QUATERNARY ENVIRONMENTS AND BIOGEOGRAPHY OF THE MALTESE ISLANDS

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Introduction

In this contribution, we describe the environmental changes of the Quaternary period and show how these have affected the Maltese environment and the development of the Maltese fauna. Early accounts of the Maltese Quaternary deposits were often constrained by the prevailing theoretical frameworks in which they were embedded. The theoretical background to the Quaternary has changed radically over the last thirty years, as new stratigraphical and chronostratigraphical methods have been adopted and as our understanding of climatic change and ecological, geomorphological, pedogenic and sedimentation processes have improved. As a result, much early work, although at the time done to the highest professional standards, is now in urgent need of reassessment. The reassessment of the early research on the Maltese Quaternary, and particularly of the renowned Maltese Quaternary faunas, enables us to examine biogeographical processes and patterns and make suggestions for future research.

The Quaternary Period

The Quaternary is the most recent period of geological time, extending up to the present day. The Quaternary Period is the latest subdivision of the Cenozoic Era (Table 1). There is still disagreement about when the Quaternary started, but most researchers operating in the Mediterranean regard its base as at the first appearance of the ostracod *Cytheropteron testudo* at the Vrica section in Calabria (Aguirre & Pasini, 1985; Harland *et al.*, 1990). This event is close to the end of the Olduvai palaeomagnetic event

and can therefore be dated to about 1.8 million years ago (Hilgen, 1991) and widely correlated (Ruddimann *et al.*, 1986; Richmond & Fullerton, 1986).

Table 1: Divisions of geological time during the last 150 million years (modified after Harland *et al.*, 1990).

Eons	Eras	Periods	Epoch	Dates (BP)
Phanerozoic	Cenozoic	Quaternary	Holocene	10,000
			Pleistocene	1,800,000
		Tertiary	Pliocene	5,200,000
			Miocene	23,300,000
			Oligocene	35,400,000
			Eocene	56,500,000
			Palaeocene	65,000,000
	Mesozoic		Cretaceous	135,000,000
			Jurassic	

Broadly, the Quaternary is the period of time known as the 'ice age', though it must be noted that this is a very eurocentric view - in Antarctica glaciation started 38 million years ago (Webb & Harwood, 1991) and Greenland had ice sheets by 7 million years ago (Larsen *et al.*, 1994). From about 3 million years ago, ice rafted debris is present in North Atlantic cores (Kennett, 1982) and evidence for terrestrial glaciation in Europe

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and North America is apparent by 2.4 million years ago (Shackleton *et al.*, 1984; Ruddimann & Raymo 1988) During the later Pliocene and Quaternary, our ancestors evolved from ape-like primates and acquired the characteristics which we associate with humanity.

Global temperature changes are caused by the complex interaction of a number of factors. The general decrease in global temperatures recorded during the Cenozoic can be attributed to a slow change in the position of land and sea and relatively abrupt changes to global circulation patterns as a result of continental drift mechanisms. Significant events include the general drift northwards of Eurasia and North America, which led to the partial isolation of the Arctic Ocean (Williams *et al.*, 1991), the opening of the seaways between Australia and Antarctica and then between South America and Antarctica (Mikolajewicz *et al.*, 1993), the closure of Tethys (Williams *et al.*, 1998), the closure of the Ithsmus of Panama (Keigwin 1978), and the rise of the Himalayas and Alps (Molnar & England 1990). Other factors, most notably the Milankovich factors of orbital eccentricity, obliquity of the ecliptic and precession of the equinoxes (Imbrie *et al*., 1984), caused short-term climatic oscillations which are superimposed on the general Cenozoic cooling trend.

In the Quaternary, global climate changed rapidly and constantly, largely as the result of the Milankovich factors (Hays *et al.*, 1976; Ruddimann *et al.*, 1986), with alternation between periods of glacial cold (stadials) and periods with temperate conditions similar to today (interglacials) (Fig. 1). Between 2.4 million years and 0.7 million years ago, the 41,000 year obliquity cycle seems to have been the dominant driver of climate change. From 0.7 million years to 0.45 million years, obliquity declined in importance and the approximately 100,000 year orbital eccentricity cycles have become more important. During the last 0.45 million years, the eccentricity cycles have been dominant, though the pattern of climate change is complex because the effects of

obliquity (periodicity 41,000 years) and the precession cycles with their periodicities of 19,000 and 23,000 years are also apparent. There were at least 96 major changes between warmth and cold during the last 2.5 million years (Ruddimann & Raymo, 1988) and superimposed on these major changes are many smaller ones (Fig. 1). Most of these changes in global temperature were extremely rapid, with the last transition from glacial to temperate taking approximately 25 years, for instance (Atkinson *et al.*, 1984).

During glacial cold periods, water evaporated from the sea, fell as snow on land and became ice in great continental ice sheets in Northern Europe and North America. These were sometimes over 3 km thick (Boulton *et al.*, 1985). The consequence of ice sheet growth was the fall of sea level. Estimates of maximum sea level fall during glacial periods vary between 118 m (Bard *et al.*, 1990) and ca.130 m (Ferland *et al.*, 1995). Sea level rose rapidly during times of rising temperature. Sea level has only been significantly higher than it is today on one occasion during the last 250,000 years, at 125,000 years before present (Harmon *et al*. 1983).

Traditionally, the Quaternary is divided into two unequal epochs. The last 10,000 years of warm climate is called the Holocene. The rest of the Quaternary, before 10,000 years ago, is called the Pleistocene. There is still considerable disagreement about how the Pleistocene should be subdivided, but Bowen (1978) and many subsequent workers have favoured the use of a timescale based upon deep-sea core V28-238 from the Pacific Ocean (Shackleton & Opdyke, 1973). In this core, major variations in global temperature can be recognised through changes in the isotopic composition of oxygen atoms in the shells of microfossils called foraminifers. The isotopic composition of oxygen in foraminifer shells is related to the isotopic composition of oxygen in seawater. This in turn varies through time because during cold periods, water molecules containing isotopically 'light' oxygen (^{16}O) are preferentially evaporated from the sea.

Precipitation falling on the land as snow and stored as glacial ice thus depletes the seawater of isotopically 'light' oxygen, leaving the sea enriched in isotopically 'heavy' oxygen (^{18}O). Foraminifer shells laid down during cold periods thus contain more 'heavy' oxygen than do shells laid down during warm periods (Emiliani, 1955).

The isotopic signature is visible in deep-sea cores and other deposits worldwide. Similar results can be seen in the same cores from studies of the proportions of fossils of cold tolerant to warmth-loving foraminifers, from other fossils like diatoms, molluscs and pollen grains, and, near the glacier margins, proportions of glacially-derived debris in the sediments of the cores (Williams *et al.*, 1998). On land, the same pattern of abrupt cyclic climate changes is shown by studies of fossil pollen, molluscs, beetles and mammal remains in lake and cave deposits and in sedimentary sequences, most remarkably the Chinese loess sequences, where temperate periods are shown by soil profiles and stadials by the accumulation of windblown dust derived from the ice sheets (Liu & Yuan, 1987).

In the deep-sea cores, the most recent warm period, the Holocene, is numbered as Oxygen Isotope (OI) Stage 1. The preceding glacial episode is numbered Stage 2. Climate oscillations are then numbered back in time, with warm periods numbered in odd numbers and cold periods numbered with even numbers (Fig.1). This scheme can be applied globally and thus can replace the various rather incomplete land-based schemes of subdivision of the Quaternary which have been used previously. The complexity of climatic change, the incompleteness of most land-based stratigraphies, and the poor resolution of most dating tools means that many older interregional correlations are problematical and terms such as Riss or Würm in the Maltese context are virtually meaningless.

From Table 2 it can be seen that the Würm glacial period of the classic Alpine sequence is equivalent to OI Stages 2-4. The Riss/Würm temperate period is equivalent to OI Stage 5. The preceding stages are, however, difficult to equate with the OI stages and are even difficult to correlate, for instance, between Bavaria and Switzerland (Table 2). Work in the classic Alpine Foreland area has shown that most of the classic stages relate to a number of temperature oscillations (Ehlers, 1986). The position is complicated because many Oxygen Isotope stages contain several temperature peaks, which can each be related to a separate land-based interglacial. Thus, in the United Kingdom, different thermal peaks within OI Stage 7 can be related to at least two different temperate periods, the earlier Ilford and later Stanton Harcourt interglacials. OI Stage 11 can be related to an earlier Swanscombe and a later Barnham interglacial (Hunt, in press). Even more confusing, the floras of the individual interglacial episodes are often remarkably similar. Thus, the British Ilford (OI Stage 7) and Ipswichian (OI Stage 5e) interglacials had virtually identical floras and were for a long time correlated. The British Hoxnian (OI Stage 9) and Swanscombe (OI Stage 11) interglacials are also similar in many ways, and both are also very similar to the Holstein (OI Stage 11) of NW Europe (Hunt in press).

The Maltese Quaternary

Quaternary deposits and fossils provide the evidence on which our reconstructions of past environmental change are based. As in many other Mediterranean countries, current understanding of the Quaternary deposits and of the chronology and nature of environmental change in the Maltese Islands is still quite limited (Hunt, 1997). Although individual deposits have been described by a number of authors, usually in terms of their vertebrate fossil content, little attention was paid to the sediments themselves until the first detailed review of the Quaternary stratigraphy of the Maltese Islands by Trechmann (1938). Since that time, our knowledge of Quaternary events elswhere has improved out of all recognition, but until recent years there was no real progress with the Maltese Quaternary; most authors (eg. Pedley *et al.*, 1990) simply using Trechmann's conceptual framework

and repeating his stratigraphic analysis. There is, therefore, an urgent need to reassess the Maltese Quaternary using modern methods. Most descriptions of the Maltese Quaternary follow Trechmann (1938) in equating European glacial periods with periods of high rainfall (pluvial periods) in the Mediterranean. Bonatti (1966) demonstrated that this is not the case, however. The use of the outdated Continental (Riss, Würm etc.) chronostratigraphic terminology in many of publications dealing with the Maltese Quaternary also hampers understanding.

The early authors, summarised by Trechmann (1938), show a general recognition of three sets of deposits: grey sediments, usually in caves, regarded as 'older' and containing bones of extinct dwarf mammals such as elephants, hippoptamus and deer, red cave and terrestrial deposits regarded as of intermediate age containing deer, and red terrestrial sediments regarded as 'younger' and containing land snails and at times bones of domestic animals (Trechmann, 1938; Pedley *et al.*, 1990). In the following sections, the most important types of Quaternary deposits found in Malta are described and corrrelated. This builds on the approach adopted in the recent review of the Maltese Quaternary by Hunt (1997).

Tufa

Calcareous tufas are sometimes associated with karstic springs; others are the result of algal deposition in calcareous rivers and lakes (Pedley, 1978). Deposition in these environments is often very rapid. Tufas are white, often chalky-looking, friable deposits made up of calcium carbonate. Tufas are often important sources of palaeoenvironmental information because of their fossil content. They may contain leaf impressions, shells and other fossils. Tufas in the Maltese Islands often contain mollusc remains (Giusti *et al.*, 1995). The Fiddien Valley Tufa provided a pollen spectrum rich in trees and shrubs, indicative of deposition in a mid to late Pleistocene interglacial (Hunt, 1997), but the deposit does not contain enough uranium to be dated using the Uranium/Thorium disequilibrium

technique (P. Rowe, written communication, 1997).

Slope deposits

Slope deposits formed in the Pleistocene during times of aridity and low temperatures, when vegetation became very sparse and very occasional extreme rainfall events caused mudflow and overland flow processes to produce great thicknesses of poorly sorted stony deposits around the base of steep slopes. The recurrence interval of these events may be very long, sometimes over 1000 years (Hunt, 1997). Similar deposits formed rapidly in the late Holocene as the result of agricultural soil erosion in many Mediterranean countries. Typically, slope deposits mantle the lower hillslopes in the Maltese Islands. They show crude downslope layering and are poorly sorted, which means they incorporate material of all sizes from clay to large boulders. In the Maltese Islands they are often reddened or cemented with calcium carbonate. Typically, they are interbedded with ancient soil profiles which mark stillstands in sedimentation during temperate periods. Slope deposit/soil profile sequences extending back at least four Oxygen Isotope stages are known from the Maltese Islands.

Fluvial deposits

Fluvial deposits are rare in Malta. Vita-Finzi (1969) proposed a model for the Mediterranean valleys, of a 'Younger Fill' - brown, silty alluvium, largely of late-Roman age, resting on or incised into an 'Older Fill' - reddened coarse gravels of Pleistocene age. The fills were supposed to have formed during periods of higher rainfall. Recent work suggests, however, that the Pleistocene gravels formed mostly during ephemeral flood events in generally arid cold-stage environments, while the 'Younger Fill' is a polyphase deposit, ranging from the Neolithic to modern times and largely resulting from river aggradation as a response to hydrological and sediment flux variations caused by deforestation and agricultural soil erosion (authors in Lewin *et al.*, 1995).

