*. 2014: 301). The observed diversification of current *Podarcis* subspecies and dispersal of these subspecies to other Maltese Islands may have been possible due to shallower sea depths during times of glacial sea level drops.

Habitat and distribution: *Podarcis filfolensis* prefers scrubland, rocky areas, gardens, and can also occasionally be found living in seabird colonies. Its current distribution is throughout the Maltese Islands including Gozo, Filfla, Selmunett Islands and Fungus Rock, and on the Italian islands of Linosa and Lampione. It has also recently been introduced to the island of Lampedusa, Italy (IUCN 2023).

Order Chiroptera Blumenbach, 1779.
Chiroptera sp. Blumenach, 1779.

Material: **2.5-3m**: 10 phalanges. **3-3.5m**: nine humeri, 13 phalanges, three ribs. **3.5-4m**: six phalanges, two ribs. **5-5.5m**: one humerus, five ribs, six phalanges. **6-6.5m:** one femur, one pelvis, four phalanges, 21 ribs. **6.5-7m**: 22 phalanges, 13 ribs, nine femurs. **7.5-end**: 10 humeri, nine phalanges, seven ribs.

Description: The material recovered mainly consisted of phalanges and ribs which are not that identifiable to species, while the humeri and femora were very similar to those of small birds. No mandibles were present in the assemblage. The process of identification presented several challenges due to absence of local postcranial reference material thus making identification of species particularly difficult.

Background: Bats present during the contemporaneous layers (‘*Pitymys melitensis*’ stage) at Għar Dalam, according to Storch (1974), included *Rhinolophus hipposideros*, *Rhinolophus euryale*, *Rhinolophus mehelyi*, *Rhinolophys blasii* and *Myotis schreibersi*. Of these species, *R. mehelyi* and *R. blasii* are now extirpated (IUCN 2023).

5.1.1 Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI)

Overall, 1697 specimens were identified to species (Table 12). A total of 1044 *Microtus melitensis* specimens, 66 *Crocidura sicula* specimens, 285 *Bufotes viridis* specimens, 170 Colubridae sp. specimens, three *Podarcis* cf. *filfolensis* specimens, and 129 Chiroptera sp. specimens were identified from the microfauna assemblage from Għar il-Fkieren. *M. melitensis* was the best represented species, comprising 62% of the total sample across the site. This was followed by *B. viridis* at 17% and Colubridae sp. at 10%. (Table 12).

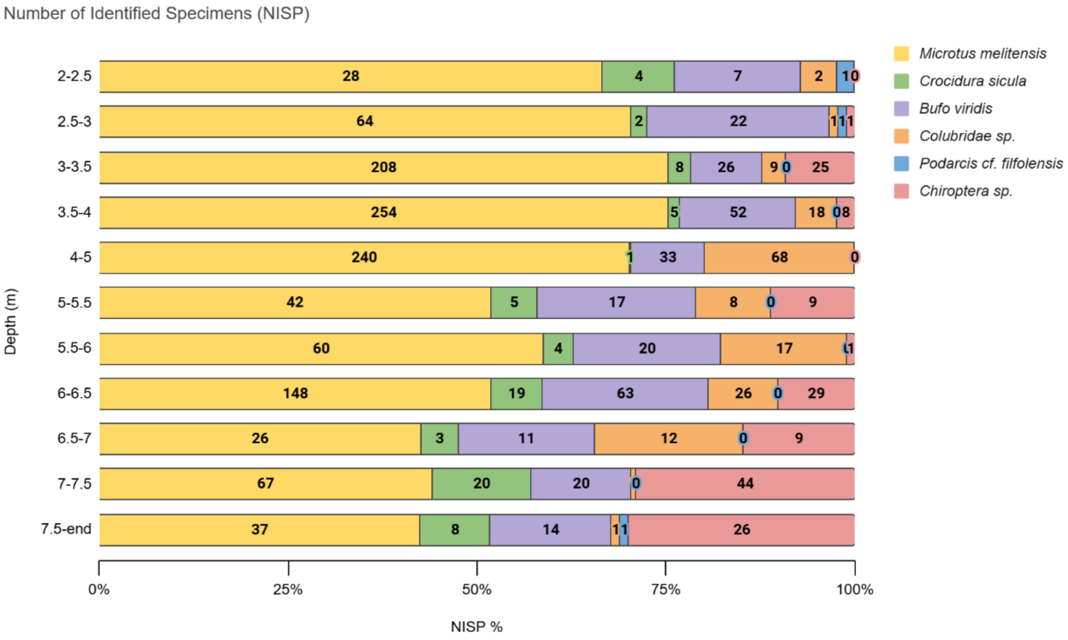


Table 10: Figure: Number of Identified Specimens (NISP) % of microfauna from Għar il-Fkieren.

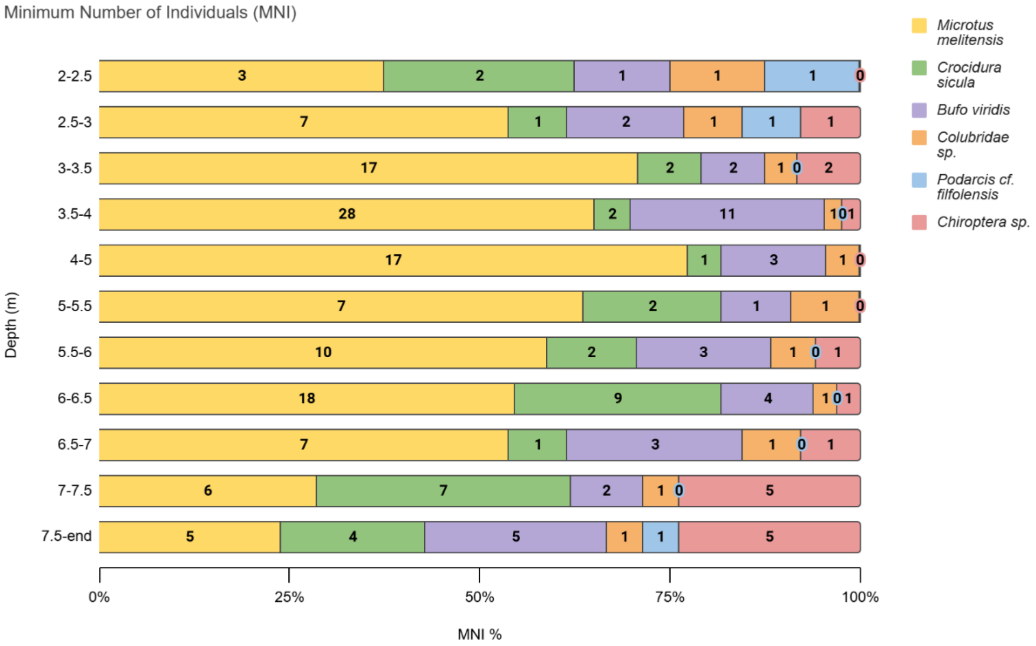


Table 11: Minimum Number of Individuals (MNI) % of microfauna from Għar il-Fkieren.

DEPTH (m)	**2-2.5**			**2.5-3**			**3-3.5**			**3.5-4**			**4-5**			**5-5.5**			**5.5-6**			**6-6.5**			**6.5-7**			**7-7.5**			**7.5-end**		
TAXA	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**	**NISP**	**MNI**	**NISP%**
Microtus melitensis	28	3	66.7	64	7	69.6	208	17	75.4	254	28	75.4	240	17	70.2	42	7	51.9	60	10	58.8	148	18	51.9	26	7	42.6	67	6	44.1	37	5	39.8
Crocidura sicula	4	2	9.5	2	1	2.2	8	2	2.9	5	2	1.5	1	1	0.3	5	2	6.2	4	2	3.9	19	9	6.7	3	1	4.9	20	7	13.2	8	4	8.6
Bufo viridis	7	1	16.7	22	2	23.9	26	2	9.4	52	11	15.4	33	3	9.6	17	1	21.0	20	3	19.6	63	4	22.1	11	3	18.0	20	2	13.2	14	5	15.1
Colubridae sp.	2	1	4.8	2	1	2.2	9	1	3.3	18	1	5.3	68	1	19.9	8	1	9.9	17	1	16.7	26	1	9.1	12	1	19.7	1	1	0.7	7	1	7.5
Podarcis cf. *filfolensis*	1	1	2.4	1	1	1.1	0	-	0.0	0	-	0.0	0	-	0.0	0	-	0.0	0	-	0.0	0	-	0.0	0	-	0.0	0	-	0.0	1	1	1.1
Chiroptera sp.	0	-	0.0	1	1	1.1	25	2	9.1	8	1	2.4	0	-	0.0	9	1	11.1	1	1	1.0	29	1	10.2	9	1	14.8	44	5	28.9	26	5	28.0

Table 12: Number of Identified Specimens (NISP), Minimum Number of Individuals (MNI), and NISP % of identified microfauna from Għar il-Fkieren.

5.2 TAPHONOMIC ANALYSIS

5.2.1 Digestion and soil corrosion

5.2.1.1 Microtus melitensis

Of the total 1124 incisors (including both isolated and in-situ teeth), 81 % showed signs of some form of chemical corrosion. Of these, 63% exhibited heavy corrosion affecting the whole tooth. This is consistent with chemical corrosion in the soil as opposed to digestive corrosion by predators which tends to produce a characteristic 'rounding' at the edges of the dental elements. The remaining 18% exhibited light to heavy signs of digestion, and 19% had no signs of digestion or soil corrosion (Figures 29-30).

5.2.1.2 Bufotes viridis

A total of seven femora, 52 humeri, 31 ilia, and 58 tibio-fibulae were taphonomically analysed based on the scheme proposed by Bisbal-Chinesta *et al*. (2020). Modifications observed include: (i) rounding based on gastric acid action; (ii) cracking due to longitudinal fractures; (iii) thinning; (iv) flaking; and (v) digestive corrosion, which causes bone loss in the articular surfaces. The anuran postcrania exhibited more signs of digestive corrosion than the arvicoline dentition, with most specimens exhibiting light to moderate digestion across all layers (Figure 31).

5.2.2 Breakage

5.2.2.1 Microtus melitensis

A total of 30 mandibles and 15 maxillae were examined for breakage using the scheme proposed by Fernández-Jalvo *et al*. (2016: 141-142) (Figure 32). Moderate to high rates of breakage were observed across all layers, with 66% having light to heavy breakage and just 4% complete specimens.

Outliers include the 5-5.5m layer, which may be attributed to the modest sample size available for that layer (six specimens). The 5.5-6m layer exhibited the highest rate of heavy breakage, with 100% of the specimens showing significant damage.

However, this sample size was also relatively small, consisting of just nine specimens.

5.2.2.2 *Bufotes viridis*

A total of seven femora, 52 humeri, 31 ilia, and 58 tibio-fibulae were examined for breakage degrees based on the scheme proposed by Bisbal-Chinesta *et al*. (2020: 4). All degrees of breakage were observed, but mostly a moderate rate of breakage was observed across all layers except for 5-5.5m, which may be attributed to the smaller sample size for this layer (Figure 33).

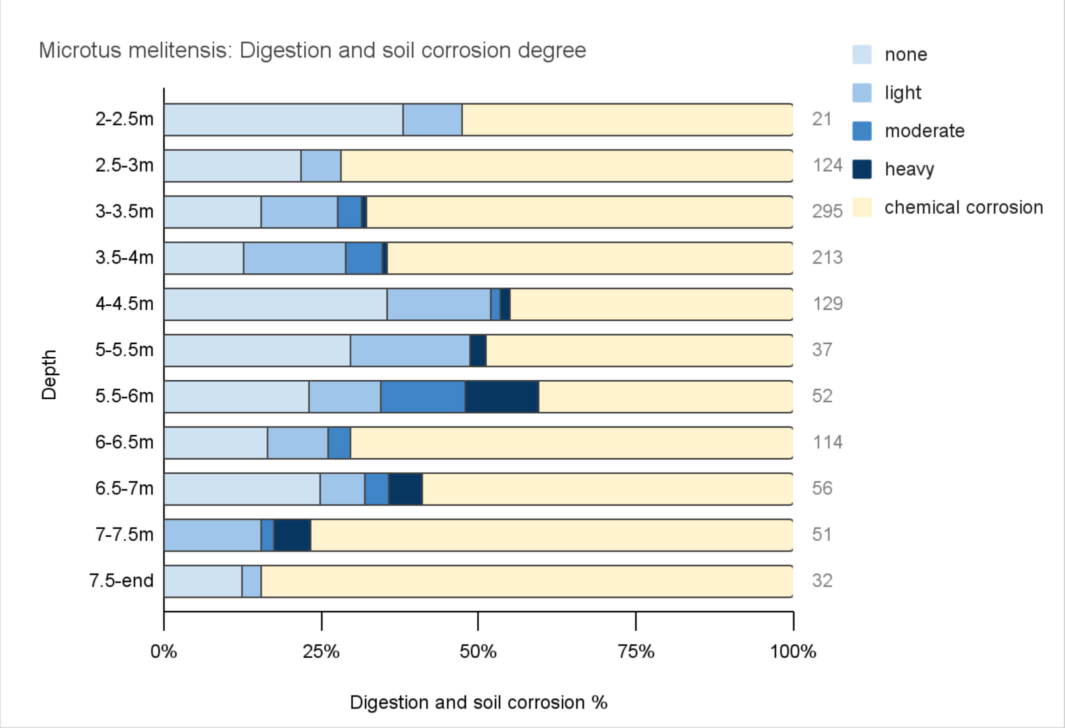


Figure 29: Microtus melitensis % digestion and chemical corrosion.

