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## **INSULAR SMALL MAMMALS FROM QUATERNARY DEPOSITS OF SICILY AND FLORES**

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# I. Introduction

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*“I do not know what I may appear to the world, but to myself I seem to have been only like a boy playing on the sea-shore, and diverting myself in now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me.”*

*Isaac Newton*

The aim of this PhD research is to detect the effect of insularity on fossil populations; in particular, to carry out the study of small mammal assemblages from Quaternary deposits on islands in order to give a contribution to the reconstruction of faunal successions in Sicily (Italy) and Flores (Indonesia), and to test the effects of evolutionary processes in insular environments.

The research on this field began to be systematic and thorough in the ‘60s; at first it was mainly a zoological field of investigation, with extensive description of biogeographic rules formulated on extant populations, from which zoologists and biogeographers, on the basis of the actual configuration of faunal communities, define evolution trends and patterns. Nevertheless, it was clear soon that these laws should have had an impact on extinct or fossil populations, and traces of the effects of isolation and endemism began to be studied on paleontological material. Whilst, working on living animals and populations, the most useful sample of study can be freely chosen among all the extant ones, often in palaeontology the sample is limited, random and its capability unpredictable. The paleontological record is by definition discontinuous, both in space and time, and palaeontologists have to work keeping in mind that the sample can be affected by many and different kind of biases, much more than in zoology. Furthermore, the sample is often found circumstantially when something else is the actual goal of the investigation or vertebrates remains and evolutionary trends were not the main goal. Sometimes fossil material can disclose its potential only after it has been found.

My research on the effects of insularity on small mammals’ palaeo-communities start from the material recovered for different purposes, mainly for archaeological and anthropological researches. The fossils, on which I am going to focus, come from three sites in Sicily (Italy) and one site on Flores (Indonesia). Isolidda 3 cave (San Vito lo Capo, Trapani, Sicily, Italy) is a late Middle Pleistocene – Upper Pleistocene site, investigated by Prof. Fabio Martini and his team of the University of Firenze in order to find ancient traces of human colonization in Sicily. This site turned to be sterile of human artefacts, but rich in vertebrate remains (among which dwarf elephants and giant dormice). Cala Mancina cave (San Vito lo Capo, Trapani, Sicily, Italy) and Oriente cave (Favignana Island, Trapani, Sicily, Italy) are Upper Pleistocene – Holocene caves, rich in stone artefacts and burials, and provided also many faunal remains of slightly endemic or cosmopolitan species. Liang Bua cave (Flores, Indonesia) has a long story of archaeological investigations, carried on by different international teams (headed by Dr. Verhoeven in the ‘50s – Utrecht, The Netherlands; Prof. Soejono in the ‘80s and ‘90s; Dr. Westaway in the last ten years – Canberra University, Australia). The striking discovery of a dwarf Pleistocene hominid in 2003 increased suddenly and hugely its popularity. The study of faunal and anthropological remains of this cave had been already addressed in the last century, but the new fame speeded up the interest in the study of all the aspects involving “The Hobbit”, *Homo floresiensis*. The excavations are still going on and the amount of small mammals remains recovered is outstanding.

The main goals of this thesis are:

1. To describe the small mammal succession of Isolidda 3, Cala Mancina, Oriente caves → which animals dwelled the area in Pleistocene/Holocene?
2. To describe (morphologically and quantitatively) the endemic species recovered → how did they look like? What did they differ in from the other species?
3. To detect the evolutionary story of the rodents considered, in particular the timing of the arrival, the traces of evolutionary processes (size increase/reduction) and timing of extinction → when did they come? How did they change? When and why did they get extinct?
4. In archaeological sites, to detect the relationship between man and mice → how did they live with man? Which was the relationship man-rodent? Did man arrival affect the faunal community?
5. To valuate the difference in faunal communities between continental islands (Sicily) and oceanic islands (Flores) → how does the insularity affect faunal communities on islands?

# Background

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*“A model is not simply a way to generate a single prediction, or set of predictions. Rather, it is a deliberately oversimplified representation of how some system should function if only a few major factors are at work. (...) Now, **why** do we **not** see the predicted result? It is the deviation from the simplified prediction, and the reasons for the deviation, that are of interest, not the oversimplified prediction in itself”*

*Heaney, 2000*

Why insular mammals have to be considered separately from continental ones?

The peculiarity of insular faunas is that they have undergone evolution under isolation. Isolated faunas have been the first ones to be studied by Darwin and Wallace and they have been crucial in the intuition and definition of the evolutionary theory. Darwin in the Galapagos Archipelago and Wallace in the Malay Archipelago were the first ones who noticed the exceptional biodiversity of these areas, the differences among species within the same taxonomical group in different islands and related these aspects to the independent evolution on each island. It was the second half of the 19<sup>th</sup> century, and the evolutionary theory was growing. Since then, many studies about the evolutionary theory were carried on, but only in 1967 a general and thorough model for the insular biogeography was published, “The theory of island biogeography” by MacArthur and Wilson. In this monograph, anticipated in 1963 by a synthetic paper (MacArthur and Wilson, 1963), they described all the factors that could affect the faunal structure on islands (characterized by low biodiversity and endemic species) and created a model, named “The Equilibrium Theory”. The main paradigm that was proposed in this monograph concerns the variation in species richness at the scale of an archipelago during ecological time: the number of species on island is related to episodes of immigration and extinction that in turn are related to the area of the island and its degree of isolation (expressed by the distance from the mainland or close islands). In other words, the number of species on islands is directly proportional to the area of an island and inverse proportional to the distance. It is called “The Equilibrium Theory” because the equilibrium between immigration and extinction is supposed. The main limits of this model are the assumption that: systems are in **equilibrium**; evolution is unimportant for explaining the species richness (**stasis**); species are equivalent with respect to their abilities to colonize and maintain populations on islands and inter-specific interactions are negligible (**species-neutral**); different islands within an archipelago have equal or comparable habitats and immigration filters (Lomolino, 2000a).

Because of this, in the last forty years many reviews, integrations and critics to the theory have been carried out. At the moment, there is agreement on the need of a new more comprehensive and general model, but a conclusive solution has not been found, yet.

According to Lomolino and Brown (2009), a new integrative theory of island biogeography should be: multi-scale; species- and process-based; inclusive of system feedback. Waiting for a new model to be developed, in the study of fossil assemblages it is good to keep in mind the eventual influence of some factors on the species richness that are emerged from forty years of island biogeography studies and, on the other hand, look for a confirmation of these hypotheses in the faunal record.

Firstly, the degree of isolation and the size of island are the first factors to be studied. According to the Equilibrium Theory, considering immigration and extinction the main forces in the determination of species-richness, area and distance from the mainland/neighbour islands affect the species-richness: larger islands and islands closer to the mainland have greater species richness at equilibrium. That is, in far and small islands biodiversity is supposed to be lower.

According to Heaney (2000), in addition to immigration and extinction, another important factor has to be taken into account: phylogenesis, which takes place on the same time-scale as colonization and extinction and can significantly increase the species-number. In fact, in isolated archipelagos, species richness is not always very low, because they support many endemic species and even endemic clades. Extinction highly impacts the fauna soon after the isolation from the mainland, but, the longer the isolation is, the higher is the number of speciation events that occur. Furthermore, colonization events are rare on remote islands, thus species-richness is mainly attributable to phylogenetic diversification. Consequently, not only area and distance are important, but also the length (in time) of the isolation from the mainland/neighbour islands.

Fox and Fox (2000) consider four more factors implied in the variation of species-richness. The habitat diversity contributes highly on variance in mammal species diversity, more than area (53.8% versus 41.8%) and these two factors are strictly related, so that habitat diversity increases with area. Furthermore, habitat disturbance (i.e. anthropic perturbation), species interaction (competition between species) and guild assembly rules (distribution of species between functional groups) are other factors that influence the number of species.

Colonization can be affected by many different factors: the location of oceanic currents, species vagility (Lomolino 2005) and serendipity (the impact of chance arrivals).

Finally, man can impact species richness by the introduction of alloctone species and its activity (that create disturbance).

To put together all these factors in a single model is not only challenging, but maybe impossible, considering also that many of these factors are correlated and stochasticity could play an important role in the achievement of colonization events.

The effects of insularity on mammals and the detection of its effects in fossil assemblages have been thoroughly investigated by Sondaar (1977). This paper represents a milestone in the studies about endemic fossil mammals from islands. Focusing on fossil assemblages from smaller oceanic islands (Mediterranean islands, Japanese archipelago, Philippines and Indonesian



archipelago), he analysed: the ways an island can be reached by; the effects of insularism on mammals bones; the implications for the systematic of endemic species; and the changes in selection mechanisms and evolution rates in insular species.