Most fluvial deposits underlie more or less flat terrace surfaces at the side of valleys. Typically, they are composed of layers of fairly well-sorted deposits, with layers of gravel laid down in-channel, and layers of silt laid down on the floodplain. The gravels tend to be typified by trough cross-bedding, the ancient equivalent of the multi-channel sedimentation style evident in many ephemeral watercourses on Malta today, which is visible as streaky or lenticular layers of fine and coarse gravel. This type of bedding is usually equated with deposition in a largely devegetated landscape with abundant sediment supply and 'flashy' discharges.

Fluvial deposits are also found in alluvial fans at the foot of steep slopes. Here, considerable thicknesses of gravel may accumulate. The fluvial gravels are often interbedded with fine-grained alluvium which shows signs of soil formation during temperate periods. Fluvial deposits in the Maltese Islands probably date from at least five stadial episodes.

Figure 1: The oxygen isotope curve for a mid-latitude site: ODP Site 607 in the mid-Atlantic. The Oxygen Isotope Stages are numbered from the top, with odd numbered stages being warm and even numbered stages being cold (after Ruddimann *et al.*, 1989).
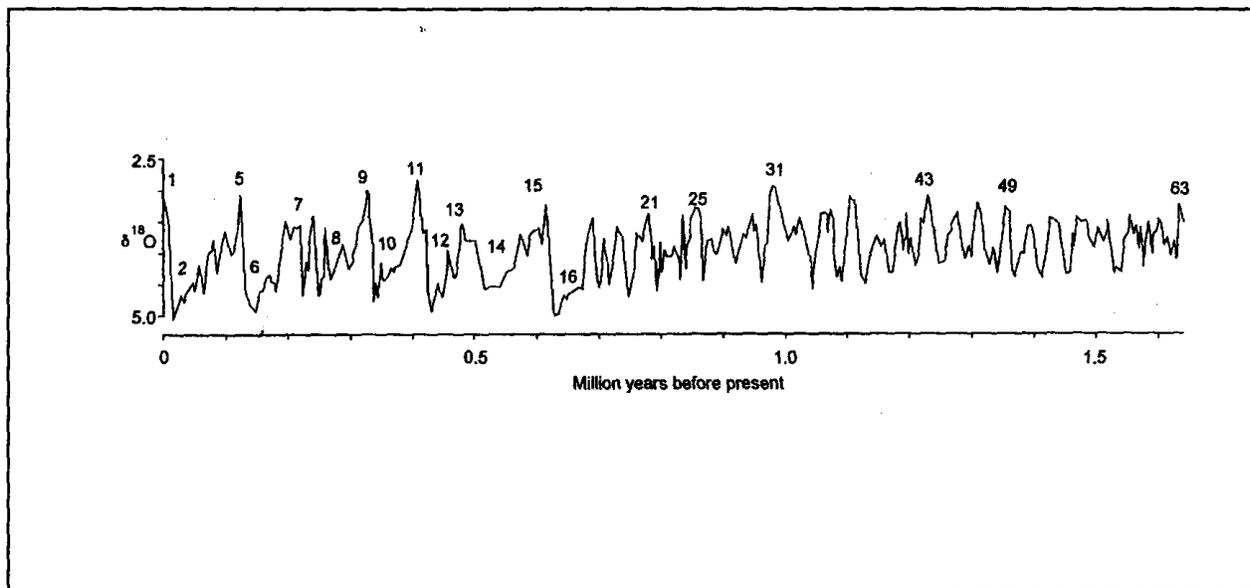
Table 2: Comparison of the Oxygen Isotope Stratigraphy for the last million years with selected regional chronologies (following Gibbard *et al.*, 1991; Ehlers, 1996; Lowe & Walker, 1997; Tzedakis *et al.*, 1997; Hunt, 1998 and Hunt, in press and unpublished)

Time of initiation (ka BP)	Oxygen Isotope Stages	Magneto-stratigraphy	Switzerland and Baden-Wurtemburg	Bavaria	North Germany	Netherlands	Britain	Italy	Greece (Tenaghi Philippon)	North America
10	1		Holocene	Holocene	Holocene	Holocene	Holocene	Holocene	Holocene	Holocene
110	2-5d		Würm	Würm	Weichselian	Weichselian	Devensian			Wisconsinian
125	5e		Krumbach	Riss-Würm	Eemian	Eemian	Ipswichian	VdC-10	Panagaion	Sangamon
190	6		Doppelwall	Late Riss	Saale	Warthe	?			Late Illinoan
250	7			?	Wacken	Saale	Stanton Harcourt Ilford	Roma I-III	Symvolon Strymon	
300	8			Early Riss	Saale (s.l.)	Drenthe	?			Early Illinoan
340	9				?	Domnitz/Wacken	Hoxnian Purfleet		Krimines Litochoris	
390	10				Fuhne	Fuhne/Mehlneck	?			Pre-Illinoan A
430	11		Sammerberg	Mindel / Riss	Holstein	Holstein/Muldsberg	Swanscombe Barnham		Lekanis	
480	12		Older Riss		Elster	Elster 1	Anglian			Pre-Illinoan B
510	13	Brunhes (normal)				Elster ½	Cromerian?			
560	14									Pre-Illinoan C
630	15			Mindel Complex		Cromerian IV / Noordbergum	Cromerian?			
690	16					Glacial C	Kennpier?			Pre-Illinoan D
720	17			Günz /Mindel?		Cromerian III / Rosmalen	Cromerian?			
780	18					Glacial B				Pre-Illinoan E
	19		Halsch-Mindel Complex	Günz Complex		Cromerian II / Westerhoven	Cromerian?			
	20	Matuyama				Helme/Glacial A				Pre-Illinoan F
	21	(*pars.,* reversed)				Cromerian I / Astern/ Wardenburg				
						Dorst				Pre-Illinoan G
900	27	Jaramillo			Pinneberg	Leerdam				
		(normal)	Uhlenberg	Uhlenberg	Elmshoorn	Linge				
1070	31				Lieth	Bavel				
					Pinnau	Menapian				
			Günz							
		Matuyama			Tornesch (TC)	Waalian 1				
		(*pars.* reversed)			Cryomer (TB)	Waalian 2				
					Tornesch (TA)	Waalian 3				
				Donau Complex						
					Lieth	Eburonian (*pars.*)				Pre-Illinoan H

Ancient soils

Slope deposits and fluvial deposits are typically interbedded with ancient soils, called palaeosoils. Palaeosoils are marked by a high clay content, typical soil structures caused by the translocation down the profile of clay and calcium carbonate, and sometimes root casts. Often, the upper layers of a soil are removed by later erosion, but the lower layers of a soil, where calcium carbonate has accumulated, become heavily cemented and extremely durable. This cemented soil is known as a calcrete. The presence of vegetation is needed to cause the stabilisation of the landscape and the formation of a soil. The palaeosoils thus mark periods of temperate climate. Palaeosoils are present in many Quaternary sequences in the Maltese Islands, reflecting soil formation during at least five temperate periods.

Coastal deposits

Coastal deposits are rare in the Maltese Islands, but well-preserved sequences occur at a number of localities along the Marfa Ridge. The ancient marine deposits are often interbedded with slope deposits - hillwash, mudflow, debris flow and scree deposits. They are usually more or less cemented together by calcrete - calcium carbonate precipitated in the subsoil by soil-forming processes.

The shoreline deposits were left by previous high stands of the sea during temperate periods. Only the back-beach deposits, which today typically form about 2-4 m above sea-level, are still preserved, now at an altitude around 1 m above modern sea level. These marine deposits are usually coarse yellowish sands with occasional seashells. They may be associated with ancient dune sands, which are very well-sorted fine sands, often of a reddish colour. It is likely that the Marfa Ridge shoreline deposits, which today lie within 1-2 m of the present sea-level, were laid down during the marine transgression of Oxygen Isotope Stage 5e. Sea level at this time was up to 6 m above present levels (Harmon *et al.*, 1983). This implies that the Marfa Ridge has subsided by approximately 6-9 m in the last 125,000 years.

Aeolian silts

Windblown silts or loess are a common sedimentary facies around the Central Mediterranean. Loess seems to have originated both as 'rock flour' from glaciated terrain in Northern Europe during glacial episodes, and as desert dust from a 'greater Sahara' to the south. Loess often caps hill-tops, and is recognisable as pale brown (though sometimes reddened) silts with often very well pronounced columnar jointing (Hunt 1997).

Cave, fissure and doline deposits

Caves and fissures are generally the result of karst solution processes, differing principally in size - fissures are too small to insert a caver's body into! Fissures may also be formed by the early stages of landslipping. Dolines are solution and collapse features in limestone, or in overburden over limestone, and often form as caves collapse. Cave deposits are an important source of information about Quaternary conditions thoughout the Mediterranean region, since in them are sometimes preserved long sedimentary sequences containing a diversity of fossil groups, including mammal, bird, reptile and amphibian bones, mollusc shells, pollen, and sometimes seeds and charcoal. They are also important sites for finding the remains of early people, and their artefacts. Cave sequences are particularly important because they often contain layers of flowstone, which can be dated by the Uranium/Thorium disequilibrium technique, although this has not yet been attempted in the Maltese context. Fissure fills are generally smaller. Doline fills are rarely investigated, but dolines are often accumulation sites for vertebrate remains and may sometimes contain waterlain deposits which are a useful source of pollen.

In the Maltese Islands, a number of cave deposits were excavated during the nineteenth and early twentieth centuries centuries. Fissure fills and cave deposits are

found regularly by quarrymen, but rarely reported. Unfortunately, most excavation records are very poor. The best-described and most important sequence is at Ghar Dalam cave (Zammit Maempel, 1989a), which is described below in some detail.

Summary of Maltese Quaternary Terrestrial Environments

During temperate stages the climate in Malta was much as the climate of today, hot in summer, cool in winter and with relatively abundant, albeit seasonal, rainfall. The Maltese landscape was well-vegetated, with forest predominating. Erosion was therefore rather ineffectual and well-structured soils formed. Humic acids produced by the plant cover and from leaf litter led to the solution of calcium carbonate from soils and from the bedrock. Some of this was reprecipitated as calcrete but much went into the groundwater, to emerge from strongly calcareous springs, whence it was reprecipitated as tufa. Other sedimentation was extremely localised, largely along the coast, where beach and dune deposits accumulated.

Temperatures fell considerably during cold stages, to the extent that there were probably severe winter frosts. Annual average rainfall diminished considerably, with aridity limiting the growth of plants. Erosion and sedimentation were pronounced because the virtually non-existent vegetation cover left the ground surface vulnerable to erosion. Very occasional extreme rainfall events led to erosion by wash, mudflow and debris-flow. This material then accumulated as slope deposits or was washed into watercourses where ephemeral floods redeposited it as valley floor gravels and alluvial fans. Long-distance wind transport and deposition of silt, both from the glaciated areas to the north and from the great deserts to the south, also took place. Much of the silt became incorporated into slope deposits.

Evidence presented by Hunt (1997), together with unpublished work discussed above, strongly suggests that the terrestrial Quaternary record can be traced back through at least four temperate stages and four cold stages in the stacked fluvial deposit/palaeosoil and slope deposit/palaeosoil sequences of the Maltese Islands. It is therefore probable that, contrary to the view of Trechmann (1938) and most other early writers, the terrestrial deposits of the Maltese Islands extend further back in time than do the vastly important fossiliferous cave sequences which are discussed below.

Quaternary faunas of the Maltese Islands

Knowledge of Maltese Quaternary faunas is limited to fossil and sub-fossil remains of vertebrates and molluscs recovered from a variety of localised deposits, all of which are apparently of Pleistocene or younger age. These comprise palaeosoils, fluvial gravels, alluvial fans, coastal conglomerates and breccias, dunes and infillings of caves and fissures as already described.

Ghar Dalam Cave

The most complete sequence discovered so far is that of the Ghar Dalam cave. The Ghar Dalam faunas are also the best studied and the only ones reliably dated, and as such are worth reviewing in some detail. Zammit Maempel (1989a) has summarised the current state of knowledge of the Ghar Dalam deposits, while more recently Savona Ventura & Mifsud (1998) have reviewed the stratigraphy.

