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First occurrence of the house mouse (*Mus musculus domesticus* Schwarz & Schwarz, 1943) in the Western Mediterranean: a zooarchaeological revision of subfossil occurrences

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This paper provides a critical analysis of archaeological small mammal collections in the Mediterranean area, from the Late Glacial to the first centuries AD, to validate the presence/absence of the house mouse through zooarchaeological criteria. The results have been synthesized through a diachronic map, whose chronological phases are related to socio-economic and cultural human evolution. The house mouse (*Mus musculus domesticus*) progression in the Mediterranean begins with a quick but limited diffusion in the Eastern Mediterranean Basin achieved around the 8th millennium BC. Until the 1st millennium BC, the invasive process seems to have stopped or drastically slowed, despite the increasing opportunities of passive transport during the Bronze Age. During the 1st millennium BC, there was mass colonization by the house mouse of the entire Western Mediterranean Basin and Northern Europe. We propose to explain this chronological gap in the colonization of the Eastern and Western Mediterranean using source-sink theory considering that the western environments acted like sinks until the first millennium BC. At that time the Western Mediterranean was fully opened to Eastern influences and migrations, and the human pressures on the environment drastically increased. This may have favoured definitively the adaptation of the house mouse to the Western commensal niches. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **84**, 429–445.

ADDITIONAL KEYWORDS: anthropization – coevolution – invasive species – phylogeography – source-sink – subfossils.

The genus *Mus* has been present in the Mediterranean area from the Middle Pleistocene, but the house mouse (*Mus musculus* sp.) diffusion from South-East Asia through Eurasia belongs to the last wave of colonization, during the Holocene. Analysing series of fossils from stratified cave fillings from 120 000 to 12 000 BC in Israel, Auffray, Tchernov & Nevo (1988) highlighted the presence of the house mouse on the shores of the Eastern Mediterranean starting from 12 000 BC only. This successful settlement must be considered to be a consequence of the development of human sedentism (small villages) and of systematic cereal harvesting and storage, more than as the result of global climate change (Tchernov 1984, 1991, 1993, 1994). The westward progression from this point, following human migrations, is presumed to have developed following two different routes, the continental one ('Danubian route'), which brought the *M. m. musculus* subspecies into Eastern, Central and

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Scandinavian Europe, and the Mediterranean route, which led the other subspecies, *M. m. domesticus*, to colonize the Mediterranean, North African and Western Europe areas (Thaler, Bonhomme & Britton-Davidian, 1981; Auffray, Vanlerberghe & Britton-Davidian, 1990).

This spread of the house mouse into Europe is, however, still poorly documented. This is mainly due to the poor sampling strategy (lack of sieving) for small mammals in archaeological sites. It may also be related to species identification problems relating to poor preservation of osteological material.

This paper aims to provide a critical review of the distribution of the house mouse in archaeological sites of the Mediterranean area. We will focus on the phylogeography of *Mus musculus domesticus* (Schwarz & Schwarz, 1943). This work is a continuation from the paper of Auffray *et al*. (1990) regarding the house mouse progression in Eurasia. Our addition to the Eurasian house mouse phylogeography consists of an improvement of the validation of the archaeological sources, using a zooarchaeological critical grid, in order to check the house mouse records in the faunal spectra from both a taxonomical and a chronological point of view. Finally, the aim is to draw up a more reliable diachronic mapping of the house mouse diffusion and discuss it in the light of human cultural evolution.

MATERIAL AND METHODS

First, a database of the archaeological occurrences of the house mouse was created (see Appendix). This database records the archaeological contexts from which small mammals have been sampled and studied. A context is a site or part of a site, which is homogeneous from the chronological and stratigraphic points of view; so, in the database nine sites with a long and complex stratigraphy have been split into several chronological contexts. Contexts are ordered according to their chronological position from the oldest to the youngest. The full collection of sites (Fig. 1A) represents 53 localities spread over the Mediterranean area.

The Central Mediterranean area as well as Northern Africa are poorly documented or not documented at all. For the first area this scarcity is due to a non-systematic collection of small mammals and, for the second, it is due to poor archaeological survey. Figure 1B shows that the archaeological contexts are spread in time from the end of the Late Glacial until the first centuries AD. The last five millennia BC include a large percentage of archaeological sites (44%).

The columns of the database in the Appendix record the presence/absence of the different murid species from the small mammal spectra with their relative frequency. Secondly, they record the different criteria that will be used globally to validate the presence/absence of the house mice in the different contexts. These criteria are based on statistical, biological and archaeological considerations.

From the statistical point of view, we have first considered the size of the subfossil small mammal collection in order to determine if the sample can be regarded as representative in terms of relative frequency of species. Samples with fewer than 30 for the minimal numbers of individuals (MNI) have been considered as unrepresentative; the absence of one species in the spectra could be due to the random effect of the small size of the sample.

From the biological point of view, we focused on the method that has been used for the interspecific distinction of the fossil remains of murids, particularly between the *Mus* species. There are no criteria for the distinction between *Apodemus* and *Mus* on the basis of postcranial bones, but both skull and tooth morphology allow a good distinction between the two genera (Chaline, 1972). The interspecific discrimination of *Mus* species, very close morphologically, is mainly based on the method of Orsini *et al*. (1983). The best discriminatory parameter among those given in this method is the zygomatic index on the skull (ZI: width of malar process anterior part/width of zygomatic arch upper part), but the distribution of the frequencies sometimes widely overlaps. The best overall criterion is the general shape of the first lower molar in occlusal view treated in Elliptic Fourier analysis (Cucchi *et al*., 2002), but because this method is very recent it has been used only for a very small number of samples. Consequently, the distinction between *Mus* species is very rarely reliable in the literature.

From an archaeological point of view, three points have been scrutinized, according to Audoin-Rouzeau & Vigne (1994), Vigne & Valladas (1996) and Vigne *et al*. (2002).

1. What is the context of the small mammal deposit? The main suspicion relating to small mammal collections from archaeological sites is the severe risk of stratigraphic disturbance, largely caused by the burrows of carnivores and rodents, but also by human activities. These have led to vertical migrations of archaeological items through different layers. The fillings of stratified caves or rock shelters are also subject to vertical migrations as a result of bioturbation. Consequently, the choice of samples for small mammal collections should include both well-sealed stratigraphies and the bottom layers of deep features such as pits, wells and silos.