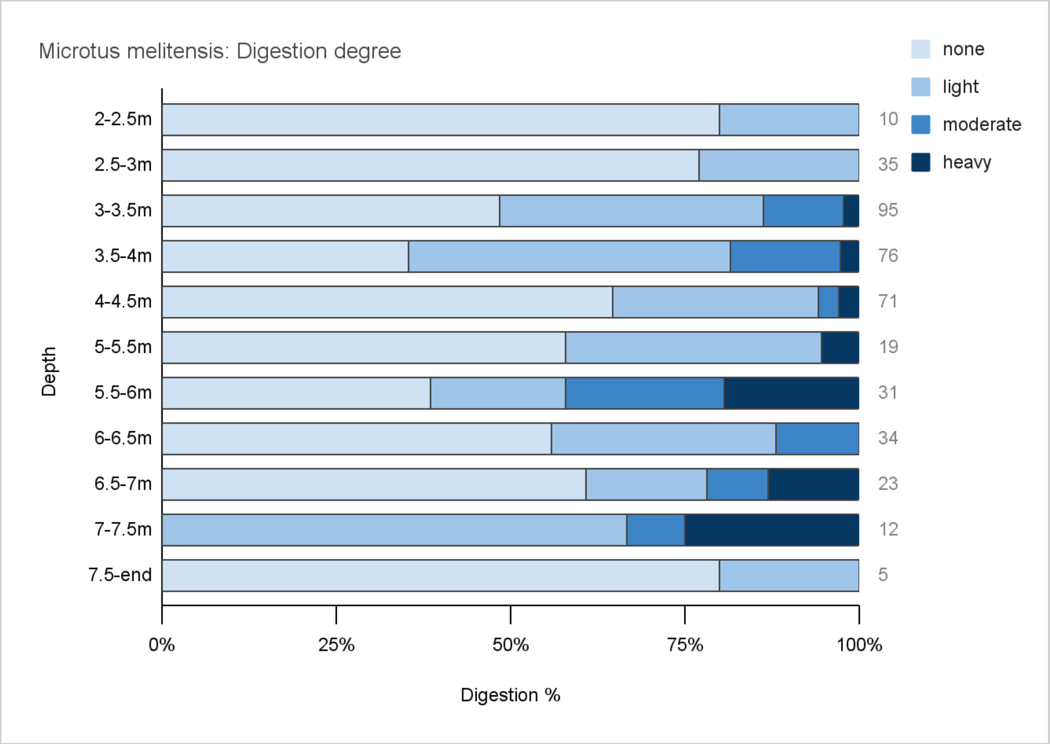


Figure 30: Microtus melitensis % digestion.

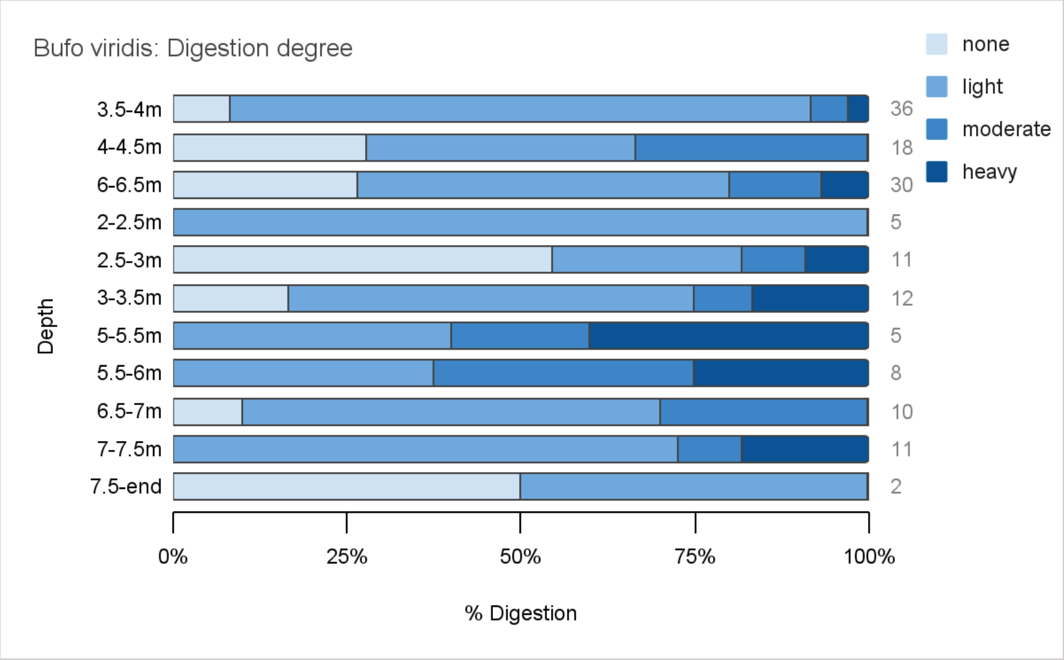


Figure 31: Bufotes viridis % digestion.

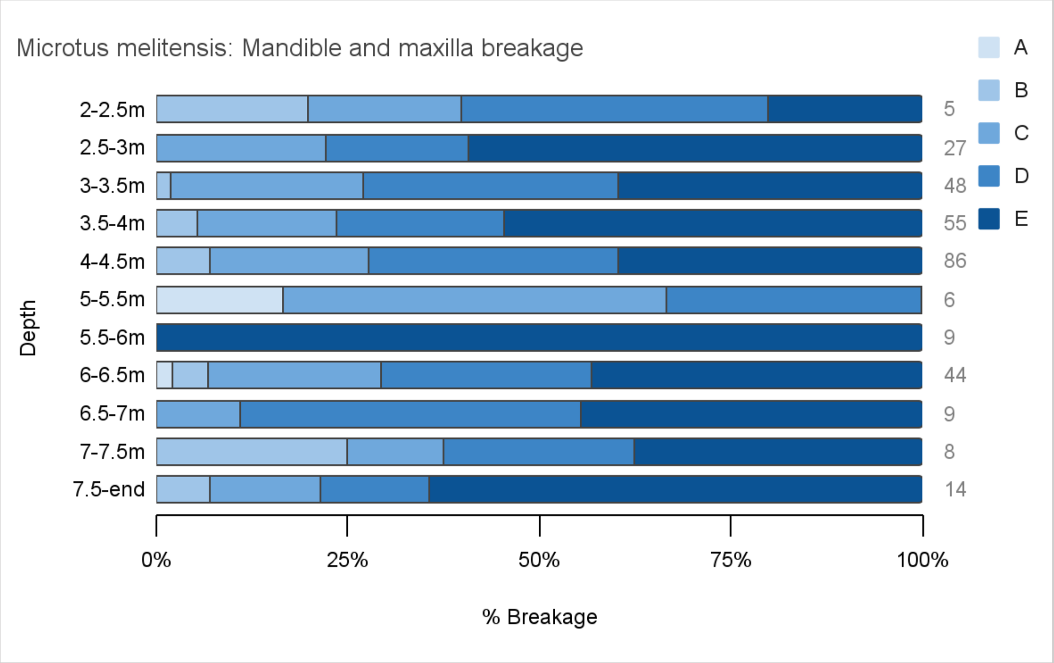


Figure 32: Breakage degrees of Microtus melitensis mandibles and maxillae based on Fernández-Jalvo et al. (2016).

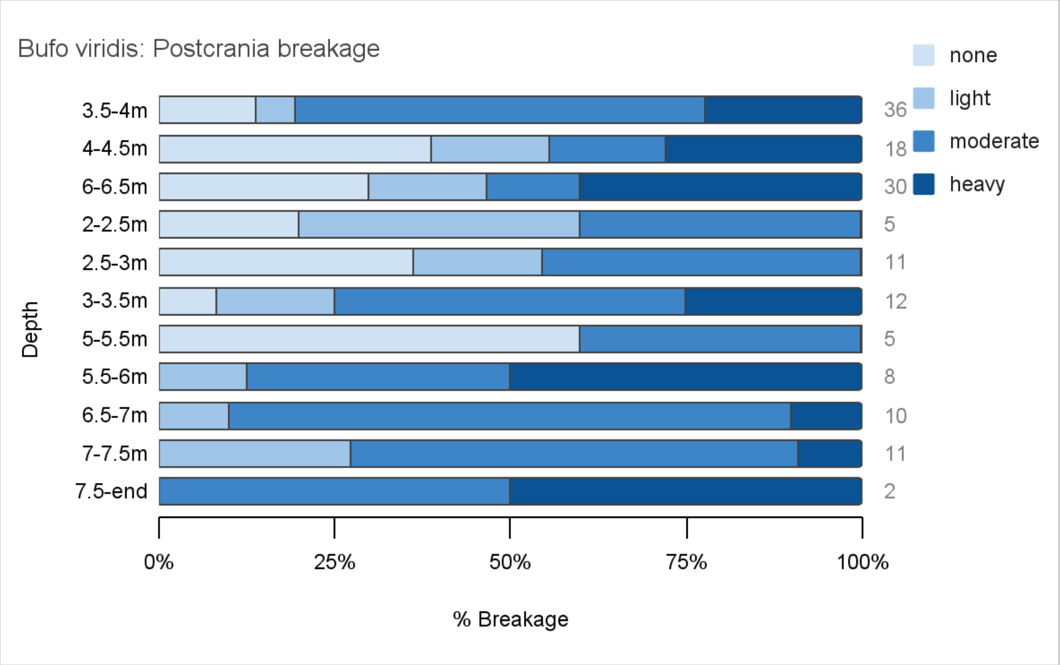


Figure 33: Bufotes viridis % postcrania breakage degrees based on scheme proposed by Bisbal-Chinesta et al. (2020).

5.2.3 General observations

Specimens throughout the assemblage showed a range of modifications, most prevalent being breakage and corrosion. Corroded specimens were corroded inhomogenously, indicating soil corrosion. Most specimens were discoloured, ranging from light discolouration to black, brown, and reddish brown. Lightly discoloured bones were generally less weathered and more well-preserved, with light signs of polishing. Light signs of weathering, rounding and splitting were also preserved. Edges of most specimens were slightly rounded. For dentition, both enamel and dentine loss were observed. A list of modifications observed on Għar il-Fkieren specimens and the suspected agents is provided in Table 13. Visual references to some of the observed modifications are provided in Figures 34-35.

Modification	Agent 1	Agent 2	Agent 3	Agent 4	Agent 5
Breakage	Carnivores	Sediment pressure	Trampling	Bioturbation	
Corrosion / Pitting	Humic acids (soil corrosion)	Organic acids	Dense low plant cover	Cave humidity	Moss and lichen
Dentine loss	Moisture	Alkaline conditions			
Discolouration: black	Manganese	Carbon stain	Fungi		
Discolouration: brown	Humic acids				
Discolouration: red	Oxydised soil				
Discolouration: light	Gley soils	Leaching			
Enamel loss	Digestion	Corrosion			
Flaking	Weathering	Sediment pressure	Digestion	Alkaline conditions	
Polishing	Wind and sand	Water and gravels	Licking	Digestion	
Rounding	Sediment and water	Wind	Digestion	Carnivores	Trampling
Splitting	Weathering	Digestion			

Table 13: Taphonomic modifications observed on Għar il-Fkieren specimens, and the suspected processes and agents which produce them. Based on Fernández-Jalvo et al. 2016: 4, Table 1.1; Fernández-Jalvo et al. 2016: 200.

