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VI

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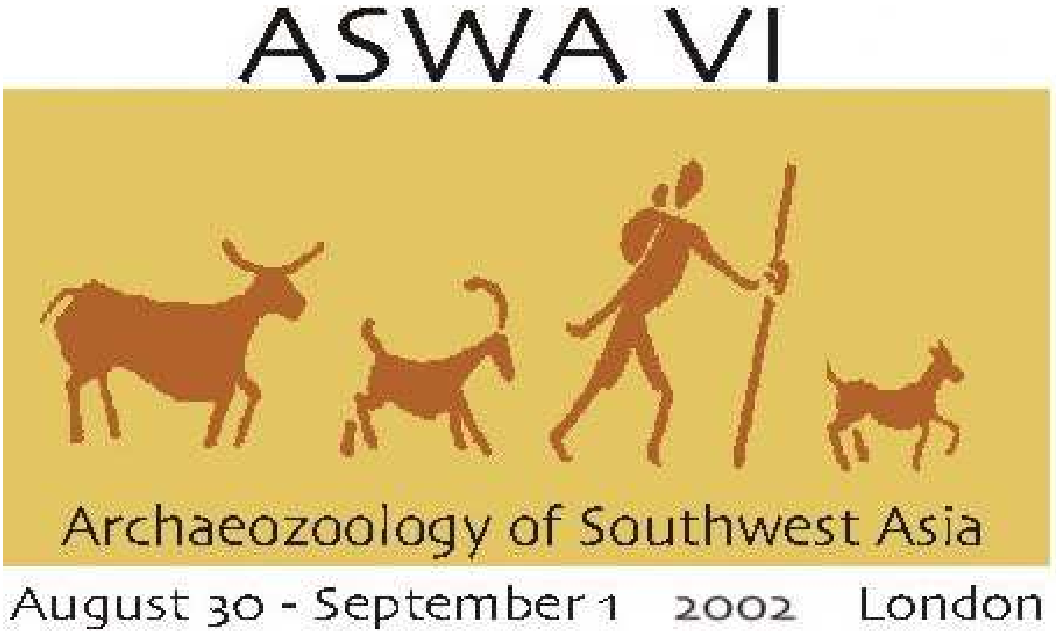

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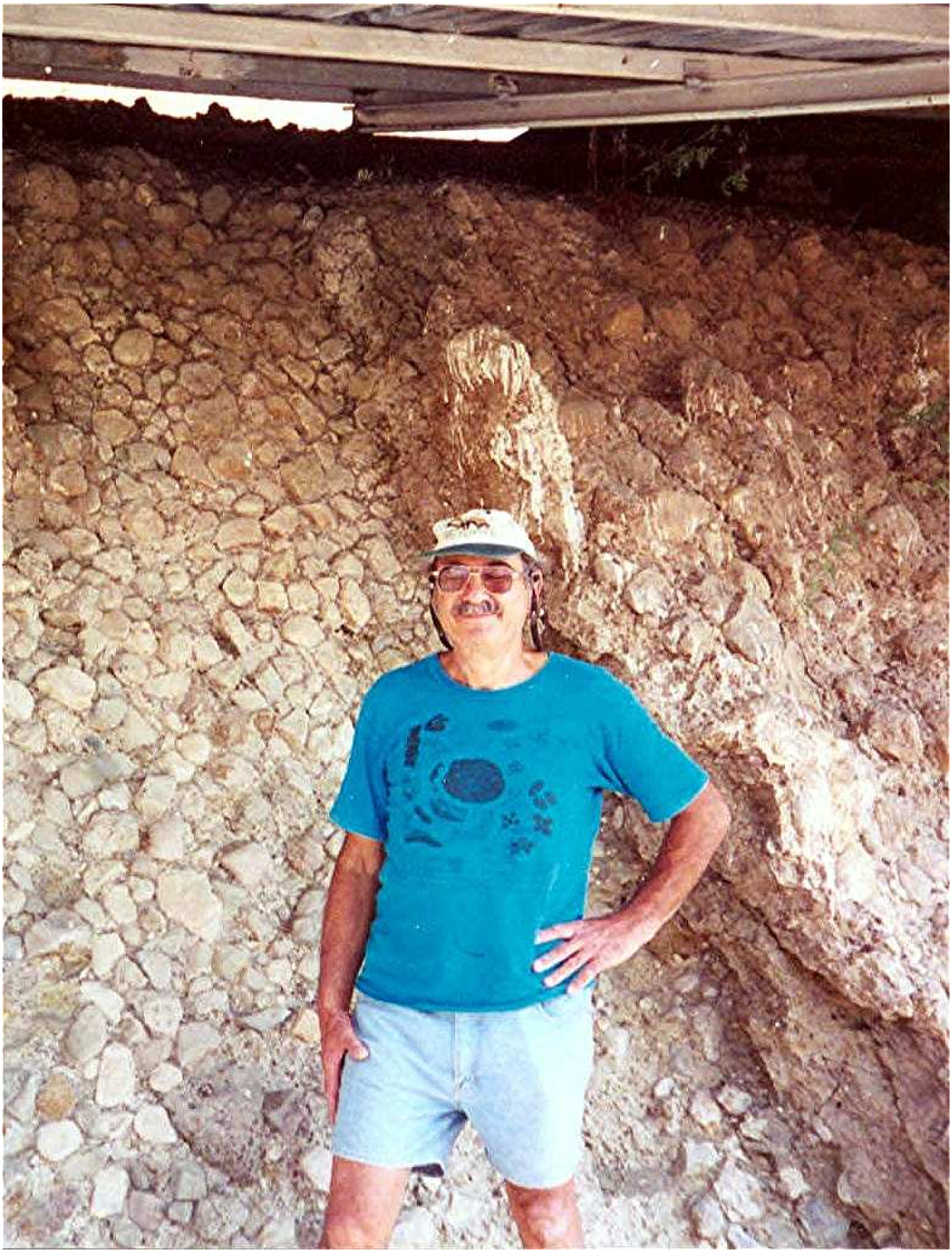

Prof.Dr. Eitan Tchernov

This volume is dedicated to the memory of Prof. Dr. Eitan Tchernov, in fond memory of his enthusiasm and support to many in the field of archaeozoology**.**

Preface

The ASWA VI meeting was held at the Institute of Archaeology, University College London, from 30th August-1st September 2002, timetabled to follow on the heels of the ICAZ meeting in Durham, UK. Over 55 participants attended the meeting, travelling from 13 countries, bringing the latest research results from our field. As usual, it was a pleasure to see so many doctoral students presenting their research – a sign for a very healthy future for zooarchaeology in south west Asia. It is still unfortunate, however, that colleagues from some Middle Eastern countries were unable to attend due to financial and political constraints.

Presentations were organized into the following six themes, which highlight the scope of the ASWA membership: Animals in Palaeolithic and Epipalaeolithic Levant; Neolithic Patterns of Animal Use; Animals in Neolithic Anatolia; Animals in the Chalcolithic and Bronze Ages; Iron Age, Nabatean and Roman Patterns of Animal Use; Animals in Ancient Egypt. There was also a poster session, and contributors were invited to submit papers to this volume.

As always with the ASWA forum, the meeting served to welcome new scholars to the group, but was also very much a reunion of old friends and colleagues who have been sharing new information and discussing issues of joint interest for many years now. In this vein, it is a great sadness that ASWA VI was the last international meeting attended by Prof. Eitan Tchernov, an original founder of the group and mentor and inspiration to so many. For many of us, it was the last time we saw Eitan, and experienced his usual incisive comment, unstoppable enthusiasm for the subject, and warm friendship. He will be greatly missed.

ASWA VI was supported by the Institute of Archaeology, UCL, who provided facilities and financial and administrative help. In particular, the organizing team was aided greatly by the administrative assistance of Jo Dullaghan at the Institute. ARC bv (Archaeological Research and Consultancy, Groningen, The Netherlands) once again shouldered the finances of the publication of the proceedings, and we are extremely grateful for their continuing support. Many thanks are also due to the postgraduate student helpers from the Institute of Archaeology who made the meeting run so smoothly: Banu Aydinoğlugil, Jenny Bredenberg, Chiori Kitagawa, Peter Popkin, and Chris Mosseri-Marlio (who also produced the logo reproduced on the frontispiece of this volume).

Many thanks to all the participants for making the meeting such a success!

Louise Martin
London 2005

Participants of the 6th ASWA Conference, held at the Institute of Archaeology, University College London.