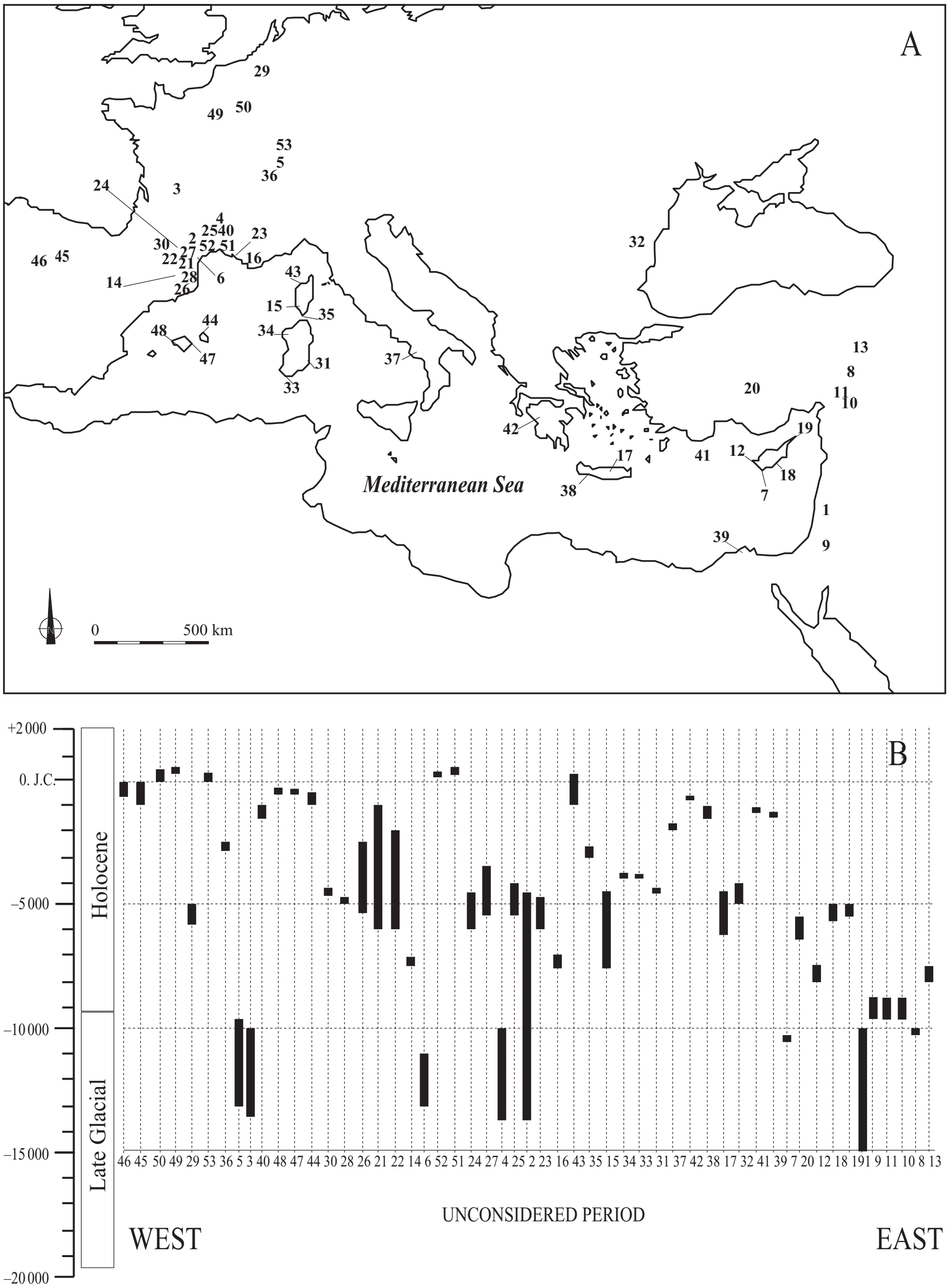


Figure 1. A, location of the 53 archaeological sites involved in the revision of subfossil house mouse occurrences. B, projection of their chronological sequences from Western to Eastern Mediterranean area. 1: Hayonim B/C, 2: L'Abeurador, 3: Bois-Ragot, 4: Rond du Barry, 5: Rochedane, 6: Espéluges, 7: Akrotiri-Aetokremnos, 8: Mureybet, 9: Netiv Hagdud, 10: Jerf el Ahmar, 11: Dja'dé, 12: Mylouthkia-Kissonerga, 13: Cafer Hüyük, 14: Cingle Vernell, 15: Monte Leone, 16: FontBregua, 17: Knossos, 18: Khirokitia, 19: Cap Andreas Kastros, 20: Catal Hüyük, 21: Cova 120, 22: Ermittons, 23: Châteauneuf-les-Martigues, 24: L'abri Jean Cros, 25: Baume d'Oullen, 26: Grotte du Frare, 27: Font-Juvenal, 28: Pasteral, 29: Place St-Lambert, 30: Villeneuve-Tolosane, 31: Corbeddu, 32: Harsova tell, 33: Grotta Rifugio, 34: Su Guanu, 35: Araguinna-Sennola, 36: Clairvaux la Motte aux Magnins, 37: Nola, 38: Kommos 1, 39: Buhen, 40: Mourre de la Barque, 41: Uluburun, 42: Nichoria, 43: Monte di Tuda, 44: Torralba d'en Salort, 45: El Soto de Medinilla, 46: La Mota, 47: Torre den Gaumès, 48: S'illot, 49: Gaillon-le-Bas, 50: Acy-Romance, 51: Lattes, 52: Canet-en-Roussillon, 53: Sierentz-Landstrasse.

2. What is the method of dating the presence of the house mouse in the archaeological site? A direct radiometric date (^{14}C) on mouse bones themselves is the best way to ensure their contemporaneity with the archaeological level in which they lay. However, this has never been done for mice bones until now, the presence of mouse remains being generally dated by the radiometric (or only cultural) dating of the layers from which they have been excavated. In addition, the reliability of ^{14}C dating depends mostly on the material on which the ^{14}C dating has been performed, as well as on the field strategy to sample this material. Indeed, wood, charcoal, bone and shell, which are the main materials for ^{14}C dating in archaeology, do not represent the same ^{14}C events, the same patterns of carbonate contamination, the same requirements for a conventional ^{14}C age and the same association with human events (for details see Strydonck *et al*., 1999). In those cases for which the dating method is mentioned, we scrutinize its reliability.
3. The last archaeological question concerns the size of the mesh used to sieve the sediment and collect the small vertebrates: more than 2 mm risks missing species of small size such as mice, even if they were present in the sediment. In addition, the quality of the sorting of the sieving refuse should also be taken into consideration (Vigne & Valladas, 1996; Vigne *et al*., 2002), but this is rarely known, and generally not very good because archaeologists extract bones directly from the sieve, without care to be exhaustive.

Once this critical examination was completed, we estimated the general reliability of the presence or absence of the house mouse for each archaeological context, according to three different levels: highly probable, probable and doubtful.

The chronology of the database has been divided into five phases according to the main changes in human history determined by technical, economical and cultural evolution. For each of these five phases a mapping of the presence and absence of mouse bones has been deduced from the database: each archaeological context has been plotted with an icon and an identification number. The icons provide two pieces of information. First is the degree of reliability in terms of sample size (fewer than 30 individuals: small circle; more than 30 individuals: large circle). The second piece of information is the level of validity of the house mouse occurrence in the sample: white for probable and highly probable absence, black for probable and highly probable presence and grey for doubtful presence.