Ghar Dalam owes its origin to a subterranean solution tunnel (phreatic tube) formed below the bed of a stream flowing through Wied Dalam. Zammit Maempel (1989a) suggests that the stream cut into its bed, eventually penetrating through the ceiling of the tunnel, and depositing its bed-load in the tunnel. Further downcutting by the stream resulted in two caves (the two terminal portions of the original tunnel) perched on either bank of the watercourse (see Fig.4 of Zammit Maempel, 1989a). The larger cave on the northeast bank of Wied Dalam is Ghar Dalam[1]. The geomorphic

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[1] The other cave on the opposite bank, known simply as the 'Second Cave', is much less deep than Ghar Dalam and only contains detrital clay which is apparently

position of the cave and the nature of the sedimentary sequence in the cave (see below) make this explanation of the origins of the cave and its fill somewhat questionable, however.

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sterile of macroscopic organic remains (Zammit Maempel, 1989a).

Table 3: The stratigraphic sequence at Ghar Dalam with the nomenclature used by various authors for the different layers and faunal stages.

Stratigraphic layer	Excavators description	Author				
		Vaufrey (1929)	Trechmann (1938)	Storch (1974)	Zammit Maempel (1985; 1989a)	Savona Ventura & Mifsud (1998)
I	Boulders	Niveau superficiel	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					

Because different authors have recognised different numbers of strata at Ghar Dalam, and have devised different nomenclatures for these, it is difficult to compare different works. Savona Ventura & Mifsud (1998) have attempted to cross-relate the main schemes. In the following discussion we follow the numbering system of the strata as given by these latter authors. This scheme is reproduced in Table 3 together with the nomenclature of the layers used by these and previous workers. A list of the vertebrate fossils recovered from these strata is given in Table 4.

The fossil remains were mostly studied in the late 19th Century and early 20th Century (see references in Zammit Maempel 1989a, and Savona Ventura & Mifsud 1998). More recently, Storch (1970) studied the micromammalian fauna, and later the chiropteran remains in more detail (Storch, 1974); Fischer & Stephan (1974) studied the avian remains, and Boessneck & Kuver (1970) those of domestic animals from the upper layers of the cave deposits. The stratigraphy of the Ghar Dalam deposits has been described by numerous authors, foremost amongst which Vaufrey (1929), Trechmann (1938), Storch (1974) and Zammit Maempel (1985; 1989a). Storch's (1974) scheme is particularly important since he based it on the micromammalian content of the deposits in an effort to produce a system which could be applied to other Quaternary deposits on the islands, and perhaps elsewhere in the Mediterranean.

The most ancient deposits at Ghar Dalam (Layer VIII) have been suggested to lie somewhere between the Late Pliocene/Early Pleistocene and the Late Pleistocene (Zammit Maempel, 1985; 1989a). These deposits, which are nearly sterile of macroscopic fossils, are overlain by a fossil-rich layer (Layer VII) suggested to be of Early Pleistocene age (according to Storch, 1974) or of Middle Pleistocene age and tentatively dated to 125,000 BP according to Zammit Maempel (1989a). Recently, Mifsud & Mifsud (1997) published the results of chemical and radiometric analyses on animal remains from Ghar Dalam and other deposits carried out by the Natural History

Museum of London[2] (see also Savona Ventura & Mifsud, 1998)[3]. These results indicate an Upper Pleistocene date for hippopotamus, deer, pig and horse remains from Ghar Dalam. In 1988, J.L. Ma and his co-workers presented a conference paper in which they gave a date of 180,000 BP (± 10%) for a hippopotamus (*Hippopotamus pentlandi*) molar from the earliest fossiliferous deposits (Layer VII) of Ghar Dalam dated using Electron Spin Resonance (ESR) (Ma *et al.*, 1988). In an unpublished manuscript, these workers revised this date to 115,000 BP (± 10,000) on the basis of additional Thorium/Uranium dating of the same molar (Bouchez *et al.*, unpublished[4]). Remains from Layer VII at Ghar Dalam have therefore been absolutely dated from the very end of the Middle Pleistocene or the earliest Upper Pleistocene. It is important to note that this does not necessarily mean that **all** the fossils from this layer are of the same age; below we shall put forward a number of lines of evidence to support the hypothesis that there may be fossils from two separate time-periods admixed together.

This earliest fossiliferous deposit (Layer VII) has yielded the remains of two species of hippopotami (*Hippopotamus pentlandi*, a dwarf species, and *H. melitensis*, which was even smaller), two or three species of pygmy elephants (*Elephas* subgenus *Palaeoloxodon*), two species of giant dormice (*Leithia cartei* and *Eliomys gollcheri*), five species of bats, a shrew (*Crocidura* cf. *russula* according to Storch, 1974), and numerous birds including a giant swan (*Cygnus falconeri*).

Apparently, Storch now regards the '*Leithia cartei*' from the lowermost fossiliferous layers of Ghar Dalam as belonging to *Eliomys* (*Maltamys*) sp. (G. Storch *in litt.* to Savona Ventura & Mifsud; see Savona Ventura & Mifsud, 1998 p.10). For this reason, Savona Ventura & Mifsud (1998) have renamed the '*Leithia cartei*' stage of Storch (1974) as the Gliridae stage.

This layer was overlain by a fossil-free pebble/small boulder layer (Layer VI) inferred to be of Upper Pleistocene age (Zammit Maempel, 1989a), which was in turn overlain by a series of fossiliferous layers containing large quantities of deer remains, also of Upper Pleistocene age (c.18,000 BP according to Zammit Maempel, 1989a). These are Layers V and IV, collectively referred to as the 'red earth layers'. Savona Ventura & Mifsud (1998) have proposed a splitting of these layers into a lower 'Carnivora stage' and an upper 'Cervus stage' on the basis of the presence of carnivores in the lower, but not in the upper red earth layers.

Apart from a dwarf form of Red Deer (*Cervus elaphus*), these layers yielded the remains of bear (*Ursus* cf. *arctos*), a small fox (*Vulpes* sp.)[5], wolf (*Canis lupus*), a vole (*Pitymys melitensis*), bats, a shrew (*Crocidura* sp.), birds, a terrapin (*Emys orbicularis*) and a toad (*Bufo bufo*). Despott (1923) reported remains of pig, horse and cow (without specifying the species or whether they were wild or domesticated) from the upper red earth layers, the first from the top layer and the other two at various depths. Human artefacts and remains have also been recovered from the red earth layers (Despott, 1918), including two taurodont molars that have been the subject of much controversy (Keith, 1918, 1924; Oakley, 1971; Mifsud & Mifsud, 1997).

A calcareous sheet separated the Deer layer from the overlying strata (Layers III, II, and I). On the basis of their micromammalian content, Storch (1974) recognised two

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[2] Previously known as the British Museum (Natural History).

[3] The results of all tests carried out on Maltese material are preserved in the manuscript records of the Department of Palaeontology, The Natural History Museum of London. Before the Mifsud father and son team published these results, only some of these data were published, possibly in semi-corrupted form (Mifsud & Mifsud, 1997).

[4] While this paper was never formally published, copies of the manuscript were made available to selected participants of the '*Early man in island environments*' conference [September 25 – 2 October 1988, Oliena, Sardinia] (David S. Reese, personal communication).

[5] According to Despott (1923) the fox remains consisted of jaws and teeth probably belonging to two distinct species.

divisions: a lower (prehistoric) *Apodemus sylvaticus* stage (Layer III) dated as Holocene and spanning from the Ghar Dalam to the Bronze Age phases of Maltese prehistory (c.7200 to 2700 BP), and an upper (historic) *Rattus rattus* stage (Layers II and I) dating from Phoenician (c.2700 BP) to modern times.

The *Apodemus sylvaticus* layer yielded remains of this species as well as Black Rat (*Rattus rattus*), bats, and a shrew (according to Storch 1974, *Crocidura russula*). The *Rattus rattus* layer yielded remains of this species as well as of Brown Rat (*Rattus norvegicus*), House mouse (*Mus musculus*), hedgehog (*Erinaceus algirus*), bats, and Pygmy shrew (*Suncus etruscus*). These layers also yielded the remains of toads and a tortoise (see Savona Ventura, 1984) as well as domestic animals including cattle, sheep, goat, pig, cat, pigeon, and domestic chicken (*Gallus gallus domesticus*). Despott (1923) also reported rabbit (without specifying the species) from these layers. Other (wild) species found were Hawfinch (*Coccothraustes coccothraustes*), a skink (*Chalcides ocellatus*), and the Painted Frog (*Discoglossus pictus*). Additionally, human remains and many cultural artefacts were recovered, including pottery shards, sling stones, flint, chert and obsidian tools and personal ornaments (reviewed by Evans, 1971).

Fossil remains of other species have also been recorded from Ghar Dalam, but it is not clear exactly which layers these were found in (Table 4). One of these species is a small horse (*Equus* sp.)[6] which according to Bate (1916) was found in association with remains of small elephants and a large chelonian, which convinced her that this equine formed part of the extinct Pleistocene fauna of Malta. Cooke (1893a) also reported the remains of horses from the superficial layers of the cave, as did Despott (1923) from both the superficial layers and the upper red earth layers. It is not at all clear whether these authors were reporting domestic horses or a wild species. Two species of

equiids are know from Sicilian deposits: the domestic horse (*Equus caballus*) and a wild ass (*Equus hydruntinus*); both apparently reached Sicily in the Upper Palaeolithic (Burgio, 1998).

Other species reported from Ghar Dalam include a vole (*Pitymys pauli*), most probably from the red earth layers (Bate, 1935), a small swan (*Cygnus equitum*), geese (*Branta bernicla* and *Branta leucopsis*), and bustards (*Tetrax campestris* and *Otis tarda*) (Bate, 1916).

Copious remains of terrestrial molluscs as well as some marine species were recovered from the superficial (historic and prehistoric) layers of the cave, and apparently also from the upper red earth layers (Cooke, 1893a; Despott, 1918, 1923; Rizzo, 1932; Trechman, 1938; Baldacchino, 1934, 1935, 1937). Terrestrial and marine shells may also have been recovered from the lower red earth layers (Despott, 1918, 1923). The marine species collected were in the main edible species and were interpreted as Neolithic kitchen debris. Echinoid spines belonging to a cidarid, (*Stylocidaris* or *Cidaris*[7], which are not edible) were suggested as being tools for decorating pottery (Despott, 1923). The terrestrial molluscs recovered were ubiquitous species still common all over the islands.

While the vast bulk of hippopotamus and elephant remains from Ghar Dalam occurred in the lower fossiliferous layer (Layer VII), remains of these animals were also found in the lower red earth layers (Layer V) (Cooke, 1893a; Despott, 1918, 1923; Canton Thompson, 1923; Baldacchino, 1934, 1935, 1936, 1937, 1938; Trechman, 1938). Isolated hippopotamus and elephant remains were also apparently found in the upper red earth layers (Layer IV) (Despott, 1923; Baldacchino, 1935; Trechman, 1938), while elephant tusks were apparently recovered from the upper red earth layers[8]

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[6] "…*an animal of about the size of a New Forest pony*." (Bate 1916 p.424).

[7] According to Despott (1923), *Cidaris*, but the commonest extant cidarid in the Maltese Islands is *Stylocidaris affinis*.

[8] Baldacchino (1937 p.xxi) states explicitly that for the elephant remains (which he reports as *Elephas mnaidriensis* and *Elephas melitensis*), "…*it was possible*

(Baldacchino, 1937; Trechman 1938). Remains of deer were most abundant in the red earth layers (Layers V and IV) but deer were also found in the prehistoric layers (Despott, 1918, 1923; Baldacchino, 1934, 1937, 1938).

Doubt exists about the actual stratigraphic provenance of these remains. Some authors argue that they may have been displaced from lower layers (from the red earth layers to the prehistoric layer for deer, and from the bone breccia layer to the red earth layers for hippopotamus and elephant) (Sinclair, 1924; Canton Thompson, 1925). Others argue that for the hippopotamus remains at least, the physical appearance of the fossils from the red earth layers is very different from those from the bone breccia layer (Cooke, 1893a; Despott, 1918, 1923; Baldacchino, 1937, 1938; see also Savona Ventura & Mifsud, 1998). Keith (1924) accounted for the presence of human remains in the red earth layers with deer, hippopotamus and elephant as due to disturbance of the layers by Neolithic people, who certainly occupied the cave, and who may have interred their dead in its soil. The presence of edible marine species of molluscs in the upper, and possibly also the lower red earth layers (Despott, 1917, 1923), lends credence to the theory that mixing of the layers may have occurred.

It is also well known (see for example, Sinclair, 1924 p.268; Baldacchino, 1936 p.xxvii) that the early excavators of the cave did not always keep exact records of where they dug or which strata the material they recovered came from. One excavator at least, refilled his trenches with the same material that he dug out (Cooke, 1893a), and one of the trenches dug by Despott was partly situated in the same area as one such refilled trench, as stated by Despott himself (Despott, 1923 p.32). Additionally, unauthorised and unrecorded excavations are also known to have taken place (Rizzo, 1932; Baldacchino, 1935; Morana, 1987; Savona Ventura & Mifsud, 1998). It is also possible that some form of natural mixing of

to ascertain that these fossil remains belonged originally to this bed and were not derived from an older stratum."

layers occurred - slumping is common in cave sediments and some predators are known to dig dens in cave floors for instance. This may have caused the stratigraphy of the cave to be laterally inconsistent, a possibility that might not have been noticed in the restricted excavations of the early researchers.