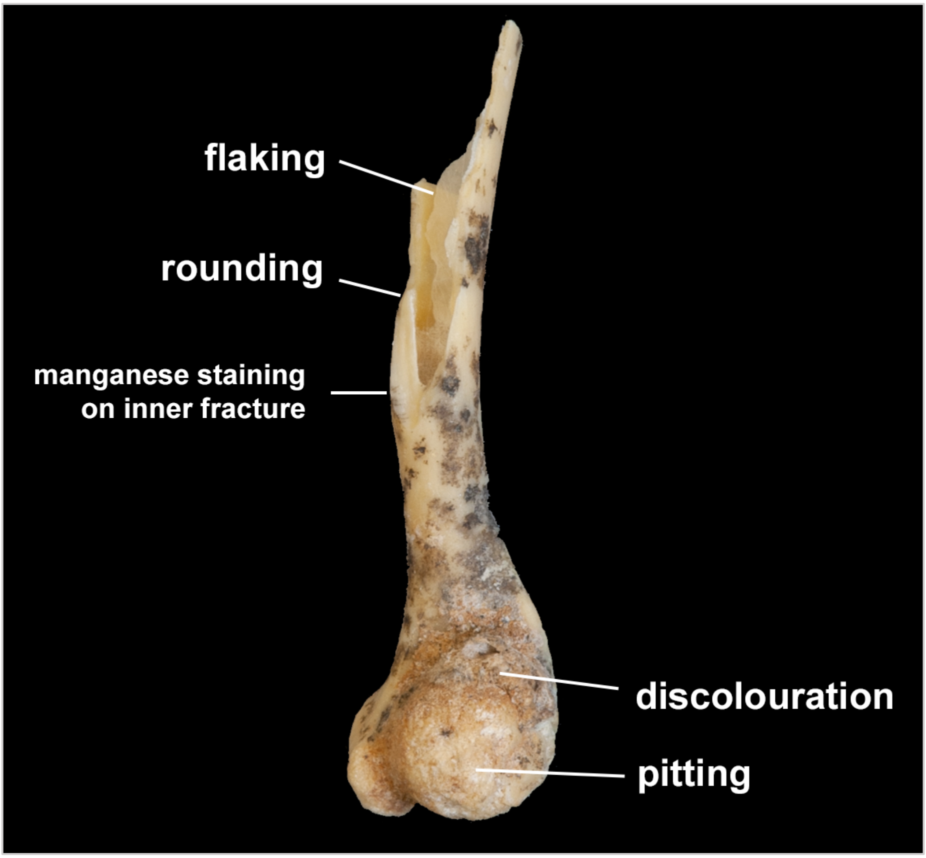


Figure 34: Specimen 3622_1 (Bufotes distal humerus) taphonomic modifications.

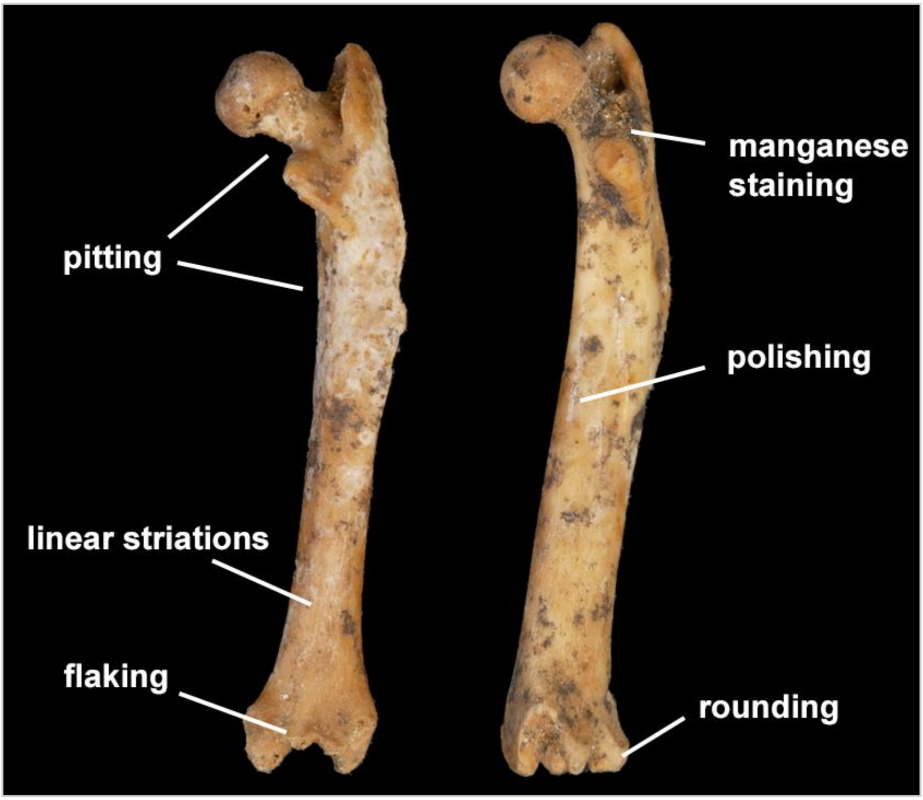


Figure 35: Specimen 3114_1A (vole femora) taphonomic modifications.

5.3 MORPHOMETRIC ANALYSIS

5.3.1 Principal Component Analysis (PCA)

A total of 183 *Microtus melitensis* femora and 47 *Bufotes viridis* humeri from Għar il-Fkieren were measured and analysed for potential cluster patterns using Principal Component Analysis (PCA). The results are presented in the following figures (Figures 36-37). The colour gradient on the plots represents the cos2 values, indicating the quality of representation for each point. Dim1 and Dim2 represent the principal components, with the spread of points across these dimensions providing insights into potential clusters or groups within the dataset. Points closer to each other on the plot are more similar in terms of the variables utilized in the PCA.

For *M. melitensis*, Dim1 and Dim2 account for 40.9 % and 25.5 % of the variance within the dataset, respectively. A high percentage of variance explained suggests that Dim1 captures a substantial portion of the variability present in the data. Consequently, factors contributing to this dimension likely play a crucial role in distinguishing patterns or characteristics among the *M. melitensis* femora.

For *Bufotes viridis*, Dim1 and Dim2 account for 85.6% and 8.8% of the total variance within the dataset, respectively. With such a high percentage of variance explained, Dim1 serves as a dominant axis in capturing the variability present in the data. Consequently, the factors influencing Dim1 are likely key determinants in differentiating characteristics among the humeri specimens.

Overall, the PCA reveals that no major clustering is observed within the datasets. Instead, the majority of the variance is contained within the primary principal components, particularly Dim1, for both *B. viridis* and *M. melitensis*. This suggests that while there may be some variation in the morphological characteristics measured, it is not sufficient to clearly delineate distinct clusters or groups within the studied population.

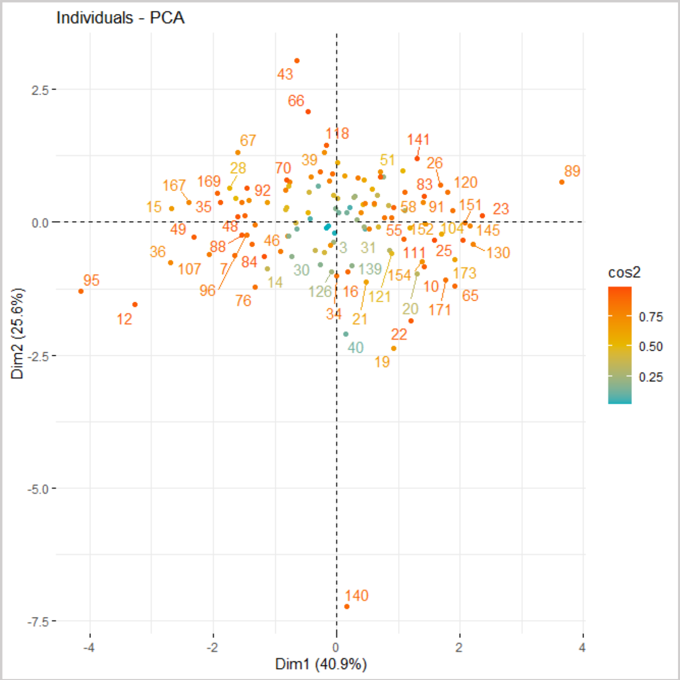


Figure 36: Microtus melitensis femur PCA from Għar il-Fkieren.

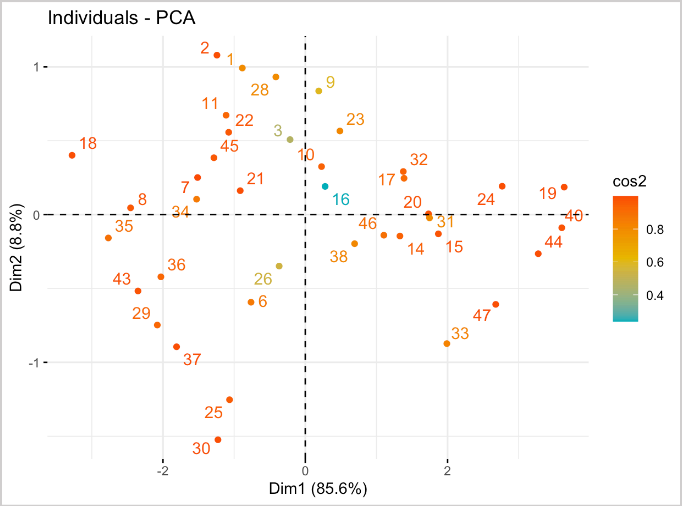


Figure 37: Bufotes viridis humerus PCA from Għar il-Fkieren.

5.3.2 Comparative morphometry

38 specimens of *Microtus melitensis* lower m1 molars from Għar Dalam and 125 specimens of *Microtus melitensis* m1 molars from Għar il-Fkieren were measured. The generated boxplot (Figure 38) compares these lower m1 measurements of *Microtus melitensis* across Għar Dalam and Għar il-Fkieren.

For Għar Dalam, the median m1 size is slightly higher compared to the normal distribution, around 2.8 mm. The interquartile range (IQR) is relatively narrow, which indicates little variability within this vole population sample. The notches in the boxplot overlap with the normal distribution, suggesting no difference in the median m1 size between Għar Dalam and the normal distribution.

For Għar il-Fkieren, the IQR is wider compared to Għar Dalam, indicating more variability within this vole sample. One specimen from Għar il-Fkieren has an unusually large size, indicated by an outlier around 3.2 mm. Despite this outlier, the notches in the boxplot for Għar il-Fkieren overlap with those of Għar Dalam, suggesting no significant difference in the median m1 size between the two sites.

In summary, while there is more variability in the m1 sizes at Għar il-Fkieren, the median sizes and overall distributions between the two sites do not show a significant difference, indicating that the variations observed are likely due to sample size and variability rather than indicating different species or significant morphological differences.

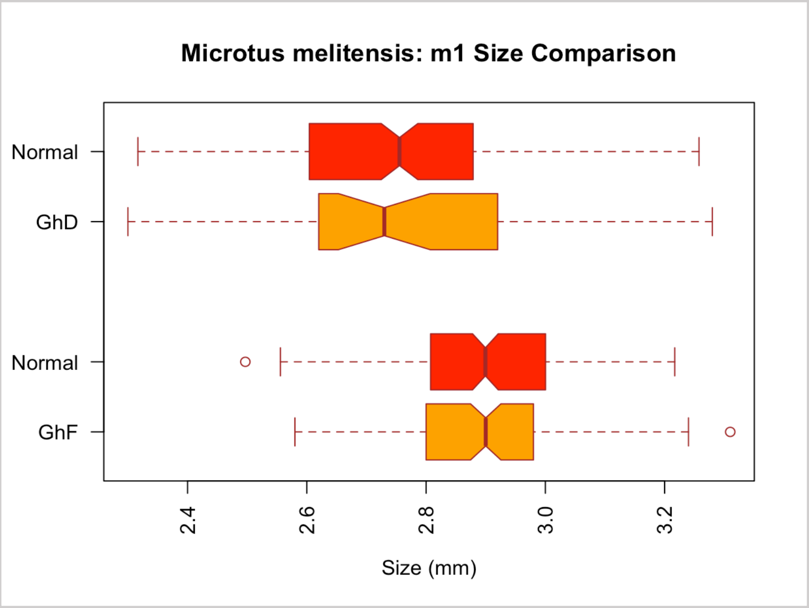


Figure 38: Microtus melitensis size comparison (mm) of lower m1 (first molars) from Għar Dalam (Għar Dalam) and Għar il-Fkieren (Għar il-Fkieren). Normal = Normal distribution.