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Preface

THE PASSIVE TRANSPORTATION OF THE HOUSE MOUSE (*Mus musculus domesticus*) TO CYPRUS: NEW INDIRECT EVIDENCE OF INTENSIVE NEOLITHIC NAVIGATION IN EASTERN MEDITERRANEAN

Thomas Cucchi[1]

Abstract

Cyprus is an important laboratory for modelling the evolution of the biogeography and human impact on flora and fauna, as well as to understanding the cultural evolution of the first Neolithic societies. Passive human transport of commensals and anthrophilous small mammals is part of this pattern, and the house mouse is one of the best-known human commensals. Thus, the first steps in its phylogeography and its morphological evolution in an island context can act as strong markers of the first humans migrations, as well as measures of the nature and intensity of trade between the island and mainland. To this end, a powerful morphological tool must be found to distinguish the commensal form from other species of the genus *Mus*. New methods in quantitative morphology, supported by mathematic models, have been highly effective for interspecific distinctions of close species and analyses of morphological evolution. The Fourier method, which is used to analyse shapes with closed outlines, was performed here on the first lower molar outlines of modern and fossil mice. First, the molar shape disparity and insular syndrome of present day mice species in the Eastern Mediterranean, was observed. Then, fossils from three preceramic sites in Cyprus were compared to the modern shape diversity. House mouse clearly displays morphological conservatism in its shape through time and space and in the absence of a morphological drift linked to insularity on Cyprus. Finally, after a discussion of the insular syndrome found in modern rodents and what is known of prehistoric seafaring it is concluded that conservatism in their shape can be explained by the existence of metapopulations of house mice living in Cyprus till the beginning of human colonisation during the Neolithic. The genetic and morphological stability of these metapopulations was maintained through intensive exchanges between Cyprus and the mainland, supported by strong nautical techniques.

Résumé

Chypre est actuellement un laboratoire important pour comprendre l'évolution culturelle des premières sociétés néolithiques ainsi que les effets anthropogènes sur la biodiversité dans la profondeur du temps. Le transport passif de petits mammifères par l’homme est une partie de ce modèle, particulièrement la souris domestique, un des commensaux les plus célèbres de l’homme. Par conséquent, la compréhension du processus de colonisation de la souris domestique et de son évolution sur une île océanique comme Chypre, peut fournir de nouvelles informations concernant la nature et l'intensité des échanges entre Chypre et le continent durant la période préhistorique. Pour atteindre cet objectif, il faut 1) que les souris commensales soient distinguées des sauvages dans les assemblages fossiles de petits mammifères et 2) que nous soyons capables de détecter des divergences morphologiques ténues. Cela représente une tâche difficile puisque le genre *Mus* est un complexe d'espèce jumelles. Néanmoins, les nouvelles méthodes en morphologie quantitative, soutenue par des modèles mathématiques, ont montré leur efficacité dans la discrimination interspécifique d’espèces proches et dans l’analyse de l’évolution morphologique. Parmi les différentes méthodes de la morphométrie géométrique, nous avons appliqué les analyses Elliptiques de Fourier sur les contours des premières molaires inférieures de souris modernes et fossiles. Ce matériel n'est pas seulement le plus résistant aux processus de la taphocenose mais il porte également un caractère ostéoscopique pouvant distinguer les souris commensales des sauvages. Le contour correspond à une projection en 2D des molaires en vue occlusale. Dans un premier temps, la disparité morphologique des souris actuelles de Méditerranée Orientale ainsi qu’un éventuel syndrome insulaire ont été observés. Ensuite, les fossiles de trois sites chypriotes du Néolithique précéramique (entre 8200 et 7000 av. J.-C.) ont été confrontés au modèle de la diversité morphologique moderne. Les résultats principaux sont le conservatisme morphologique de la souris domestique à travers le temps et l'espace ainsi que l'absence de dérive morphologique liée à l'insularité. Finalement, après une discussion sur le syndrome insulaire des rongeurs modernes et l'état de la connaissance sur la navigation de pleine mer pendant la préhistoire, nous avons conclu que ce conservatisme de forme pourrait s’expliquer par l’existence de métapopulations de souris domestiques à Chypre, dont la stabilité génétique et morphologique a été entretenue à la faveur d’échanges intensifs entre Chypre et le continent soutenus par une technique nautique forte, dés que les premières communautés néolithiques ont colonisé Chypre.

Key Words: Rodents, Preceramic Neolithic, Fourier analysis, shape, island evolution, metapopulations.

Mots Clés: Rongeurs, Néolitique précéramique, analyse de Fourier, forme, syndrome insulaire, métapopulations.

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Introduction

Only few authors have used small commensal mammals in order to understand ancient human societies. Eitan Tchernov was one of first scientists who employed these biological relationships between humans and animals as markers of settlement size and duration as well as the degree of sedentism (Tchernov 1984, 1991). Indeed, human sedentism at the end of Late Glacial Period in favourable environments such as the Levantine Corridor and the Zagros had an impact on the natural ecosystem in the vicinity of settlements. An ecotone between human activities and the natural habitat became a new ecological niche, which only species with special colonization skills could occupy.

Vigne (1999a) has integrated these species in his model of evolutionary biogeography which employs the example of large Mediterranean islands. He has demonstrated, as have others (Olson and James 1982, 1984; Cherry 1981), the way "true islands" can be a laboratory for modelling biogeographic evolution and human impact on fauna and flora. In isolated contexts, the anthropogenic flow of mammals can be considered an obvious process. Based on this pattern, mammalian faunas of the Mediterranean islands were completely altered following human colonization (Vigne and Alcover 1985; Vigne 1988, 1990, 1999a; Blondel and Vigne 1993). One point in this model concerns migration through passive transport (human sea traffic) of small anthropophilous or commensal mammals (rat, mouse, fieldmouse, shrew) between the 5th and the 2nd millennia BC. For Vigne, the diffusion of these micro mammals was a marker of the level and nature of trade as well as of human demography (Vigne 1994). The presence of black rat (*Rattus rattus*) most usefully illustrates diffusion. Its phylogeography was interpreted both in terms of human increases in population, urbanization and intensification in trade (Audoin-Rouzeau and Vigne 1994).

The case of the house mouse is less well documented and, as a true human commensal, the reconstruction of its phylogeography across the large true Mediterranean islands should be very informative on the first migrations of human societies. This aim of this paper is to study the evolution of tooth shape in current and fossil mouse populations on large islands such as Cyprus, using a technique that is powerful and yet sensitive enough to detect discrete morphological drifts linked to genetic factors in a closed evolutionary context. Following a discussion of island syndrome in house mouse populations, results will be examined with reference to Neolithic seafaring.

The house mouse: a case study in archaeozoology

Palaeontologists generally agree that the genus *Mus* has an Asian origin. It appears in the Indo-Pakistani area 7 million years ago (Jacobs 1978). They spread from this nuclear area, and subsequent allopatric speciations produced the structure of the current mouse taxonomic complex. In Eurasia, biomolecular studies (Bonhomme *et al* 1984) have clarified the taxonomy of the mouse, which was long considered monospecific because morphologically they are not diverse (Schwartz and Schwartz 1943). The current mouse population is made up of five taxa. Three wild species occur in circum-Mediterranean habitats: *Mus spretus* in the western Basin, *Mus macedonicus* in the eastern one, and *Mus spiciligus* in Central Europe. They live sympatrically with two commensal sub-species in Eurasia, *Mus musculus musculus* in Northern Europe and *Mus musculus domesticus* in Southern Europe (including the Mediterranean islands). Theoretically, a first wave of diffusion during interglacial periods of the Pleistocene could have been at the origin of the current wild species distribution (Auffray *et al* 1990). A second wave took place during the Holocene and corresponds to house mouse diffusion. In addition to the taxonomic identification of mouse species, genetics has also allowed for the distinction of morphological criteria for separating species (Orsini *et al* 1983). Consequently, the presence of the house mouse has been established at the Natufian site of Hayonim in Israel (Auffray *et al* 1988). The new ecological niche resulting from human sedentary communities appears to have allowed this species to gain an important advantage over wild species such as *Mus macedonicus*, which is present in the area until the Acheulean period. Once it became commensal, the house mouse would have benefited from human migrations to colonise the globe.

In spite of its passive transportation, molecular, biogeographical and archaeozoological data seem to agree that the house mouse made a slow progression (for a review see Auffray *et al* 1990), and it is considered to have diffused into the Mediterranean during the Bronze Age, taking advantage of the increase in sailing and trade, reaching the Western European mainland during the Iron Age. Following Vigne (1994) one can question why the house mouse does not appear to have belonged to the ecological package associated with Neolithic diffusion.