RESULTS: DIACHRONIC MAPPING BY PHASE

PHASE 1: 12 000–8500 BC – UPPER PALAEOLITHIC, EPIPALAEOLITHIC AND MESOLITHIC PERIODS

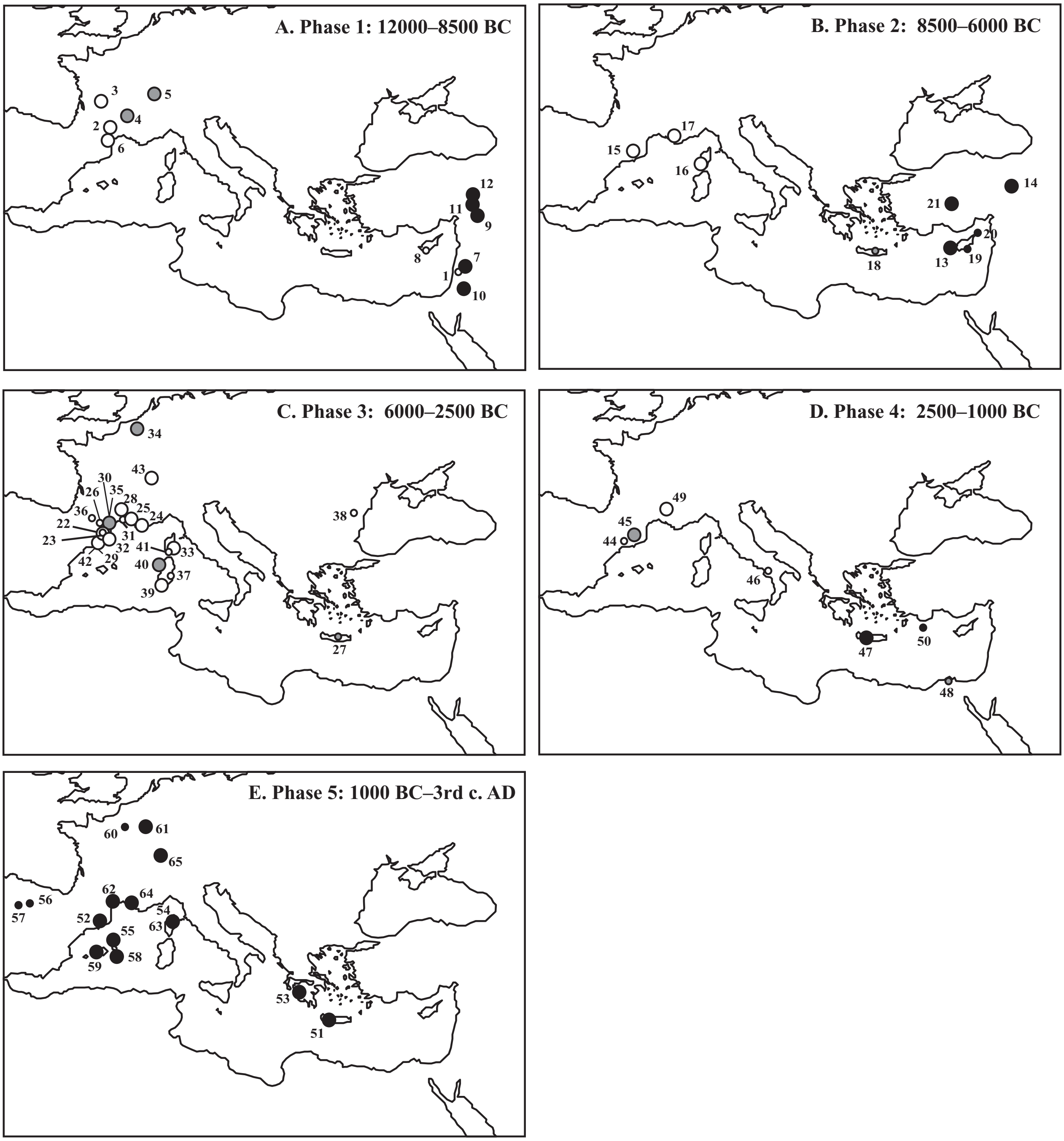
General historical framework

In Europe, this phase is marked by wide climatic oscillations, which end *c.* 9200 BC with the abrupt Holocene warming (Magny, 1995, 2004), but these climatic changes were much less marked in the Near East (Sanlaville, 1997). During this period, human communities were still hunter-gatherers. In Europe, Magdalenian, Epigravettian, Epipalaeolithic and Mesolithic communities remained mobile over large areas (Djindjian, Koslowski & Otte, 1999). In the Near East, between 12 000 and 10 300 BC, cultural evolution is obvious in the subsistence strategies of the foragers, which generally ranged from semisedentary groups to small mobile bands. Sedentary Natufian hamlets were established and then larger open-field sites of Pre-Pottery Neolithic A (PPNA) in the Levantine corridor (Bar-Yosef & Meadows, 1995; Aurenche & Kozlowski, 1999).

Mapping the presence/absence of the house mouse (Fig. 2A)

The projection of the probable and highly probable occurrences of the house mouse for phase 1 coincides with the limits of the sites that belong to the Natufian heritage. In those sites the house mouse has adapted to the new ecological niche created by long-term human settlements. The commensal niche seems to be fully colonized by *Mus musculus domesticus* in the Levantine corridor because this species is found in caves and rock shelters as well as from open-field PPNA sites such as Jerf el Ahmar, Mureybet and Dja'dé. Although it can be argued that the presence of the house mouse in cave deposits does not represent clear evidence of synchronous occupation by humans and mice, because of possible accumulations of raptor pellets following human abandonment of the sites (Ervynck, 2002), the presence of house mice in the occupation layers of houses is clear evidence of a commensal way of life.

In Cyprus, the house mouse is absent from the Epipalaeolithic site of Akrotiri-Aetokremnos (Simmons, 1999: 69) but the sample size is too small to be representative. By contrast, three French Epipalaeolithic sites with a significant sample size and which were carefully studied do not contain any house mouse remains; the only documented (and sometimes abundant) small murid was the wood mouse (*Apodemus* sp.). Based on these reliable data, the presence of very few remains of *Mus musculus* sp. in Rochedanes (MNI = 2) and in the cave of Rond du Barry (MNI = 1), within significant samples (respectively 539 and 511


A. Phase 1: 12000–8500 BC

B. Phase 2: 8500–6000 BC

C. Phase 3: 6000–2500 BC

D. Phase 4: 2500–1000 BC

E. Phase 5: 1000 BC–3rd c. AD

Figure 2. A–E, diachronic mapping of the subfossil house mouse occurrences in the Mediterranean area, according to five chronological phases. The numbers used for each map refer to the inventory numbers of the database in the Appendix. The size of the dots corresponds to the size of the fossil collections: a small circle represents fewer than 30 MNI and a large circle 30 MNI or more. A black dot represents a validated presence of house mouse, a grey circle a doubtful presence and a white circle a validated absence.

individuals), appears doubtful. The fossil remains have not yet been revisited from a taxonomic point of view nor directly radiocarbon dated. However, it would be surprising that a population of house mice could have survived both the cold climate of these latitudes at that time, given the competition with the wood mouse (which is highly dominant in the faunal spectrum), and out of the protection of the commensal niche (people were still nomadic foragers). We propose that this documentation of house mouse should either be referred to as *Mus* sp., assuming the presence of *Mus spretus* (Lataste, 1983) in the area, at least for Rochedanes, or considered as modern pollution of current house mouse in archaeological layers due to vertical migration and inappropriate selection in small fauna sampling.

PHASE 2: 8500–6000 BC – NEOLITHIC EMERGENCE AND SPREAD

General historical framework

The Neolithic phenomenon is a series of mechanisms that made humans change from an economy of predation to an economy of production and that occurred in different places of the world. For our purpose, we are interested in the Neolithic that emerged from the Near East (the 'Fertile Crescent') and diffused all around Eurasia, thereby determining its cultural and biological diversity. The whole period is situated at the Holocene optimum climate (warm and moist), which reached its highest point at the end of this period. This period provides the first clear evidence of domesticated plants and animals from archaeological remains. Domestication was not yet completed when the farming culture spread out from its origin, as we can see in Cyprus, which was colonized from 8200 BC (Guilaine *et al*., 2000).

The diffusion of the Neolithic which emerged from the maturation area of the Levantine corridor (Pre-Pottery Neolithic B, PPNB) did not seem to go further than Central Anatolia. The western diffusion to the Aegean seems to have been one millennium later and corresponds to the emergence of a new Neolithic culture. By the end of the 7th millennium BC, the Aegean, Balkan and Italian–Adriatic areas had been colonized by the Neolithic diffusion.

The societies that achieved the technical skills that allowed animal and plant domestication took their knowledge in their westward progression as well as their livestock. This involved the first large ecological human impact. This transfer is particularly well highlighted by the Neolithic colonization of the Mediterranean islands (Cherry, 1981, 1990; Vigne & Alcover, 1985; Blondel & Vigne, 1993; Vigne, 1999). In these islands, the endemic fauna, in which there was no wild ancestor of domestic animals, was replaced by an invasive fauna comprising farm animals and feral populations derived from escapees from the transferred livestock. In this ecological package the passive transport of the house mouse could have been expected, given that humans transferred other anthrophilous small mammals early to the Mediterranean islands (Vigne, 1994a). The question is whether the house mouse followed this progression, which should have brought it out of its primary area of diffusion in Central Anatolia and Cyprus.