5.4 HABITAT WEIGHTING

Identified species (*Microtus melitensis*, *Bufotes viridis*, *Crocidura sicula* and *Podarcis* cf. *filfolensis*) at all depths within Għar il-Fkieren were included in the habitat weighting, combining observations from both NISP % (Number of Identified Specimens) (Figure 39) and MNI % (Minimum Number of Individuals) (Figure 40).

Depth 2-2.5m: Both %NISP and %MNI data show a predominant presence of shrubland species, constituting over 50% of the assemblage. Forest species follow with a significant proportion, although markedly less than successive depths. Minor components include grassland species and rocky habitat species, with the latter being slightly more pronounced in the MNI data.

Depth 2.5-3 m: Shrubland species remain dominant across both datasets. An increased proportion of forest species is noted, especially in %NISP. Grassland species make a minor appearance.

Depths 3-3.5 m - 6.5-7m: Shrubland species continue to be the most prevalent in both %NISP and %MNI, with forest species present in almost equal proportions. Grassland species presence is minimal.

Depth 7-7.5m: Shrubland species dominate, with a marked decrease in forest species. A small presence of grassland species is still noted.

Depth 7.5-end: Shrubland species are still predominant in both datasets. The reduction in forest species compared to the previous depth is more pronounced, and a minor increase is observed in rocky habitat species.

Overall, both %NISP and %MNI consistently indicate a dominance of shrubland and forest habitats across all depths. Minor variations exist, such as a slightly higher representation of rocky habitat in the %MNI. Depth-specific trends include an increase in forest species at certain depths and a consistent presence of shrubland species throughout. These findings suggest that the fossil assemblage is predominantly composed of species from shrubland and forest habitats, with minor contributions from grassland and rocky habitats.

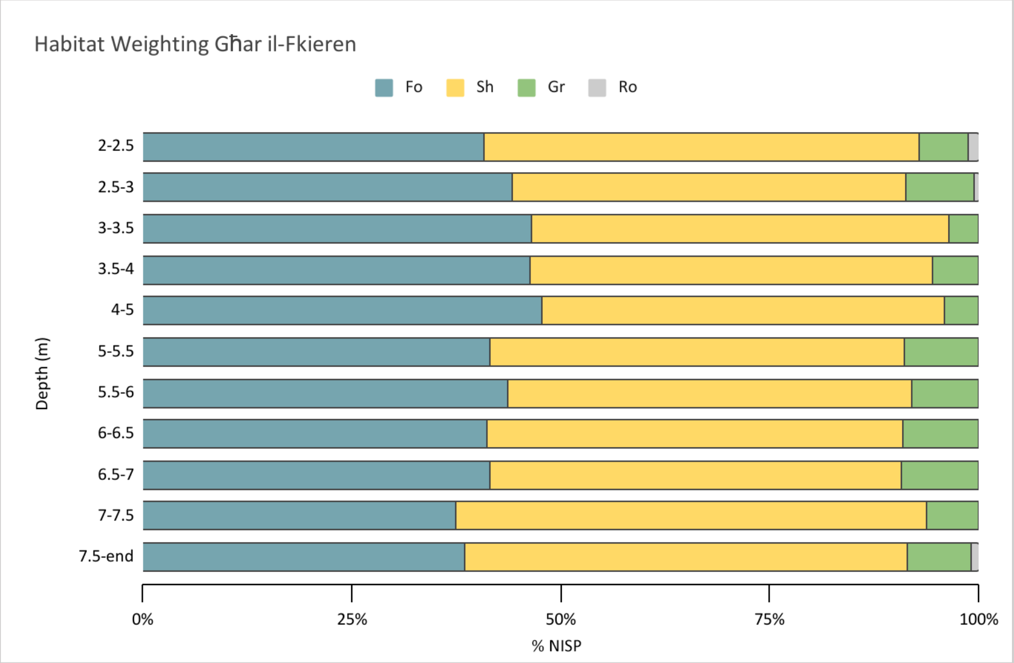


Figure 39: Habitat Weighting (NISP %) from Għar il-Fkieren. Fo = Forest; Sh = Shrub; Gr = Grass; Ro = Rocky.

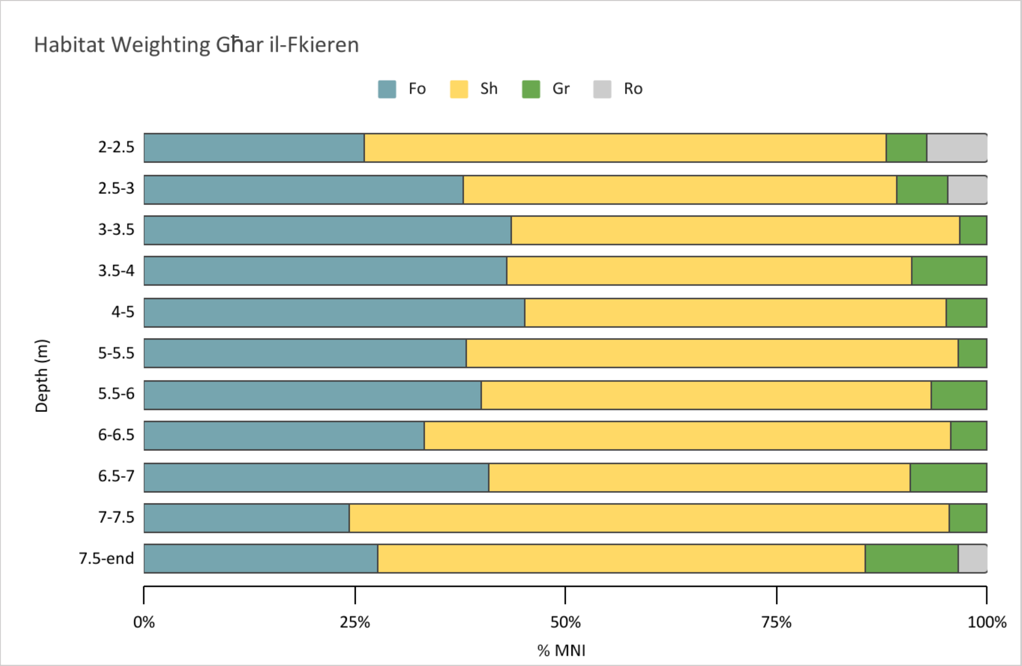


Figure 40: Habitat Weighting (MNI %) from Għar il-Fkieren. Fo = Forest; Sh = Shrub; Gr = Grass; Ro = Rocky.

6 DISCUSSION

6.1 SUMMARY OF RESULTS

In addition to several taxa already known from Malta (the extinct vole *Microtus (Terricola) melitensis*, the shrew *Crocidura sicula*, and the extirpated toad *Bufotes viridis*), the analysis of the Għar il-Fkieren microfauna assemblage revealed some previously undocumented taxa from Quaternary sites. These included *Podarcis* cf. *filfolensis* and *Colubridae* sp. The latter is of particular note, since it challenges the commonly held view that Malta's colubrids were introduced to the islands only relatively recently. This is also the first time *Podarcis* cf. *filfolensis* was identified from a Quaternary site, although small lacertids have been identified from Ta' Gandja fissure (Adams 1866). It is possible due to lack of robust screening methods, *Podarcis* were missed during earlier investigations of other sites owing to the very small size of the remains.

Microtus melitensis was the best represented taxon, followed by *Bufotes viridis* and *Colubridae* sp. The remaining species contributed minimally but consistently to the overall faunal composition, and there was generally little variation in species abundance between layers except for at the deepest levels where Chiroptera sp. remains seemed more abundant and the rest of the species seemed more evenly distributed, especially with regards to %MNI.

Taphonomic analysis indicated that *M. melitensis* remains exhibited moderate signs of predator digestion. In contrast, *B. viridis* remains displayed much higher degrees of digestion compared to *M. melitensis*. Both species exhibited high rates of skeletal breakage, with *M. melitensis* showing a slightly higher overall breakage rate. Corrosive pitting, natural linear striations, rounding, flaking, and discoloration were also noted on many of the observed specimens, although these modifications varied considerably.

PCA of *M. melitensis* femora and *B. viridis* humeri revealed that the morphological variability within each species was primarily captured along a single principal axis, with no significant clustering observed within the datasets. These results suggest that while there is morphological variation within each species, it is not sufficient to form distinct clusters which would be statistically significant.

The boxplot comparative analysis of *M. melitensis* molar sizes from the Għar il-Fkieren and Għar Dalam sites showed that while there was more variability in the m1 sizes at Għar il-Fkieren, the median sizes and overall distribution between the two sites were not statistically significant. The IQR for Għar il-Fkieren was wider, indicating more variability in the sample, but the median sizes between the two sites overlapped, suggesting no significant morphological difference between the populations.

Habitat weighting results, derived from living examples or closest living relatives of the identified species, indicated a predominance of shrubland species, followed by forest species, with minor variations at the shallowest and deepest stratigraphic depths. There was typically a minimal presence of species associated with rocky and grassland habitats. Depth-specific trends showed shrubland species as the most prevalent, with forest species making up a significant proportion but decreasing in dominance at the deeper layers. Grassland species were minimally present throughout the layers, while rocky habitat species showed a slight increase at the shallowest and deepest stratigraphic levels.

6.2 INTERPRETATION OF FINDINGS

6.2.1 Faunal composition and environmental implications

The high percentages of NISP and MNI for *M. melitensis* and *B. viridis* indicate both better preservation of these remains and a higher prevalence of these species around the site, suggesting they were well-adapted to the local environment. The dominance of *M. melitensis* and *B. viridis*, alongside the presence of *C. sicula* and *P.* cf. *filfolensis*, points to a primarily shrubland and forest environment, consistent with habitat weighting results.

The higher prevalence of *Chiroptera* sp. in deeper layers may suggest cave or crevice environments suitable for bat roosting, as the crevice may have been much larger prior to sediment infill. However, data on bat species roosting in vertical cave environments appears limited. The minimal variation in species composition across different layers implies a relatively rapid depositional process, coupled with environmental stability during this short period.

The macrofauna, although requiring further study, indicate that carnivores such as *Vulpes vulpes* (red fox), *Canis lupus* (wolf), and *Ursus* cf. *arctos* (brown bear), along with large herbivores like *P. mnaidriensis* and *H. pentlandi*, were absent by the time of Għar il-Fkieren deposition (Table 5). These findings align with those at Għar Dalam, except for the absence of *Bos* and *Equus*, which are present in the Upper Red Earth IV layers at Għar Dalam during this period but not at Għar il-Fkieren. Tortoises (likely *Emys orbicularis*) and deer (likely *Cervus elaphus*) were highly abundant at Għar il-Fkieren, as shown by preliminary and ongoing analyses. *Cervus elaphus* is well-adapted to forest and shrub habitat, while *Emys orbicularis* is a species preferring wetland habitat, suggesting further that the area around Għar il-Fkieren was forested and experienced much wetter than present conditions to support the proliferation of these species.

The timing and extinction or extirpation of the larger herbivores and carnivores likely occurred somewhere between 167 – 80 ka, due to their presence in the Lower Red Earth V, but absence in the succeeding Upper Red Earth IV Għar Dalam layers (see Table 5; Figure 13). This may be linked with lack available medium-sized prey within insular environments and habitat loss due to shrinking island size (Masini *et al*. 2008). While conditions may have been favourable during the time of their dispersal, large mammalian carnivores are rare on islands due to these disadvantages. Malta has experienced shrinking island size since the LGM (Last Glacial Maximum) when it was at its maximum size (Prampolini *et al.* 2017) (Figure 41). The only comparable glacial maximum is the PGM (penultimate glacial Maximum) which occurred c. 140 ka, which was succeeded by Holocene levels of warming at around 135 ka (Benjamin *et al.* 2017). This could suggest favourable conditions (connectivity to Sicily and larger habitat area in the Maltese Islands) for large carnivore dispersal, followed rapidly by Holocene-like warm conditions and sea levels, which would explain their rapid extinction within the islands.

The microfauna, on the other hand, are consistent with the Upper Red Earth IV layers at Għar Dalam and show continuity with the Lower Red Earth V layers. This indicates that the environment between c. 167 to 53 ka was favourable enough for the microfauna assemblage to survive, potentially continuously from 167 ka to the Holocene (Table 14). This confirms Masini *et al*. (2008)'s observations that small mammals tend to be more resilient to extinction within insular environments.