The apparent time gap between the first appearance of the house mouse in the circum Mediterranean area and its subsequent diffusion might be less dramatic if more systematic sediment sieving was undertaken on archaeological sites, allowing for the retrieval of microfauna, and if morphological distinctions could be made on broken archaeological remains.

The method

The problem of distinguishing between species in archaeological remains is well known. Discriminating between close species requires morphoscopic criteria or the use of biometric techniques. Generally speaking, however, archaeozoologists are unable to go below the genus level because of the subjectivity of the morphological criteria, biological variability and the low number of available fossils. Even if there were many biometric techniques utilizing uni- and bivariate statistical analyses of linear and angular parameters for quantifying formal differences, these are always size dependant. Furthermore, it is difficult to be sure that the distance between two groups is a real biological distance as opposed to a distance due to environmental factors. Since the 1980s, new mathematical techniques have been developed where comparisons are based only on shape rather than size (Temple 1992).

The problem of distinguishing between species is more complex with mice because they all tend to be con-specific. Sympatric species may be distinguished on the basis of biometrical analyses of skulls. The zygomatic index (ZI: width of the anterior part of the malar process /width of the upper part of the zygomatic arch), published by Orsini *et al* (1983), has proven to be one of the best discriminatory parameters. This method has shown its efficiency when linked to a discriminate analysis on measurement sets (Auffray *et al* 1988). However, complete skulls are almost never preserved in archaeological contexts and isolated teeth are much more common.

Commensal sub-species from wild species (*Mus spretus*/*Mus macedonicus*) can be distinguished from each other using morphoscopic critera on the anterior lobe of the first lower molars (M_1) (Orsini 1982). This criterion supposes that the tubercle in the wild species is more developed (Fig. 1), having a more tetralobic shape compared to the anterior wear pattern on the molar. The tubercles of the commensal species are more trilobic. From one point of view this critera is too subjective because it depends on the degree of wear. The difference in tubercle development should, nevertheless, be expressed on the two-dimensional occlusal outlines of the M_1. In palaeontology, studies concerning tooth specialization in a Pliocene murid (*Stephanomys*) have shown that "the outline describes effec-

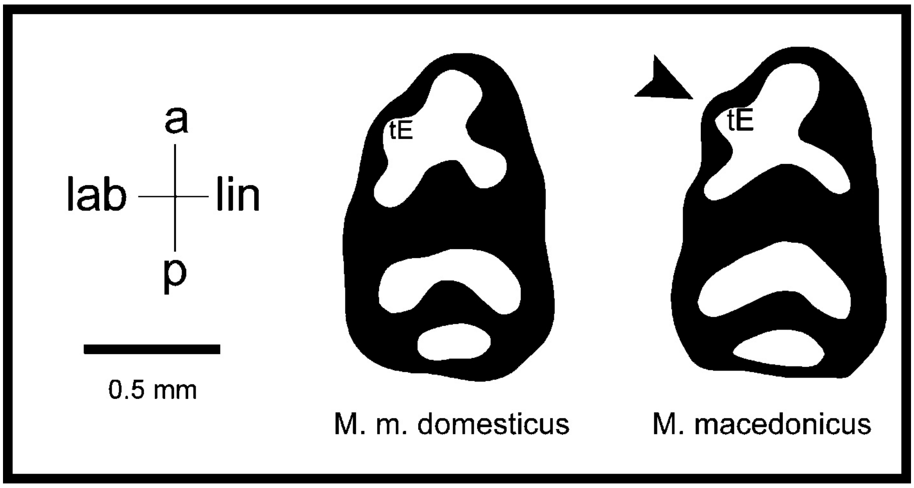

Fig. 1. Morphoscopic differences on the first lower molar between house mouse (here: *Mus musculus domesticus*) and wild mouse species (here *Mus macedonicus*) after Orsini *et al* 1983 (tE = tubercul E, a = anterior, p = posterior, lab = labial, lin = lingual.).

tively the location of the tubercles characteristics of the tooth morphology" (Renaud *et al* 1999: 859). Among the different methods used in outlining shape analysis, the Fourier method (Rholf and Archie 1984) most powerfully generates a set of shape-representative variables suitable for statistical comparisons between samples (Crampton 1995). Among the numerous Fourier methods available, elliptic Fourier decomposition (Khul and Giardina 1982) has already proven its worth in taxonomic description (Ferson *et al* 1985).

The principle of the elliptic Fourier transform (Fig. 2) consists of projecting the M_1 in its occlusal view in a 2D plan to obtain a closed outline. Two periodic functions are provided by curvilinear abscissa variations all along the outline, based on the *x* and *y* coordinates. Each function is then broken down into a series of trigonometric functions of decreasing wavelength called harmonics. Each harmonic is expressed in terms of *sinus* and *cosinus* developed from four coefficients called Fourier coefficients. These coefficients are the shape descriptors of the tooth outline. They can be used as variables in multivariate statistical analyses.

For each M_1, the *x* and *y* coordinates of the 64 points equally spaced along a manual drawn outline on the image of the M_1 are automatically extracted using an optical image analyser (Optymas 6.0). An elliptic Fourier transform is applied on this 64 point matrix of the coordinates using © NTSYS-pc 2.0 software.

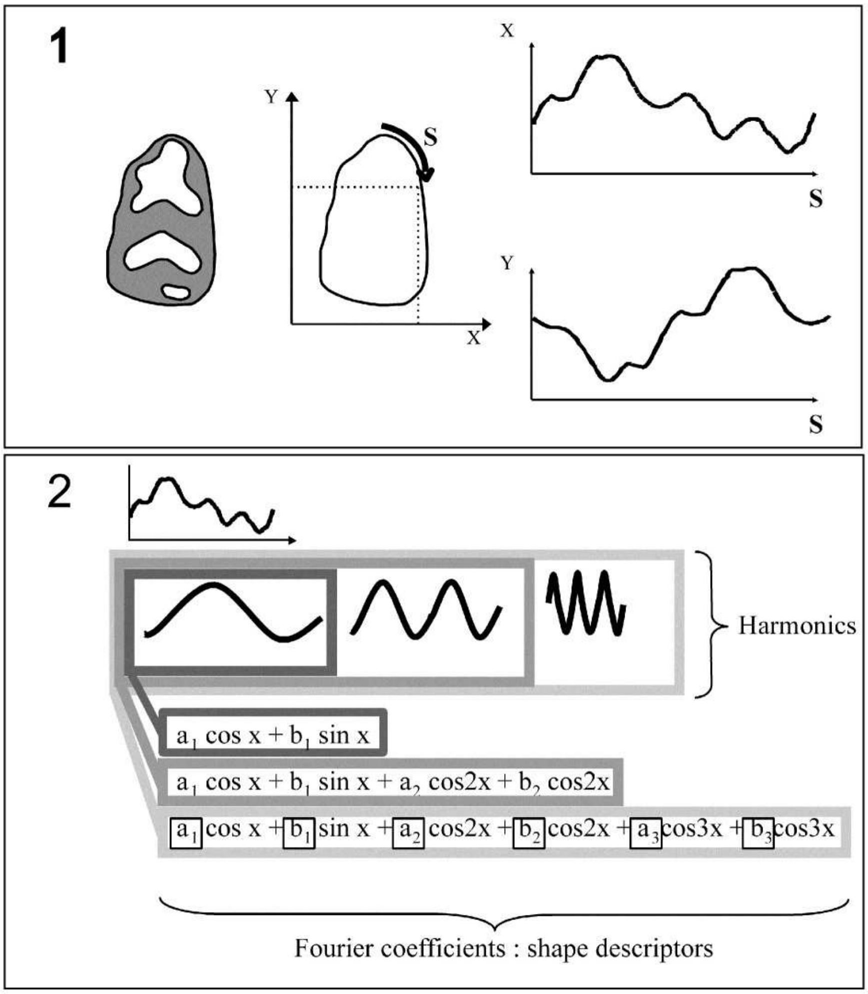

Fig. 2. Principle of the Elliptic Fourier analysis. 1: The 2D projection of a molar in occlusal view consists of two periodic functions based on the curvilinear abscissa variations on *x* and *y* coordinates (S). 2: Fourier transform principle (from V. Debat, unpublished).