Mapping the presence/absence of the house mouse (Fig. 2B)

The only positive answer to the question above comes from some murid remains recorded from the Early Neolithic layers of Knossos, in Crete (Appendix, no. 18). Although we have not yet observed these remains, we know that they are only postcranial bones (V. Isaakidou, pers. comm.). Given that interspecific discrimination between murid species on postcranial bones is extremely difficult, the taxonomic attribution to *Mus*, for this site, should probably much more cautiously be changed into a general attribution such as 'small murid', i.e. either *Apodemus*, which is present in Crete, or *Mus minotaurus* (Bate, 1942) and *Mus batae* (Mayew, 1977), the Pleistocene forms, which could have survived the human colonization, or a putative invasive *Mus musculus domesticus*. We therefore consider that this occurrence is doubtful. For the Central Mediterranean area, there are no other reports of house mouse for this phase. Water sieving of large samples in the Early Neolithic site at Trasano (Matera) gave very few small vertebrate bones but no mice (J.-D. Vigne, unpubl. data). We have already mentioned the scarcity of archaeological small mammal collections from these regions. The question remains: did the house mouse fail to follow the Neolithic diffusion up to the Italian shores or does the absence of mice reflect sampling bias? Phase 3 probably helps to find a solution.

PHASE 3: 6000–2500 BC – NEOLITHIC DIFFUSION IN EUROPE

General historical framework

The Neolithic diffusion in the Western Mediterranean and in Central Europe, according to the two separated axes of human and cultural transfer, followed a pattern of rapid progression. The further diffusion of the Neolithic was arrhythmic, with alternations of quick and slow phases linked to the adaptation and renewal of the cultural traits facing the biotic and abiotic factors of the colonized environments (Guilaine, 2000a). The colonization of the western Mediterranean shores from Italy to Spain and then to Portugal, supposedly realized by coastal navigation, was completed in 800 years. For the Occidental culture of Central Europe, after a long period of adaptation from the Mediterranean Neolithic of the Aegean and the Balkans to the ecology of Temperate Europe, the diffusion up to the Parisian Basin was rapid.

Mapping the presence/absence of the house mouse (Fig. 2C)

For this phase, we found no data from the Eastern and Central Mediterranean area, except for Knossos (with the same questions as above) and a small sample with poor reliability from the Romanian site of Harsova tell.

In Western Europe, ten sites gave reliable small mammal samples with no evidence of the house mouse. Five less reliable sites gave the same result (nos. 23, 26, 31, 41, 43). This sheds doubt on the three other sites (nos. 30–35, 34, 40) in which the house mouse was recorded. These doubts are confirmed by analysis of each of these data:

1. The mention of house mice in the 'Place St Lambert' excavations, in Liège (Belgium; no. 34) is doubtful because: (i) half of the small mammal species of the spectrum are composed of forest species (wood mouse, red squirrel and bank vole) and there was only one house mouse in a total of 48 individual small mammals examined; and (ii) we have no absolute dating for this context. The collection method seems to have been appropriate but we do not know if the sample originates from the upper or from the lower layers of the pits; so in the absence of any taphonomic analysis, we cannot exclude the possibility that these house mouse bones result from a stratigraphic intrusion. This possibility is even probable given the abundance in the spectrum of three genera of burrowing rodents. Indeed, *Arvicola terrestris* (Linnaeus, 1758) (Meylan, 1977), *Microtus arvalis* (Pallas, 1758) (Niethammer & Krapp, 1982) and *Apodemus sylvaticus* (Linnaeus, 1758) (Niethammer, 1978) have many burrows 20–25 cm deep and some even 25–70 cm deep. So if the small mammals samples were not deposited in deep and rapidly filled structures, the few house mouse remains in Neolithic layers could be the result of modern bones taken down by these rodents. As we cannot exclude that this insubstantial occurrence of house mouse results from pollution by vertical migration of recent remains, it cannot be considered as evidence of the presence of the house mouse in Belgium during the Neolithic.
2. Sample nos. 30 and 35 represent two phases of the Font-Juvénal shelter (Aude, France). For this site, the study of which dates to the early 1980s, the biochemical revision of the *Mus* species was not available. At that time and according to Le Louarn & St-Girons (1977: 154), all mice from Western Europe were considered as subspecies of *Mus musculus*, including the outdoor species *Mus spretus*. The claims should be revised to *Mus* sp. (J.-C. Marquet, pers. comm.). Taking into account the low percentage of *Mus* in both small mammal assemblages at Font-Juvénal (no. 30: 2%; no. 35: 2.6%), *M. spretus* is much more probable than *M. musculus*.
3. No. 40 is a Sardinian cave, but which is poorly dated and has an unreliable stratigraphy. For example, in the Neolithic layer, together with the mouse remains is the presence of the black rat (*Rattus rattus* Linnaeus, 1758), which is known to have been absent from this area before the second half of the 1st millennium BC (Vigne & Valladas, 1996). This documentation of house mouse must be considered to be the consequence of modern contamination due to stratigraphic disturbance.

Consequently, even during this phase 3, which covers the strong demographic, cultural and ecological spread of the Neolithic farmers *mode de vie* over the whole Mediterranean basin, the house mouse did not take advantage of the opportunities to colonize westward.

PHASE 4: 2500–1000 BC – BRONZE AGE AND INTENSIFICATION OF THE EXCHANGES IN THE MEDITERRANEAN SEA

General historical framework

This phase belongs to the Subboreal chronozone. It is a phase of both climate deterioration and increase of human impact on the vegetation. In the Near East, from the 16th to the 11th centuries BC, several empires and cities emerged, such as the Theban Empire, the Hittite and the Assyrian kingdoms, Babylon, etc. In Europe, the civilizations of the Bronze Age were also organized into a hierarchy, but if exchanges existed they did not reach the level of economic interactions between the Near East empires. All these hierarchical societies comprised an elite of warriors and merchants, but were still based on herders and farmers. During this period, long-distance exchanges of material and knowledge between human communities drastically increased. This was due first to the development of new hierarchical organization of the societies, but also to improvements in ship manufacture and in sea-faring techniques, mainly known from civilizations around the Aegean islands. This might have favoured the colonization of the entire Eastern Mediterranean basin by the house mouse.

Mapping the presence/absence of the house mouse (Fig. 2D)

Despite the small number of sites, the house mouse is clearly recorded at Kommos 1, in Crete (no. 47). Only four sites are available in the Western Europe area. Three of these sites, one of which is fully reliable (Mourre de la Barque, no. 49), gave no evidence for the house mouse. The fourth (Cova 120, Catalonia, no. 45) gave a more convincing mention of the house mouse, but the poor chronology as well as problems with species diagnosis have also led us to reject this occurrence. The Italian site of Nola (excavated by C. Albore) provides a suitable archaeological context because the farmer–herder hamlet was destroyed and petrified by a volcanic eruption of Mount Vesuvius, similar to that which affected Pompeii several centuries later. Remains of small mammals with no mice have been found inside an enclosure. Thus, this context, despite the small size of the sample, is nevertheless the most convincing for the absence of the house mouse in Western Europe during the Bronze Age. However, this conclusion is based on only a few sites.

PHASE 5: 1000 BC – 3RD CENTURY AD – IRON AGE

General historical framework

Iron metallurgy existed from the 11th century BC and also spread from East to West. This period marked the increase of the socio-economic traits that had emerged during the previous phase. Indeed, in the Western Mediterranean commercial traffic became more organized and North–South axes of exchange emerged together with intensive human urbanization. Social hierarchy also increased with a stronger expression of power through demonstrations of status. Eastern influence is strong in the Western Mediterranean and archaeological remains have demonstrated how trade through the Mediterranean Sea became more regular, diversified and intensive.

Mapping the presence/absence of the house mouse (Fig. 2E)

Both sites of the Central Mediterranean area and the 13 sites of Western Europe dating to phase 5 yielded remains of the house mouse. In general, for these samples, dating and determinations are very reliable. In addition, the house mouse dominates in frequency in all the samples. This massive presence strengthens the interpretation that we gave to the low rates of occurrence of house mouse during the previous phases. The earliest sites in this phase are known from Western Mediterranean islands such as Corsica and the Balearic Islands and date to the first half of the 1st millennium BC. Documentation on mainland Europe is only slightly later, dating from the 6–4th centuries in Spain and in both the South and the North of France. This phase clearly represents the invasion of Western Europe by the house mouse.