Re-examination of the stratigraphic sequence at Ghar Dalam using modern sedimentological techniques is clearly urgently necessary, since the early excavators neglected other than the most cursory descriptions of the cave sediments and many of the scientific problems discussed above could be addressed simply. A number of observations can be made already, based on material on display in the Ghar Dalam Museum and examination from a distance of the preserved stratigraphic column in the cave.

Examination of fragments of Layer VII on display in the Ghar Dalam Museum indicates clearly that this is **not** a waterlain deposit. The deposit is unsorted and unbedded and there is no sign of the imbrication (common particle orientation) that would be expected with a fluvial sediment. Zammit Maempel (1989a) notes that the early excavators found the animal bones in this layer in "*pell mell occurrence*". The lack of sorting, bedding and imbrication is suggestive of a mass flow deposit of some kind. Fossil material of widely different ages is very likely to have become incorporated in the mass flow, probably as existing quaternary deposits became liquified under saturated conditions and formed a mudflow.

The pebble layers (VI, for instance) are likely to be lag deposits left by local shallow wash events. The red cave earths of layers V, VI, II and I appear to be 'normal' cave earths of terrestrial origin, laid down by a mixture of airfall dust, small-scale rockfall and granular disintegration of the cave roof, small scale wash, the traction of sediment into the cave by animals and people and so forth. Such layers tend to accumulate when there is a relatively abundant sediment supply, perhaps because of an incomplete

vegetation cover caused by climatic extremes (layers V, VI) or farming (layers I, II). The thin calcareous sheet at the base of Layer III is most probably of stalagmitic origin and early Holocene date, reflecting abundant vegetation as an acid source and relatively high rainfall to dissolve calcium carbonate, together with the cessation of the clastic sediment supply, probably because of a relatively complete vegetation cover (see discussion of Tufa, above).

Table 4: List of vertebrate species identified from the Quaternary deposits at Ghar Dalam (see Table 3 for description and numbering of layers) and those known from Maltese sites other than Ghar Dalam, with an indication of their occurrence in Sicily.

SPECIES	DESCRIPTION AND NOTES	Malta					Sicily
		Ghar Dalam				Not known from Ghar Dalam	
		Superficial layers I, II, III	Red earth layers IV, V	Bone breccia VI, VII	Unknown stratigraphic provenance		
Amphibia							
Discoglossus pictus	*Painted frog*	+	-	-	-	-	+
Bufo bufo	*Common toad*	(?)+	+	-	-	-	-
Bufo viridis	*Green toad*	+	-	-	-	-	+
Reptilia Testudines							
Geochelone robusta	*Extinct giant tortoise*	-	-	-	+	-	+
Testudo sp.	*Tortoise*	+	-	-	-	-	+
Emys orbicularis	*European pond terrapin*	-	+	-	-	-	+
Reptilia Sauria							
Lacerta siculimelitensis	*Extinct giant lizard*	-	-	-	-	+	+
(?) Podarcis sp.	*Wall lizard*	-	-	-	-	+	(?)+
Chalcides ocellatus	*Ocellated skink*	+	-	-	-	-	-
Aves							
Cygnus equitum	*Swan*	-	-	-	+	-	*Sicilian fossil birds have been little studied*
Cygnus falconeri	*Extinct Maltese giant swan*	-	-	+	-	-	
Cygnus sp.	*Swan*	-	-	-	-	+	
Anser sp.	*Goose*	-	-	-	-	+	
Branta bernicla	*Brent goose*	-	-	-	+	-	
Branta leucopsis	*Barnacle goose*	-	-	-	+	-	
Anas acuta	*Pintail duck*	-	-	+	-	-	
Marmaronetta angustirostris	*Marbled teal*	-	-	-	-	+	
Hieraeetus fasciatus	*Bonelli's eagle*	-	-	-	-	+	
Gyps melitensis	*Extinct Maltese vulture*	-	-	-	-	+	
Alectoris graeca	*Rock partridge*	-	-	+	-	-	
Coturnix coturnix	*Quail*	-	-	+	-	-	
Grus melitensis	*Extinct Maltese crane*	-	-	-	-	+	
Grus grus	*Common crane*	-	-	-	-	+	
Tetrax campestris	*Bustard*	-	-	-	+	-	
Otis tarda	*Great Bustard*	-	-	-	+	-	
Gallus gallus domesticus	*Domestic chicken*	+	-	-	-	-	
Scoloplax ghardalamensis	*Extinct Maltese woodcock*	-	+	+	-	-	
Columba melitensis	*Extinct Maltese dove*	-	-	-	-	+	
Columba livia	*Domestic pigeon*	+	-	-	-	-	
Otus scops	*Scops owl*	-	-	+	-	-	
Tyto alba	*Barn owl*	-	-	+	-	-	
Strix melitensis	*Extinct Maltese tawny owl*	-	-	-	-	+	
Hirudo sp.	*Swallow*	-	.	+	-	-	
Turdus sp.	*Thrush*	-	+	+	-	-	
Sturnus vulgaris	*Starling*	-	-	+	-	-	
unidentified estrildid	*Waxbill*	-	+	-	-	-	
Carduelis chloris	*Greenfinch*	-	-	+	-	-	
Coccothraustes coccothraustes	*Hawfinch*	+	-	+	-	-	
Insectivora							
Crocidura cf. russula	*White-toothed shrew (all records of Maltese Quaternary Crocidura probably refer to C. esuae; see Hutterer, 1990; 1991).*	-	-	+	-	-	-
Crocidura russula		+	-	-	-	-	+
Crocidura sp.		-	+	-	-	-	+
Suncus etruscus	*Pygmy shrew*	+	-	-	-	-	-
Erinaceus algirus	*Algerian hedgehog*	+	-	-	-	-	-

Order / Species	Common name						
Chiroptera							
Rhinolophus hipposideros	Lesser horseshoe bat	+	+	+	-	-	+
Rhinolophus mehelyi mehelyi	Mehely's horseshoe bat	-	+	-	-	-	+
Rhinolophus mehelyi	Extinct Maltese race of	-	-	+	-	-	-
birzebbugensis	Mehely's horseshoe bat	+	+	-	-	-	-
Rhinolophus euryale	Mediterranean horseshoe bat	-	+	+	-	-	+
Rhinolophus blasii	Blasius' horseshoe bat	+	-	-	-	-	-
Myotis blythi	Lesser mouse-eared bat	-	-	+	-	-	-
Myotis exilis	Mouse-eared bat	-	-	+	-	-	-
Myotis bechsteini robutus	Extinct Maltese race of Bechstein's mouse-eared bat	-	-	+	-	-	-
Myotis ghardalamensis	Extinct Maltese mouse-eared bat	-	-	+	-	-	+
Myotis capaccinii	Long-fingered bat	-	-	+	-	-	-
Eptesicus praeglacialis	Extinct Maltese serotine	+	-	-	-	-	-
Vespertilio murinus	Parti-coloured bat	+	-	+	-	-	-
Pipistrellus pipistrellus	Common pipistrelle	-	+	+	-	-	+
Miniopterus schreibersi	Schreiber's bat						
Lagomorpha							
'Rabbit'	(?) domestic rabbit	+	-	-	-	-	+
Rodentia Gliridae							
Eliomys (Maltamys) gollcheri	All are extinct dormice showing	-	-	+	-	-	+
Eliomys (Maltamys)	different degrees of gigantism	-	-	-	-	+	+
wiedincitensis		-	-	+	-	-	+
Leithia cartei		-	-	-	-	+	+
Leithia melitensis		-	-	-	-	+	-
Leithia aff. melitensis							
Rodentia Muridae							
Pitymys pauli	Extinct pine vole	-	(?)+	-	-	-	-
Pitymys melitensis	Extinct Maltese pine vole	-	+	-	-	-	-
Rattus rattus	Brown rat	+	-	-	-	-	+
Rattus norvegicus	Black rat	+	-	-	-	-	+
Apodemus sylvaticus	Wood mouse	+	-	-	-	-	+
Mus musculus	House mouse	+	-	-	-	-	+
Carnivora Ursidae							
Ursus cf. arctos	Brown bear (? small form)	-	+	-	-	-	+
Carnivora Canidae							
Vulpes sp. (? Vulpes)	Fox (? small form)	-	+	-	-	-	+
Canis lupus	Wolf	-	+	-	-	-	+
Carnivora Mustelidae							
Lutra euxena	Extinct Maltese otter	-	-	-	-	+	-
Carnivora Felidae							
Felis catus	Domestic cat	+	-	-	-	-	+
Proboscida							
Elephas (Palaeoloxodon) falconeri	All are extinct pygmy elephants showing different degrees of nanism	-	-	+	-	-	+
Elephas (Palaeoloxodon) melitensis		-	(?)+	+	-	-	+
Elephas (Palaeoloxodon) mnaidriensis		-	(?)+	+	-	-	+
Perissodactyla Equidae							
Equus sp.	(?) Extinct wild ass	-	+	(?)+	-	-	(?)
Equus caballus	Domestic horse	-	-	-	-	-	+
Artiodactyla Suidae							
Sus sp.	(?) Wild boar	-	+	-	-	-	+
Sus scrofa domestica	Domestic pig	+	-	-	-	-	+
Artiodactyla Hippopotamidae	All are extinct pygmy hippopotami showing different degrees of nanism						
Hippopotamus pentlandi		-	-	+	-	-	+
Hippopotamus melitensis		-	-	+	-	-	(?)+
Artiodactyla Bovidae							
Bos sp.	(?) Wild cattle	-	+	-	-	-	+
Bos taurus	Domestic cattle	+	-	-	-	-	+
Capra hircus	Domestic goat	+	-	-	-	-	+
Ovis aries	Domestic sheep	+	-	-	-	-	+
Artiodactyla Cervidae							
Cervus elaphus	Red deer	-	-	-	-	(?)+	+
Cervus elaphus siciliae	Extinct pygmy red deer	-	+	-	-	-	+
(?) Dama dama	Fallow deer	-	-	-	-	+	(?)+

Other sites

Fissure infills and cave sediments from various parts of the islands have yielded fossils of the islands' Pleistocene fauna (see lists by Adams, 1870, 1877; Tagliaferro, 1915; Bate, 1916, 1935; Baldacchino, 1936, 1937, 1938; Trechman, 1938; Böhme & Zammit Maempel, 1982; Zammit Maempel & De Bruijn, 1982; Savona Ventura, 1984; for an account of the excavations by T.A.B. Spratt, A. Leith Adams and J.H.Cooke see Zammit Maempel, 1989b). These included several of the species reported from Ghar Dalam, as well as others not known from this site (Table 4). In very few sites was a stratigraphy present, and in no case was a detailed record of the excavations kept. It is therefore not possible to relate these sites to the Ghar Dalam stratigraphy other then by a gross comparison of the fauna. Similarly, no dating, other than by comparison of faunas, exists for any site. Moreover, almost none of these sites still exist, precluding an investigation using modern techniques.

Species recorded from these fissures and caves include the same hippopotami, elephants, and deer as found at Ghar Dalam, as well as dormice (*Leithia melitensis, Leithia cartei, Eliomys gollcheri* and *Eliomys wiedincitensis*) (De Bruijn, 1966; Zammit Maempel & De Bruijn, 1982), voles (*Pitymys* spp.), shrews (*Crocidura* cf. *russula* according to Bate, 1935), bats (*Rhinolophus* sp.), a mustelid (*Lutra euxena*; Bate, 1935), a bear (*Ursus* sp.) as well as various avian, reptilian and amphibian remains (see the following and references therein: Spratt, 1867; Adams, 1863, 1864, 1865, 1866a,b, 1867, 1868, 1870, 1874a,b, 1877; Cooke, 1893a; Tagliaferro, 1915; Bate, 1916, 1935; Trechmann, 1938; Northcote, 1981-83, 1982a,b,c, 1984; Böhme & Zammit Maempel, 1982; Zammit Maempel & de Bruijn, 1982; Savona Ventura, 1984).

Many Quaternary deposits, especially the supposedly younger ones that tend to include few or no vertebrate remains, are rich in the fossil and subfossil remains of brackish water, freshwater and terrestrial molluscs (Murray, 1890; Cooke, 1891, 1896; Baldacchino, 1936, 1937, 1938; Trechmann, 1938; Pedley, 1980; Giusti *et al.*, 1995; Hunt, 1997). Many of these species are still extant in the Maltese Islands, however, a number, especially freshwater forms, are no longer found alive (Giusti *et al.*, 1995).