About the presence of mammals on islands, beyond the dispersal model, there is also the “Vicariance theory” (Wiley, 1988). According to Sondaar and the dispersalists, an island can be reached by natural rafts, swimming or drifting by sweepstakes routes. He thought that the landbridge concept, that implies the formation of a landbridge that allows animals to cross water barriers, is unlikely in most cases, because it would be necessary to imply big tectonic changes. Beyond these ways, the vicariance model, insularisms on islands are the consequence of the rise of barriers within the island and the mainland, which caused the isolation and speciation (Wiley, 1988).

The overseas dispersal implies a peculiar structure in mammal community, since not all the species have the same chances to disperse and cross sea-barriers; according to Sondaar, the presence of an “elephant-deer” fauna (that is common to Mediterranean and Indonesian islands) can be symptomatic of an overseas dispersal event by sweepstakes routes.

The size change in insular mammals, also known as “the island rule” (Foster, 1963; van Valen, 1973) was reviewed on fossil mammals by Sondaar (1977), who enounces the causes that drive to size reduction in large mammals and the size increase in small ones. Size change has been one of the major topics debated in the next 35 years (Case, 1978; Heaney, 1978; Lomolino, 2005), and systematic studies brought to two opposite conclusions: Lomolino (2005) assesses the generality of the island rule, while Meiri et al. (2008) wonder if the island rule is “made to be broken”, since in their analysis size variation seems to be a clade-specific response to insularity instead of size related.

Studies about morphological adaptations to insular conditions have also been investigated thoroughly; nevertheless, since in this thesis I am going to focus exclusively on dental remains, I will not take them into account.

Two important points raised by Sondaar (1977) concern the variation and the phylogenesis of insular forms. He detected great size variation that exceeds the one recorded in mainland forms and he hypothesizes that maybe different species evolved from the same ancestors are present and it is impossible to recognize them in the fossil remains. Furthermore in islands, evolutionary dynamics are different, with higher evolutionary rates, high degree of adaptation and plasticity and many episodes of parallelism. Consequently, classical parameters used in the identification of continental forms will often not be useful in the classification of island ones.

The presence or absence of these features in the fossil assemblages investigated, will tell something more about the evolutionary dynamics on Sicily and Flores and something more about the faunal successions and history of these two islands.



# Summary

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The thesis is structured in three main parts.

Part 1 deals with faunal successions in Sicily. The material investigated comes from three different caves: Isolidda 3, Cala Mancina and Oriente (CHAPTER II). Since this material has already been partially studied in my Master thesis, I will not deal with the general faunal association, but I will focus on two particular taxa whose systematic is still problematic.

*Microtus (Terricola)* nova species records the first occurrence of voles in Quaternary deposits of Sicily; I will provide a morphological description of dental remains and in a joint work with the University of Palermo I will try to reconstruct the phylogeny of this vole and its implication on Sicilian palaeo-biogeography (CHAPTER III).

The study of Sicilian *Crocidura* has always been challenging, both in recent that in fossil records, since the presence of an extinct species *Crocidura esuae* and the recent species *Crocidura sicula* are still widely debated. I will describe and determinate the fossil material (CHAPTER IV).

Part 2 will deal with the analysis of Liang Bua small mammal assemblage. After a brief introduction on Flores, vertebrate successions on the island and the Liang Bua cave description (CHAPTER V), murids of different size will be considered separately: small (CHAPTER VI), medium (CHAPTER VII) and large (CHAPTER VIII) size murids. Finally, general considerations on the small mammal association will be made (CHAPTER IX).

Part 3 (CHAPTER X) represents the conclusive part of the thesis; I will compare the Sicilian assemblages with the Liang Bua one, in order to see the impact on the faunal fossil association of completely different insular conditions (Sicily, a continental island very close to the mainland; Flores, an oceanic island surrounded by islands).



# PART 1: SICILY

## II. Quaternary faunal successions in Sicily

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Faunal successions in Sicily are arranged in biochrones named “Faunal Complexes” (FC).

Early Miocene is represented by a single find, a *Gomphotherium* molar found in marine sediments from Burgio locality (Trapani); a scarcely diversified Late Miocene fauna from Gravitelli (Kotsakis, 1986; Rook et al., 2006) has been found. Since Sicily was not an island at that time, the faunal association has all the features of a continental fauna. In fact, Sicily as an insular system is a young geographical entity; till Early-Middle Pleistocene it was not a stable geological entity, because of the extensive tectonic activity from the Early Pleistocene, which led to the creation of deep marine basins. Only at the end of Early Pleistocene Sicily became a true island.

The oldest Faunal Complex (FC) is **Monte-Pellegrino FC** (Bonfiglio et al., 2002), which derives its name from the area near Palermo, where faunal remains referable to this old complex have been retrieved in three outcrops. This complex is dated to Early Pleistocene. The following species are documented (Bonfiglio et al., 2002):

- *Pannonictis arzilla*
- *Asoriculus burgioi*
- *Apodemus maximus*
- *Leithia* sp.
- *Maltamys* cf. *gollcheri*
- *Pellegrinia panormensis*
- *Hypolagus* sp.

Very few faunal elements can be confidently traced back to their continental ancestors in regard to the two oldest biochrons. According to Masini and Sarà (1998), the Monte Pellegrino FC has a complex origin and taxa dispersed along different routes (European and African origin) in different time slices, and the dormice possibly derive *in situ* from older and unknown population phases. Two taxa have a clear European affinity (*Hypolagus* and *Pannonictis*) and suggest an eventual relation with the Late Villafranchian Faunal Units of the Italian peninsula (Masini and Sala, 2007). These peculiar populations might have formed by successive dispersal events during a long time span, and were in existence on the island during a time interval that roughly encompasses part of the Late Villafranchian and likely the early Galerian.

During the late Middle Pleistocene, Sicily was temporarily connected with southern Calabria through filtering barriers of decreasing intensity (Bonfiglio et al., 2008). The next faunal complex is the *Elephas falconeri* FC, whose beginning is assumed at about 0.9 – 0.8 Ma (ca MIS 22). This estimated age is based on stratigraphic relationships among vertebrate deposits, marine deposits and local successions of marine terraces (correlated with the MIS curve) (Di Maggio et al., 1999; Bonfiglio et al., 2003). The Aminoacid Racemisation (AAR) dating of some fossils of “*Elephas*” *falconeri* yielded an age of  $455 \pm 90$  ka (Belluomini and Bada, 1985). The stratigraphic gap between the first documentations of this Faunal Complex and Monte Pellegrino FC, do not allow a precise evaluation of the dispersal timing.

The taxa included in *Elephas falconeri* FC (Bonfiglio et al., 2002) are:

- *Vulpes* sp.
- *Lutra trinacriae*
- *Elephas falconeri*
- *Crocidura esuae*
- *Leithia cartei*
- *Leithia melitensis*
- *Maltamys gollcheri*

The “*E. falconeri*” FC is renewed respect to the Monte Pellegrino FC, with the exception of the dormice *Maltamys gollcheri*, which likely represents a descendant of the dormice of the preceding FC. No clear correlation with the fauna from the mainland can be done based on faunal content since this FC is characterized by a very low biodiversity and by high degree of endemism. Among endemic species, *Leithia* (giant dormouse) has been always considered a distant relative of *Eliomys* (a genus present thorough the Neogene and Quaternary in Europe). The affinities of *Crocidura esuae* are not clear, yet; the genus *Crocidura* is widespread in Africa and is present in the Italian peninsula since at least the Gelasian. Even the affinities of the very dwarf elephant are still unclear. If, as suggested by Ferretti (2008), it belongs to genus *Paleoloxodon* and if its dispersal derives from the Italian peninsula, *P. antiquus* is its possible ancestor and thus the appearance of this species cannot be much older than the Brunhes-Matuyama boundary.

The relations among vertebrate deposits, marine coastal deposits, marine terraces and the AAR dating (Di Maggio et al. 1999; Bonfiglio et al., 2003) indicate that this FC was already in existence at about 0.5 Ma, and its origin is not well defined. It doesn't show any trace of the fast and deep faunal dynamics that affect the mammalian population on the mainland, due to the very strong geographic isolation of the “proto” Sicily at that time.

With the transition from the *E. falconeri* to the following *Elephas mnaidriensis* FC, Sicily passed from the condition of an “oceanic like island”, similar to Sardinia and characterised by severe barriers to dispersals, to that of a “continental like island”, a land that experienced frequent faunal exchanges with the mainland and that became a part of the mainland when emerged corridors were, temporarily, in existence.

According to Bonfiglio et al. (2002), the characteristic taxa of this faunal complex are:

- *Panthera leo*
- *Crocota crocota* cf. *spelaea*
- *Canis lupus*

- *Lutra trinacriae*
- *Ursus cf. arctos*
- *Elephas mnaidriensis*
- *Sus scrofa*
- *Hippopotamus pentlandi*
- *Cervus elaphus siciliae*
- *Dama carburangelensis*
- *Bos primigenius siciliae*
- *Bison priscus siciliae*
- *Erinaceus europaeus*
- *Crocidura aff. esuae*
- *Leithia cf. melitensis*
- *Maltamys cf. wiendincitensis*

The dating of the beginning of the “*Elephas*” *mnaidriensis* (= *Palaeoloxodon mnaidriensis*) FC is somewhat problematic, as well.