DISCUSSION

GENERAL FEATURES OF THE HOUSE MOUSE DIFFUSION

Given that fossil data from Northern Africa are missing, we are only able to consider the house mouse progression on the northern shore of the Mediterranean Sea. According to our data, the house mouse pattern of diffusion seems to have proceeded in three steps:

1. First was a rapid but limited diffusion in the Eastern Mediterranean Basin, following the primary diffusion of the PPNB out of its maturation area (the Levantine corridor). The house mouse perhaps reached Crete by the beginning of the 7th millennium BC in the same wave, but this is far from certain; the colonization of Crete is authentically documented only at the time of the Minoan period, during the 3rd millennium BC. At the present state of knowledge, this first expansion wave of the house mouse seems to have been over a rather short geographical extension and achieved around 7800 BC.
2. Between the end of the 8th millennium and the 1st millennium BC there is no reliable documentation of the house mouse in Central and Western Europe, and the invasive process seems to have stopped or drastically slowed. The record in the Minoan period in Crete, however, suggests a slowing down rather than a complete cessation. Regardless, even the increase in the opportunities for passive transportation of commensal small vertebrates of the Bronze Age did not seem to have been decisive in the Mediterranean invasion by the house mouse. This is the main change with reference to the conclusions of Auffray *et al*. (1990), who claimed a successful colonization of Western Europe at least during the Early Bronze Age (2500 BC).
3. From the end of the first half of the last millennium BC, the house mouse showed mass colonization over a short time span and covering the entire Western Mediterranean Basin and north-west Europe.

It should be noted that the house mouse colonized Western Europe only slightly earlier than the black rat (*c.* 2nd century BC; Vigne & Valladas, 1996; Ervynck, 2002).

HOUSE MOUSE AND HUMANS: A PATTERN OF COEVOLUTION?

Why did colonization by house mice in the Western Mediterranean not occur until the Iron Age, when it would have been expected that the species would have benefited from ecological transfer and passive transportation during Neolithic migrations and, later, during Bronze Age maritime exchanges in the Eastern and Central Mediterranean sea? What prevented westward diffusion of the house mouse at those times?

Given that the Bronze Age, which was characterized by an increase in sea faring, is now under challenge as the earliest date for the western diffusion, it is no longer possible to put forward passive transportation via human boats as the only factor for successful colonization by house mice. According to the biological definition of commensalism, the house mouse relationship with humans should depend only on food supply and possible protection against climatic variations and predation, without either harm or benefit from the latter. In fact, the interaction between house mice and humans is more complex than a simple one-way relationship. House mice can become a pest for harvests when their population is uncontrolled and forms plagues (Newsome & Crowcroft, 1971; Singleton *et al.*, 2005, this issue), as well as for food storage by wasting and soiling with urine. Today, mice are not as dangerous as rats for the spread of epidemic diseases but remain a source of pathogenic agents. During the Neolithic, the epidemiological impact of house mice on humans and on domestic ungulates is unknown. Under the prevailing conditions, the house mouse may have not just been an opportunistic pest in its relationships with humans, but also a real parasite against which human societies had to adapt in order to protect their sources of subsistence. On the other hand, house mouse populations benefited from human cultural and economic evolution to colonize new environments and increase their range and population size. Consequently, commensalism of the house mouse may have evolved into parasitism of humans in unbalanced situations, such as those that generate mouse plagues. Therefore, this relationship between house mice and humans should be regarded as a potential co-evolutionary pattern.

Successful colonization in the house mouse reflects human cultural evolution because it depends on two main factors:

1. migrant flow related to qualitative and quantitative evolution in maritime traffic and exchanges;
2. the presence and the vacuity of commensal niches, which are closely linked to the level of anthropization of new environments and to the presence of possible commensal competitors. Tchernov (1984, 1991) has demonstrated, through the first sedentary settlements in the Natufian period, that commensalism is a consequence of both intensive human pressure on natural habitats and increases in plant usage leading to the creation of a new ecological niche available for anthropophilous species. This anthropization of the environment should have provided a decrease of predation and of interspecific competition. It should also have increased the food availability for mice and provided protection against meteorological variation and climatic change.

However, the fact that the house mouse did not follow the human Neolithic wave indicates that disconnections are possible between farmer societies and the house mouse, and suggests that the relationship also depends on other and more complicated factors. One of these may result from the progressive adaptation to the commensal niche. Indeed, it is possible that the Western Europe commensal niche, in wetter climatic environments, required adaptation slightly different from that which had allowed mice to become commensal in the more arid regions of the Near East (see Berry & Scriven, 2005, this issue). Even if it should have been favoured by the probable founding, on the colonization front, of numerous small pioneer populations subjected to rapid evolution, the adaptation to this new kind of commensal niche might have taken a few centuries or millennia. However, this evolutionary explanation must be first confronted by at least three other hypotheses: (i) a level of immigration flow, i.e. of sea traffic, that was too low; (ii) too little anthropization in Western areas that was too low compared with the large villages or towns of the Eastern Mediterranean; and (iii) competition with another anthropophilous species such as the wood mouse, which was also a good candidate for the commensal niche during the Neolithic.

House mouse migrant flow and sea traffic in the Mediterranean Sea

We have very little data regarding boats and sea traffic in the Mediterranean Basin before the Bronze Age. No Neolithic wrecks have ever been found. Boats in the Eastern Mediterranean are only known starting from the late Neolithic, as a result of Egyptian steles and Aegean frescoes. They were rather large boats with decks (Vigié, 1979; Pomey, 1997). In the Western Mediterranean, the only known Neolithic boats were wooden launches with a monoxyle keel (Italy, Fugazzola-Delpino, D'Eugenio & Pessina, 1993).

Finally, we only have indirect evidence of successful boat journeys during the Neolithic, through human and animal colonizations of the Mediterranean islands. All were reached by humans relatively easily as early as the beginning of the Holocene: Cyprus was visited by hunter-fisher-gatherers during the 10th millennium BC (Simmons, 1999), then colonized by Neolithic people at the end of the 9th millennium, and Corsica was settled by Mesolithic groups during the 9–8th millennia (Vigne, 1999).

The transfer of small mammals to the large Mediterranean islands provides more precise information. Plotting the dates for immigration of small mammals to the five large 'true' Mediterranean islands during the last five millennia BC, Vigne (1999) observed that immigration took place on all five islands mainly during the 5th and 4th millennia BC. This may be interpreted as the consequence of both the increase of sea faring during the last part of the Neolithic period and, at the same time, the appearance of boats with decks, in the shelter of which small mammals could hide more easily, significantly increasing their immigration flow. By contrast, our geometric morphometric analysis of molar shape in fossils from Cyprus compared with modern house mice has demonstrated that, in a period of two millennia following the arrival of the latter on the island at the end of the 9th millennium BC (Cucchi *et al*., 2002), the shape remained unchanged. This shape conservation has been interpreted in terms of intensive migrant flow by boats, preventing genetic and morphological drift (Cucchi, in press). These observations show, first, that sea faring existed for a long time before the Bronze Age and, second, that intensive interaction by sea faring occurred from 8200 BC between Cyprus and the close mainland.

For the 3rd and 2nd millennia BC, archaeological and historical sources indicate that the increase of exchanges and sea traffic was still mainly focused in the Eastern Mediterranean Basin (Rougé, 1975; Anon, 1979; Pomey, 1997). From the 3rd millennium, the Eastern basin is dominated by Aegean thalassocraty first centred on Cyclad archipelagos and then on Crete with the succession of Minoan and Mycenaean civilizations. During the 2nd millennium BC the Canaanite people living on the Syro-Palestinian coast (their most famous cities were Ugarit and Byblos) controlled trade routes connecting Egypt, Mesopotamia, the Hittite Empire, Cyprus, Crete and the lands beyond. Although archaeology has demonstrated that there were contacts between the Mycenaean world and the Tyrrhenian Sea, particularly with the discovery of Achaean artefacts in the Lipari Islands, maritime trade was mainly monopolized by exchanges between the Eastern Mediterranean civilizations. It was not until the first Phoenician (9–6th century BC) and then Greek (8–6th century BC) colonizations of Central and Western areas that the Mediterranean Sea became widely opened to trade in both directions.