Correlation with Sicilian Quaternary faunas

As has been observed many times, starting with the earliest studies of the Maltese Quaternary fossil faunas, these are very similar to those from Sicily, and indeed are almost certainly derived from them. It is therefore instructive to compare the Maltese with the Sicilian faunas.

An account of the earlier studies on the Sicilian Quaternary faunas has been given by Kotsakis (1979), and more recently by Burgio (1998). The modern study of these faunas owes its origin to the seminal work of Kotsakis (1979) that was followed by many tens of publications (see the extensive bibliographies in Bonfiglio, 1991; Bonfiglio & Burgio, 1992 and in Burgio, 1998). Until relatively recently, several different faunas were recognised from Sicily, spanning from the Late Pliocene-Lower Pleistocene *Pellegrinia* fauna, to the very late Upper Pleistocene-early Holocene *Equus hydruntinus* fauna. Between these two, several other faunal stages and sub-stages were recognised, characterised by different species of elephant and hippopotamus (Kotsakis, 1979; Burgio, 1998).

In 1991, Bada and his co-workers dated a large number of Sicilian Quaternary mammals belonging to *Elephas mnaidriensis*, *Elephas falconeri*, *Elephas antiquus*, *Hippopotamus pentlandi* and the deer *Praemegaceros carburangelensis* and *Cervus elaphus siciliae*, using isoleucine epimerization, and discovered that their ages fell into two groups with no overlap between them (Bada *et al.*, 1991). One group with an average age of 455,000 (±90,000) BP comprised all the elephants except some specimens of *Elephas mnaidriensis*. The other group, with an average age of 200,000 (±40,000) BP comprised all the other species,

and some specimens of *Elephas mnaidriensis*. Bada *et al.* (1991) interpreted their data as suggesting that Sicily experienced at least two immigrations of megafauna: an early Middle Pleistocene one characterised by elephants, including *Elephas falconeri* and endemic micromammals (glirids and soricids), and a mid-Middle Pleistocene one characterised by *Elephas mnaidriensis,* hippopotamus, cervids, bovids and carnivores.

On the basis of this and other studies, four Sicilian faunal stages are currently recognised (Table 5).

Nothing remotely similar to the Late Pliocene-Lower Pleistocene *Pellegrinia* fauna of Sicily has been discovered on the Maltese Islands. On the basis of the single Thorium/Uranium date of 115,000 (±10,000) BP for a *Hippopotamus pentlandi* molar from Ghar Dalam (Bouchez *et al.*, unpublished), it would appear that the earliest Quaternary fauna known from Ghar Dalam (that from Layer VII) belongs to the third wave of Sicilian immigrants. However, there is one problem with this interpretation: the occurrence of *Elephas falconeri* admixed with *Elephas mnaidriensis* and hippopotamus remains. In Sicily, such an admixture is only known from one site, where, however, the deposit has been reworked (Bada *et al.*, 1991). In fact, Bonfiglio & Burgio (1992) have shown that in Sicilian deposits of different types (colluvial and alluvial deposits, cave and fissure infills, lacustrine deposits, and coastal plain deposits), two separate Middle Pleistocene faunal associations (e.g. the *Elephas falconeri* fauna and the *Elephas mnaidriensis* fauna) of considerably different ages are consistently present.

The Sicilian and Maltese Quaternary faunas are so similar to each other that it is difficult to imagine that two distinct Middle Pleistocene faunas occur in Sicily but only one, which includes species from **both** Sicilian faunas, in the Maltese Islands. The bone breccia of the basal fossiliferous layer (Layer VII) at Ghar Dalam may actually represents two separate faunas

corresponding to the Sicilian ones reworked together. Dating more fossils from this layer, especially the various species of elephants present, would be a good test of this hypothesis.

All the other faunal associations younger that the basal one but older than the Holocene deposits (i.e. Layers IV, V and VI) are simply variants of the *Elephas mnaidriensis* fauna of Sicily, probably reflecting different palaeo- or depositional environments.

Evolutionary, biogeographical and palaeoecological aspects

The Quaternary fossil faunas of the Maltese Islands show strong affinities with the European faunas of the same period, particularly those of Sicily. Many of the Pleistocene species known from the Maltese Islands occurred also in Sicily (Caloi *et al.*, 1988; Bonfiglio, 1992; see Table 4). Of these, many are apparently Siculo-Maltese endemics, since they are only known from Sicily (and the circum-Sicilian islands) and the Maltese Islands. The present day biota of these islands is also very similar, and in large part the Maltese biota is a sub-set of the Sicilian one (Francini Corti & Laza, 1973; Di Martino & Raimondo, 1979; Lanfranco, 1984; Schembri, 1992).

The present day Maltese biota includes a relatively large number of Siculo-Maltese endemisims; it also includes a substantial number of exclusively Maltese endemic taxa (Lanfranco, 1987, 1989b; Schembri, 1992). These fall into two categories. One set of endemics is apparently of Tertiary origin and reached the Maltese Islands at an early date possibly at the very end of the Miocene or during the Pliocene. These have developed in isolation for an extended period of time, in some cases sufficiently long to differentiate also at the supra-specific level. Many such species have no close living relatives, and the fossil record generally gives no clues as to their ancestry. Such species are termed palaeoendemic. The second set of endemics has clearly been derived from Sicilian ancestors relatively recently (Pleistocene to Recent) and only

show a relatively weak differentiation, sometimes only at infra-specific level. These are termed neoendemic.

Table 5: The four currently recognised Sicilian Quaternary faunas, with an indication of their characteristic mammalian species and of their age (modified from Burgio, 1998).

Fauna	*Pellegrinia panormensis* fauna	*Elephas falconeri* fauna	*Elephas mnaidriensis* fauna	*Equus hydruntinus* fauna
Characteristic species	*Apodemus maximus* *Maltamys* cf. *gollcheri* *Pellegrinia panormensis* *Hypolagus* sp. *Episoriculus* n.sp. *Mustelercta arzilla*	*Leithia melitensis* *Leithia cartei* *Crocidura esuae* *Lutra trinacriae* *Elephas falconeri* *Elephas* cf. *mnaidriensis*	*Leithia melitensis* *Maltamys wiedincitensis* *Crocidura esuae* *Crocuta crocuta spelaea* *Panthera leo spelaea* *Canis lupus* *Ursus arctos* *Elephas antiquus leonardii* *Elephas* sp. (? cf. *antiquus*) *Elephas mnaidriensis* *Sus scrofa* *Hippopotamus pentlandi* *Hippopotamus* sp. *Cervus elaphus siciliae* *Megaceros carburangelensis* *Bos promigenius siciliae* *Bison priscus siciliae*	*Hystrix cristata* ?*Pytimis savi* ?*Lepus europaeus* *Erinaceus europaeus* *Crocidura sp* ?*Lynx lynx* *Felis sylvestris* *Canis lupus* *Vulpes vulpes* *Equus caballus* *Equus hydruntinus* *Sus scrofa* *Cervus elaphus elaphus* *Bos primigenius primigenius*
Age	Late Pliocene – Lower Pleistocene	early Middle Pleistocene	mid-Middle Pleistocene	Very late Upper Pleistocene – early Holocene

It is not difficult to trace in broad terms the sequence of events that led to the development of the extinct and extant biotas of the Maltese Islands. Shortly after their formation, the Maltese Islands received an influx of immigrant biota from Sicily, which in turn had received its biota from the European mainland. The Siculo-Maltese populations must have become isolated for a sufficiently long period of time to allow development of an endemic Siculo-Maltese biota in the Pleistocene. However, the Pleistocene biota of the Maltese Islands also included a few exclusively Maltese elements, so presumably the Maltese Islands must have been at least semi-isolated from Sicily. At the end of the Pleistocene, some groups became extinct. The first influx of immigrants to the Maltese Islands gave rise to the Pleistocene endemics (both Siculo-Maltese and exclusively Maltese) and presumably also to the present day palaeoendemics, while later arrivals, both during the Pleistocene and more recently, gave rise to the neoendemics.

While the outline biogeography is perhaps clear, the details are very obscure and a great many questions remain unanswered. For example, when did the first influx of immigrants occur? When and for how long were the Sicilian and Maltese biotas isolated during the Pleistocene? Was this isolation total or only partial? Why did certain forms become extinct at the end of the Pleistocene? How and when did the ancestors of the present day neoendemics reach the islands? Note that here and in the preceding paragraph, by isolation is meant reproductive isolation of populations. This is probably related to actual physical isolation of the Maltese Islands and Sicily, but physical isolation is not a prerequisite for genetic isolation: populations may become genetically isolated even if geographically confluent and conversely, gene flow can occur even in the presence of a geographical barrier between two populations. Therefore, another set of questions arises about the relative contributions of genetic and geographical isolation on the biogeography of the Maltese Islands.

Yet another set of questions concerns the contribution of the environment to the development of the island biotas, which show a number of peculiarities when compared to continental ones, including a reduced number of species, lack of particular groups, species which are larger when compared to their mainland ancestors

(gigantism), others that are smaller (nanism), flightlessness in birds, and changes in both habit and habitat of species when compared to their mainland relatives. The particular environment found on the islands (both the physical environment [for example, uneven terrain, poor vegetation cover, etc.] and the biotic one [for example, very small gene pools, reduced competition from certain species, lack of certain types of predators, lack of resources forcing intense intraspecific competition etc.]) must have played as important a role as genetic isolation for these adaptations to arise. This aspect has been largely unexplored, at least in the local context.

What follows is a review of selected groups of Quaternary biota of the Maltese Islands in order to analyse what information they provide on the biogeography and palaeoecology of the region and on the evolution of the groups themselves.

Reptiles

Of particular interest amongst the Maltese herpetological remains are those of giant tortoises (*Geochelone* spp.) and a giant lizard (*Lacerta siculimelitensis*). Remains of the former were found in various Pleistocene deposits from Malta, including those from Zebbug, Mnajdra Gap, and Corradino Hill and possibly Ghar Dalam (see review by Savona Ventura, 1984). Individuals of three sizes have been found, which have received different names: *G. spratti* for small sized individuals (tibia length c.85 mm), *G. robusta* for medium sized ones (tibia length 105-132 mm), and *G. robustissima* for the largest individuals (tibia length c.170 mm) (Savona Ventura, 1984). However, these are now regarded as a single, variable species, *Geochelone robusta* (Caloi *et al.*, 1986), which may have weighed up to 90 kg and reached lengths of up to 1.2 m.

The associated fauna included another chelonian (the terrapin *Emys orbicularis*), elephants (*Elephas* spp.), the glirid *Leithia melitensis*, and the giant swan *Cygnus falconeri*. This fauna is intermediate between that found in Layers VII and V at Ghar Dalam (Table 4).

Remains of *Lacerta siculimelitensis*, a large species estimated to have reached a total length (body + tail) of 0.70-0.75 m, were recovered from Pleistocene deposits from Ta' Kandja, Benghisa Gap and Wied Incita all on Malta (see Böhme & Zammit Maempel, 1982 and review therein). In all three cases these were associated with the remains of smaller individuals, possibly belonging to a different species (? *Podarcis* sp.), while in the first two sites mentioned, remains of *Elephas falconeri* were also found. At Wied Incita, remains of *Ursus* cf. *arctos*, the glirid *Eliomys wiedincitensis*, birds and chelonians were also present. The Wied Incita deposit has been suggested to date from the very late Pleistocene (Böhme & Zammit Maempel, 1982). *L. siculimelitensis* is also known from Sicily where it has been found in "Würmian" (=supposedly Upper Pleistocene) deposits with *Elephas falconeri* (Böhme & Zammit Maempel, 1982). Belluomini & Bada (1985) and Bada et al. (1991) have dated Sicilian *Elephas falconeri* as mid-Pleistocene. This suggests that Böhme & Zammit Maempel's date for the Wied Incita deposit is too young.

The associated fauna at Wied Incita and particularly the presence of bear remains might be taken to suggest that *L. siculimelitensis* was coeval with the fauna from Layer V at Ghar Dalam (Table 4). The presence of elephant fossils with the *Lacerta* remains at Ta' Kandja and Benghisa Gap does not invalidate this assignation since (i) elephant remains were also found in Layer V at Ghar Dalam (see section on Ghar Dalam above), and (ii) the Ta' Kandja and Benghisa Gap sediments were apparently deposited by running water (Böhme & Zammit Maempel, 1982).