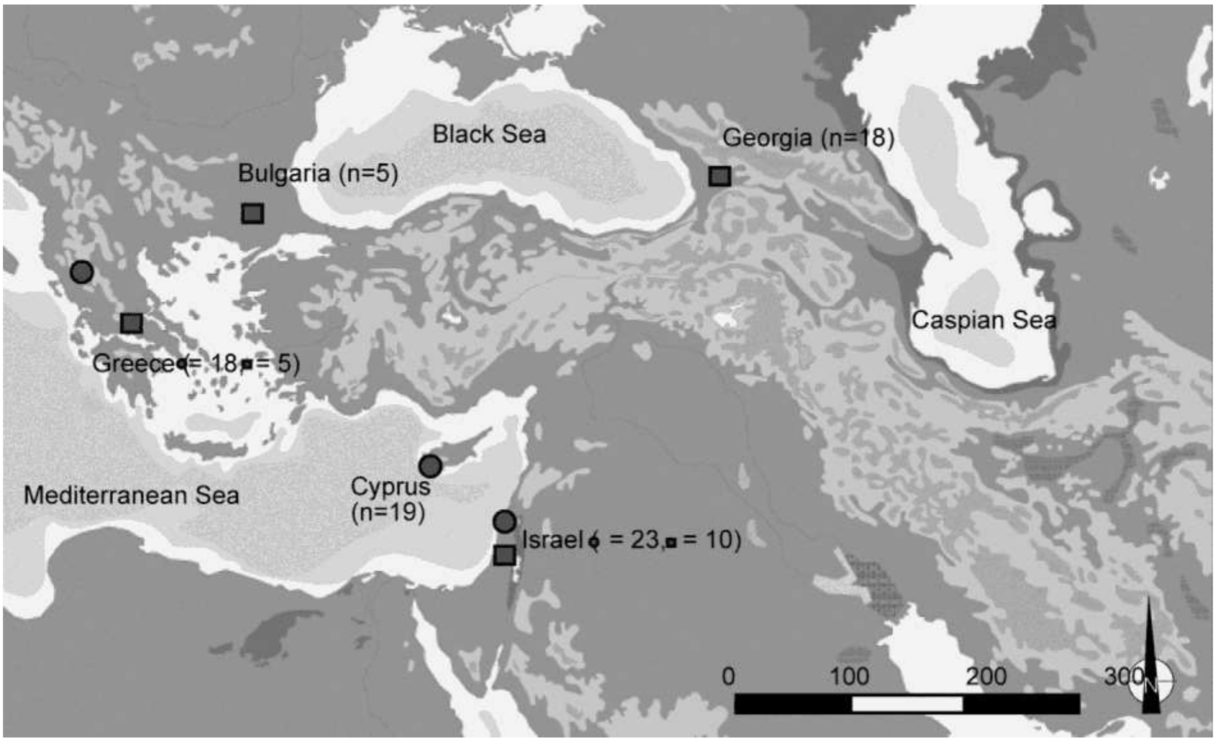

Fig. 3. Locations and sample sizes of the seven recent mouse specimens from the Eastern Mediterranean. The full circles represent *Mus musculus domesticus* samples. The full squares represent the *Mus macedonicus* samples (GeoAtlas ©).

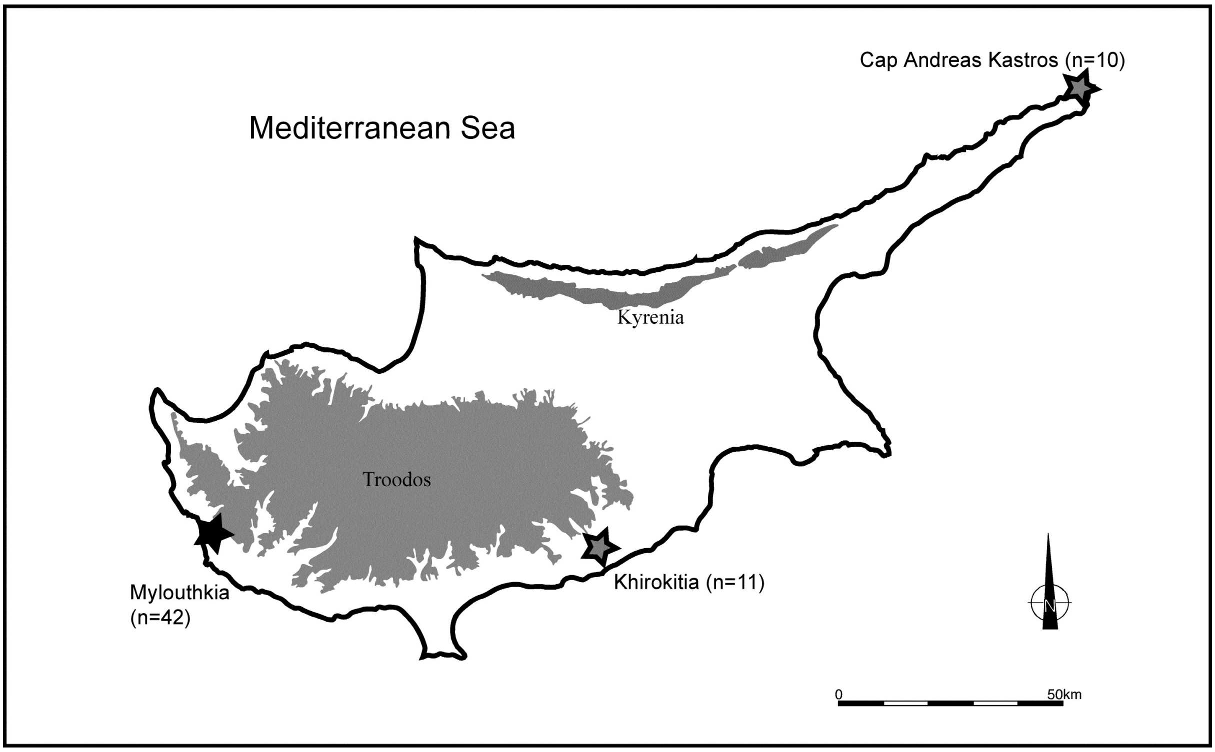

Fig. 4. Locations and size of samples of fossil mice in Cyprus considered in this paper.

This method has two principal advantages. The size standardization of the Fourier coefficient yields a coefficient dependent only on shape by dividing all the Fourier coefficients by the area of each $M_{1,}$ producing a size estimator. The second advantage of this method is that permits reconstruction of the M_1 outline, which corresponds to any set of Fourier coefficients using the inverse Fourier Transform principle. This allows the average molar shape (consensus) of a population or a fossil group to be displayed.

Material

First, we looked at differences in the shapes of recent M_1 teeth in sympatric mouse species in the circum Eastern Mediterranean area, in genetically identified specimens from seven localities in Greece, Bulgaria, Georgia and Israel (see Fig. 3 for location and size of samples) provided by the Institut des Sciences de l'Evolution de Montpellier (ISEM). In order to identify island syndrome possibly effecting tooth shape, a sample from Cyprus was analysed (trapped live by S.J. Davis in Khirokitian Valley). These mice were biometrically identified using the zygomatic index. Only the commensal sub-species were sampled in these locations.

The fossil samples come from three Neolithic sites on Cyprus, which range in date over the whole of the Aceramic Neolithic period on the island (Fig. 4). The earliest sample comes from Kissonerga-Mylouthkia (Peltenburg *et al* 2001). Kissonerga-Mylouthkia is a coastal site, badly damaged by modern development activity and excavated by Paul Croft (Lemba Archaeological Project of the University of Edinburgh). Together with Shillourokombos (Guilaine *et al* 2000), this site corresponds to the first Neolithic colonisation of the island and places Cyprus within the general framework of the PPNB cultural and demographic diffusion. Two water wells, numbers 116 and 133, were dated respectively from the end of the 9th and 8th millennia cal. BC, and are the most interesting features at the site. Dug into the smooth *havara* calcareous sediment down to depths of up to 8 meters, these wells trapped numerous micro vertebrates, which had fallen to the bottom of these wells when they were used as sources of water (for taphonomic analyses see Cucchi 2001). The faunal assemblage is mainly composed of murid remains. Altogether 42 M_1 teeth from murids were analysed, including 30 specimens from Well 116 and 12 from Well 133.

The Aceramic Neolithic villages of Khirokitia (n=11) and Cap Andreas Kastros (n=10) provided other mouse samples and can be assigned to the well-known Khirokitia phase of the 7th millennium cal BC. (Le Brun 1981, 1989). These samples have been sorted by S. Davis and D. Helmer from wet-sieved stratigraphical units such as pits and hearth sediments inside the houses.

Results.

How many harmonics were the results based on?