AAR dating by Bada et al. (1991) yielded an age of  $200 \pm 40$  ka for mammal remains belonging to this FC. ESR dating by Rhodes (1996) at Contrada Fusco yielded ages of  $146,8 \pm 28,7$  ka (L.U. method) and  $88,2 \pm 19,5$  ka (E.U. method). The occurrence of a marine deposit dated to the Tyrrhenian (MIS 5e) superposed to continental layers containing the mammals, however, indicates that the age of the Contrada Fusco fossil assemblage is older than 125 ka. The stratigraphic correlations among vertebrate deposits, marine deposits and marine terraces show that the taxa here documented were well established on the island before the Tyrrhenian (0.125 Ma) (Di Maggio, 1999; Bonfiglio et al., 2003). The occurrence of *Maltamys* and *Leithia*, associated to *Hippopotamus pentlandi* in the lower deposits of Site K22 (San Vito Lo Capo, Trapani) at the top of a marine deposit possibly correlated with MIS 11, also suggests that the beginning of this FC could be older than MIS 8.

The “*Elephas*” *mnaidriensis* FC marks a deep faunal renewal in the large mammal community. All the taxa which dispersed to the island to form this faunal complex came from the Italian peninsula: the endemic fallow deer *Dama carburangelensis*; *Bison priscus siciliae*, a steppe wisent reduced in size; *Cervus elaphus siciliae*, a moderately dwarfed red deer; *Hippopotamus pentlandi*.

The faunas referred to this faunal complex include several carnivores, among which top predators like the cave lion and the cave spotted hyena. The occurrence of a community of predators and the relatively low degree of endemic modification of the ungulates – most of them are reduced in size but not at such an extent as observed in other Mediterranean islands - indicate by one side that the faunal exchanges with the continental peninsula were easier, and by the other that the surface of the island was large enough to sustain a well developed mammalian trophic chain for long time spans. The latter consideration is supported by paleogeographical reconstructions showing that, during glacial marine low stands, the island was decidedly larger than now owing to the emerged continental platforms, particularly at the western and south-eastern corners (Malta island included). Fossil evidences do not allow assessing whether the faunal elements of this complex dispersed on the island with a single wave, or if the arrivals are more scattered in time.

The next faunal complex, **San Teodoro-Contrada Pianetti FC**, is dated to the Last Glacial Maximum; a preliminary radiometric  $^{230}\text{Th}/^{234}\text{U}$  dating carried on a speleothem at the top of a

fossiliferous level containing mammals of this FC in the San Teodoro cave yielded an age of 32.0 ± 4 ka (Bonfiglio et al., 2008). Nevertheless, a tentative age of 70 ka (MIS4) is proposed for the beginning of this Faunal Complex (Bonfiglio et al., 2003). It represents an important faunal renewal that regards particularly small mammals. This is the species list (Bonfiglio et al., 2002):

- *Crocuta crocuta* cf. *spelaea*
- *Canis* cf. *lupus*
- *Vulpes vulpes*
- *Ursus* cf. *arctos*
- *Elephas mnaidriensis*
- *Sus scrofa*
- *Equus hydruntinus*
- *Cervus elaphus siciliae*
- *Bos primigenius siciliae*
- *Erinacues* cf. *europaeus*
- *Crocidura* cf. *sicula*
- *Apodemus* cf. *silvaticus*
- *Microtus (Terricola)* ex gr. *savii*

Whilst endemic small mammals are extinct and replaced by taxa from the mainland (*Microtus (Terricola)*, *Apodemus* cf. *silvaticus*, *Crocidura* cf. *sicula*, etc.), this FC includes several large mammals that were present in the previous faunal complex. The dispersal of a fossorial small mammal from the continent - *Microtus (Terricola)* ex. gr. *savii* - suggests that a sort of land bridge was in existence. This faunal composition also opens the intriguing question whether the same taxon from the mainland might have entered the island more than once, giving rise to analogous endemics in successive time slices. This possibility cannot be ruled out especially for most widespread ruminants, like the red deer and the auroch.

The dispersals that gave origin to the following **Castello FC** most likely took place during the Last Glacial Maximum (MIS 2) dated at about 24-20 ka. However, radiometric <sup>14</sup>C dating on Epigravettian levels insist on 14.0 – 11.0 ka (not calibrated; Martini, 1997). The faunal association is the following (Bonfiglio et al., 2002):

- *Canis lupus*
- *Vulpes vulpes*
- *Equus caballus*
- *Equus hydruntinus*
- *Sus scrofa*
- *Cervus elaphus*
- *Bos primigenius*
- *Erinaceus europaeus*
- *Crocidura* cf. *sicula*
- *Microtus (Terricola)* ex gr. *savii*
- *Apodemus* sp.
- *Lepus europaeus* (recte *L. corsicanus*)

The Castello Faunal Complex represents the mammalian population of the island in the last part of the Pleniglacial until the Holocene. Endemic taxa are extinct, as well as large predators, the fauna



from Sicily looks like a less diversified version of the coeval fauna from the peninsula. A consistent connection with a land corridor likely gave origin to these faunas. Nevertheless, among rodents, species of *Microtus* (*M. arvalis* and *M. agrestis*), *Chionomys nivalis* and *Myodes glareolus* are absent. The water vole *Arvicola amphibius*, as well as glirids (*Glis*, *Eliomys*, *Muscardinus*), are documented only in the Holocene faunas. All these “absences” can be explained or by some peculiar features of the corridor connecting the island to southern Calabria (i.e. lagoon and wet terrains), or to the refuge role played by the Tyrrhenian side of the peninsula during the stadial phases of the last glacial cycles.

In the **Holocene**, we assist to the establishment of a faunal association that is very similar to the mainland one:

- *Canis cf. lupus*
- *Vulpes vulpes*
- *Felis silvestris*
- *Martes* sp.
- *Mustela cf. nivalis*
- *Ursus* sp.
- *Monachus monachus*
- *Sus scrofa*
- *Cervus* sp.
- *Bos primigenius*
- *Erinaceus europaeus*
- *Crocidura* sp.
- *Microtus (Terricola) cf. savii*
- *Apodemus* sp.
- *Arvicola amphibus*
- *Mioxus glis*

Recent arrivals could also be related to the human presence on the island since the Last Glacial Maximum (since San Teodoro-Pianetti FC). Accidentally or intentionally, man can transport animals during his moving. Ancient human documentations are not clear, yet, and the first sure documentations of human presence in Sicily date only to Late Glacial, in association with Epigravettian lithic industries.

In conclusion, dealing with Sicilian faunal successions, it seems that climate affects faunal turnovers mainly (if not exclusively) as a promoter of dispersals from the mainland. The fact that, in the passage from one faunal complex to the other, there is not a complete renewal of the faunal association, but many species last for long, make a sweepstake route more likely in many cases (above all in ancient complexes, when biodiversity is low).

The palaeontological/archaeological deposits investigated by the University of Firenze in 2004 yielded many vertebrate remains. Among them, small mammals have been useful to better understand the faunal successions in Sicily. Part of the material has been studied in my Master thesis; in that occasion I described the small mammal association, focused on giant dormice from Isolidda 3 and began the morphometric study of *Crocidura* sp. and *Microtus (Terricola)* sp. In the following paragraph I will make a brief reference to the archeological and environmental setting,

necessary for the understanding of the next chapters about the systematic study of two taxa recovered in these deposits.

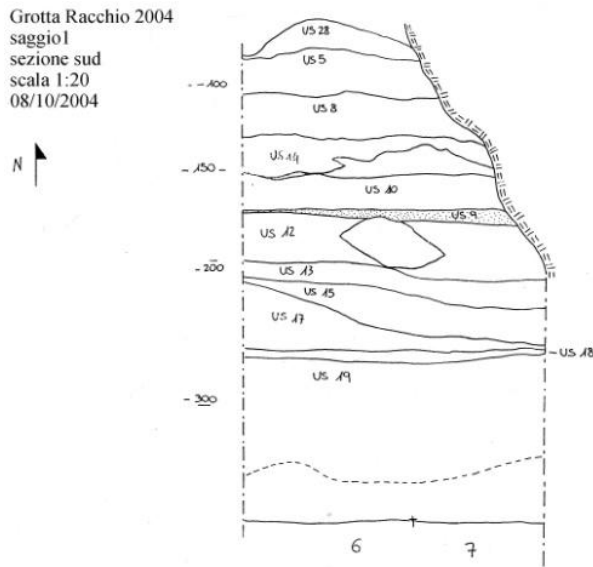


Figure II-1: : field stratigraphy of Isolidda 3 cave

Isolidda group is made up of five cavities, opening on the oriental slope of the San Vito Lo Capo promontory (Macari, Trapani, Sicily). All the caves are located at 60-70m above sea level and are residuals of wider cavities digged by the sea. Isolidda 3 (according to Mannino, 1962) is made up of 2 superposed cavities; the upper one is filled with marine deposit, cemented at its base; the lower is wide and has a high vault. In the latter there is a continental deposit with faunal remains that will be taken into account in this thesis. A trench of about 4m<sup>2</sup> has been excavated and five different stratigraphic horizons yielded small faunal remains (Figure II-1):

1. US12: red with clay matrix
  2. US 13: similar to US12, but orange-red. Calcareous skeleton.
  3. US15: silty-clay, dark red with manganese.
  4. US17: silty-clay, red with white laminations. High sloping
  5. US19: red with sandy matrix.
- Between US 17 and US15 there is an erosion surface (US16); between US17 and US19 there is a cemented layer (US18).