The precise timing of the extinction of *M. melitensis* remains undetermined. However, considering the habitat preferences of its close relative *M. savii*, which favours forested environments, it can be inferred that this species likely faced significant environmental challenges. Since the beginning of the Holocene epoch, Malta has experienced a considerable reduction in rainfall and woodland coverage. Consequently, *M. melitensis* may have gone extinct due to these environmental pressures. However, since it had already proved resilient to PGM levels of environmental pressure, its extinction has most likely occurred post-human intervention, when the species encountered competition from other rodents introduced by humans, such as *Apodemus sylvaticus* (wood mouse) and *Rattus rattus* (black rat).

Meanwhile, *B. viridis* appears to no longer inhabit the Maltese, surviving only in more northern Palearctic regions with wetter and more wooded environments (IUCN 2023). Although it is still unclear when *B. viridis* became extirpated, the decline of *B. viridis* in Malta can likely be attributed to similar environmental pressures, including human-driven habitat loss and the reduction of freshwater sources. These factors, along with the overall drier and less wooded conditions in Malta since the Holocene, likely contributed to the extirpation of this species from the islands.

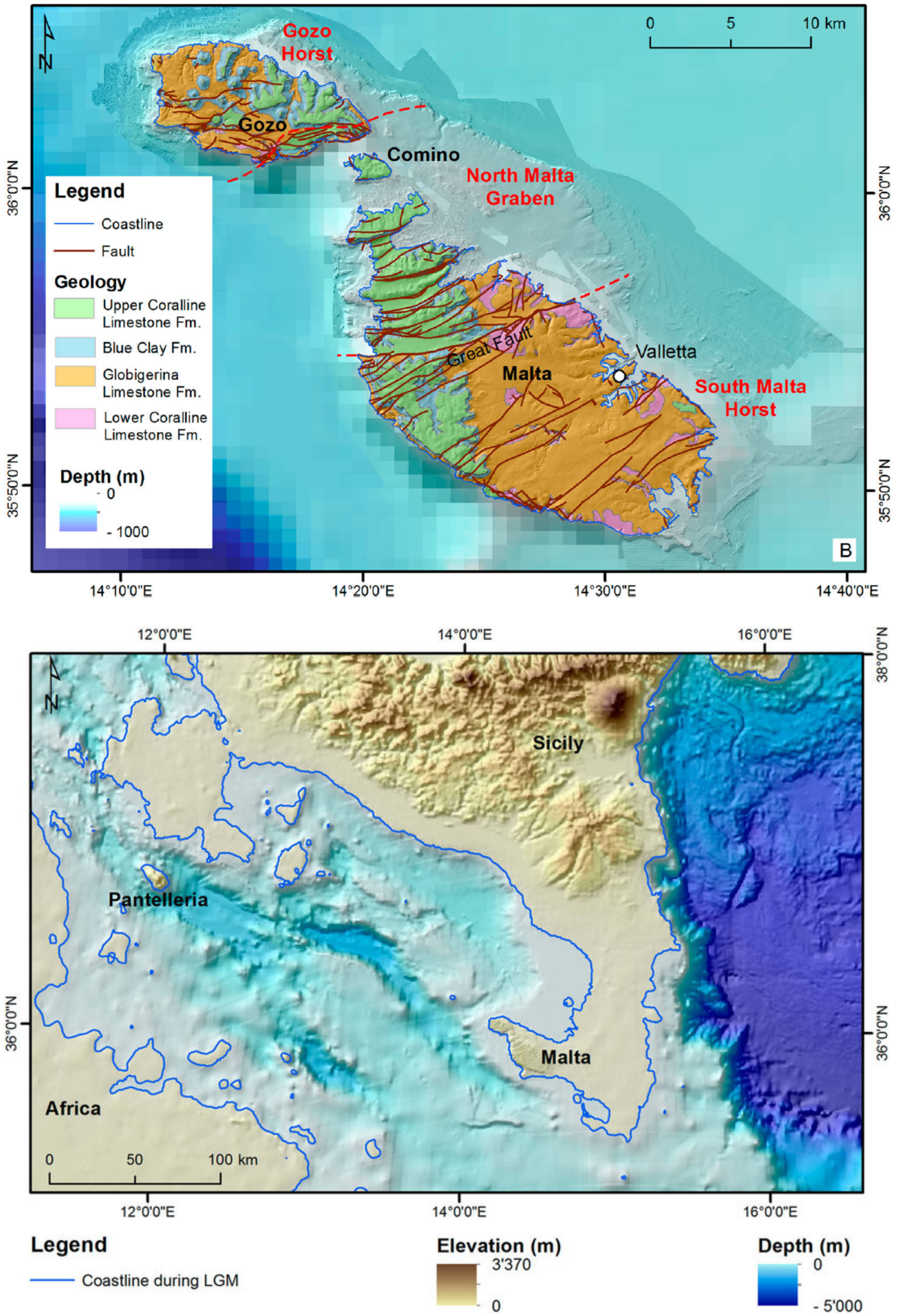


Figure 41: Top: Geological setting of the Maltese Islands and bathymetry surrounding the archipelago, showing current sea levels and palaeoshore (Prampolini et al. 2017, after Oil Exploration Directorate, 1993). Bottom: The Maltese Islands during the Last Glacial Maximum (LGM) (Prampolini et al. 2017).

6.2.2 Taphonomic analysis

6.2.2.1 Microtus melitensis

According to Andrews (1990: 163), the observed taphonomic signatures for the *Microtus* specimens align closely with those of mustelid accumulations, where selective predation is not proportionate to prey abundance. In the site examined by Andrews, the microstratigraphy of the layer also corresponded to mud flow from outside the cave. The breakage rates of crania (= 92%) and digestion of molars and incisors (= 14-18 %) were comparable to the levels observed in Għar il-Fkieren *Microtus*: crania breakage (= 96%) and corrosion (= 18%).

Mustela nivalis vulgaris (least weasel) has only been confirmed from one undated Quaternary deposit (Wied il- Ħesri Cave), tentatively present during the late Middle Pleistocene based on associated fossil fauna. Present-day *M. nivalis* is well adapted to forest/shrub habitat and the available prey in Għar il-Fkieren aligns with its dietary preferences (IUCN 2023). It remains to be confirmed if this carnivore is conclusively present in the macrofaunal assemblage.

However, it is important to note that the sample size for the Andrews (1990: 163) mustelid assemblage was much smaller (MNI = 30) and did not account for the very high rate of chemical corrosion seen here. It is also possible that chemical corrosion has masked any original digestive corrosion. Thus, any interpretations of potential predators must be approached with caution. The low rates of digestion despite the large number of *Microtus* elements in the assemblage seem to agree with observed rates of predation on small mammal species, which Andrews (1990: 25) notes always seem to hover around 5% regardless of population size. Thus, the effect of predation on population size is more pronounced in smaller populations and assemblages (Andrews 1990: 25).

The moderate rate of predator digestion (18%), including pitting and rounding, indicates that some of the remains were subjected to predation. Meanwhile, the high rate of chemical corrosion (63.3%) suggests that post-mortem environmental factors, such as soil corrosion and moisture, played a major role in the degradation of the bones (Fernández-Jalvo *et al*. 2016: 4). The very high breakage rate of crania (maxillae and mandibles) (96%) is also indicative of significant post-mortem mechanical processes such as sediment pressure and bioturbation (Fernández-Jalvo *et al*. 2016: 4).

6.2.2.2 Bufotes viridis

The higher levels of digestion marks observed in the remains (82%) suggest that predation was a more significant factor affecting this species, although it is again possible that soil corrosion and abrasion has caused similar rounding and corrosive effects. Additionally, the breakage rate was substantial at 80%, suggesting that both predation and other taphonomic processes contributed to the preservation of the remains.

Taphonomic studies on amphibian remains by Pinto-Llona and Andrews (1999: 418) suggest that such high levels of digestion and breakage most closely resemble the effects of mustelid predation. Mustelids are known for their specific predation behaviours which result in considerable digestion and breakage of bones (Figure 42). However, it is essential to note that significant breakage may also be caused by other agents, such as sediment pressure, trampling and bioturbation, contributing to the breakage levels observed (Fernández-Jalvo et al. 2016: 4).

Given these factors, it is possible that these remains accumulated in part due to predators that leave similar digestive signatures, but lesser breakage signatures compared to mustelids. Compared to the bivariate plot by Pinto-Llona and Andrews (1999: 418) (Figure 42), species confirmed to be present during the Pleistocene in Malta include *Tyto alba* (barn owl), *Asio flammeus* (short-eared owl), and *Strix aluco* (tawny owl) (Borg 1999).

Among these, *S. aluco* appears to be the most likely predator for several reasons. Firstly, *S. aluco* has a higher preference for amphibians in its diet, accounting for 34% of its prey items (Roulin and Dubey 2013). Moreover, *S. aluco*'s habitat preferences align with the inferred environmental conditions of Late Pleistocene Malta, since it typically inhabits forested areas (IUCN 2023). This preference for forested habitats and amphibian predation further supports the hypothesis that *S. aluco,* or an avian predator with similar digestive patterns and diet preferences, may have been a primary predator contributing to the *Bufotes* digestion and breakage patterns.

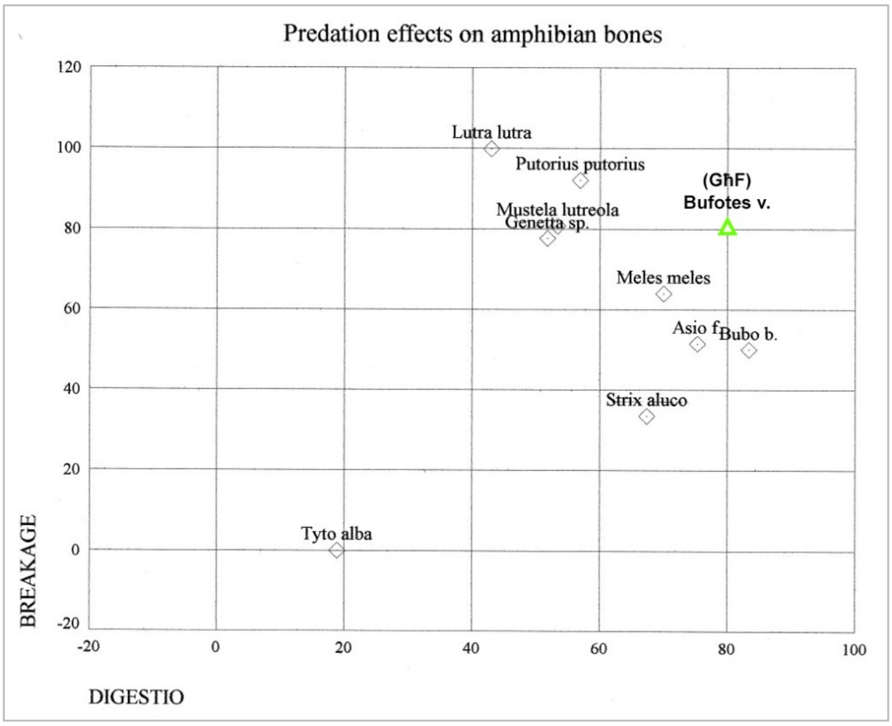


Figure 42: Bivariate plot of predation effects on amphibian bones from Pinto Llona and Andrews (1999: 418), with added values from B. viridis Għar il-Fkieren sample.

6.2.2.3 Site formation and accumulation processes

These geological features form due to a focused water flow which causes inhomogenous corrosion, especially in the highly porous and permeable Quaternary limestone matrices (Lipar *et al*. 2021). The presence of carbonic acid from rainwater and soil CO_2 is the main agent of the erosion responsible for the formation of karst solution pipe fissures. Although the rate of solutional erosion may vary greatly depending on local conditions, it can be relatively rapid due to the exposed limestone and lack of overlying residue (Andrews 1990: 91). Determining the timeframe between deepest and earliest sediments of the fissure is however currently not possible, since minimum U-series dates have only been acquired from SU 11 (approx. depth 2.5 – 3 m) (Table 1).

Many of the observed postcrania display light vertical linear striations parallel to the bone fibres which are suggestive of weathering (Fernández-Jalvo *et al*. 2016: 4). Weathering refers to surface modifications made by exposure to sunlight, temperature change, wind, and rain (Andrews 1990: 10). The observed striations, otherwise called 'splitting', are less pronounced if the bones were exposed in a shaded environment rather than exposed to direct sunlight (Pinto Llona and Andrews 1999: 423), suggesting that the bones were deposited post-mortem after either short periods of sunlit subaerial exposure, or longer times in shaded areas. This is potentially a further indication that the area around Għar il-Fkieren may have been forested, and/or that episodic flooding during the Late Pleistocene was much more frequent than previously thought. According to Hunt (1997: 108), erosion and sedimentation was particularly pronounced in Mediterranean countries during stadial episodes, where there was no vegetation cover and severe winter frosts. This would lead occasional extreme rainfall events led to the mass transport and accumulation of sediments by wash, mud and debris flow processes (Hunt 1999: 9). Għar il-Fkieren dates (c .63 – 53 ka) place it at the transition from the glacial period MIS 4 to the warmer MIS 3c (c. 60 ka), potentially explaining such flooding events.