Based on Renaud *et al* (1996), we have measured the variation coefficient of amplitude of the first thirteen harmonics performed on the outline of two different individuals measured ten times. Figure 5 show that after the 7th harmonic, the 'noise' caused by variation in factors such as light and positioning during optical measurement reduced the reproducibility of the measures. Consequently, the coefficients from the eight harmonic on were left out of the statistical analysis. The 0th and 1st harmonic were also excluded: harmonic 0 refers to the perimeter of the best fitting ellipse for the molar (=size) and harmonic 1 corresponds to the residues from standardisation. Hence, there are only six harmonics, which closely describe our M_1 outlines. PCAs were performed on a variance-covariance set of the Fourier coefficients of the six harmonics kept for the analysis (24 variables).

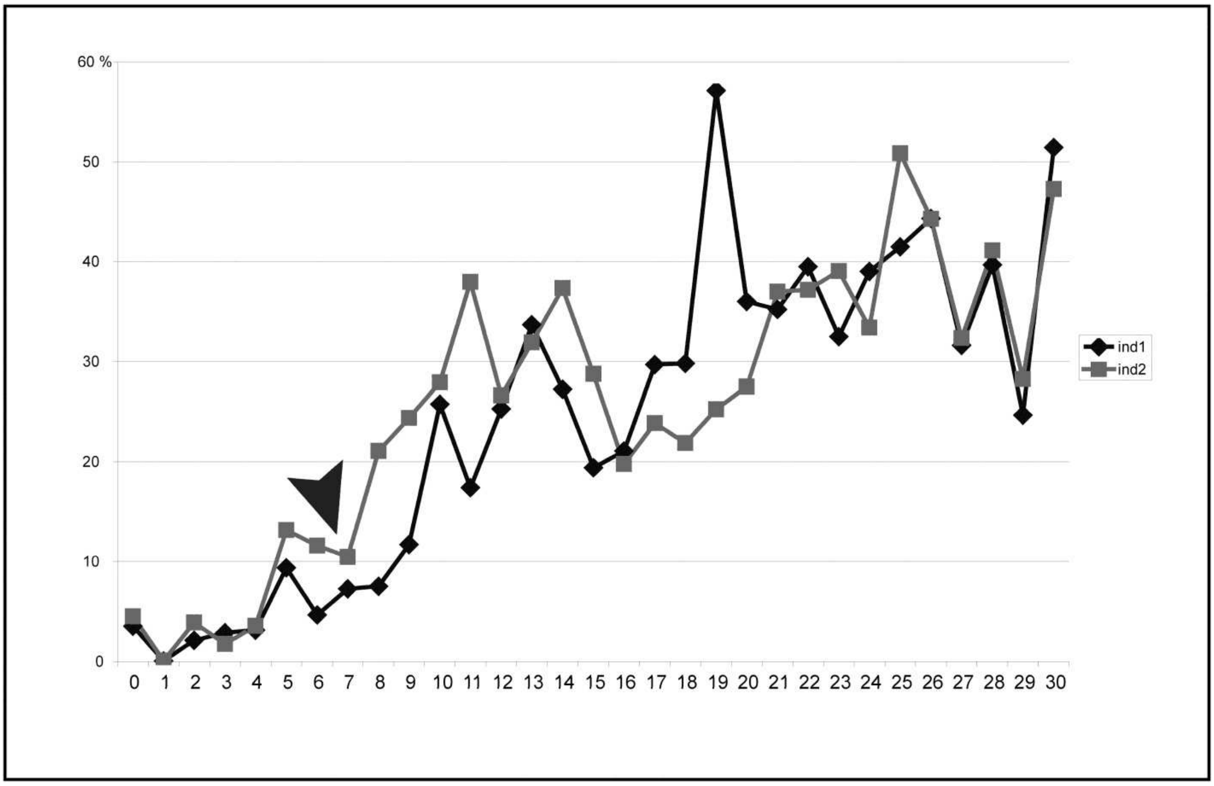

Fig. 5. Coefficient of variation of the amplitude of the first thirteen harmonics on ten repeated measurements carried out on two individuals. Amplitude of an harmonic is calculated as $a_n^2 + b_n^2 + c_n^2 + d_n^2$.

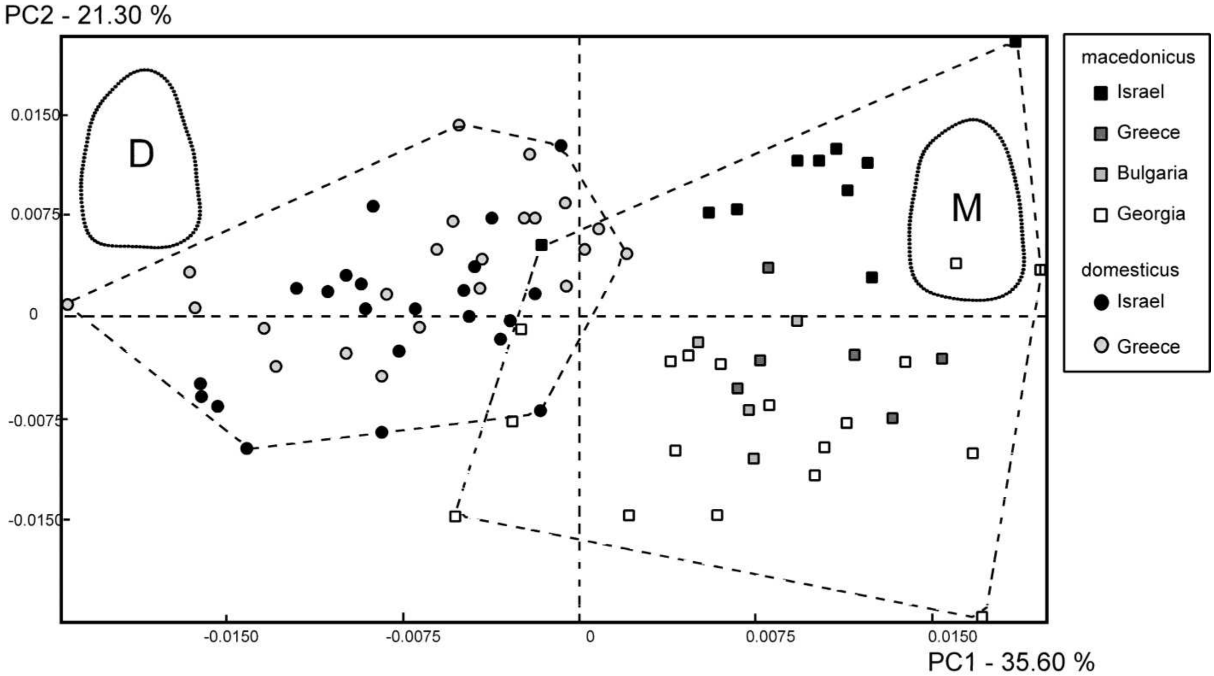

Fig. 6. Projection PC1*PC2 of the PCA of Var/Covar matrix of Fourier coefficients of current mainland samples with reconstructed with the average shape of the reconstructed outlines of *Mus musculus domesticus* (D) and *Mus macedonicus* (M).

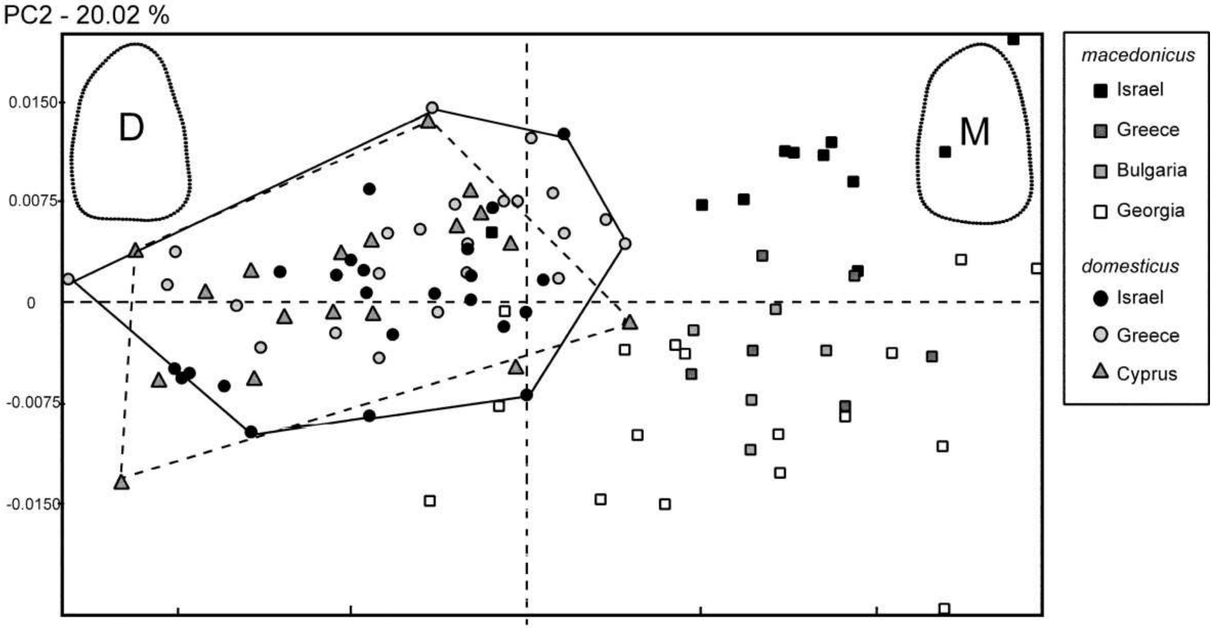

Fig. 7. Projection PC1*PC2 of the PCA of Var/Covar matrix of Fourier coefficients of recent mainland samples and recent house mice from Cyprus.