Despite the intense research, no anthropic remains have been recovered (neither bones nor artifacts). Large mammals were few, but important. In the basal stratigraphic unit (US19) there are well preserved remains of *Elephas mnaidrensis* and *Canis lupus*. In US15 *Sus scrofa* and *Cervus elaphus siciliae* have been recovered; since US13 Bovidae make their appearance and in US12 *Cervus elaphus siciliae* was replaced by *Cervus elaphus*. Four unidentified remains of elephant teeth have been found in US12; since the last elephant attested in Sicily is *Elephas mnaidrensis*, these remains are likely to belong to this species.

Small mammals were very abundant (MNI=2697), but only four species were recovered: 2 giant dormice (*Leithia melitensis* and *Maltamys wiedincitensis*), an endemic shrew (*Crocidura esuae*) and *Microtus (Terricola)* n. sp. (Figure II-2).

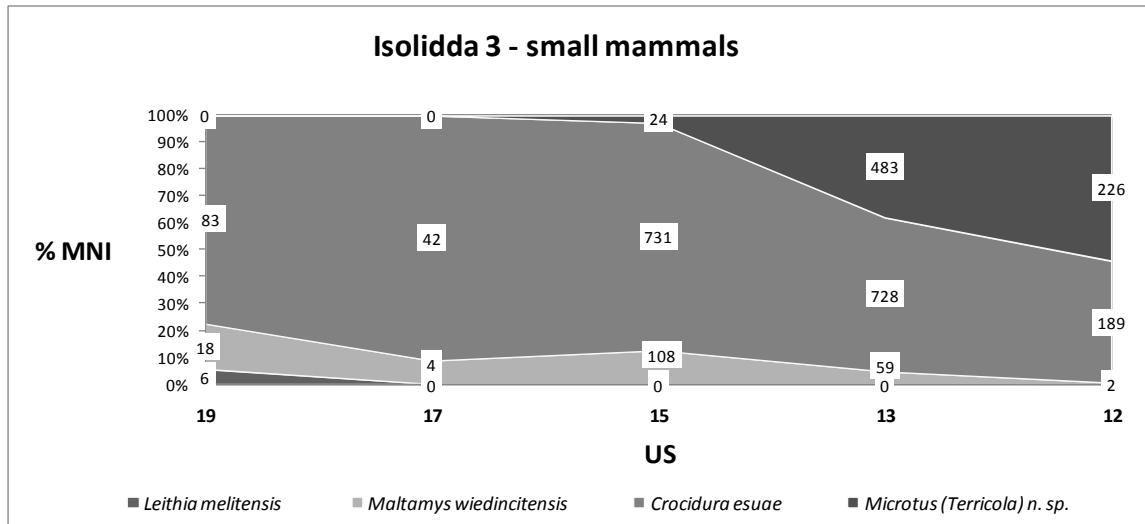


Figure II-2: small mammal seccession at Isolidda 3 cave. Variation in the relative abundance (expressed by minimum number of individuals=MNI) of species along the stratigraphy (US)

Giant dormice have already been studied in my Master thesis; results of the morphometric analysis and the comparison with other samples from the literature are illustrated in Fogure II-3 and Figure II-4.

From the analysis, the dormice have dimensions comparable to the ones reported in literature. Only the sample of *Leithia ex gr. melitensis–cartei* from Contrada Pianetti in smaller, as already noticed in Bonfiglio et al. (1997).

From the small mammal succession, it is noticeable the disappearance of *Leithia melitensis*, that is present only in US19, and the first occurrence of a vole, *Microtus (Terricola) n. sp.* In the next chapter I will face the problem of the systematic of this vole, which resulted to be different from the already known *M. (T.) savii* of Sicily. Together with it, new large mammals reach the island.

## *Leithia melitensis*

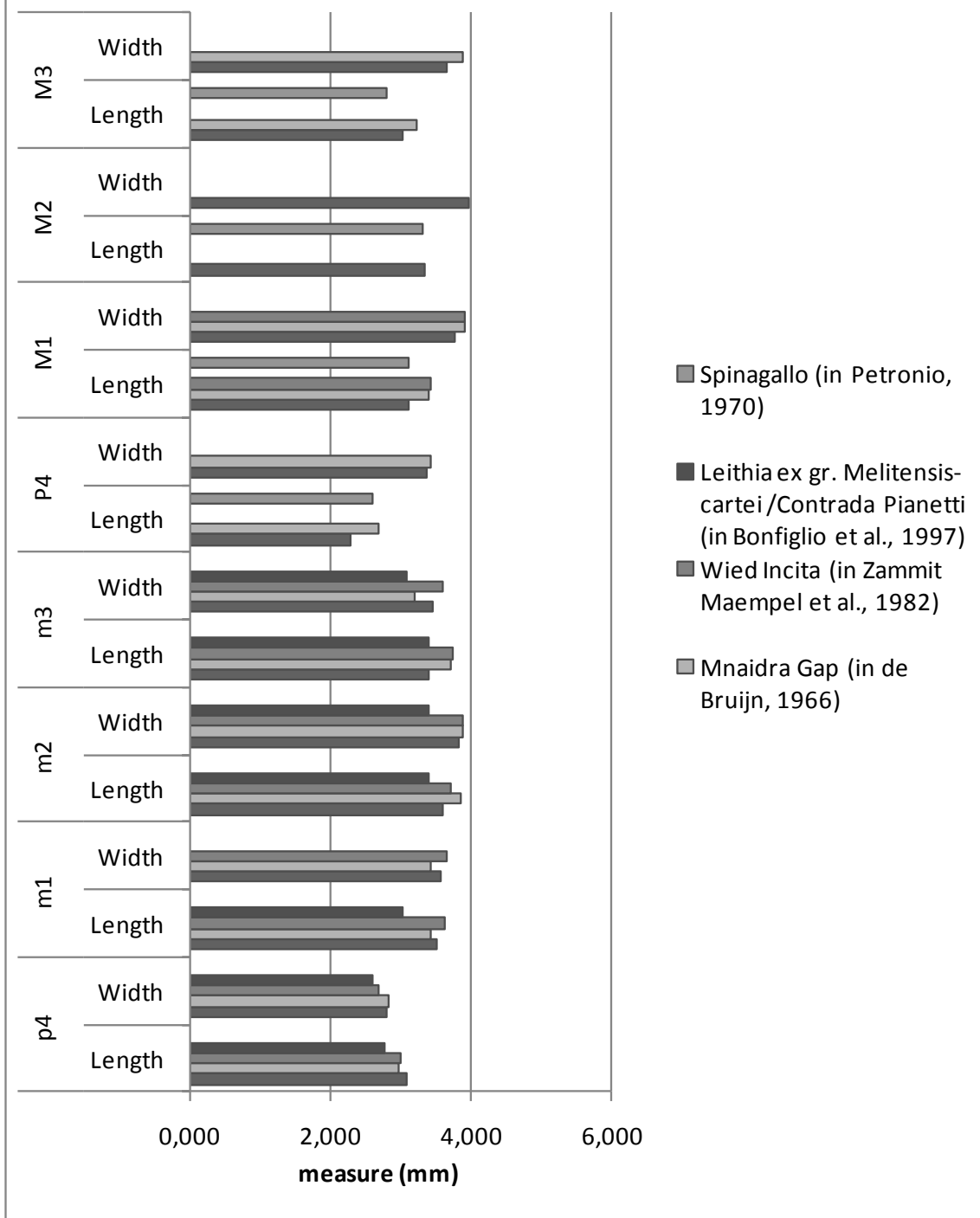


Figure II-3: comparison among measurements of *Leithia melitensis* from Isoldda 3 cave and the other samples published in the literature. m= lower molar. M= upper molar