Anthropization and urbanism: the gap between the Eastern and Western Mediterranean Basin

We have discussed above the antiquity of a sedentary way of life (10th millennium BC) and agriculture (9th millennium BC) in the Near East. However, the intensification of housing is the most important condition for the existence of the commensal niche. In the Near East, villages became rapidly larger from the 10th to the 8th millennium (see references in Guilaine, 2000b). Small villages are known as early as the 10th millennium Natufian. Large villages with more than 10–15 mud brick and stone houses and with collective buildings for cereal storage are documented as early as the 9th millennium PPNA Neolithic. Large villages of more than one hectare and with numerous houses, all built on the same plan, are known all through the 8th millennium BC. The first real cities are recorded from the 6th millennium BC in the Near East and not before the 3rd millennium BC in the Aegean area.

By contrast, in Western Europe, true villages did not appear before the middle of the 6th millennium BC at the earliest, and they were composed of fewer than ten wooden or stone dwellings. Large Neolithic villages did not exist in Western Europe, except in a few areas such as the south-east Italy (Pugglia). This situation did not change fundamentally during the Bronze Age. In the Western Mediterranean, urban development did not occur before the end of the last millennium BC, the first large conglomerations being the Etruscan small cities and the Celtic *oppida*.

The wood mouse (Apodemus sp.): a competitor for the commensal niche in Western Europe?

The last element we should take into account in understanding the chronological delay in the westward diffusion of house mice is the presence of potential autochthonous competitors in the commensal niche of Western Mediterranean areas. The most probable competitor is the wood mouse, comprising two species, *Apodemus sylvaticus* and *A. flavicollis*, the fossil teeth of which are indistinguishable using classical morphological methods. Currently, the genus *Apodemus* is found throughout Europe, except in northern Scandinavia and Finland, east to the Altai and in the Himalayan mountains. It is also found in parts of central and south-western Asia, the Himalayas, north-western Africa, the British Isles and nearby islands (Nowak, 1991). It has been present in Western Europe since the Pliocene (Chaline, 1972). During the Quaternary glacial phases, the European Mediterranean peninsulas played a role as refugia (Michaux *et al*., 2003). The earliest mention of fossils in northern Europe are dated to the Boreal period, so it is probable that the wood mouse colonized northern parts of Europe only at the beginning of the Holocene (Pascal *et al*., 2003: 313). In all the archaeological sites from the Central and Western Mediterranean, the wood mouse is dominant among the rodents before the invasion of the house mouse. Its presence is clearly documented in deposits from houses in Neolithic settlements in France (Vigne, 1997). It was one of the first anthropophilous wild species to be transferred to Corsica by boat during the Neolithic, long before house mice (Vigne, 1994a). This is evidence of commensalism of this species, confirmed by current observations (J.-C. Auffray, unpubl. data). Following Vigne (1997), we can say that the wood mouse might have occupied the commensal niche in Europe as soon as it was available, i.e. before the arrival of the house mouse.

In an environment poorly anthropized such as the Western Mediterranean Basin before the late Bronze Age, the house mouse would have been out-competed by the wood mouse (Berry, Cuthbert & Peters, 1982), the commensal populations of which could be regularly reinforced by native wild populations. In addition, house mice had no chance to compete with the autochthonous small mammals in the wild, away from the mild influence of the Mediterranean climate.

HOUSE MOUSE FOSSILS FROM THE CANARY ISLANDS

The Canary Islands are outside of the area considered in this paper but they are integral to the question of the spread of the house mouse westward. Indeed, subfossils of *Mus musculus* sp. have been described in small mammal collections from two volcanic tube in-fills in Fuerteventura. The first sample of house mouse remains comes from Cueva Villaverde and was located in a level underlying a horizon dated to 1730 ± 50 years BP (Carrascosa & Lopez-Martinez, 1988). Calibration of this ^{14}C date using CALIB REV4.4.2 (Stuiver & Reimer, 1993) provides the following range: AD 140–423 (2σ), which suggests an arrival of the house mouse on the island between the 2nd and the 5th centuries AD, i.e. during Roman times. This date is coherent with the rhythm of house mouse dispersal previously described for the Western Mediterranean.

More recently, in Cueva del Llano, mice remains determined as *Mus musculus* sp. from a level dated to 7000 years BP suggest that house mouse immigration might have taken place before the first human settlements (Castillo, Martin-Gonzalez & Coello, 2001). The calibration provides an immigration date between 6400 and 5300 BC. This very early occurrence, however, raises a number of questions.

If these prehistoric house mice from the Canary Islands really were derived from the mainland *Mus musculus* pool, it would mean that the house mouse dispersal followed an 'African route' in parallel to the Mediterranean one, and that the diffusion was faster in the former than in the latter, bringing the house mouse to eastern parts of Northern Africa around the 7th millennium BC at the latest. In contrast to the northern Mediterranean coastline, in this area, the house mouse would have followed the Neolithic progression. Unfortunately, this area is archaeologically poorly documented, but the few radiometric dates available allow us to at least consider the possibility of a 'neolithization' of North Africa at this early date. Fuerteventura is a volcanic island, which today lies more than 100 km from the mainland, and the earliest evidence for human arrival in the Canaries, from adjacent parts of Africa, has been dated to around 6th/5th centuries BC (Martín de Guzman, 1978; Onrubia Pintado, 1987). Given the geographical distance (which may not now be very different from that which existed around the 7th millennium BC) and the likely absence of any human passive transport (the house mouse appears to have always been dependant upon passive transport to colonize less distant islands such as Corsica or Cyprus), it seems most unlikely for the house mouse to have reached and settled Fuerteventura. Nevertheless, we can envisage that the exploration of the Canary Islands by Neolithic people, without real colonization, would have allowed the importation of house mice without leaving any material trace. House mice would then be the only evidence of their visit.

Consequently, there is much uncertainty regarding the nature of mice remains from level 9 in Cueva del Llano. Moreover, the method of interspecific determination is not described for this site. The only description of this subfossil house mouse is available for Cueva Villaverde. Carrascosa & Lopez-Martinez (1988) provided a complete morphological analysis of the taxa. Although this shares several characters with reference specimens of *Mus musculus* sp. (only two specimens from Gran Canaria) – mainly the trilobed anterior part of the lower molar – it also shares accessory cusps in the labial part with current *Mus spretus*. These accessory cusps have never been described for house mouse. Finally, numerous characters are peculiar, such as the zygomatic coefficient, which is, with the trilobed anterior part of the M_1, one of the most discriminatory parameters used to distinguish house mouse from outdoor species (Orsini *et al*., 1983). A survey of the current genetic and morphological diversity of mice in Fuerteventura should be carried out and then compared with subfossil material in order to establish the precise nature of mice from Fuerteventura. For the moment, the possibility that this mouse is actually an endemic species such as *Malpaisomys insularis* cannot be ruled out. The current house mouse, *Mus musculus domesticus*, would have been introduced later.

SYNTHESIS AND CONCLUSIONS

Zooarchaeological data show that the house mouse diffusion from the East to the West of the Mediterranean Basin took several millennia and thus followed complex dynamics. Because the house mouse cannot live on its own, especially under non-Mediterranean climates, but requires human commensalism, these dynamics must reflect cultural evolution of human societies. The development of a sedentary way of life and then farming, economic and cultural change allowed the house mouse to spread and colonize the Eastern Mediterranean basin. Contrary to what we could have expected, neither the western Neolithic diffusion nor the technical evolution of sea faring during the Bronze Age promoted the colonization of the Western Mediterranean before the Iron Age.