The same water flows responsible for the formation of the fissure can also cause chemical and mechanical erosion, as well as the transport of bones, leading to physical damage and dispersion. Markers of such corrosion and pitting are evident on many of the specimens, although the levels of preservation vary. The acidity in the surrounding matrix, caused by the replacement reaction of limestone and clay, is likely responsible for the significant number of specimens exhibiting corrosion or pitting modifications. This acidic replacement reaction is a common feature of Quaternary Mediterranean 'terra rossa' sediments (Merino and Banerjee 2008).

Although further and more in-depth specialist analysis needs to be done on the cave to ascertain the exact formation processes, the fissure was likely eroded by groundwater, creating a subsurface fissure. The cavemouth was then opened by landscape erosion processes (Figure 7), effectively creating a trap which may have caused animals to perished by falling into the fissure rather than being transported into it post-mortem (Andrews 1999: 90-94). Specimens which show very light to no signs of weathering or discoloration may also have been deposited through other means. Andrews (1990: 10) notes that owl pellets or scat afford a layer of protection to the bone, and less surface modifications can generally be observed on bone deposited through these means. These pellets may have been deposited by owls roosting in nearby trees at higher elevations (Figure 43). This hypothesis is supported by the habitat weighting results suggesting that the area around Għar il-Fkieren was quite wooded.

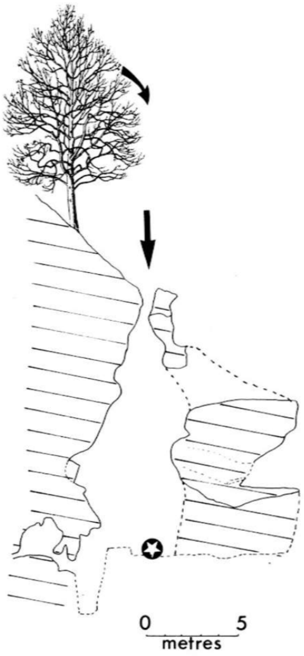


Figure 43: Schematic section of Tornewton Cave, showing how owl pellets can be deposited directly through points of entry in vertical cave systems (Andrews 1990: 96).

The consistent presence of chemical corrosion and minimal digestion across multiple layers for *M. melitensis*, along with variable digestion and breakage in *B. viridis*, point to a range of taphonomic factors at play, including weathering, predation and soil movement. The high rate of breakage and soil corrosion points to post-mortem disturbances such as flooding and soil transportation as the most significant factors affecting the taphonomy of the assemblage, with predation playing a smaller role in the accumulation of remains.

6.2.3 Morphometric analysis and insular gigantism

The boxplot analysis confirmed that both Għar Dalam and Għar il-Fkieren *M. melitensis* m1 lengths exhibit very little variation in size. Locatelli (2010) analysed both mainland and Maltese vole specimens from Għar Dalam, noting that *M. melitensis* is significantly larger. When comparing *M. melitensis* from Għar Dalam MIS 6 specimens, it appears that this species did not undergo much morphological change in size. Insular species can persist for long periods with little to no variation within strongly isolated areas, resulting in morphological stasis (Locatelli 2010).

In the Orkney islands, *Microtus* voles have been observed to grow approximately 5% in body mass in just around 5000 years, although influenced by factors such as human occupation in the Neolithic (Cucchi *et al*. 2014). While Moncunill-Solé *et al*. (2016) suggest that certain small mammals do not grow larger due to phylogenetic factors, gigantism in voles has also been observed in insular North American islands (Schlis-Elias and Malaney 2022), confirming that these micromammals can experience the phenomenon of gigantism (Cucchi *et al*. 2014).

The size difference between the Sicilian populations and *M. melitensis* (Locatelli 2010) suggests that *M. melitensis* underwent a trend towards gigantism sometime before its introduction during MIS 6 and remained relatively stable until its reappearance at Għar il-Fkieren during MIS 4-3.

6.2.4 Habitat weighting and paleoenvironmental reconstruction

The habitat weighting analysis revealed that the faunal assemblage at Għar il-Fkieren is primarily composed of species associated with shrubland and forest environments, likely also having a freshwater source nearby to support the *B. viridis* population. The presence of species such as *M. melitensis*, *B. viridis*, *C. sicula*, and *P*. cf. *filfolensis*, which thrive in these habitats, further supports this conclusion. This is consistent with other paleoenvironmental evidence from the region, which shows a prevalence of forested areas during interglacial periods (Allen *et al*. 1999; Watts *et al*. 2000).

These findings support Hunt (1999: 29)'s hypothesis that the Pleistocene taxa recorded from the contemporaneous Għar Dalam Upper Red Earth layers indicated warm climate and some woodland. However, the dates from Għar il-Fkieren (c. 63 – 53 ka) and the recent U-series dates from Għar Dalam (c. 80 – 20 ka) do not align with his suggestion of a Late Glacial (13 - 11 ka) age. Instead, they confirm such warm and wooded conditions during MIS 4-3 (c. 63 – 53 ka).

Based on the taphonomy of the assemblage and site, it appears that flash floods were also a feature of the palaeoclimate, matching current climate records which show that flooding occurs far more frequently in certain areas of the Mediterranean than in other parts of Europe (Gaume *et al*. 2009; Llassat *et al*. 2010). This is attributed to the regional climate, which is susceptible to short, intense bursts of rainfall. The topography surrounding the Mediterranean Sea causes low-level atmospheric flows to converge and warm, moist air masses from the sea to rise, resulting in active convection and increased rainfall intensity (Guame et *al*. 2016). This is intriguing, as it suggests that flash flooding has been a characteristic of the Mediterranean climate since before the rise in human population and human induced climate change during the Holocene.

Figure 44: Forest in the Zakros Canyon, Crete, as an approximation of the landscape around Għar il-Fkieren during the Late Pleistocene. Image: Yooga, Wikipedia Commons.

As discussed in section 6.2.1, the flash flooding may be linked to the MIS 4 – 3 transition, wherein glacial conditions gave way to warmer conditions. However, the fact that there is a relatively stable pattern of relative abundance and habitat weighting throughout the Għar il-Fkieren sequence could also mean that local climate change caused by the transition was not pronounced enough to cause major habitat changes.

6.2.5 Summary of findings

The faunal composition at Għar il-Fkieren remains relatively consistent throughout the sequence and indicates a primarily shrubland and forest environment with available freshwater sources for the duration of its deposition, based on the habitat preferences of the identified species.

The taphonomic analysis of the remains from Għar il-Fkieren provides insight into the accumulation processes and environmental influences affecting the *M. melitensis* and *B. viridis* specimens. Although predation (possibly by mustelids and/or owls) played a small role in the accumulation of the assemblage, the high rates of chemical corrosion and minimal digestion across multiple layers pointed to post-mortem disturbances such as flooding and soil transportation as the main taphonomic agents.

The variation in bone discoloration and the presence of light vertical striations parallel to the bone fibres suggest different burial modes and weathering due to periods of subaerial exposure. Some of these specimens may also have been deposited through falling into the fissure or through owl pellets. The site formation processes reveal that carbonic acid from rainwater and soil CO_2 was the main agent of erosion responsible for forming karst solution pipe fissures like Għar il-Fkieren. Water flows causing the fissure also led to chemical and mechanical erosion and bone transport, causing physical damage and dispersion. The acidity from limestone and clay reactions likely contributed to bone corrosion, as indicated by the presence of typical Quaternary Mediterranean 'terra rossa' sediments. Flash flooding appeared to be a characteristic feature of the

Mediterranean climate, linked to regional climate patterns and intense rainfall events during cold stages.

M. melitensis likely faced extinction post-Holocene due to reduced rainfall, woodland coverage, and competition from introduced rodents, while *B. viridis* likely became extirpated due to similar environmental pressures and human-driven habitat loss. However, the strong evidence of continuity of *M. melitensis* and *B. viridis* survivorship from approximately 167 to 53 ka highlights small animal resilience to glacial-interglacial climate changes. Meanwhile, the extinction of carnivores is likely linked to the extreme weather oscillation between the PGM and succeeding MIS 5e extreme warming event, which caused decreased land size and created insular conditions.

6.3 CONTEXT OF FINDINGS IN A BROADER LATE PLEISTOCENE MEDITERRANEAN CONTEXT

Allen *et al*. (1999) demonstrated that vegetation changes in the Mediterranean could occur within less than 200 years, indicating the region's sensitivity to climatic shifts. Over the past 65 ka, the Southern Mediterranean experienced particularly severe climate fluctuations, with rapid transitions between forest and wooded steppe environments, occurring on average every 142 years. These rapid alternations suggest a highly dynamic ecosystem responding swiftly to climatic ameliorations and deteriorations.

Between 60 - 50ka, a consistent presence of wooded taxa but predominance of steppe taxa is observed in the pollen records at Lago di Monticchio (Allen *et al*. 1999, Figure 2). This is not altogether inconsistent with the habitat weighting results from the Għar il-Fkieren microfauna assemblage, which shows a predominance of shrub, although local conditions seem to be more generally forested than what is observed in the Lago di Monticchio pollen records between the broad range of 60 – 50 ka. The habitat weighting more closely aligns with the Lago di Monticchio pollen records between 66 – 64 ka and 50 – 55 ka, which show an increasing trend towards forested conditions.

The continuous sediment accumulation at Għar il-Fkieren, devoid of calcium carbonate layers or hiatuses, also indicates a relatively stable depositional environment during MIS 4-3, suggesting that the Maltese islands may have experienced localised climatic conditions that were less volatile than those of the broader Southern Mediterranean. The continuous sediment record and the consistent presence of certain species support the idea that Malta may have offered more stable habitats during times of broader environmental upheaval. This would agree with the suggestion made by Watts *et al*. 2000 that when the site is sufficiently far from very cold areas affected by glacial-age climate, this allows the development of species-rich forest within individual warm phases.

It is likely that warm or temperate adapted species may have dispersed southward into the Maltese Islands during periods of glaciation, where conditions were more favourable (Schmitt 2007), after which they continued to evolve in insular conditions. For instance, the evolutionary and demographic history of *P. filfolensis* as inferred by Salvi *et al*. (2014), suggest that in non-continental regions like coastal areas and islands, local climate conditions were less severe during glacial periods. Furthermore, glacio-eustatic sea-level lowering during glacials resulted in a significant increase in terrestrial habitat availability in coastal areas, which decreased the necessity for species to expand outwards into other regions during subsequent marine highstands (Schmitt 2007).

Based on such genetic studies, relative dating and comparisons to Sicilian faunal complexes, it is possible that a dispersal event occurred around 900 ka during the pronounced MIS 22 lowstand (Martínez-Dios *et al*. 2021). Bonfiglio *et al*. (2002) suggest that an Early Pleistocene African dispersal hypothesis should be reconsidered based on evidence of tectonic changes of sea bed depth (Kelling and Stanley 1972). Masini *et al*. (2008) also note the ‘Monte Pellegrino’ Sicilian faunal complexes show a polyphasic origin, with some fauna originating from Europe and others with clear African affinities (*Pellegrinia panormensis* and *Crocidura esuae*). The ancestry of these species certainly suggest links with Africa, at least during the Late Miocene (Dubey *et al*. 2008). However, the major uncertainties regarding the

‘Monte Pellegrino’ dates and lack of Maltese palaeontological sites dated earlier than the late Middle Pleistocene currently complicate further analyses of this potential dispersal event (Masini *et al*. 2008).

Pedley (2011) argues for a 690 ka MIS 16 dispersal based on the phylogenetic study of *C. sicula* (Dubey *et al*. 2008). However, this phylogenetic study and the presence of *C. esuae* in Sicilian deposits are currently the only secure piece of evidence for this hypothesis, aside from relative dating from stratigraphic data of the Spinagallo *E. falconeri* (Pedley and Grasso 2002).