## *Maltamys wiedincitensis*

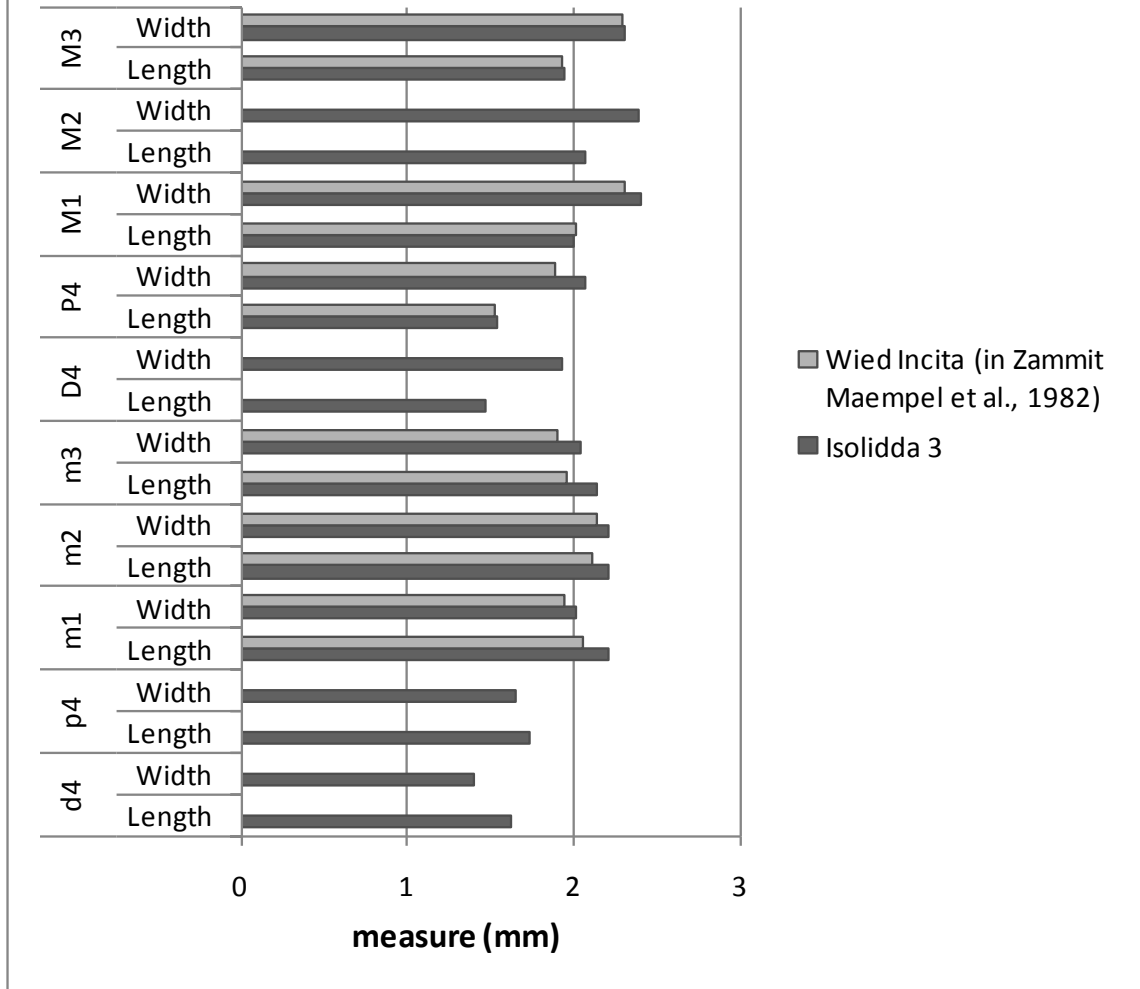


Figure II-4: comparison among measurements of *Maltamys wiedincitensis* from Isoldda 3 cave and the other samples published in the literature. Minuscule letters are for lower teeth; capitol letters for upper teeth.

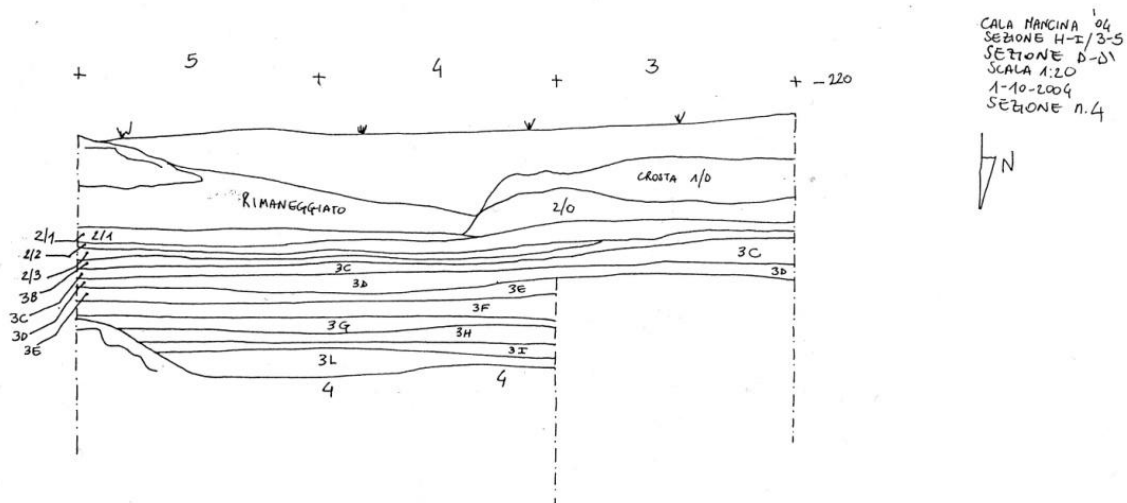


Figure II-5: Field stratigraphy of Cala Mancina cave

Cala Mancina cave is located at San Vito lo Capo, Sicily. It consists of a small cave-rockshelter opening ca. 8 m above sea level. Layers 2 and 3 document Mesolithic cave occupations with lithic assemblages ascribed to a local Epigravettian tradition (from ca. 9.5 to 8.5 year BP; Lo Vetro and Martini, in press) (Figure II-5). In Layer 3 (horizons 3b and 3c) two radiometric  $^{14}\text{C}$  dating have been made, which date the Mesolithic occupation to  $8,467 \pm 55$  BP (7,600-7,450 BC cal.  $2\sigma$ ) e  $9,332 \pm 60$  BP (8,760-8,420 BC cal.  $2\sigma$ ) respectively.

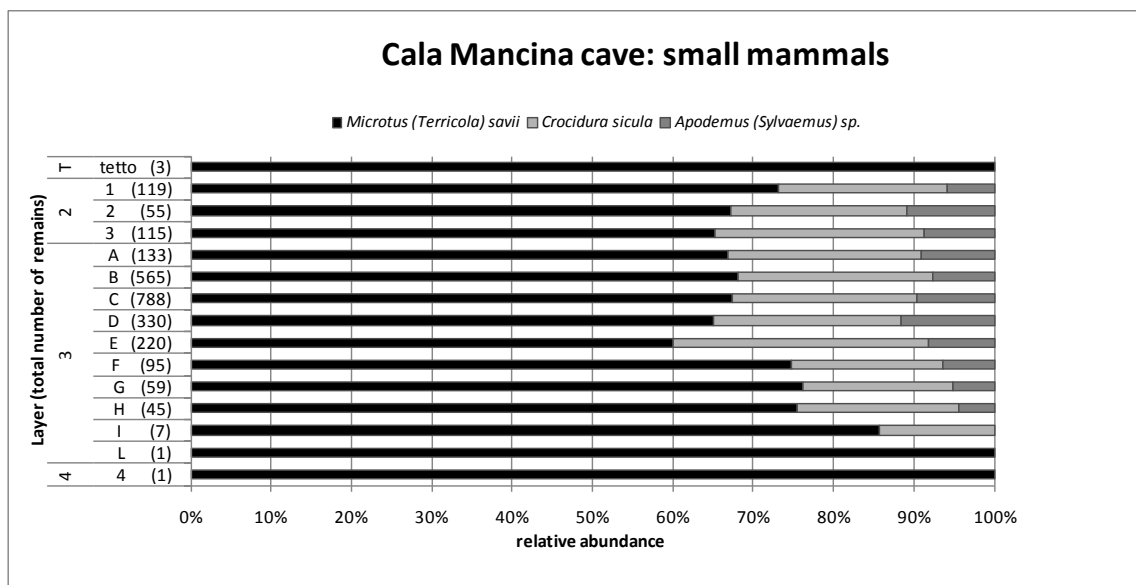


Figure II-6: variation of the relative abundance of small mammals in the stratigraphy of Cala Mancina cave.

Only three species of small mammals have been recovered in this deposit, despite the outstanding amount of fossil remains recovered (3062): *Microtus (Terricola) savii*, *Crocidura sicula* and *Apodemus (Sylvaemus) sp.* (Figure II-6). The vole and the shrew are dominant in the whole deposit, indicating a mainly dry climate. The increase in the relative abundance of the mouse *Apodemus (Sylvaemus) sp.* and the correspondent decrease of the vole *Microtus (Terricola) savii* could indicate a slight decrease in the dryness in layers 3/D and 2/2.