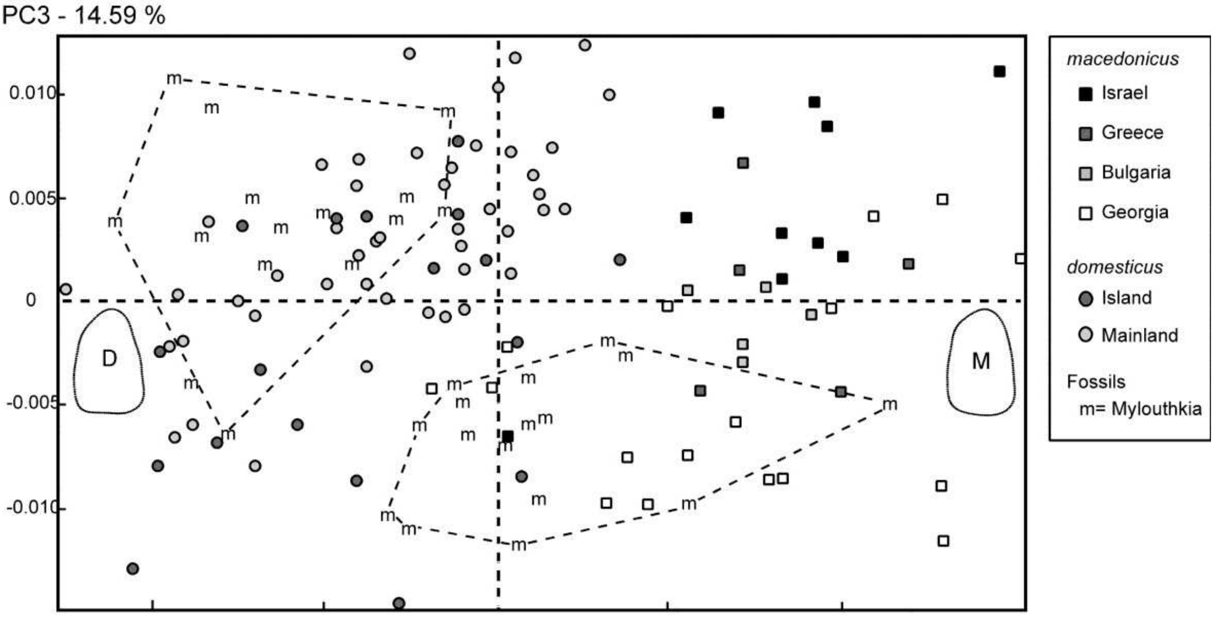

Fig. 8. Projection PC1*PC3 of the PCA of Var/Covar matrix of Fourier coefficients for recent mainland and island samples with fossils from Mylouthkia (m).

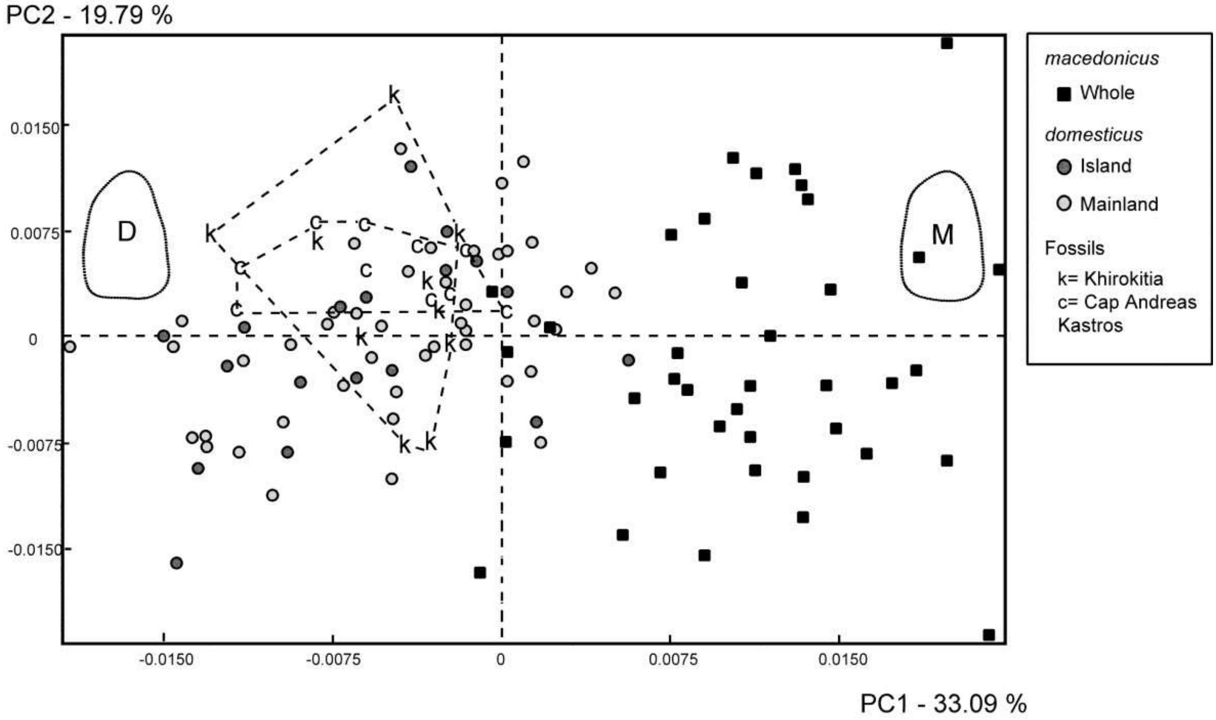

Fig. 9. Projection PC1*PC2 of the PCA of Var/Covar matrix of Fourier coefficients for recent mainland and island samples with fossils from Khirokitia (k) and Cap Andreas Kastros (c).

Current shape differences in Eastern Mediterranean mouse species

We have already demonstrated that Fourier analysis could be a powerful tool for objectively distinguishing the commensal species from the wild one based on the outline of the molar shape (Cucchi *et al* 2002). This is shown here in Fig. 6 where the genetic reference material from mainland mice are projected on the two first PCs (55 % variance). House and wild mice can be clearly distinguished on this projection based on the shape of the respective outlines of their M_1. Wild mice had a triangular form and house mice had a rectangular shape.

We tried to see if the shape of recent Cyprian house mouse M_1 teeth were affected by island syndrome (Fig. 7). The three first PCs representing respectively 34, 19 and 11 % of the between group variance, clearly display no morphological drift in recent house mice. The shape variability of the house mouse M_1 from Cyprus in this figure was superimposed on teeth from mainland house mice.

Hence, the island syndrome, involving changes in demography, reproduction and behaviour (Adler and Levin 1994) of island vertebrates, is characterized by particular morphological traits, which cannot be found with the house mouse on Cyprus based on the molar shape. For the moment, island syndrome in rodents has been described as including increases in body size and, particularly for *Rattus* and *Mus*, as an increase in size of the manducatory system. This syndrome effect has been observed only on small islands and interpreted as a consequence of the loss of interspecific competition and predation linked with the poor diversity on small islands (Vigne *et al* 1993). Although the island isolation effect is now well known for change in body size, the same trends in morphological traits are less known.