Birds

The most thoroughly studied avian fossils are those of the extinct Maltese cranes and swans. A large (c.8 kg - see Northcote, 1982a,b) endemic crane, *Grus melitensis*, was described by Lydekker (1890) from Pleistocene deposits from Zebbug, Malta, while additional material of the same species was obtained from Tal-Gnien by

Dorothea M.A.Bate and from Mnajdra Gap by Andrew Leith Adams (Northcote, 1982a). On the basis of the associated fauna, the Mnajdra material was tentatively dated at 135,000-115,000 BP by Northcote (1984). Northcote showed that this crane was sympatric with another smaller species (*Grus grus*) (Northcote, 1982b), and that *Grus melitensis* did not appear to have reduced powers of flight as previously supposed (Northcote, 1984).

An endemic swan, *Cygnus falconeri*, was described by Parker (1865) from the Zebbug Pleistocene deposits, while remains of the same species are also known from Tal-Gnien, Mnajdra and Ghar Dalam (Northcote 1982c, 1981-83). Northcote (1982c, 1981-83) has shown that this swan was a very large species, weighing some 17.5kg and with a wingspan of some 3m, and that it was probably flightless. Additionally, it was a good walker on land and the very small salt gland indicated that it probably fed mainly on terrestrial plants.

Both the endemic crane and the endemic swan were associated with remains of elephants, hippopotami, glirids and chelonians (Adams, 1870), suggesting that they belonged to the same fauna as that of Layer VII at Ghar Dalam (Table 4).

Glirids

Four species of fossil Gliridae (dormice) are known from the Maltese Islands. Adams (1863) described two of these (as *Myoxus*): *Leithia melitensis*, which is a large sized species, and the slightly smaller *L. cartei*. These Siculo-Maltese Pleistocene species are very closely related and differ mainly in size. Another two glirids belonging to the genus *Eliomys*, *E. gollcheri* (originally described as *Hypnomys*) and *E. wiedincitensis*, were described by De Bruijn (1966) and by Zammit Maempel & De Bruijn (1982), respectively. *E. wiedincitensis* is larger than *E. gollcheri*, but both are smaller than the two *Leithia* species. Zammit Maempel & De Bruijn (1982) instituted the new subgenus *Maltamys* for the two Maltese *Eliomys* and hypothesised on their phylogeny. According to these authors a species of *Eliomys* (s.str.)

from the European mainland spread throughout the western Mediterranean area during the Messinian. During the Pliocene, populations of this species which became isolated on various islands developed along separate lines to give rise to different endemic subgenera and species: *E.* (*Hypnomys*) *waldreni* in the Balearics, *E.* (*Thyrrhenoglis*) *figariensis* in Sardinia, and *E.* (*Maltamys*) *gollcheri* in Sicily and the Maltese Islands. Each of these species then evolved further by Late Pleistocene times – in the case of Sicily and the Maltese Islands, into the endemic *E.* (*M.*) *wiedincitensis*. This scenario implies a period of Plio-Pleistocenic isolation for the Siculo-Maltese Islands sufficiently long for the evolution of an endemic supraspecific taxon (the subgenus *Maltamys*).

The case of the *Leithia* species is not so clear-cut. *Leithia* shows some affinities with *Eliomys* subgenus *Maltamys*, but there are also important differences, which led Zammit Maempel & De Bruijn (1982) to suggest that the similarities may be due to convergent evolution. These authors have also suggested that the two *Leithia* are chronosubspecies, representing a continuous evolutionary line from some unknown ancestor invading from the mainland, as in the case of *Maltamys*. The occurrence of remains of *L. melitensis* and *L. cartei* in the same deposits suggests that they were coeval (De Bruijn, 1966) or, as suggested above, that Layer VII is mixed. Following the former hypothesis, it would appear that the original mainland ancestor gave rise to two sympatric species, when populations became cut off on Sicily and Malta. By the Late Pleistocene, one of these (*L.melitensis*) may have given rise to what may be another distinct species or chrono-subspecies – referred to as *Leithia* aff. *melitensis* by Zammit Maempel & De Bruijn (1982).

From an analysis of the associated fauna, it would appear that *L. melitensis*, *L. cartei* and *E.* (*Maltamys*) *gollcheri* form part of the fauna represented in Layer VII at Ghar Dalam, while *E.*(*M.*) *wiedincitensis* and *Leithia* aff. *melitensis* are part of the fauna represented in Layer V (Table 4).

Carnivora

The Pleistocene Carnivora of the Maltese Islands are represented by four species: brown bear *Ursus* cf. *arctos*[9], a fox *Vulpes* sp., wolf *Canis lupus*, and an otter *Lutra euxena*. With the exception of the otter, all the other species are best known from the Ghar Dalam deposits, where they occur in Layer V (Table 4). Although fossils of carnivores are very rare in Maltese deposits, evidence of their activity is more widespread; for example, the fossil elephant remains which Spratt (1867) excavated from the Zebbug Cave (Wied il-Kbir) showed signs of gnawing, as did the elephant remains recovered by Andrew Leith Adams from Mnajdra Gap (Cooke, 1892).

An extinct endemic otter, *Lutra euxena,* was described by Bate (1935) from the Pleistocene of Tal-Gnien, Malta (as *Nesolutra euxena*). Of the other extinct Pleistocene species of insular otters known (Willemsen, 1992), the closest to the Maltese species is *Lutra trinacriae* from Sicily (Burgio & Fiore, 1988). However, the Sicilian and Maltese species have many important differences, showing that they shared the same ancestor but developed along different lines, presumably after the Sicilian and Maltese populations became separated. The faunas associated with *L. trinacriae* and *L. euxena* are also very similar and Burgio & Fiore (1988) have suggested a Middle to Upper Pleistocene date for these assemblages. According to these authors the Sicilian and Maltese otters were both fish-eating marine species, however the Maltese *Lutra euxena* was more adapted to terrestrial life.

Elephants

Three species of endemic fossil Siculo-Maltese elephants (*Elephas* subgenus *Palaeoloxodon*) have been described: *Elephas mnaidriensis*, which was some 1.9 m high, *E. falconeri*, which was only some 0.9 m high[10], and an intermediate form between the two which has been called *Elephas melitensis*, but which is now usually synonymised with *E. falconeri*. All appear to be related to the common European mainland species *Elephas antiquus*, which reached a height of 3.5-4.0 m and fossils of which have also been found in Sicily[11]. Vaufrey (1929) has postulated that the smallest form evolved from *E. antiquus* via the intermediate sized forms during the Middle to Upper Pleistocene (i.e. *antiquus → mnaidriensis → melitensis → falconeri*). Burgio & Cani (1988) compared the faunas associated with *E. falconeri* and *E. mnaidriensis* in Sicily and concluded that these are very different. For example, apart from the elephants themselves, few other species are common to both; additionally, while the *falconeri* fauna includes endemic forms, that of *mnaidriensis* is little different from the continental latest Upper Pleistocene-Holocene fauna. Furthermore, the stratigraphy does not support Vaufrey's hypothesis; according to Burgio & Cani (1988) remains of *E. mnaidriensis* have always been found immediately below Palaeolithic deposits without any *E. falconeri* remains in between, as required by Vaufrey's scheme. Moreover, on the Hyblean plateau, *E. falconeri* remains were found in older strata, below those containing *E. mnaidriensis* (Bonfiglio & Insacco, 1992). Amino acid racemisation dating of Sicilian *E. falconeri* from Spinagallo Cave and of *E. mnaidriensis* from Puntali Cave support an older age for the former: *E. falconeri* 550,000 BP (Middle Pleistocene), *E. mnaidriensis* 180,000 BP (late Middle Pleistocene to

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[9] Bear remains recovered from Maltese deposits consist of teeth and an almost complete left ramus of the mandible. Cooke (1892) attributed this ramus to *Ursus arctos* (brown bear). In a subsequent paper (Cooke, 1893b) he referred to it as *Ursus ferox*. This jawbone is similar to that of brown bear but since some of the diagnostic characters are missing it is best referred to as *Ursus* cf. *arctos*. It also appears to belong to a form significantly smaller than continental *U.arctos* (Zammit Maempel, 1989a).

[10] This and other figures quoted are estimates of the average size of full-grown individuals, however, the Siculo-Maltese fossil elephants were apparently sexually dimorphic with males being larger than females (Ambrosetti, 1968). Roth (1990) gives an estimated shoulder height of 1.3 m for male and 1.0 m for female *Elephas falconeri* from Sicily.

[11] The Sicilian fossil *Elephas antiquus* have a somewhat reduced size relative to the continental species and for this reason were named as a separate subspecies (*Elephas antiquus leonardii*) by Aguirre (1968-69).

Upper Pleistocene) (Belluomini & Bada, 1985).

Burgio & Cani (1988) suggest a phylogeny for the Siculo-Maltese elephants based on repeated invasions and extinctions (i.e. faunal turnovers; see Table 5). *E. antiqus*[12] first invaded Sicily and Malta during the Middle Pleistocene. In the absence of predators, the populations isolated on these islands evolved into a dwarf form – *E. falconeri* – which later became extinct, perhaps due to a change in climate. A second invasion by *E. antiquus* occurred in Upper Pleistocene times. When again isolated, these populations gave rise to *E. mnaidriensis*, however, because the associated fauna now included predators, reduction in size was not as favoured as previously, and *E. mniadriensis* did not become as dwarfed as *E. falconeri*. A further change in climate caused the extinction of this fauna[13].

In Sicily, two groups of *Elephas mnaidriensis* fossils apparently occur: an older group forming part of the early Middle Pleistocene *Elephas falconeri* fauna, and a younger group forming part of the mid-Middle Pleistocene *Elephas mnaidriensis - Hippopotamus pentlandi* fauna (Bada *et al.*, 1991; Bonfiglio & Insacco, 1992). It has been suggested that these two groups may actually belong to unrelated species that are morphologically similar due to convergence (Bada *et al.*, 1991). If this hypothesis is

correct, and, as suggested by us (see section on correlation with the Sicilian faunas, above), both these Sicilian faunas are represented in the Maltese Islands, then the status of local '*Elephas mnaidriensis*' fossils, as well as those of *Elephas melitensis*, needs to be re-assessed to ascertain whether the former belong to the 'old' or 'young' 'E. *mnaidriensis*', and whether the latter is a good species and possibly synonymous with either of the two groups currently included in '*Elephas mnaidriensis*'.

Deer

Remains of deer have been found in many Maltese Upper Pleistocene and early Holocene deposits. The deer remains recovered from some prehistoric sites (e.g. Pike, 1971), and the human remains and artefacts found mixed with deer remains in Layer IV at Ghar Dalam, suggests that deer may have been contemporaneous with the earliest human inhabitants of the Maltese Islands. In fact, it has been suggested that deer may have become extinct partly due to hunting pressure from the early settlers coupled with habitat destruction correlated with the introduction of agriculture to the islands (Thake, 1985).

The Maltese deer remains have been attributed to red deer, *Cervus elaphus* (Smith Woodward in Cooke, 1893a; Bate, 1916), although according to Despott (1918) the deer remains from Ghar Dalam "*unquestionably belonged to two species, as some of the antlers were at the base as much as 3 inches in diameter*." Remains of "*Cervus dama*" (= *Dama dama*) were apparently found by Andrew Leith Adams in a fissure at Valletta (see Zammit Maempel, 1989b legend to Plate 67); Bate (1916) lists "*Cervus dama*" with a question mark, suggesting that she considered this record doubtful. It is interesting to note that in Sicily, abundant remains of Middle Pleistocene deer originally attributed to *Dama dama* have been assigned to a pygmy megacerine deer *Praemegaceros carburangelensis* (Gliozzi & Malatesta, 1982). It would not be surprising if this species would also prove to be present among the Maltese deer material.

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[12] Although most authorities subscribe to the view that the Siculo-Maltese fossil elephants are all derived from *Elephas antiquus* or a close relative, there are some dissenting opinions. For example, Lister & Bahn (1994) postulate an ancestry for *Elephas falconeri* from early mammoth (possibly *Mammuthus meridionalis*) stock. This hypothesis gains support from the geological distribution of the putative ancestors since *Mammuthus meridionalis* is a Lower to Middle Pleistocene species, while *Elephas antiquus* is a Middle to Upper Pleistocene one. An early Middle Pleistocene age for *Elephas falconeri* of Sicily such as found by Bada *et al.* (1991) fits in better with derivation of this species from *Mammuthus meridionalis* than from *Elephas antiquus*. If this hypothesis is correct, *Elephas falconeri* should be renamed *Mammuthus falconeri*, as proposed by Mol *et al.* (1996).

[13] Burgio & Cani (1988) postulate a third invasion of fauna ("fauna a *Equus hydruntinus*") occurred in the Upper Palaeolithic, however, this time no species of elephant were included (Table 5).