Oriente cave is a coastal cave located in Favignana Island, in the Egadi Archipelago (Sicily) at ca. 40 m above sea level (Martini et al., 2007b). The stratigraphy is arranged in 7 main units (Figure II-7).

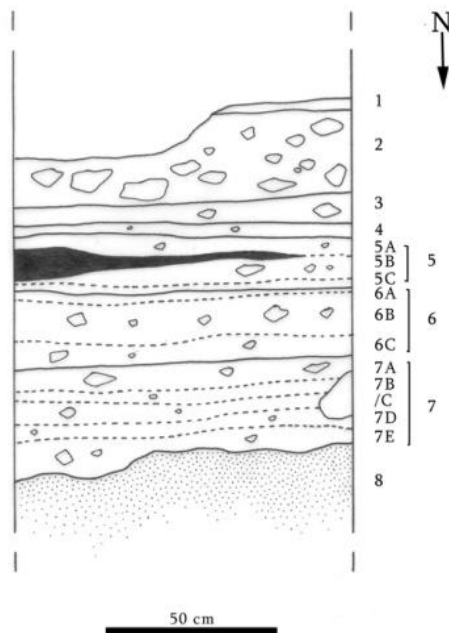
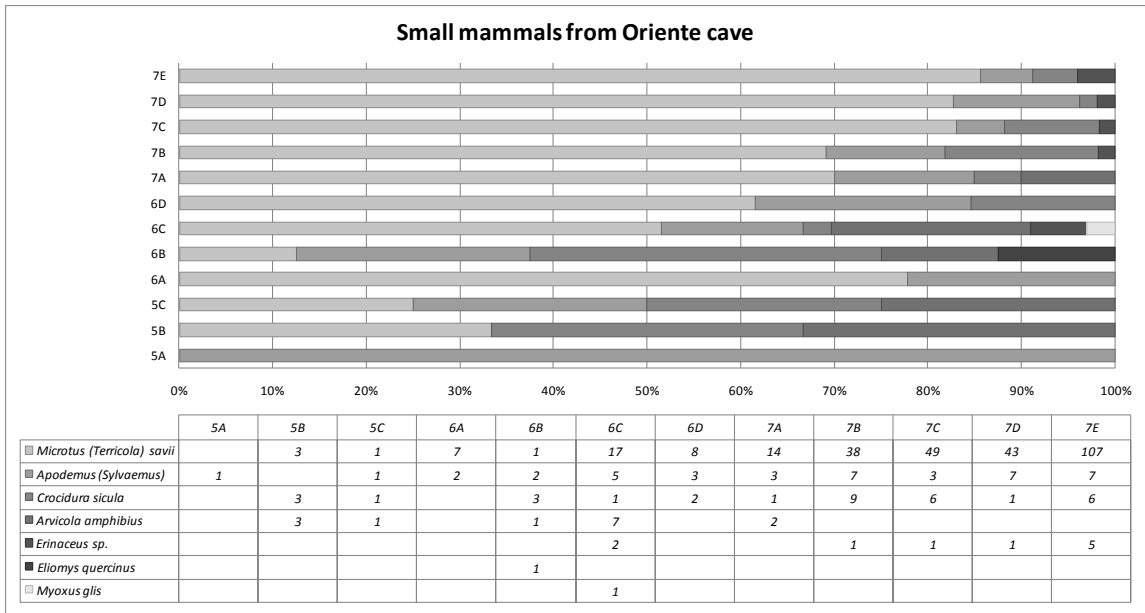


Figure II-7: field stratigraphy of Oriente cave

Unit 7 provides evidence of Epigravettian culture; Mesolithic occupation phases are recorded in units 6 and 5 (Martini et al., in press). Unit 5 provides cultural evidence related to the end of the local Mesolithic and the beginning of the Neolithic in Sicily. The Mesolithic succession provided very scarce large mammal remains, and in Unit 5 rare domestic (*Ovis* vel *Capra*) species appear. Shellfish are relatively abundant, with the genera *Patella* and *Osilinus* being most common (Martini et al., in press). Small mammals remains come from Units 7, 6 and 5. From Unit 4 upwards, protohistoric occupation begins and in the uppermost layers there are evidence of a historic frequentation of the cave. Every layer has been dated by  $^{14}\text{C}$  and calibrated; Unit 7

ranges from around 12ka to 8 ka BC; layer 6 from 8 ka to 7.5 ka and Layer 5 is around 6 ka.

About small mammals, the biodiversity in this deposit is higher than the one recorded at Cala Mancina cave. Seven different species have been recorded; one shrew, *Crocidura sicula*; one hedgehog, *Erinaceus* sp.; two Glires, *Eliomys quercinus* and *Myoxus glis*; one murid, *Apodemus (Sylvaemus)* sp.; and one vole, *Microtus (Terricola) savii*. Despite the higher biodiversity, the remains recovered are far fewer than at Isolida 3 and Cala Mancina caves, with a total amount of 388 identified remains (Figure II-8).



**Figure II-8: variation in the relative abundance of small mammals at Oriente cave**

The only endemic species is *Crocidura sicula*; all the others are animals well spread in the peninsula, as well. *Arvicola amphibius* occurs exclusively in Holocene layers, in agreement with Bonfiglio et al. (2002); it usually indicates the nearness to water. The Savi vole is dominant in all the Late Glacial layers, indicating a dry climate; nevertheless, its relative abundance decreases progressively, indicating an increase in the humidity during Holocene. No significant palaeo-ecological inferences are possible in the uppermost layers, since the total number of remains is very low (only 14 identified remains in Unit 6).



# III. *Microtus (Terricola)* (Mammalia, Rodentia) of Sicily

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*“In realtà ogni ramo del sapere è una disciplina comparata; qualunque descrizione, sia in campo umanistico sia scientifico, tiene conto di somiglianze e divergenze. Persino nella storia della musica è impossibile studiare le Messe di Palestrina senza accostarle a quelle di Orlando di Lasso o di Tomas Luis Victoria, o ai mottetti dello stesso autore. Tutto il nostro pensiero è una forma di comparazione: parlare di cielo azzurro vuol dire paragonarlo a un cielo grigio o rosso. Walter Wiora ha senz’altro ragione quando sottolinea che la comparazione può denotare tutt’al più un metodo, ma non un ramo del sapere”.*

*Curt Sachs, Le sorgenti della musica*

## 1. Introduction

The vole *Microtus (Terricola) savii* is widely spread all over Italy, with the exception of the northeast and Sardinia. Many questions about its origin and evolution are still unresolved. According to Tougard et al. (2008), *M. (T.) savii* originated in Italy and it has close relationships with *M. (T.) multiplex*. Four subspecies are recognized nowadays: *Microtus (Terricola) savii savii* (de Sélys Longchamps, 1838) spread through northern and central Italy; *Microtus (Terricola) savii nebrodensis* (Minà Palumbo, 1868) from Sicily; *Microtus (Terricola) savii tolfetanus* (Contoli, 2003) from Latium and *Microtus (Terricola) savii niethammericus* (Contoli, 2003) from Basilicata, Abruzzo and Apulia.

This chapter deals with the fossils of the subgenus *Terricola* from Sicily. The study has been carried out in collaboration with the University of Palermo; in particular, the Dr. Daria Petruso studied most of the Sicilian samples and Ghar Dalam for her PhD thesis, Giovanni Surdi studied the Grotta Grande di Scario cave, Serratura cave, extant samples from Cascina and S. Miniato, whereas Chiara Dalla Valle worked on Cavallo cave. Federico Masini and Benedetto Sala coordinated the work. I studied the samples from Isolidda 3, Oriente and Cala Mancina caves. This work has been presented to the SEQs Conference (2009) at Orce and has been submitted to Quaternary International.

## **History of research**

The occurrence of a distinct species *Microtus (Terricola) brachycercus* (von Lehmann, 1961), closely related to the Savi vole, is recognised in the Calabria peninsula, based on karyological features (Galleni, 1995; Galleni et al., 1992; 1994; 1998; Wilson and Reeder, 2005). The phylogenetic distance of the Northern and Central Italian populations of *M. (T.) savii* from *M. (T.) brachycercus* has been confirmed by molecular analyses of Jaarola et al. (2004) and Castiglia et al. (2008). The latter authors found also a greater affinity of the Calabria species with populations referred to *M. (T.) savii niethammericus* by Contoli (2003). Such results lead Contoli and Nappi (2009) to place the subspecies “*niethammericus*” within the species *M. (T.) brachycercus*. The morphological distinction between the Calabrian voles (namely from Aspromonte) and southern Italian, particularly Sicilian, populations, was first noted by De Luca (1998) and illustrated by Petruso (2003) based on measurements and morphological indexes of the first lower molar ( $M_1$ ). On the other hand, “small differences” between the Calabrian vole and vole samples from northern, central and southern Italy were detected by Nappi et al. (2005) using Canonical Discriminant Analysis on a set of linear measurement of the  $M_1$ . These authors concluded that if the Calabrian vole is proven to be a distinct species from the Savi vole, separation must have been achieved recently. Multivariate morphological analysis carried on first lower molars by Piras et al. (2010), based on geometrical morphometric methods, apparently confirms the morphological distance of Calabrian populations from some samples of *M. (T.) savii* from southern Italy and two samples from central and northern Italy.