Differences in fossil M_1 shapes

We have already shown that at Mylouthkia, two sympatric species of mice were trapped in wells (Cucchi *et al* 2002). In this paper, the first group was the commensal sub-species *Mus musculus domesticus*. The identification of the second species was more problematic, with a choice between Mus *macedonicus* related to morphological drift from long isolation or s mouse with a different geographic origin in Israel. Based on new mtDNA data, *Mus macedonicus* is a polytypic species with one clade occuring in the north of the distribution area and the second in the south (Israel) (Orth *et al* 2002). This genetic distance is interpreted as a consequence of these mice having lived in two possible glacial refuges during the Pleistocene, of the Caucasian mountains. In order to answer the question of the geographical origin of the *Mus macedonicus* in Cyprus, new individuals were added to the reference material because *macedonicus* species are found scattered within its geographical area. With these additions to the reference material, a distinction between the two species may be found on factorial plan PC1*PC3 (Fig. 8). This plan seems to confirm the idea that the form of the *macedonicus* $M_{1,}$ although it diverges from variations in shape found on the mainland, is related to morphological drift as a consequence of isolation and stochastic processes.

One millennium later, the assemblages from Khirokitia and Cap Andreas Kastros (Fig. 9) comprised only the commensal sub-species *Mus musculus domesticus*. In the strict commensal context of the Aceramic Neolithic village, only the commensal form,. *Mus macedonicus* seems to have been present in the anthropogenic sphere. Concerning the shape of the fossil house mouse M_1, no morphological drift can be observed when it is compared to recent mainland and insular reference specimens.

These results show the morphological conservatism of house mouse molar shape through time (between fossils and current individuals as well as between fossils over a one millennium timescale) and space (between the mainland and the island and in different localities on the island) in this part of the Mediterranean.

Discussion

Cyprus is a "true" island.

Cyprus in an oceanic island, which emerged from the oceanic platform through subduction during the Miocene (Constantinou 1982). Unlike other Mediterranean islands, the maximum regression of sea levels during the Pleistocene caused by glaciations never meant that this island was linked with the mainland either with a land bridge or through reduction in the width of the sea channels (Van Andel, 1989, 1990). That is to say, the distance between Cyprus and the mainland coast remained greater than 80 km even during the earliest Neolithic. This distance represented a significant obstacle for the natural spread of the house mouse on naturals rafts while migration by swimming is inconceivable for such a small mammal. An attempt to quantify the waves of migration was made in order to compare the flow of mammalian migration during the Upper Pleistocene and the Holocene in large Mediterranean islands using paleontological and archeozoological lists (Vigne 1999a). This migration rate shows that in Cyprus the migratory inflow increased 24 times. Hence, this clearly shows that Cypriot mammal migration and diversity represents an anthropogenic inflow during the Neolithic diffusion. Thus, if no land bridge existed to ease house mouse migration to Cyprus and if this species presence is linked with Neolithic settlement, the most likely hypothesis is that the human population was responsible for their introduction as part of an ecological package when people colonized Cyprus in the 9th millennium cal BC. Biogeographic studies of the Mediterranean islands confirm this hypothesis since they established that even if the spread could have occurred naturally, not a single commensal species arrived or survived on uninhabited islands (Cheylan 1984).

The island syndrome in house mouse populations

Given Cyprus' isolation and the very small number of founder individuals, conventional wisdom would predict a massive loss of genetic variability and an increasing differentiation in the M_1 tooth form within the mouse colony. These syndromes are best known as founder effect and genetic drift. The whole future reaction and adjustment of the colonizing group depends largely on the alleles and their frequency in the original members i.e. on stochastic factors. The sample which set up the founder population probably had the major part of the alleles in the ancestral population but the difference with the mainland lies in a higher proportion of rare alleles in island populations (Ridley 1996). Here, the island syndrome in mice populations will be described using three examples.

The analysis of the genetic structure of Western island Mediterranean populations of the house mouse have shown that there is no genetic decrease in variability due to founder effect on this islands but rather a rapid increase in genetic differentiation (Navajas y Navarro and Britton-Davidian 1989). This genetic differentiation is a consequence of multiple introductions due to multiple migrations from localities around the Mediterranean and particularly from Middle East populations. These multiple founding events, with addition of several new alleles, maintained the mean heterozygotisy but changed allelic frequencies to allow, together with geographic isolation and stochastic processes, rare variants in genetic structure.

The study of Madeira island house mouse populations has shown that they underwent a rapid chromosomal evolution (Britton-Davidian *et al* 2000). The topography of the island is characterized by steep mountains separated by narrow valleys. These closed spaces are the only areas where humans can settle together with their commensals. Each valley corresponds to particular distinct chromosomal demes of house mouse. Considering that house mice were mainly introduced during Portuguese colonization in the fifteenth century, this chromosomal differentiation has been interpreted as a consequence of isolation of house mouse populations in the different valleys, leading to chromosomal fusions and reproductive isolation in only five centuries.

In another isolated geographical context, in the Valtellina and Orobian Alps (Northern Italy), geometric morphometric analyses on skulls and mandibles were used to describe the patterns in shape changes between demes. The results show that the phenotypical changes follow chromosomal speciation and also take place over a short time span (Corti and Rohlf 2001).

To sum up, house mouse genetic, karyotypic and morphometric structures react very quickly to geographic isolation and stochastic processes. The founder effect seems to have been an important factor only on very small islands. According to Nei, Maruyama and Chakraborty (1975) the severity of a founder effect is more dependent on the rate of population increase following the bottleneck than on the size of the founder populations. The barriers preventing from gene introgression are different between small and large islands. The black rat may be used as a heuristic model of adaptation on small islands. The social modifications involve inter-individual tolerance leading to stable and high populations densities with panmixy explaining the surprising genetic diversity of this population (Cheylan *et al* 1998). These behavioural adaptations are also mentioned for other rodents (Adler and Levins 1994) and house mouse (Gray and Hurst 1998). Nonetheless, despite this good relationship between resident animals, black rats behave aggressively towards newcomers (Granjon and Cheylan 1990) thus, circumventing gene introgression despite migrant inflow. On large islands, this density compensation in association with a decrease in antagonistic behaviours was not observed because the size of the population permitted dispersal, thus, avoiding density and social stress. Large islands have higher species diversity implying greater competition and predation. They are therefore characterized by more unstable and smaller local population sizes. In both cases, gene flow via new migrants is not an easy venture.

On Cyprus, one of the most isolated of the Mediterranean islands, a drift in house mouse fossil shape in the M_1 tooth would be expected with respect to recent mainland reference specimens. However, no morphological drift was observed either in the same locality over one millennium or in various scattered localities far away from each other over one millennium. To maintain such morphological conservatism, the migration events must have been intensive enough to allow gene flow to pass through ecological and behavioural barriers. The Aceramic Neolithic settlements such as Mylouthkia, Khirokitia and Cap Andreas Kastros must have served as locations for house mouse metapopulations on Cyprus in accordance with the mainland/island model (Harrison 1991). This model takes into account that there are different episodes of island decolonisation from mainland sources which make the island populations resistant to extinction and genetic drift. The link is through a uni-directional flow of migrants coming from different mainland sources (Fig 10). Only when a migration or decolonisation rate is strong enough can it lead to a sporadic genetic introgression among the populations on isolated islands and contribute to the maintenance or increase in the genetic variability, avoiding genetic drift or differentiation (Gaggiotti 1996) and, at the same time, morphological drift. Hence, the study of house mouse island migrations leads to the question of human maritime traffic.

Very little information is available concerning the use of boats in the Mediterranean before the Bronze Age so that the gaps in our knowledge must be filled in with indirect evidence.

The existence of viable craft and offshore sailing is evident in Late and Final Palaeolithic times in several parts of the world (Vigne 1989; Cherry 1990). Recent research has highlighted the fact that Mediterranean islands were visited and sometimes colonized by hunter-gatherers mostly from the 9th millennium BC (Vigne 2000). It is probable that the carrying capacity of large islands would have been attractive and landing on them represented scheduled ventures in sea-going craft capable of making long voyages. Nonetheless, It is difficult to clearly differentiate between real hunter-gatherer colonization and seasonal visits to these islands. Indeed archaeological evidence is poor (Cherry 1981, Sondaar *et al* 1986; Simmons 1988; Vigne and Desse-Berset 1995).

The earliest presence of humans on large Mediterranean islands is found on Cyprus with the small settlement of Akrotiri Aetokremnos dated to the 9th millennium BC (Simmons 1988, 1991). Other evidence closely follows this evidence from Corsica and Sardinia, which were visited within the same time scale in the second part of the 8th millennium BC. Corsica is, for the moment, has been most intensively investigated in terms of early settlements. The amount of information on the Preneolithic on Corsica has radically increased since 1990 with the discovery of six Mesolithic sites (Vigne and Desse-Berset 1995, Vigne *et al* 1998b, Vigne 1999b). In Sardinia, only the site of Porto Leccio (Tozzi 1996) has yielded clear evidence for Mesolithic settlement.