The Maltese *Cervus elaphus* belonged to a dwarf form similar to one that inhabited Sicily and which has been named *Cervus elaphus siciliae* (Gliozzi *et al.*, 1993). Zammit Maempel (1989a) figures the longest (259 mm) and shortest (152 mm) femora of this species housed in the Ghar Dalam Museum collections. On the basis of the mean femur length (274 mm) of modern European red deer (*Cervus elaphus hippelaphus*), the extinct Maltese deer had a height at the shoulder of between 0.83 m and 1.40 m. However, Gliozzi *et al.* (1993) estimate that the Maltese populations had an average shoulder height of 0.7-0.8 m, making them smaller than the Sicilian populations (shoulder height: 0.8-0.9 m; Gliozzi *et al.,* 1993). Surprisingly, no detailed studies on the Maltese *Cervus elaphus* seem to have been carried out, apart from the tantalising information given in passing by Zammit Maempel (1989a pp.48-51), and while Gliozzi *et al.* (1993) who studied extensive material from Sicily consider the Sicilian and Maltese red deer as conspecific, this needs to be confirmed by detailed osteological and biometric studies on Maltese material.

Burgio & Di Patti (1990) have postulated repeated invasions and extinctions to explain the occurrence of remains of *Cervus elaphus* in Sicilian Quaternary deposits. These authors suggest that *Cervus elaphus* from the Italian peninsula invaded Sicily and then developed in isolation, eventually giving rise to the dwarf form *C. elaphus siciliae* which was associated with the Middle Pleistocene *Elephas mnaidriensis* fauna (Table 5). This fauna eventually became extinct and a second invasion of *C. elaphus* occurred, became isolated, and gave rise to a slightly dwarfed form which was a member of the Upper Palaeolithic *Equus hydruntinus* fauna (Table 5). These populations eventually also became extinct, possibly due to human activities.

Zammit Maempel (1989a) suggests that deer reached Malta from Sicily after having already become somewhat dwarfed. The same author does not seem to subscribe to the idea of repeated invasions of the Maltese

Islands, as he states that he has traced a "*graduated sequence*" of sizes of deer bones in the Ghar Dalam collections. To him this suggests a "*a local progressive stunting*[14] *event*" (Zammit Maempel, 1989a).

Terrestrial Mollusca

Trechmann (1938) listed about 20 species of fossil snails from Maltese Quaternary deposits, describing some eight taxa as endemic extinct forms. The fossil terrestrial Mollusca of the Maltese Islands received no further attention until the extant and extinct non-marine species were revised by Giusti *et al.* (1995). These authors placed Trechmann's taxa in synonymy with extant species, with one exception all still living in the Maltese Islands. The single exception is *Xeromunda durieui* which is locally extinct, although common all along the African shores of the western Mediterranean, in southern Italy, and in Cyprus.

Giusti *et al.* (1995) also studied more recently collected molluscan material from a wide variety of Quaternary deposits from the Maltese Islands. They recorded a total of 42 fossil and sub-fossil species, of which all but eight are presently living in the Maltese Islands (Table 6). Of these eight extinct forms, four are species that either live in freshwater wetlands that are perennially wet, or are associated with very damp habitats. All of these species were found in a lacustrine deposit at Wied tal-Bahrija

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[14] It is unfortunate that some authors have used the term 'stunting' to describe the phenomenon of insular nanism. Stunting implies reduced growth due to environmental stress. Insular nanism is an evolutionary process resulting in reduced body size compared to the ancestral population. This may be partly a response to intra- and inter-specific competition for limiting environmental resources but it may be due to other factors as well (for example, lack of predators). Insular nanism is not a one-to-one reduction in size but is usually allometric and involves numerous morphological adaptations apart from small size, including in cranial and dental morphology as well as in that of the appendicular skeleton. As an example of the morphological changes accompanying nanism in *Elephas falconeri*, and their possible adaptive significance, see Sondaar & Boekschoten (1967) and Mol *et al.*, (1996). For adaptations of Mediterranean Pleistocene herbivores, including deer, to the insular environment see Caloi & Palombo (1990) and Palombo (1996).

(Malta) where they form part of a suite of freshwater-associated species, some of which still occur at Bahrija and/or in other freshwater habitats in the Maltese Islands. Giusti *et al.* (1995) have interpreted these species as indicative of past much wetter conditions than currently occur in the Maltese Islands. Unfortunately, this deposit has not yet been dated. The other four locally extinct species (*Orculella templorum*, *Siciliaria* cf. s*eptemplicata*, *Xeromunda durieui* and *Trochoidea* cf. *caroni*) are all associated with xeric habitats.

Table 6: Fossil non-marine Mollusca known from the Maltese Islands, with an indication of status (LF – living and fossil; F – fossil only) and habitat (modified from Giusti *et al*., 1995)

Species	Status	Habitat
Gastropoda		
Pomatias sulcatus	LF	Ubiquitous
Pseudamnicola moussonii	LF	Freshwater; springs
Ovatella myosotis	LF	Brackish water; amphibious; saline marshlands
Carychium cf. *schlickumi*	LF	Freshwater; springs
Lymnaea truncatula	LF	Freshwater; amphibious; ponds and slow-moving water
Planorbis planorbis	LF	Freshwater; slow-moving water
Planorbis moquini	LF	Freshwater; springs
Gyraulus crista	F	Freshwater; wetlands
Bulinus cf. *truncatus*	F	Freshwater; wetlands
Ancylus fluviatilis	LF	Freshwater; running water
Oxyloma elegans	F	Humid environments; wetlands
Vertigo cf. *antivertigo*	F	Humid environments; wetlands
Truncatellina callicratis	LF	Leaf litter
Orculella templorurn	F	Xeric environments
Granopupa granum	LF	Xeric environments especially karstland
Vallonia pulchella	LF	Humid environments; wetlands
Chondrula pupa	LF	Ubiquitous
Vitrea contracta	LF	Humid environments; leaf litter
Vitrea sp.	LF	Humid environments; leaf litter
Oxychilus draparnaudi	LF	Damp environments
Cecilioides acicula	LF	Subterranean; soil
Hohenwartiana hohenwarti	LF	Subterranean; clayey soil
Rumina decollata	LF	Xeric environments
Siciliaria cf. *septemplicata*	F	Xeric environments
Lampedusa imitatrix	LF	Xeric environments especially karstland
Muticaria macrostoma	LF	Xeric environments especially karstland
Papillifera papillaris	LF	Ubiquitous
Sphincterochila candidissima	LF	Xeric environments especially coastal karstland
Xerotricha apicina	LF	Xeric coastal environments
Trochoidea spratti	LF	Xeric environments especially karstland
Trochoidea cf. *caroni*	F	Grassy habitats
Cernuella caruanae	LF	Ubiquitous
Cernuella cf. *cisalpina*	LF	Ubiquitous
Cernuella cf. *virgata*	LF	Grassy coastal habitats
Xeromunda durieui	F	Xeric environments
Cochlicella acuta	LF	Ubiquitous
Theba pisana	LF	Ubiquitous; especially common in coastal habitats
Marmorana melitensis	LF	Xeric rocky habitats receiving some shade
Eobania vermiculata	LF	Ubiquitous
Cantareus aspersum	LF	Ubiquitous
Bivalvia		
Pisidium casertanum	LF	Freshwater; springs
Pisidium personatum	LF	Freshwater; springs

Palaeoenvironment

The study of the Quaternary deposits of the Maltese Islands and the fossils they contain has thrown some light on the palaeoenvironment of the islands at the time. Trechmann (1938) postulated that Ghar Dalam and other caves were eroded during a pre-Chellian pluvial period, that the earliest bone deposits date from the Chellian[15], and that there followed an arid period during the Mindel-Riss interglacial (i.e. 290,000-190,000 BP), in turn followed by another pluvial period (post-Riss). The discussion above clearly makes this hypothesis untenable.

On the basis of the fossil Chiroptera from Layer VII of Ghar Dalam cave, Storch (1974) deduced a Mediterranean climate and the presence of large bodies of freshwater, forests with high trees and open areas. Storch (1974) considered this layer to be of Early Pleistocene age. Later stages showed a reduction in habitat diversity. The supposedly Middle Pleistocene fossil avifauna from Ghar Dalam indicated the presence of open country poor in vegetation or with stands of trees, and possibly, the presence of standing water (Fischer & Stephan, 1974). Taxa such as bustards and quail are certainly indicators of open steppe or desert vegetation. Assessment of the other fauna of layer VII is difficult because of the number of extinct taxa. Most extant doormice are woodland species. Hippos and elephants (apart from most mammoths) in the Pleistocene in Europe are usually found in association with signs of woodland, though in Africa today they are more often associated with savanna. The wild ass is a steppe and montane species. Either a mixed habitat, with some woodland and some open ground, or, more likely, a mixing of the fauna from two or more layers is probable.

More helpful conclusions can be drawn from the fauna of the later layers. In the Red Earth layers (IV, V), the presence of

European pond terrapin points to relatively mild conditions – this species is thermally limited in Europe today (Stuart, 1982). Pine voles today are found in woods and grassland. Wild boar and brown bear are woodland animals. Most other taxa are catholic in their habitat requirements, but a number have predominantly southern European distributions and waxbills today are an African family. The exception is the wild ass: a steppe or montane species. A warm climate and at least some woodland are indicated by most of this fauna, although it is possible that the mixture of species reflects rapidly oscillating climate not resolved by the crude methods of the early excavators. The evidence for warmth and probably oscillating conditions implies a Late-Glacial (13,000-11,000 BP) rather than glacial maximum age for these layers.

The fauna of the superficial layers (I, II, III) is heavily influenced by humans, but a number of wood-edge species are present, including the hawfinch, white-toothed shrew and pygmy shrew, and some bats. The Algerian hedgehog is typical of Mediterranean scrub. A partially wooded biotype was probably present.

Origins of the Maltese Quaternary and Holocene biotas

The affinities of the Maltese Quaternary and Holocene biotas are clearly with those of Sicily (Francini Corti & Laza, 1973; Di Martino & Raimondo, 1979; Lanfranco, 1984; Bonfiglio, 1992; Schembri, 1992). While many workers have pointed this out, the first coherent hypothesis on the origin of the Maltese Quaternary and Holocene biotas was put forward by Thake (1985) to explain the occurrence and distribution of a group of (extant) clausiliid land snails endemic to the Maltese Islands, the Pelagian Islands, and the Hyblean region of Sicily. Two genera occur: the genus *Lampedusa* is endemic to the Maltese Islands (where Thake recognised three endemic species) and the Pelagian Islands (one endemic species); and the genus *Muticaria* which is endemic to the Maltese Islands (where Thake recognised four species, three of which are endemic) and the Hyblean region of Sicily (one species,

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[15] The 'Chellian' is a Palaeolithic culture stage which at the time was usually equated with the Günz-Mindel interglacial (i.e. 600,000-400,000 BP).

according to Thake also occurring on the Maltese Islands).

Thake (1985) interpreted the extant species of *Lampedusa* as the descendants of an ancient clausiliid stock that colonised the areas now occupied by the Pelagian and Maltese island groups, from Sicily in Messinian times, when the whole Pelagian Block[16] was emerged during the Messinian salinity event. From these colonisers, the present species of *Lampedusa* differentiated in isolation following submergence of the land connections between the two island groups and Sicily. Thake postulated that the ancestral clausiliid stock remaining in Sicily gave rise to the genus *Muticaria*, and that these *Muticaria* from Sicily invaded the Maltese Islands during periods of low sea-levels when the two areas became joined by land-bridges during the Pleistocene glaciations. On the basis of conchological and distributional data, Thake hypothesised that two separate invasions by *Muticaria* may have occurred. Each invading population then developed in isolation following severance of the land connection with Sicily, giving rise to the extant *Muticaria* of the Maltese Islands.

Thake's (1985) biogeographical model has been recently re-examined by Giusti *et al.* (1995). These authors reviewed the taxonomy and phylogeny of the clausiliid taxa considered by Thake, using classical conchological and anatomical analyses as well as modern molecular techniques. They concluded that three biological species of *Lampedusa* occur. *L. lopadusae*, endemic to the islands of Lampedusa and Lampione, and *L. imitatrix*, endemic to the islands of Malta and Filfla, are derived from a common mainland ancestor that colonised the areas in question in pre-Quaternary times (see Giusti *et al.* 1995 pp.341-342 for a discussion of the possible ancestral species). The third

species, *L. melitensis*, endemic to the island of Malta, has differentiated more recently from *L. imitatrix*.

Giusti *et al.* (1995) also confirmed that *Muticaria* is a good genus, but do not agree with Thake's (1985) interpretation of the species placed in it. According to Giusti *et al.* (1995) only two biological species occur: *M. macrostoma* endemic to the Maltese Islands (except Filfla), and *M. syracusana* endemic to southeastern Sicily. Both species have numerous conchological forms that were assigned specific or infraspecific status in the past, but which molecular genetic analysis has shown to be little more than local demes. On the basis of this analysis, Thake's model for speciation in *Muticaria* is obviously incorrect and *M. syracusana* and *M. macrostoma* are likely to have arisen by allopatric speciation from a common *macrostoma*-like ancestor that lived in Sicily and reached the Maltese Islands in a single colonisation event (Giusti *et al.*, 1995). It is not clear when this event took place. On the basis of the weak morphological and genetic differentiation between *M. syracusana* and *M. macrostoma*, it is likely that it did not occur before the start of the Quaternary (Giusti *et al.*, 1995).