Recent high-resolution pollen studies, such as Sassoon *et al*. (2023), also provide insights into the climatic and vegetational shifts during the transition between MIS 12 – 10 (c. 478 – 424 ka). The study highlights the transition from a glacial to an interglacial period, characterised by a marked shift in vegetation from cold-adapted species to temperate and Mediterranean taxa. This transition period, particularly during MIS 11, is noted for its relatively stable and warm conditions, which contrasts with the severe glacial conditions of MIS 12. The stable and warm conditions during MIS 11, as identified in the Alboran Sea pollen record (Sassoon *et al*. 2023), suggest that the southwestern Mediterranean region provided a stable ecological niche during periods of climatic deterioration. However, MIS 12-11 occurs during a time of no secure palaeontological evidence from either Malta or Sicily to compare to this pollen record.

The findings from Għar il-Fkieren, however, support Petruso *et al*. (2011)’s hypothesis of a dispersal event occurring during the Penultimate Glacial Maximum (PGM) at MIS 6a. This marine highstand possibly introduced a new faunal complex from Sicily, specifically the ‘Grotta San Teodoro Pianetti’ faunal complex. Petruso *et al*. (2011)’s analysis of Sicilian and Maltese Pleistocene voles revealed that *M. melitensis* samples from Għar Dalam exhibited a mix of both primitive and more evolved characteristics, indicating a descent from primitive Sicilian *savii* populations, such as the Isolidda 3 *Microtus* vole. The analysis also indicated genetic drift, which led to the significant size observed in *M. melitensis* specimens compared to coeval Sicilian voles.

Identifying the timing of faunal dispersals from Sicily to Malta is complex and requires more comprehensive data. Herridge (2010) also notes that correlating stratigraphic and faunal data from Maltese and Sicilian Quaternary sites presents significant challenges. The lack of comprehensive geological data and absolute dates from both Sicilian and Maltese sites hinders the establishment of stronger links between climate, environment, and faunal dispersal pathways.

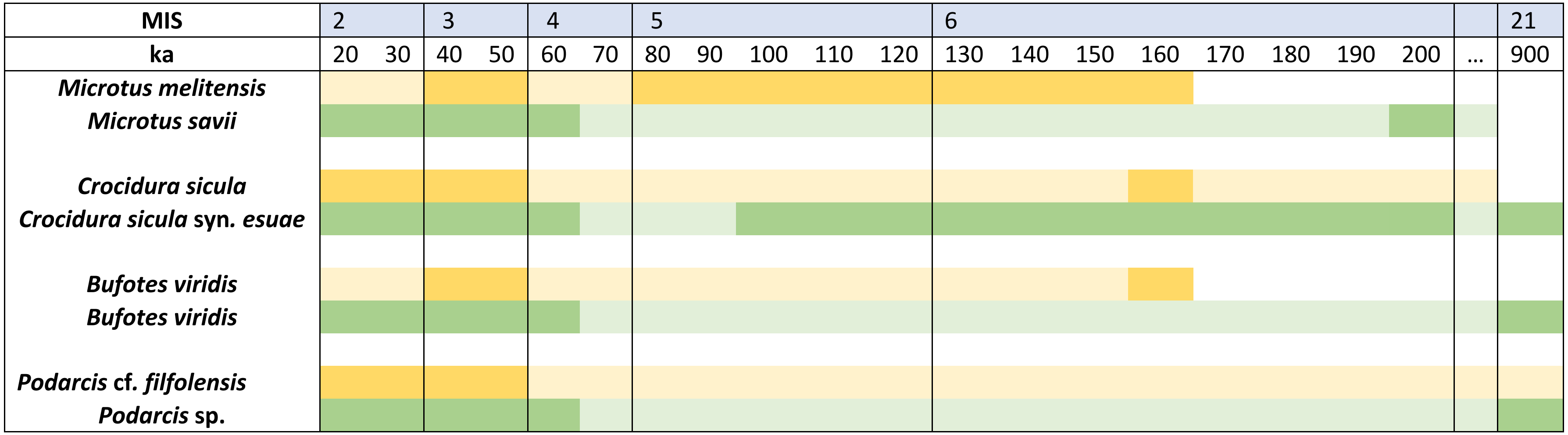
In conclusion, the findings at Għar il-Fkieren have expanded our understanding of the Late Pleistocene Mediterranean climate and environment by providing strong evidence that localised climate change in remote island contexts can be less pronounced than on the mainland. It also suggests that flash flooding was already a feature of Mediterranean island and coastal climates before human-driven climate changes in the Holocene.

The findings also provide more context to understand climate driven faunal dispersals from Sicily, and suggest tentative dates based on the palaeontological and climatic evidence (Table 14 - Table 15).

This study represents the first detailed taxonomic and taphonomic study of microfauna from the Maltese Islands and a rare example for Mediterranean Islands generally. By combining taxonomic data with studies of bone preservation and surface modifications, the present study has provided novel insights into the MIS 4-3 climate and ecology of Malta, as well as the specific site formation processes at the new site of Għar il-Fkieren. Although limited to a small assemblage from a single site, the present study highlights the value of microfauna studies for palaeoenvironmental and palaeoecological reconstructions, and for the study of island dynamics with respects to faunal dispersals and 'island rule' effects.

Sicily	Site	Date (ka)	MIS	MIS Dispersal?	Malta	Site	Date (ka)	MIS
Bufo* cf. *viridis	Monte Pellegrino	900	21	6	***Bufo viridis***	Għar Dalam	167.3 - 151.2	6
Bufo viridis	Grotta San Teodoro	70 - 32	4 - 3	6	***Bufo viridis***	Għar il-Fkieren	63 - 53	4-3
***Podarcis* sp.**	Grotta San Teodoro	70 - 32	4 - 3	?	***Podarcis* cf. *filfolensis***	Għar il-Fkieren	63 - 53	4-3
***Lacerta* sp.**	Monte Pellegrino	900	21	?	***Lacerta sp.***	Middle Cave (Adams)	?	?
Coluber* cf. *viridiflavus	Monte Pellegrino	900	21	?	**Colubridae sp.**	Għar il-Fkieren	63 - 53	4-3
Crocidura esuae	Monte Pellegrino, Spinagallo, Isolidda 3	900, Pre-Tyrrhenian	21	?	***Crocidura* cf. *russula* syn. *C. sicula***	Għar Dalam	Before 165.9	6d or older
Crocidura* aff. *esuae	K22	200 - 88	7 - 5	?	***Crocidura sicula***	Għar Dalam	167.3 - 151.2	6
Crocidura sicula	Grotta San Teodoro	70 - 32	4 - 3	?	***Crocidura sicula***	Għar il-Fkieren	63 - 53	4-3
Microtus (Terricola) savii	Isolidda 3	Pre-Tyrrhenian (?)		6	***Microtus melitensis***	Għar Dalam	167.3 - 151.2	6
Microtus (Terricola) savii	Grotta San Teodoro	70 -32	4 - 3	6, 4(?)	***Microtus melitensis***	Għar il-Fkieren	63 - 53	4-3

Table 14: Hypothesised faunal dispersals based on Bonfiglio et al. (2002) faunal complexes, Locatelli (2007), Petruso et al. (2011), Marra (2013). Sicilian dates reproduced from Masini et al. (2008, Appendix; p.75-76). Malta dates from Uranium-series disequilibria (D'Souza 2016).



MIS	2		3		4		5					6									21
ka	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	180	190	200	…	900
Microtus melitensis	▨	▨	🟨	🟨	▨	▨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨						
Microtus savii	🟩	🟩	🟩	🟩	🟩	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	🟩	▨	
Crocidura sicula	🟨	🟨	🟨	🟨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	🟨	▨	▨	▨	▨	▨	
Crocidura sicula* syn. *esuae	🟩	🟩	🟩	🟩	🟩	▨	▨	▨	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	▨	🟩
Bufotes viridis	▨	▨	🟨	🟨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	🟨						
Bufotes viridis	🟩	🟩	🟩	🟩	🟩	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	🟩
Podarcis* cf. *filfolensis	🟨	🟨	🟨	🟨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
***Podarcis* sp.**	🟩	🟩	🟩	🟩	🟩	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	🟩

Table 15: Related species present in Maltese Islands (yellow) and Sicily (green) based on the dating and fossil data in Table 14. Lighter sections indicate uncertain periods of species continuity.

6.4 LIMITATIONS OF STUDY

Excavation documentation and mixed strategies: Rescue excavations, driven by the urgency to salvage palaeontological data before site destruction, often face the challenge of balancing speed with documentation. This necessity can result in sparse records of the excavation process, hindering a comprehensive understanding of the site's context and the interpretation of collected data. At Għar il-Fkieren, this lack of detailed documentation posed a significant obstacle to fully grasping the site's stratigraphy.

Complicating matters further, the excavation at Għar il-Fkieren initially employed mixed strategies. The early stages involved excavating by Stratigraphic Units (SUs), followed by a shift to a spit and depth approach. This variation in excavation and documentation methods introduced complexity to the interpretation of site stratigraphy and layering. To address this challenge, an effort was made to standardise the excavation system by converting SUs to their approximate depths. This standardisation aimed to streamline the analysis process and provide a clearer understanding of the site's stratigraphy.

Sampling bias: Despite efforts to evenly sample across stratigraphy, certain layers may be overrepresented or underrepresented, leading to potential biases in stratigraphic interpretation.

Taxonomic identification challenges: Giovas and LeFebvre (2018: 37) highlight methodological challenges in taxonomic identification, particularly regarding the reliance on analogy and inference. Taxonomic identification of archaeological remains can be complex and prone to subjective interpretation, leading to potential inaccuracies or uncertainties in species identification. The lack of local reference material further compounds these issues, as visual material from published sources and online catalogues may vary in quality and reliability. Although zooarchaeology's reliance on analogous specimen identifications is an inherent epistemological part of studying past phenomena and processes (Giovas and LeFebvre 2018: 37), methodological transparency in the identification process was implemented to improve the scientific rigour of the study.

Interpretive uncertainties: While microfauna can provide valuable insights into past environments, interpretations may still be subject to uncertainties and alternative explanations. For instance, habitats of extinct species are based on the assumption that the closest living relative lives in a similar habitat.

Comparative analysis challenges: Comparing taxa from different sites can be challenging due to differences in preservation, recording methods, sampling methods, and environmental conditions.

Dating limitations: The current U-series dates are limited to six dates between roughly 63 – 53 ka (minimum age estimates) all retrieved from the same stratigraphic context (SU 11, approx. depth 2.5 – 3 m) (Table 1). The absence of reliable dates from the deepest layers of the site challenged confident interpretations of the timeframe and stratigraphy.

Taphonomic interpretation difficulties: Lack of taphonomic references for the particular karst and Mediterranean soil environment caused difficulty in identifying whether pitting on bone was caused by digestion or soil corrosion. Acidic corrosion and rounding caused by soil movement may have obscured lighter signs of digestion. Where possible, this was solved by examining how much of the surface area was corroded; inhomogeneous pitting is recorded as a sign of corrosion while concentrated corrosion and rounding at edges are recorded as a sign of digestion.

MNI difficulty: Selective transport and destruction of more fragile elements is a common occurrence in sites affected by soil movement and natural processes of deposition which are not dependent on natural in-situ death (Andrews 1990). This causes a collection bias which affects NISP and complicates the calculation of MNI, as it may over or underrepresent the species abundance. In addition, very small delicate elements like those of small lizards and squamates, and potentially bats, may not have been recovered. In fact, bats were not identifiable to species due to the elements being mostly phalanges and ribs. Snakes, in particular, can be difficult to estimate both in terms of NISP and MNI. Since there is a large amount of vertebrae and a small number of cranial elements, they may be over-represented in NISP. They may also be under-represented in MNI, since an estimate cannot be easily determined based on vertebrae.

6.5 FUTURE RESEARCH

The most pressing need to further understand the climatic and stratigraphic context of Għar il-Fkieren is to secure more reliable dating across the sequence, especially at the deeper layers. This is essential to provide a solid timeframe on which to base further interpretations.

Future research should also incorporate isotopic analysis, which could offer further insights into past environmental conditions, such as mean annual precipitation and other climatic patterns, adding another layer of understanding to the ecological context of the assemblage.

While preliminary studies on the macrofauna have been conducted, a comprehensive understanding of the ecosystem and habitat of the site during the Late Pleistocene requires combining observations and species abundance data of both microfauna and macrofauna. This integrated approach will provide a more holistic view of the biodiversity and ecological interactions within the environment.