Nappi et al. (2006), working with the methodology of Nappi et al. (2005) on some fifty samples distributed all over Italy and Sicily (but not Calabria), detected a morphological differentiation between north-central and southern populations of Italy. The authors infer the existence of a latitudinal gradient (a morphocline) based on the analogies between the intraspecific differences within the Italian populations and the interspecific differences within the Western European group - between the northern *multiplex-subterraneus* group (sensu Chaline, 1972) and the southern *Microtus (Terricola) duodecimcostatus* (de Sélys Longchamps, 1839). Conversely, Piras et al. (2010) deny the significance of differences between central and southern populations and claim the influence of a “more complex climatic effect” and the importance of phylogeographic relationships in modeling the variability among *Microtus (Terricola)* populations and species. The same authors had already in an earlier paper (Piras et al., 2009) shown some correlations between the morphological variation of the anterior portion of the first lower molar and the climatic fluctuations as expressed by the  $\delta^{18}\text{O}$  climatic proxy.

Even though the extant vole populations from Sicily were referred to *M. (T.) savii nebrodensis* in the critical revision of Contoli (2003), diverging opinions are expressed in the literature for what concerns their actual phylogenetic relationships, taxonomy and origin. Castiglia et al. (2008) evidenced a noteworthy distance in Cytochrome b haplotypes (7%) between some specimens from Ficuzza (Palermo, western Sicily) and those of the *savii - brachycercus* group, which almost suggests a distinct specific status for the former population. On the other hand, Nappi et al. (2006) on the basis of morphological analysis, demonstrated that the Sicilian *Microtus (Terricola)* falls in the southern group of *savii*, having, however, some distinctive features in the anterior part of the first molar. Piras et al. (2010) do not detect any significant difference between the Sicilian populations and the Savi vole from the Italian peninsula.

Fossil remains of the subgenus *M. (Terricola)* are, sometime in great abundance, present in many Sicilian deposits from the late Middle - Late Pleistocene. However, until the 1990s, the published record was limited to a specimen from La Costiera (PA; Burgio and Kotsakis, 1987). As a matter of fact, upto then little attention was given by palaeontologists to non-endemic small mammals from Sicily and very little (if any) sediment from the hundredseventy Quaternary deposits known on the island had been sieved for collecting micro fauna (Petruoso, et al, 2008). Even fewer works, specifically addressed to the detailed analysis of the Savi vole morphology, have been produced with the purpose to clarify the relationships between the Sicilian populations and the peninsular ones. The first finding, reported by Burgio and Kotsakis (1987) from the site La Costiera, consisted of a unique remain (a mandible fragment) referred to as “*Pitimys=Microtus (Terricola)* cf. *savii*” and tentatively ascribed to the Late Glacial Castello Faunal Complex (FC). Subsequently Tagliacozzo (1993) documents the diffusion of *Microtus (Terricola)* in the early Holocene deposit of Uzzo cave (San Vito lo Capo, TP) and confirms its occurrence in pre - Holocene (Late Glacial) levels. Bonfiglio et al. (1997) describe samples from two new fossil sites and refer them to *M. (T.) ex gr. savii*: the Late Pleistocene sample from Contrada Pianetti (RG), later referred by Bonfiglio et al. (2002) to the Grotta di San Teodoro – Pianetti FC (MIS4-2) and a sample from the Late Pleistocene layer of site K22 (San Vito lo Capo, TP). The authors stress the differences between the two fossil populations and suggest they could have derived from two distinct dispersal events from the continent, the older of which gave rise to the the Contrada Pianetti vole. The first comparative study of the extant Savi vole from Sicily, an extant population from Aspromonte and the Late Pleistocene sample from site K22 was carried on shortly thereafter (De Luca, 1998). In the comparison, all the analyzed populations were attributed to the *savii* group, with the exception of the sample from Calabria, which showed morphological features closer to the *multiplex-subterraneus* group. A deeper and more extended comparative analysis of the fossil material of this species from more numerous Late Pleistocene – Early Holocene Sicilian sites (San Teodoro Cave, Acquedolci, ME; Uzzo Cave, Castello shelter, PA; K22) was carried on by Petruoso (2003), who attributed all the Sicilian samples to the *savii* group and detected a more complex and assorted coexistence of different characters in the Maltese sample from the Last Glacial deposit of Ghar Dalam (Malta; Storch, 1974). The comparison demonstrated the wide size variation among the populations, ascribable to different micro-environmental features. In 2007, Locatelli analyzed the late Middle Pleistocene-Late Pleistocene vole remains from Isolidda 3 cave (San Vito lo Capo, TP). The results show a marked difference between these old Sicilian populations and the aforementioned younger ones. A detailed study of the San Teodoro vole remains is reported in Bonfiglio et al. (2008), pointing out the morphological differences between samples coming from different sectors and different layers of the cave.

Despite the efforts of the last ten years, the details of the dispersal history of this vole in Sicily and the question if it reached the island only one time, and then evolved in Sicily, with sporadic contacts with the mainland populations, or if it reached the island more than once, is still particularly challenging. Morphological divergence as a result of geographical isolation from the peninsular populations would indicate endemic processes , while greater similarities with the peninsular samples of different ages would be indicative of possible connections with the mainland. The aim of this study is to detect, by the morphometrical analysis of the first lower molar of *Microtus (Terricola) ex gr. savii* of extant and fossil Sicilian populations and their comparison with peninsular and Western European samples, the possible similarities between different populations that could suggest a strict phylogenetic relation. Thus the dispersal events of this vole during late Middle - Late Pleistocene could be outlined hypothesizing the presence of

temporary land bridges with the mainland, giving in this way also a contribution to the reconstruction of the Sicilian paleobiogeography.

## 2. Materials and methods

The systematic study was carried out using morphometric analysis on first lower molars of voles from Isolidda 3, Cala Mancina and Oriente caves. Subsequently, other populations of *Microtus (Terricola)* have been taken into account, for a total of 22 localities, including 13 fossil deposits and 9 extant populations. As in some fossil sites with a clear stratigraphic succession (Isolidda 3 cave, Cavallo cave, Grotta Grande di Scario cave, Uzzo cave and San Teodoro cave), specimens from different levels have been analysed separately, the total amount of samples analysed is 34. The location of the sites is shown in Figure III-1