Of the Corsican sites, the Monte Leone shelter provides clear proof of a successful colonization of Corsica by Mesolithic communities exploiting a large range of local resources including marine fish and shells, endemic mammals and avifauna (Vigne *et al* 1996). Finally, the example of Franchthi cave in the southern Argolid (Greece) with the presence of Melian obsidian and tuna bones which first appear in the late Upper Palaeolithic and Mesolithic contexts respectively in the cave, provides a clear indication for sea-going craft and two-way crossings well before the advent of agriculture (Perlès 1979).

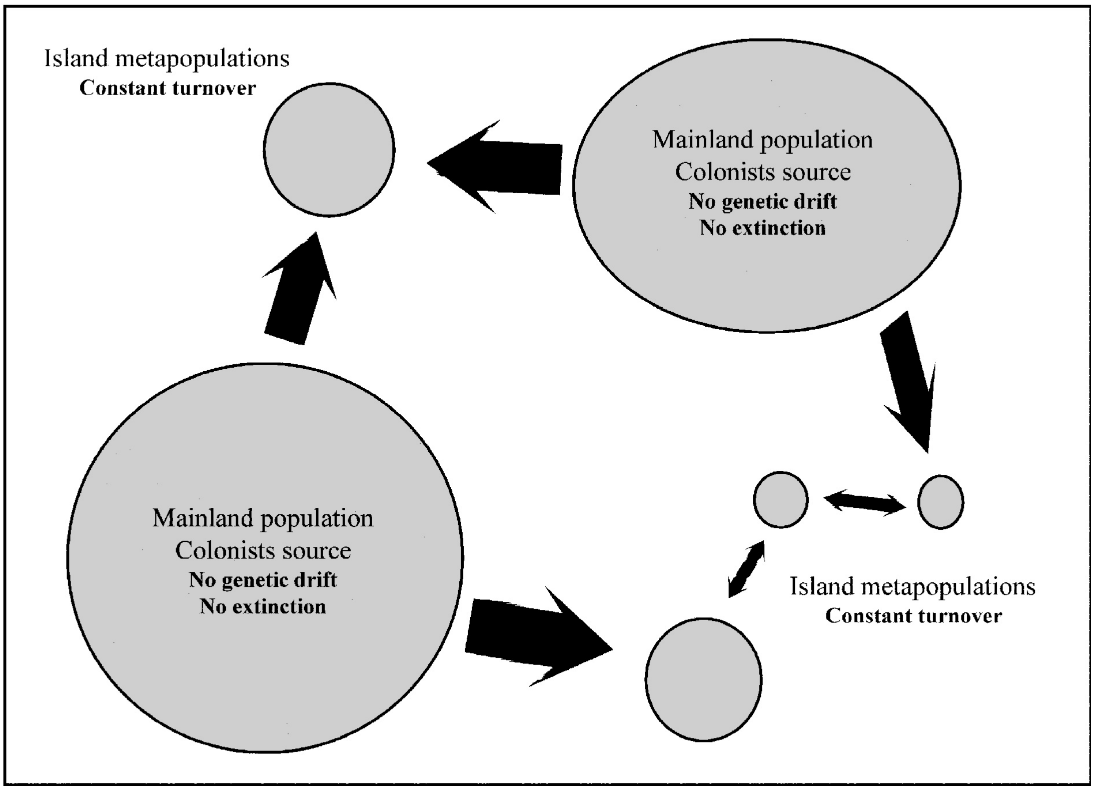

Fig. 10. Mainland/island metapopulations model.

Very little is known about nautical technology for this early period since the earliest sea-going craft recovered from underwater archaeological survey work dates to before the Late Bronze age (1300 BC). The best example is the Uluburun shipwreck discovered along the southwestern coast of Turkey and excavated between 1984 and 1994. For the Neolithic period the only evidence for boats come from the hollow-log vessel carved from a single tree trunk (monoxylon) and found in Bercy on the banks of the Seine (5^{th} millennium BC) and two terracotta scale model crafts and the large hollow-log craft found in Bracciano lake (Italy) (Delpino and Mineo 1995) which come from early Neolithic contexts (6^{th} millennium BC). Despite their importance for understanding navigation across lakes and down rivers as well as Neolithic exchange possibilities they still are not evidence for Neolithic seafaring technology. Nevertheless, in 1995 and 1998, the model from Bracciano inspired a researcher with a Polish team to reconstruct Neolithic seafaring (Monoxylon expeditions 1 and 2). They took two experimental voyages with a hollow-log craft of more than 6 meters dug out of the trunk of an oak tree. First, with eleven persons on board, they crossed the Aegean from Samos to Attica in eleven days. The second expedition followed a sea path from Sicily to Latium, then along the coasts of Liguria and Catalonia finally landing in southern Portugal. In 1969, Greek researchers concerned with Neolithic sea routes undertook an experimental voyage and sailing using a craft made of bundles of papyrus (Tzalas 1993). This time the venture aimed at following a sea route from Melos, with its obsidian sources exploited in the Mesolithic but mostly in the Neolithic period, to the southern Argolid where Franchthi cave is located. Even if all these experiments suggest that long sea voyages could have been undertaken in the Neolithic with these kinds of crafts it is impossible to be sure that this technology was used in boat construction during the Neolithic.

A modelled colonization of Crete shows that the Neolithic colonization of a large island is a highly scheduled venture. The model proposes that under circumstances of a single colonising event, a viable minimum number of farming colonists should be 40 for the founder group, with a total implied cargo (animals, plants, water) of around 20,000 kg (Broodbank and Strasser 1991). This is a good argument for a change in nautical technology between hunter-gatherer craft, thought to be made for lightness, mobility and easy handling (Johnstone, 1988) based on ethnographic examples from around the world, and those of Neolithic colonists with larger watertight boats that could transport large live cargoes. Others go further and propose a correlation between the increase in the introduction of small mammals onto islands as stowaways (5^{th}-4^{th} millennia BC) with the development of superstructures on boats such as decks under which small mammals were able to hide (Vigne 1998a, 1999a).

The question of exchange through sea traffic has already been considered with regard to diffusion of raw materials whose sources were limited such as obsidian, flint and also prestigious objects. They have shown that Neolithic communities did not live within closed areas but engaged in exchange on a large scale. However, the intensity of these exchanges is difficult to assess. The changes in the rate of obsidian coming into mainland sites is a good marker although the amounts of obsidian are mostly useful as qualitative markers rather than quantitative ones except in the case of Shillourokombos (Briois *et al* 1997). On the other hand, the introduction of mammals to islands would be good markers if we assume they were introduced in multiple events with small numbers of individuals. Based on genetic parameters, in order to maintain a viable population in a new biota these events should be numerous enough to establish a species, especially if several failures are taken into account (Vigne 1998a, 2000).

I propose using the shape conservatism in the M_1 in Cypriot house mouse populations as a strong quantifiable argument with which to approach questions concerning the intensity of sea traffic. Indeed, as we have already argued, the house mice depended on human populations for passive transport to reach Cyprus. The second strong evidence for the intensification of sea traffic lies in the rapid genetic and morphological drift in mouse populations in isolated contexts. Finally, a migrant flow can become a gene flow insuring genetic and morphologic stability only after intensive migration is followed by successful colonisations. Based on these three points, the shape conservatism of the M_1 of house mouse in Cyprus since the end of the 9^{th} millennium BC is the consequence of intensive trade links between Cyprus and the mainland in this part of the Mediterranean. We do not know if these mice then became widely distributed all around the island and we prefer to talk about human settlements rather than house mouse metapopulations. The boats coming from the mainland with house mouse stowaways attracted by seeds or legumes stored on board resulted in a continuous inflow of new individuals contributing to the genetic diversity of the island with genes from the mainland. This inflow brought new genes to the metapopulations or settled new populations based on an extinction recolonisation model. In both cases, the fossil metapopulations on Cyprus produce the same morphological image in terms of the M_1 of these mice populations. We can now provide new indirect evidence for a region of early intensive trade in the Mediterranean six millennia before the Mediterranean sea-faring states of the Bronze Age, at least in the Eastern Mediterranean Basin. The sea does not seem to have represented a barrier for the first farmers. With the study of these mouse populations we now have another element to show sea travel was advanced enough to permit planned colonization by large communities and ecological transplantation as well as frequent return travel.

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