In summary, as suggested by Thake (albeit based on incorrect data), the emerged parts of the Pelagian Block, including what are now the Maltese and Pelagian island groups and Hyblean Sicily, were originally colonised by species from the surrounding emerged lands, mainly the European mainland, during sea-level lows associated with the Messinian salinity event. At the end of the Miocene, after much of the Pelagian Block became inundated, some of these colonisers differentiated in isolation on the still emerged land-masses, one of which was the Maltese complex. During the Quaternary, the Maltese Islands experienced further colonisation episodes, mainly from Sicily, followed by development in isolation of the populations that managed to gain a foothold. What is uncertain is whether these Quaternary colonisations occurred across land-bridges which formed during the marine regressions associated with the

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[16] The Pelagian Block is the foreland margin of the African continental plate and consists of thick carbonate deposits extending from the southeastern part of Sicily to the coast of Tunisia. Much of this platform is now submerged and the only exposed parts are the Hyblean region of Sicily, the Maltese and Pelagian archipelagos, and the Tunisian coast (Pedley *et al.*, 1978; Pedley 1990; Grasso & Pedley 1985).

Pleistocene glaciations (as suggested by Thake and by others – see for example, Francini Corti & Lanza, 1973), or due to jump dispersal across the channel separating the Maltese group from Sicily. The latter mechanism may have been facilitated by a narrowing of the marine barrier by the Pleistocenic marine regressions.

Bonfiglio (1992) compared the Quaternary vertebrate faunas of Sicily and Malta and concluded that the two Middle Pleistocene Sicilian *Elephas* faunas (see Table 5) are both represented on the Maltese Islands. On the basis of this she postulated that the Maltese Islands and Sicily must have been connected by land-bridges at least in the early Middle Pleistocene and in late Middle to Upper Pleistocene times.

The nature of the animals that actually managed to colonise the islands from Sicily (especially micromammals and terrestrial molluscs which are not able to swim) suggests a direct land connection on several occasions. During the Pleistocene glacial stages, sea level fell by approximately 120-130 m (Bard *et al.*, 1990; Ferland *et al.*, 1995) with the last sea-level minimum about 22,000-17,000 years ago. The drop in sea-level needed to connect Malta to Sicily is currently 155m[17] but it is possible that sedimentation and tectonics have caused the depth of the channel to fluctuate in the past.

The hypothesis of an original influx of biota shortly after the formation of the Maltese Islands, when they became connected with the Sicilian mainland during the Messinian salinity event, followed by a long period of isolation during the Pliocene and Lower to Middle Pleistocene, fits well with both what is known about the extinct Quaternary endemic fauna, and the occurrence of living palaeoendemic species in the Maltese Islands.

This scenario explains the origin and differentiation of such extinct endemic

Maltese Quaternary vertebrates as: (1) the Maltese dwarf hippopotamus (*Hippopotamus melitensis*), derived from a Siculo-Maltese species, *Hippopotamus pentlandi*, in turn probably derived from *Hippopotamus amphibius* (Caloi & Palombo, 1982; Capasso Barbato & Petronio, 1983), a widely distributed species in Europe in Plio-Pleistocene times; (2) the Maltese dwarf elephants (*Elephas* subgenus *Palaeoloxodon*), closely related to (if not conspecific with) the Sicilian dwarf elephants; (3) The giant dormouse L*eithia* aff. *melitensis*, apparently derived from *L. melitensis*, a species occuring on both Malta and Sicily (Zammit Maempel & De Bruijn, 1982; (4) the Maltese bats: *Rhinolophus mehelyi birzebbugensis* and *Myotis ghardalamensis*, related respectively to *Rhinolophus mehelyi* and *Myotis blythi/Myotis myotis* (Storch, 1974); and (5) certain aquatic birds, apparently with poor powers of flight (although for the Giant Maltese Crane, *Grus melitensis*, the presumed reduced power of flight has been thrown in doubt [Northcote, 1984]), closely related to similar species which occurred in Sicily (Bate, 1916; Harrison, 1979).

Some extant endemic taxa appear to be derived from the pre-Quaternary Mediterranean biota and have no living close relatives (Di Martino & Raimondo, 1979; Lanfranco, 1987, 1989a; Schembri 1992). Amongst the best known of these palaeoendemic taxa are the vascular plants. The principal palaeoendemic flowering plants are the Maltese Cliff-orache (*Cremnophyton lanfrancoi*), Maltese Rock-centaury (*Palaeocyanus crassifolius*), Maltese Salt-tree (*Darniella melitensis*), Maltese Fleabane (*Chiliadenus bocconei*), Maltese Hyoseris (*Hyoseris frutescens*), and Maltese Dwarf Garlic (*Allium lojaconei*) (Lanfranco 1984, 1987, 1989a,b). The genera *Cremnophyton* and *Palaeocyanus* are monotypic and therefore are also endemic to the Maltese Islands. *Palaeocyanus* is most closely related to the genus *Centaurea* but is more 'primitive' than this and related genera. *Cremnophyton* is related to the ancestors of *Atriplex* (Lanfranco 1987, 1989a, 1989b). These entities may either be

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[17] With the present bathymetry, a drop of 100m in sea-level would leave a channel less than 14km wide separating Malta from Sicily.

relicts of previously widespread Tertiary taxa, or else may have developed *in situ* in the Maltese Islands following a long period of Plio-Pleistocenic isolation after initial colonisation by an ancestral stock during the Upper Miocene.

Other endemic species are very similar to Sicilian and other mainland species. Such neoendemic species are presumed to have evolved more recently (post-Tertiary) than the palaeoendemics (Schembri, 1992). Examples include the Maltese Sea-lavender (*Limonium melitense*), Zerapha's Sea-lavender (*Limonium zeraphae*), Maltese Pyramidal Orchid (*Anacamptis urvilleana*; see also Del Prete & Mazzola, 1995), and Maltese Sea-chamomile (*Anthemis urvilleana*) among the flowering plants (Lanfranco 1987, 1989a, b), and the Maltese Wall Lizard (*Podarcis filfolensis*) and its various races among the animals (Lanza, 1972).

Island endemics probably resulted from extremely small colonising populations. Such small populations are unlikely to have reflected accurately the characteristics of the whole parent population and therefore may have shown some level of differentiation from the start of their isolated development. This phenomenon is known as the founder effect. Very small populations are known to evolve exceedingly rapidly (Stanley, 1979; Lister 1989) so it is possible that the evolution of the endemic taxa and especially the appearance of traits such as nanism and gigantism took at most only a few thousand years. Without accurately dated fossil evidence, identification of neo- and palaeoendemics must remain rather speculative.

In summary, it appears therefore that Sicily and the surrounding islands received their initial influx of biota during the Messinian via land-bridges which would have been relatively broad (i.e. corridors[18]). These immigrants may have come from both southern Europe and northern Africa, but there is no completely unequivocal evidence of any direct African connections either in the extinct Quaternary biota or in the extant one (although *Pellegrinia* and *Maltemys* have been interpreted as of African origin; Azzaroli, 1990; and *Xeromunda durieui* is a southern European and North African species). Inundation of the central Mediterranean at the beginning of the Pliocene resulted in a long period of isolation of the biota, which continued probably until some time during the Lower or early Middle Pleistocene. During this period there must have been significant changes in the original biota, resulting in the *Pellegrinia panormensis* fauna of Sicily (Table 5). No equivalent to this fauna has been found in the Maltese Islands, although some of the extant Maltese palaeoendemic taxa may be derived from forms that originally colonised the group at this time.

A marine regression sometime during the Lower or early Middle Pleistocene, perhaps Oxygen Isotope Stage 16 (690,000 years ago), which is known to have been a time of very extensive glaciation (e.g. Hunt 1998) seems to have facilitated a second round of immigration into Sicily and the Maltese Islands. This was followed by another long period of isolation during which distinctive island forms, including giant (e.g. glirids), pygmy (e.g. elephants), and flightless (e.g. the Maltese swan) species, developed on the various islands of the Siculo-Maltese archipelago (Sicily was not a single landmass during the Lower Pleistocene, and the Hyblean Plateau at least was separated from northwestern Sicily by a narrow channel). In Sicily, this fauna has been termed the *Elephas falconeri* fauna (Table 5). In the Maltese Islands, this fauna was ecologically unbalanced[19] suggesting that colonisation took place across a barrier rather than via a landbridge (i.e. sweepstake[20] or pendel[21] dispersal).

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[18] Corridor: a broad land connection allowing faunal interchange from one region to another (Simpson, 1940; Cox & Moore, 1993).

[19] An unbalanced fauna is one missing certain functional groups, for example, carnivores (Sondaar, 1977)

[20] Sweepstake dispersal: chance dispersal across a wide biogeographical obstacle (Simpson, 1940; Cox & Moore, 1993).

Elephants are estimated to swim as much as 48 km (Johnson, 1978). Some components of this fauna may also have been derived from pre-Pleistocene ancestral species (e.g. *Eliomys* (*Maltamys*) *gollcheri*).

Another marine regression sometime during the later Middle Pleistocene, possibly Oxygen Isotope Stage 8 (300,000 years ago), though the probably much greater regression of Stage 12 (490,000 years ago) cannot be totally ruled out, facilitated a third round of immigration into Sicily and the Maltese Islands. Possibly, this regression resulted in actual physical connection of mainland Italy with Sicily (and of Sicily with the Maltese group?), since the new fauna (the *Elephas mnaidriensis* fuana) was nearly balanced (Table 5). Perhaps as a result, nanism was much less pronounced than in the previous fauna, although still evident. This fauna must have experienced a period of isolation since there was some development of distinct island forms. Compared with Sicily, the Maltese *Elephas mnaidriensis* assemblage had a somewhat reduced number of species (Table 5). This might suggest a partial barrier to dispersal (a filter[22]), or simply that the land area of the Maltese archipelago was insufficient to carry the same number of species as the larger land area of Sicily.

Another wave of immigration occurred towards the end of the Pleistocene, probably during the sea level lowstand during Oxygen Isotope Stage 2 (22,000-17,000 years ago). In Sicily this resulted in the *Equus hydruntinus* fauna (Table 5). The mechanisms that facilitated this immigration are not clear, though Oxygen Isotope Stage 2 equates with an extremely extensive glaciation and thus resulted in a significantly low sea level stand. Neither is it clear whether there was a direct land connection with the Maltese Islands, since only a few elements from the Sicilian *Equus hydruntinus* fauna are represented in the

Maltese Islands. This suggests jump-dispersal across a sea barrier, facilitated by low sea levels, although given the presence of small animals such as pine voles and toads it is possible, again, that there was a land bridge but that the area of the Maltese Islands, once isolated, was insufficient to support the full diversity of the Sicilian fauna. In the case of the Maltese Islands, the next influx of species is correlated with human presence on the islands.

The history or the Maltese biota therefore appears to consist of a series of turnovers (replacement of one biota by another). It would be very interesting to discover why these turnovers occurred. Possibilities include: immigration by a new biota that replaces an older one; changes in the physical size of the islands as a result of eustatic[23] sea-level fluctuations; arrival of predators in a previously predator-free ecosystem (the arrival of man is a special case of this!); and environmental changes, possibly related to climatic changes. Possibly, all of these have operated at one time or another in the biogeographic history of the Maltese Islands.

Concluding Statement

This review takes the analyses of the Quaternary biota, biogeography and environment as far as they can be taken without substantial fresh data. Most of the suggestions we make, such as the mixed nature of the fauna in Layer VII at Ghar Dalam and the timing of the faunal immigration pulses, are testable hypotheses which now need exploration using modern multidisciplinary methods. The Maltese Quaternary deposits can provide answers to pressing problems concerning how species adapt to the stresses of environmental change and the isolation of small populations. These are fundamental to our understanding of the evolutionary process. It is important that the rich, if damaged, heritage of Quaternary deposits and fossils in the Maltese Islands is recognised for its potential to answer these questions, and is

[21] Pendel dispersal: dispersal across a barrier (e.g. a narrow strait) that is easily crossed by some organisms but not by others (Dermitakis & Sondaar, 1978).

[22] Filter: a narrow land connection with obstacles to the free dispersal of organisms across it (Simpson, 1940; Cox & Moore, 1993).

[23] Eustasy: a simultaneous global rise or fall in sea-level due to a rise or fall of the ocean.

not simply relegated to the status of a historical curiosity.

Acknowledgements

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