We propose to integrate historical and biological traits, using the source-sink concept (Dias, 1996), to explain this two-step diffusion separated by a gap of 5000 years. We suggest that a hierarchical diffusion (Hengeveld, 1989) to the West by means of jumps of a few individuals from Eastern population sources must have occurred as a result of human migrations through the Mediterranean Sea during the Neolithic dispersal and Aegean explorations. These new environments to which house mouse migrants had been transferred may have played the role of dispersal-sink for the more western dispersal process.

However, there was no more westerly colonization for several reasons, and these probably acted together. First, maritime exchanges were very limited between the Eastern and Western Mediterranean Basin until the beginning of the 1st millennium BC. Consequently, the migratory flow to the Western Basin should have been too weak to maintain stable pioneer populations for a long time. Secondly, among the different biotic and abiotic factors the migrants had to face during their spread, the problem of the ecological niches available is very important. There are striking differences between East and West in the size and activity of Neolithic villages, and also then of the protohistorical cities. Whereas the commensal niche was well represented and established over several millennia in the Levant, the niche was very poorly represented and less stable in Western Europe until the first large pre-Roman cities and Celtic *oppida* of the 1st millennium BC. Third, in Western Europe, the commensal niche was probably occupied by the wood mouse long before the house mouse arrived, and competition between the two species must have favoured the wood mouse until larger and more stable commensal environments developed, especially outside of the Mediterranean area.

Consequently, it is not necessary to put forward a long and progressive biological adaptation to the commensal niche by the house mouse, which was probably achieved as early as the late Natufian or early PPN in the Near East. A low immigration rate as well as a weakly settled and non-vacant commensal niche could explain the delay for the westward house mouse colonization.

During the last millennium BC, the increase of migrant flow as a result of more intensive trading in both East and West directions, as well as increasing human pressure on the environment, may have definitively favoured the house mouse adaptation to the western commensal niches. The house mouse could then overwhelm the wood mouse and succeed in colonizing Europe in its entirety.

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APPENDIX

Database of murids from circum-Mediterranean archaeological collections with house mouse presence/absence reliability after zooarchaeological evaluation of the data

Archaeological site	Country	Chronological period	Description	Dating	Small mammals collection	Sample size	*Apodemus.* sp.	Feral mouse	*Mus* sp.	*M. musculus* sp.	Taxonomic method	References	Reviewed by	House mouse presence/absence
1 Hayonim B/C	Israel	15000–12000 BC	cave	^{14}C mat. un.	WS?	?		X			Morphometric	Auffray *et al.* (1988)		Cons. as probable
2 L'Abeurador	France	13500–10000 BC	cave	^{14}C mat. un.	WS?	MNI = 1612	(mni = 74)				Morphometric	Mistrot (2001)		Cons. as certain
3 La grotte du Bois-Ragot	France	13500–10000 BC	cave	^{14}C mat. un.	WS?	MNI = 279	(mni = 16)				Morphometric	Marquet (1993)		Cons. as certain
4 La grotte du Rond du Barry	France	13500–10000 BC	cave	^{14}C mat. un.	WS?	MNI = 511	(mni = 26)			(mni = 1)	Morphometric	Marquet (1993)		Cons. as doubtful
5 Rochedane	France	13000–9500 BC	rock shelter	^{14}C mat. un.	?	MNI = 539	(mni = 35)			(mni = 2)	Morphometric	Chaline (1972)	Marquet (1993)	Cons. as doubtful
6 Espéluges	France	13000–11000 BC	rock shelter	Charcoal ^{14}C	WS < 2 mm	MNI = 153	(mni = 3)				?	Omnès *et al.* (1980)		Cons. as probable
7 Hayonim B	Israel	12000–10000 BC	cave	^{14}C mat. un.	?	MNI = 33		X		X	Morphometric	Auffray *et al.* (1988)		Cons. as certain
8 Akrotiri-Aetokremnos	Cyprus	10500 BC	rock shelter	Shell ^{14}C	WS?	'several'		X			Morphometric	Reese (1999)		Cons. as probable
9 Mureybet	Syria	10200–10000 BC	habitat's layer	^{14}C mat. un.	WS?	MNI = 256				(mni = 2)	Fourier analysis	A. Haydar, unpubl. data	T. Cucchi, unpubl. data	Cons. as certain
10 Netiv Hagdud	Israel	9500–8500 BC	habitat's layer	^{14}C mat. un.	?	NR = 301				(nr = 61)	Morphometric	Tchernov (1994)		Cons. as probable
11 Jerf el Ahmar	Syria	9500–8500 BC	habitat's layer	^{14}C mat. un.	WS?	MNI = 78				(mni = 1)	Fourier analysis	A. Haydar, unpubl. data	T. Cucchi, unpubl. data	Cons. as certain
12 Dja'de	Syria	9500–8500 BC	habitat's layer	^{14}C mat. un.	WS?	MNI = 63				(mni = 6)	Fourier analysis	A. Haydar, unpubl. data	T. Cucchi, unpubl. data	Cons. as certain
13 Mylouthkia	Cyprus	8200/7000 BC	well	Charcoal ^{14}C	WS < 2 mm	MNI = 35		(mni = 19)		(mni = 16)	Fourier analysis	Cucchi (2001), Cucchi *et al.* (2002)		Cons. as certain
14 Cafer Hüyük	Turkey	8000–7500 BC	habitat's layer	^{14}C mat. un.	DS	MNI = 38		(mni = 4)		(mni = 34)	Fourier analysis	T. Cucchi, unpubl. data		Cons. as certain
15 Cingle Vernell	Spain	7500 BC	Rock shelter	^{14}C mat. un.	WS < 2 mm	MNI = 54	(mni = 37)				Morphometric	Alcade Gurt (1986)		Cons. as probable
16 Monte Leone	France	7500–7000 BC	Rock shelter	^{14}C mat. un.	WS < 2 mm	MNI = 124					Morphometric	Vigne, Bailon & Cuisin (1997)		Cons. as certain
17 FontBregoua	France	7500–7000 BC	cave	^{14}C mat. un.	WS?	MNI = 2017	(mni = 1342)				Morphometric	Poitevin (1984), Poitevin, Bayle & Courtin (1990)	Bayle (1993)	Cons. as certain
18 Knossos	Greece	6600–5800 BC	?	Shell ^{14}C	DS	?			X		?	Jarman (1996)		Cons. as doubtful
19 Khirokitia	Cyprus	7th mill. BC	habitat's layer	Charcoal ^{14}C	WS?	MNI = 8				(mni = 8)	Fourier analysis	Davis (1989)	Cucchi (in press)	Cons. as certain
20 Cap Andreas Kastros	Cyprus	7th mill. BC	habitat's layer	no ^{14}C	WS?	MNI = 5				(mni = 5)	Fourier analysis	Helmer (1981)	Cucchi (in press)	Cons. as certain
21 Catal Hüyük	Turkey	6500–5500 BC	grave	^{14}C mat. un.	'good'	NRT = 837				X	Morphometric	Brothwell (1981)		Cons. as certain
22 Cova 120	Spain	6000–3000 BC	habitat (silo)	no ^{14}C	WS < 2 mm	MNI = 55	(mni = 49)				Morphometric	Alcade Gurt (1986)		Cons. as certain
23 Ermitons	Spain	6000–2000 BC	karst (layer)	no ^{14}C	WS < 2 mm	MNI = 11	(mni = 4)				Morphometric	Alcade Gurt (1986)		Cons. as probable
24 FontBregoua	France	6000–4700 BC	cave	^{14}C mat. un.	WS?	MNI = 569	(mni = 292)				Morphoscopic	Poitevin (1984), Poitevin *et al.* (1990)	Bayle (1993)	Cons. as certain
25 Château-neuf-les Martigues	France	6000–4700 BC	rock shelter	^{14}C	WS?	MNI = 202	(mni = 17)				Morphoscopic	Poitevin (1984), Poitevin *et al.* (1990)	Bayle (1993)	Cons. as certain
26 L'abri Jean-Cros	France	6000–4700 BC	rock shelter	no ^{14}C	?	MNI?	(mni = 1)				Morphoscopic	Poulain (1979)		Cons. as probable
27 Knossos	Greece	5700–4700 BC	?	Shell ^{14}C	DS	?			X		?	Jarman (1996)		Cons. as probable
28 Baume d'Oullen	France	5500–4000 BC	?	?	WS < 2 mm	MNI = 60	(mni = 20)				Morphometric	D. Helmer & J.-D. Vigne, unpubl. data		Cons. as certain
29 Grotte du Frare	Spain	5500–5000 BC	cave	^{14}C mat. un.	WS < 2 mm	MNI = 99	(mni = 37)				Morphometric	Alcade Gurt (1986)		Cons. as certain
30 Font-Juvenal	France	5500–5000 BC	rock shelter	^{14}C mat. un.	WS?	MNI = 531	(mni = 216)			(mni = 9)	Morphoscopic	Marquet (1987, 1993)	Bayle (1993)	Cons. as doubtful