The analysis of bird remains from Għar il-Fkieren is also crucial for interpreting the taphonomic processes affecting the assemblage, particularly the role of avian predators in shaping the faunal composition. A detailed examination of these remains could confirm or challenge current interpretations of taphonomic patterns observed in the assemblage. Taphonomic studies should also explore the effects of predation by species other than mammals and owls, such as herons and storks, to elucidate patterns of prey selection and consumption by these predators, thereby contributing to a more comprehensive understanding of the fossil assemblage.

An area of particular interest is the effect of snake predation on prey remains. Studies focused on the distinctive marks and patterns left by snake digestion and consumption could offer valuable insights. These studies should compare the damage to bones caused by snake predation with that caused by other predators to distinguish between different predatory behaviours and their impacts on the faunal assemblage.

A more detailed taphonomic analysis of weathering, cracking, splitting, and bone fractures in Mediterranean karst 'terra rossa' environments is also necessary. This analysis should employ techniques such as Scanning Electron Microscopy (SEM) to examine the microstructural changes in bones. SEM microscopy can reveal fine details of surface alterations and fracture patterns, providing a deeper understanding of the post-mortem history of the remains. Such studies could help differentiate between various taphonomic agents and processes, such as soil chemistry, mechanical pressure, and weathering. Furthermore, SEM microscopy could uncover micro-wear patterns and other subtle taphonomic features not visible through traditional microscopic methods. These features might include micro-cracks, pitting, and other surface modifications indicating specific environmental conditions or post-mortem treatments. By understanding these features, the interpretation of the depositional and post-depositional history of the faunal assemblage can be further refined.

Further avenues of research could include:

- Palynological studies on the sediments, despite the difficulties in pollen preservation in Maltese soil.
- Localised climate studies, such as speleothem dating, are also recommended.

- A comparison between shrew and vole sizes on Sicily and Malta assemblages to study gigantism or founding population effects in greater depth.

- Phylogenetic tracing of species to explore Malta as a Messinian North Africa dispersal pathway.

- A detailed morphological analysis between *Pitymys pauli* and *Microtus melitensis* to better understand their relationship.

- The study of reptilian and squamate remains in both Malta and Sicily warrants further investigation to address their palaeontological context, specifically the timeline and mechanisms of their introduction to the islands.

- More focused geological studies of the Mediterranean seabed between Malta and Sicily, to understand potential land connections during glacial Pleistocene lowstands further back than the Late Glacial Maximum.

- Focused fauna studies on the period from MIS 3 to the Neolithic to understand when Pleistocene species became extinct (*Microtus melitensis*) or extirpated (*Bufotes viridis*) and why.

7 CONCLUSION

The main objective of this research was to identify and understand the faunal assemblage from Għar il-Fkieren, for use as proxies for the Late Pleistocene local climate and environment. It aimed to provide insights into how the site and assemblage were formed against the backdrop of global Pleistocene glacial-interglacial dynamics, and elucidate the interplay between climatic fluctuations, environmental conditions, and the composition of Malta's Pleistocene faunal assemblages.

This conclusion will revisit the research questions, discussing how the findings have illuminated various aspects of these inquiries. It will also identify areas requiring further investigation and underscore the significance of the results.

The study aimed to identify which species were present for the duration of the assemblage's formation and calculate the relative abundance of species. Results of the taxonomic identification showed that the most abundant taxa were *Microtus melitensis*, the extinct Maltese vole, followed by *Bufotes viridis*, the extirpated European green toad and *Crocidura sicula*, the endemic Sicilian shrew. Notable identifications included *Podarcis* cf. *filfolensis*, an endemic species not yet recorded in the Maltese Quaternary, although Adams (1866) had noted the presence of 'small lacertids' at Ta' Gandja fissure. Various postcranial elements were assigned to *Chiroptera* sp., which represented a small portion of the assemblage especially in the deeper layers, possibly representing the cave being used for roosting shortly after the cave mouth was eroded, exposing the fissure. Finally, a small colubrid species was also identified, representing the first time Squamata were recorded in a Quaternary site.

The identification of *Colubridae* sp. was a significant find which challenges the prevailing view that snakes were only introduced recently to the Maltese Islands.

The presence of *Podarcis* cf. *filfolensis* and *Colubridae* sp. also highlights the importance of screening for small remains, since it is highly likely these were missed due to lack of screening procedures in the past. The identification of these two species represents a fresh insight into the origins of Maltese herpetofauna, which were since not significantly well-represented or discussed in Maltese Pleistocene records. This should be of significant interest to researchers interested in the origin, dispersal, and evolution of Mediterranean herpetofauna.

A further goal was to use the relative abundance of species to elucidate aspects of the Late Pleistocene climate and environment. The relative abundance, which allowed calculation of habitat weighting, suggested a predominance of shrub and forest habitat, with wetter conditions that could support a significant amphibian and tortoise population. The consistent pattern of species abundance throughout the site stratigraphy also indicated that this habitat was relatively stable during the duration of the site's deposition. These findings roughly correspond with southern Mediterranean pollen records from MIS 4-3 and support hypotheses that islands and coastal areas can experience localised climate conditions which are more subtle than broader climate change cycles. This study represents the first detailed study of microfauna as proxies for the Maltese palaeoenvironment, presenting an unprecendented insight into localised Late Pleistocene climate conditions.

Additionally, the study undertook the first taphonomic analyses of a Maltese Quaternary microfaunal assemblage, providing insight into the site formation processes of Għar il-Fkieren. Preliminary geological assessments suggest the site was initially formed by rain draining through the soil, dissolving the limestone and eroding it into a fissure beneath the surface. Eventually, the erosion opened the mouth of the fissure, exposing a cave entrance. The similar faunal composition across the sequence and similarity of sediments, along with absence of calcium carbonate layers, indicates that the fissure was filled by occasional flooding in a relatively short time span. The taphonomic analysis of the assemblage also points to mostly physical modifications as a result of sediment pressure and cave corrosion, rather than predation. Finally, once the cave was filled, it was again sealed which preserved the bone rich deposit inside.

The findings suggest that flash floods were a feature of Mediterranean island and coastal climates before Holocene climate change and align with Hunt's (1997, 1999) hypothesis that occasional extreme flood events and high sedimentation rates were common in the Maltese Pleistocene during glacial or cold stages. The dating of the site (c. 63 – 53 ka) corresponding with the transition between MIS 4-3 provided further evidence of this localised climatic feature.

While most of the bone were affected by sediment transport and weather, some of these were more well preserved and their preservation may be attributed to predation or natural death by falling into the cave. Further quantification and analyses of these specimens indicated the potential identification of *Mustela nivalis* and/or *Strix aluco* as predators by proxy. However, the study highlighted the limitations of identifying predators in assemblages dominated by such a diverse range of taphonomic modifications occurring in Mediterranean 'terra rossa' karst environments, mainly infilled by sediments and affected by acidic corrosion. Further taphonomic, geochemical and geological assessments of Quaternary 'terra rossa' sites would provide a useful insight into the specific processes involved in these contexts. However, the study also highlighted the importance of not only taxonomic, but taphonomic analyses which deepen the interpretation of site formation and local climatic conditions.

The research also aimed to further understand the climatic patterns and environmental changes which precipitated the extinction of Maltese Late Pleistocene endemic species. The findings suggest that *M. melitensis*, *C. sicula* and *B. viridis* likely survived continuously between c. 167 ka (MIS 6) to c. 63 - 53 ka (MIS 4-3), as evidenced by their presence both in Għar Dalam's Lower – Upper Red Earth layers and Għar il-Fkieren, while carnivores from the Lower Red Earth layers (c. 167 – 151 ka) appear to have gone extinct shortly after their arrival. The timing of their dispersal has been linked to the PGM (Penultimate Glacial Maximum) at

MIS 6a (c. 140 ka), while their extinction has been linked to the rapid onset of Holocene-like conditions at MIS 5e (135 ka), which would have drastically reduced island size, available prey and habitat range.

This confirms Masini *et al*. (2008)'s comparison of dispersal and extinction patterns between large and small mammals in Sicily and Sardinia, which revealed that small-sized mammals tend to survive longer, particularly in isolated systems. Additionally, it supports the observations by Van der Made (1999) and later by Masini *et al*. (2002a) that large carnivores tend to go extinct quickly in insular environments, explaining the rarity of large mammalian carnivores on islands. This highlights the importance of ecological perspectives in understanding changes in taxonomic diversity on islands.

Further work should explore the time span between MIS 4-3 to the beginning of the Holocene, to determine the causes of the extinction of *Microtus melitensis* and extirpation of *Bufotes viridis*.

The study also aimed to further understand the timing and causes faunal turnovers occurring from Sicily during the Pleistocene by correlating Maltese and Sicilian dates, faunal complexes, phylogenetic data and new information gleaned from the taxa identified at Għar il-Fkieren. Research into the faunal complexes of Għar Dalam provide hints of a climate driven faunal dispersal potentially during MIS 6e, where fauna dispersed to the islands from Sicily preceding the Għar Dalam Lower Red Earth faunal complex. However, correlating the data proved challenging due to the lack of absolute dates, highlighting the significant research gaps in the narrative of the Għar Dalam site and the need for more secure dating of layers. The discovery of herpetofauna with genetic links to much older Sicilian assemblages, however, provide hints that older dispersals may have occurred during previous marine lowstands.

This research also used morphometric analysis to elucidate aspects about the phylogenetic ancestry of species and insular evolution on islands. Morphometric comparisons of *M. melitensis* from both Għar Dalam and Għar il-Fkieren provided valuable insights into the effects of insularity on island species. This research builds upon the study by Petruso *et al*. (2011), which posits that *M. melitensis* descended from the Sicilian *M. savii* and likely dispersed earlier than its first recorded presence at Għar Dalam during MIS 6c. Petruso *et al*. (2011) observed that the Maltese *M. melitensis* exhibited a size increase characteristic of gigantism compared to its ancestral Sicilian form. This size increase is likely attributed to the stable and isolated insular conditions on the islands.

This study's morphometric analysis of *M. melitensis* remains from both Għar Dalam MIS 6 specimens and Għar il-Fkieren MIS 3 specimens revealed no significant size difference. This lack of size increase suggests that *M. melitensis* underwent morphological stasis between MIS 6 and MIS 3, supporting the hypothesis that the isolated and stable environmental conditions on the islands played a crucial role in maintaining the morphological traits of *M. melitensis* over extended periods. This provided further insight into the unique evolutionary effects of insularity on small mammals.

However, more work is needed to understand the evolutionary phenomena of gigantism and the 'founder effect' in the Maltese Pleistocene. The founder effect refers to the phenomenon where a small group of individuals, not representative of the population they come from, disperses and founds a new population, leading to genetic differences. Hunt (1999: 32) raises this possibility with reference to the size increase seen in various island endemics, suggesting that the initial colonising population may have had unique traits that were then amplified and evolved quite rapidly in the isolated environment of Malta. This concept is also discussed by Stanley (1979) and Lister (1989), who emphasize the potential for significant evolutionary changes in small, isolated populations due to limited genetic diversity and selective pressures unique to insular environments.

The findings from this study contribute to our understanding of insular evolution by highlighting the interplay between environmental conditions and morphological changes. They underscore the importance of further research to disentangle the relative contributions of insularity, genetic drift, and founder effects in shaping the evolutionary trajectories of island species. Such research would provide a more comprehensive understanding of how isolated environments influence species evolution and contribute to the broader field of evolutionary biology. Moreover, the research underscores the importance of long-term ecological stability in fostering evolutionary stasis in island species. The consistent size of *M. melitensis* demonstrates how island ecosystems, due to their isolation and stability, can preserve specific morphological characteristics in species over millennia. Further comparative studies with other insular species could provide deeper insights into the broader patterns of insular evolution and the factors contributing to morphological stasis in isolated environments.

This study represents the first focused palaeontological study of Maltese Pleistocene microvertebrates which are not derived from Għar Dalam or other Pleistocene sites of unreliable date, providing an important comparative assemblage. The data from Għar il-Fkieren underscore the potential for localised stability in island environments, highlighting the importance of detailed, site-specific studies in reconstructing past climates and understanding factors contributing to species survival and ecosystem stability during periods of global change. Islands often exhibit unique climatic and ecological conditions that can differ significantly from nearby mainland areas, underscoring the need for localised palaeoenvironmental studies. By examining these environments in detail, researchers can gain insights into broader patterns of climate change and species survival during periods of global climatic instability. This research emphasises the role of microfauna as markers for these localised palaeoenvironments and advances our understanding of how climatic and environmental factors influenced faunal assemblages in Malta during the Late Pleistocene. The findings contribute to broader discussions on climate change, species adaptation, and survival, and have implications for both academic research and practical conservation efforts, particularly in island contexts.

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