33 Monte Leone	France	5000–4500 BC	rock shelter	Charcoal ^{14}C	WS < 2 mm	MNI = 90				Morphometric	Vigne *et al.* (1997)		Cons. as certain
34 Place St-Lambert	Belgium	5th mill. BC	pit	no ^{14}C	WS?	*N* = 48	(nr = 9)		(nr = 1)	?	Cordy & Stassart (1982)		Cons. as doubtful
35 Font-Juvenal	France	4700–3200 BC	rock shelter	^{14}C mat. un.	WS?	MNI = 234	(mni = 112)		(mni = 6)	Morphoscopic	Marquet (1987); 1993	Bayle (1993)	Cons. as doubtful
36 Villeneuve-Tolosane	France	4500 BC	?	?	WS?	NR = 101				Morphometric	A. Tresset, unpubl. data		Cons. as probable
37 Corbeddu-cave	Italy	4300 BC	cave	Charcoal ^{14}C	?	?	('very rare')			?	Sondaar *et al.* (1984)		Cons. as probable
38 Harsova Tell	Romania	5/4th mill. BC	?	?	?	?				Morphoscopic	T. Cucchi, unpubl. data		Cons. as doubtful
39 Grotta rifugio	Italy	3500 BC	cave	?	?	MNI = 192	(mni = 7)			?	Agosti (1980)		Cons. as probable
40 Su Guanu	Italy	3500 BC	cave	^{14}C mat. un.	WS?	NR = 1429	(nr = 954)		(*n* = 92)	?	Sanges & Alcover (1980)		Cons. as doubtful
41 Araguinna-Sennola	France	3000 BC	rock shelter	^{14}C mat. un.	DS		X			Morphometric	Vigne (1988)		Cons. as probable
42 Grotte du Frare	Spain	3000–2500 BC	cave	^{14}C mat. un.	WS < 2 mm	MNI = 58	(mni = 19)			Morphometric	Alcade Gurt (1986)		Cons. as certain
43 Clairvaux la Motte	France	2800–2700 BC	habitat	Charcoal ^{14}C	WS < 2 mm	MNI = 8	(nr = 14)			Morphometric	Vigne (1997)		Cons. as probable
44 Grotte du Frare aux Magnins	Spain	2500–2400 BC	cave	^{14}C mat. un.	WS < 2 mm	MNI = 17	(mni = 8)			Morphometric	Alcade Gurt (1986)		Cons. as certain
45 Cova 120	Spain	2500–2000 BC	grave	no ^{14}C	WS < 2 mm	MNI = 114	(mni = 70)		(mni = 2)	Morphometric	Alcade Gurt (1986)		Cons. as doubtful
46 Nola	Italy	1800 BC	enclosure	^{14}C mat. un.	?	MNI = 13	(mni = 3)			Morphoscopic	T. Cucchi, unpubl. data		Cons. as probable
47 Kommos 1	Greece	1700–1400 BC	town (all layers)	no ^{14}C	WS < 2 mm	'big'	X		'most abundant'	Morphometric	Payne (1995)		Cons. as certain
48 Buhen	Egypt	1700 BC	?	?	?	'not saved'			X	?	Brothwell (1981)		Cons. as doubtful
49 Mourre de la Barque	France	1400–1000 BC	cave	Shell ^{14}C	WS < 2 mm	?	X			Morphometric	Renault *et al.* (1997)		Cons. as probable
50 Uluburun	Turkey	1300 BC	shipwreck	no ^{14}C	?	?			(mni = 1)	Morphoscopic	T. Cucchi, unpubl. data		Cons. as certain
51 Kommos 1	Greece	1000 BC	town (all layers)	no ^{14}C	WS < 2 mm	'big'			'most abundant'	Morphometric	Payne (1995)		Cons. as certain
52 Cova 120	Spain	1000 BC	grave	^{14}C mat. un.	WS < 2 mm	MNI = 31	(mni = 18)		(mni = 6)	Morphometric	Alcade Gurt (1986)		Cons. as probable
53 Nichoria	Greece	850–750 BC	Pithos	Shell ^{14}C	WS?	MNI = 167	(mni = 100)		(mni = 20)	Morphoscopic	Sloan & Duncan (1978)		Cons. as probable
54 Monte di Tuda	France	9–5th c. BC	cave porch	Bone ^{14}C	WS < 2 mm	MNI = 1633	X		X	Morphometric	Vigne & Valladas (1996)		Cons. as certain
55 Torralba d'en Salort	Spain	9–4th c. BC	habitat	Charcoal ^{14}C	?	MNI = 2124	(mni = 454)		(mni = 1106)	?	Sanders & Reumer (1984)		Cons. as probable
56 El Soto de Medinilla	Spain	6–3rd c. BC	habitat	?	WS?	MNI = ?			(mni = 1)	Morphometric	Muniz *et al.* (1995)		Cons. as probable
57 La Mota	Spain	6–3rd c. BC	habitat	?	WS?	MNI = ?			(mni = 6)	Morphometric	Muniz *et al.* (1995)		Cons. as probable
58 Torre den Gaumés	Spain	5th c. BC	?	?	DS	?		X	X	Morphoscopic	T. Cucchi, unpubl. data		Cons. as doubtful
59 S'illot	Spain	400–150 c. BC	?	?	?	?	X		X	?	Uerpmann (1971)		Cons. as probable
60 Gaillon-le-bas	France	5–4th c. BC	pit	?	WS < 2 mm	NR = 24	X		X	Morphoscopic	Vigne (1994b)		Cons. as probable
61 Acy-Romance	France	400–100 c. BC	habitat (silo)	^{14}C mat. un.	WS > 2 mm	MNI = 109	(mni = 15)		(mni = 13)	Morphometric	Vigne (1992)	Lesur (1999)	Cons. as certain
62 Lattes	France	4/3rd c. BC	habitat	^{14}C mat. un.	DS	MNI = 119	(nr = 3)		(nr = 72)	Morphoscopic	Poitevin & Senegas (1999)	Pomes (2002)	Cons. as certain
63 Monte di Tuda	France	4/3rd c. BC	cave porch	Bone ^{14}C	WS < 2 mm	MNI = 883	X		X	Morphometric	Vigne & Valladas (1996)		Cons. as certain
64 Canet-en-Rousillon	France	50–60 AD	habitat (silo)	^{14}C mat. un.	WS?	MNI = 58			(mni = 20)	Morphometric	C. Callou & J.-D. Vigne, unpubl. data		Cons. as certain
65 Sierentz-Land strasse	France	1–3rd c. AD	pits	?	WS < 2 mm	MNI = 56	(mni = 1)		(mni = 6)	Morphometric	Vigne, Bailon & Vallet (1994)		Cons. as certain

Refer to Figure 1A, B for site locations. ^{14}C mat.un., ^{14}C dating with material unrecorded; DS, dry sieving; WS?, wet sieving with mesh size unknown, WS > 2 mm, wet sieving with mesh size larger than 2 mm; WS < 2 mm, wet sieving with mesh size smaller than 2 mm; MNI, minimal number of individuals; NR, number of remains; NRT, number of remains in total, Cons., considered.