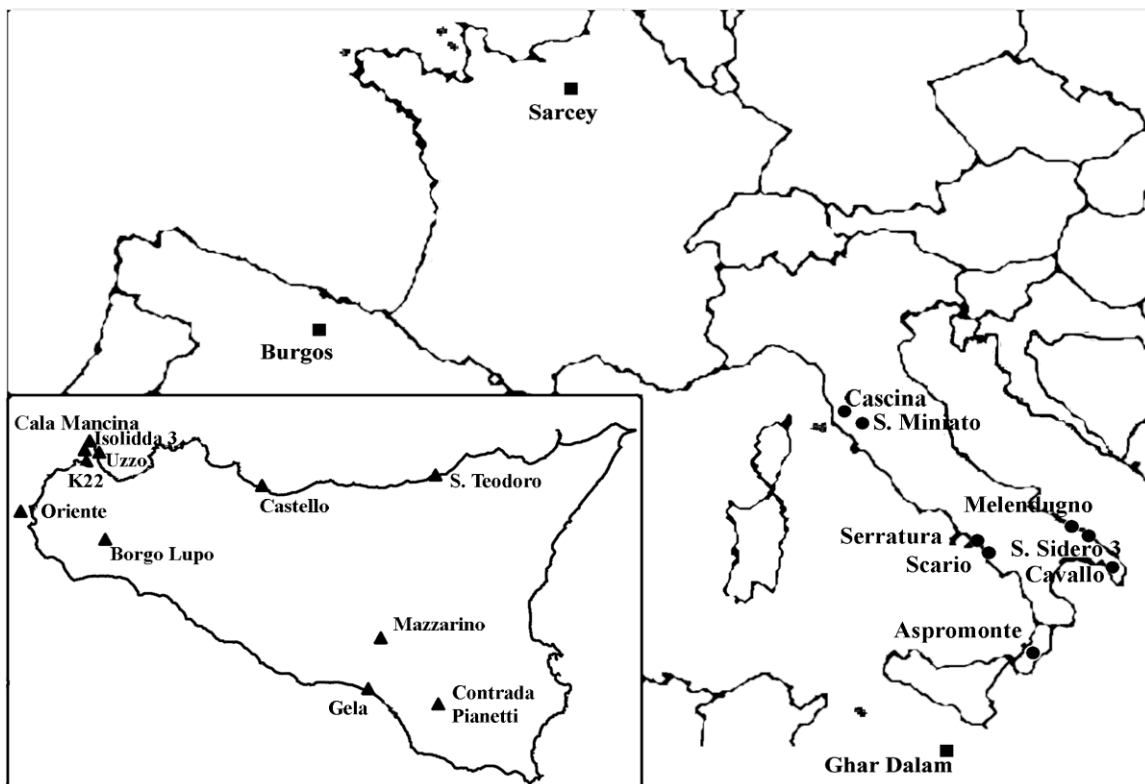
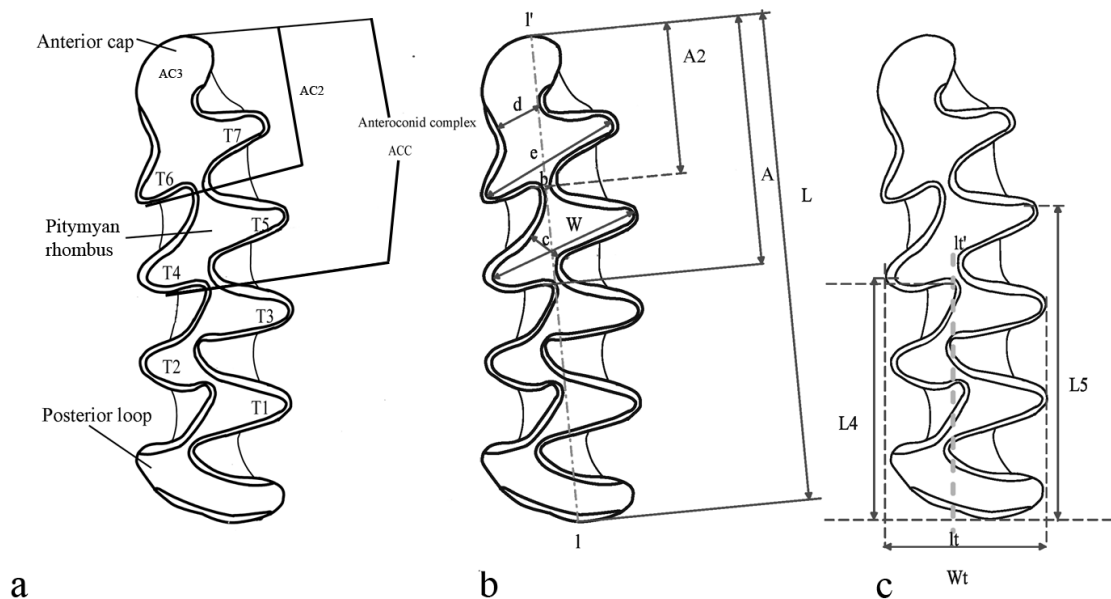


Figure III-1: Location map of samples of *Microtus (Terricola)* considered in the analysis

The samples used in the analysis have been chosen for both chronological and geographical reasons. With regard to Sicilian samples, all the known fossil sites with *Microtus (Terricola)* have been considered (with the exception of the single specimen from La Costiera, which went lost), while the extant populations come from localities with different geographical features (some of them are located near coastal areas, while others are close to mountain chains). From the Italian peninsula samples from sites coeval with the Sicilian ones and located in different regions of Italy were chosen, in order to discern geographical data from chronological ones. Two extant populations from outside Italy, belonging to *Microtus (Terricola) subterraneus* (France) and

*Microtus (Terricola) lusitanicus* (Spain), have been included as a sort of “out-group” for comparisons. The list of the localities, fossil and extant ones, together with the age of their deposits (single or distinguished into different levels), the distinctive code used in the diagrams, the number of specimens of each sample and the references for the chronology of fossil sites, are given in Table III-1.

Measurements were taken according to the plan proposed by Van der Meulen (1973) and modified by Masini (in Bonfiglio et al., 1997; Masini et al., 2005) with the integration of some measures according with the Brunet-Lecomte and Chaline scheme (1992; Figure III-2) with a Leica MZ8 orthoplan microscope; at Ferrara university it was provided with the positioning stage Parker 4508DM (straight-line accuracy  $2\mu\text{m}$ ). The nomenclature used follows Van der Meulen (1973) and Rekovets and Nadachowski (1995). In Arvicolinae only first lower molar is diagnostic, while third upper molar can give some additional information. All the other teeth do not show any significant difference among species. For this reason, the morphological description will focus more on these teeth.



**Figure III-2: nomenclature (a) and plan of measurements (b and c), modified after van der Meulen (1973), Bonfiglio et al. (2002) and Masini (2005)**

The analysis has been carried out by bivariate diagrams using the measurements and morphological indexes computed from the single measures such as: AL ( $A/L*100$ ), A2A ( $A2/A*100$ ), BW ( $B/W*100$ ), CW ( $C/W*100$ ), DW ( $D/W*100$ ), DE ( $D/E*100$ ), L45 ( $L4/L5*100$ ). To trace the evolutionary pattern and to find out possible relations between different populations, the mean values of each measurement or morphological indexes are plotted on the abscissa, while on the vertical axis discrete intervals of time (time slices), related to important paleoclimatic events are reported. Principal Component Analysis (PCA) with correlation metric has been carried out on the means of measurements and indexes of the considered samples using the PAST software (Hammer et al., 2001).

Locality	Age	Code	N	Reference for the chronology of fossil sites
Sarcey-Rhone (FR)	Extant	sub	5	
Lamilla-Burgos (E)	Extant	lus	27	
Melendugno (LE)	Extant	Mel	32	
San Miniato (PI)	Extant	Smin	38	
Cascina (PI)	Extant	Cas	45	
Aspromonte (RC)	Extant	Asp	30	
Borgo Lupo (TP)	Extant	BLu	22	
Piana di Gela (CL)	Extant	Gel	26	
Mazzarino (CL)	Extant	Maz	12	
Uzzo Cave (TP)	Early Holocene Mesolithic 1	UZmI	39	Tagliacozzo, 1993
Uzzo Cave (TP)	Early Holocene Mesolithic 2	UZmII	32	Tagliacozzo, 1993
Uzzo Cave (TP)	Early Holocene Neolithic	UZn	15	Tagliacozzo, 1993
Cala Mancina (TP)	Early Holocene	MAN	60	Martini et al., in press b
Castello shelter(PA)	Late Glacial - Holocene (MIS2-1)	RC	6	Petruso, 2003
Oriente Cave -Favignana island (TP)	Late Glacial (MIS2)	OR	41	Martini et al., in press a
Serratura Cave (SA)	Late Glacial (MIS2)	SER	96	Martini, 1993; Bertolini et al., 1996
Cavallo Cave (LE) layer B	Late Glacial (MIS2)	CavB	29	Palma di Cesnola et al., 1964
K22 (TP)	Würm (MIS3-2 ?)	K22	35	Petruso, 1996; De Luca, 1997; Di Maggio et al., 1999
S.Teodoro Cave (ME) trench 1998	Würm (MIS3)	TEO98	22	Bonfiglio et al., 2008
S.Teodoro Cave (ME) trench 2003-04 ABC sectors	Würm (MIS3)	TEOABC	12	Bonfiglio et al., 2008
S.Teodoro Cave (ME) trench 2003-04 D sector	Würm (MIS3)	TEOD	16	Bonfiglio et al., 2008
Cavallo Cave (LE) layer F	Würm (MIS3)	CavF	45	Palma di Cesnola et al., 1964
Contrada Pianetti (RG)	Würm (MIS3)	CP	31	Bonfiglio et al. 1997
Ghar Dalam Cave (Malta)	Würm ?	GD	28	Storch, 1974
Grande Cave, Scario (SA) trench A	Post-Tyrrhenian (MIS5d-a)	GGSA	18	Abbazzi et Masini, 1998; Boscato et Ronchitelli, 2004; Ronchitelli et al., 1998, 2008
Grande Cave, Scario (SA) trench F	Post-Tyrrhenian (MIS5d-a)	GGSF	24	Abbazzi et Masini, 1998; Boscato et Ronchitelli, 2004; Ronchitelli et al., 1998, 2008
Cavallo Cave (LE) layer M	Post-Tyrrhenian (MIS5d-a)	CavM	45	Sarti et al., 2002
San Sidero 3 (LE)	Post-Tyrrhenian (MIS5 s.L)	SS3	24	De Giulì, 1983
Cavallo Cave (LE) layer N	Eemian (MIS5e)	CavN	33	Sarti et al., 2002
Grande Cave, Scario (SA) trench C lower	Pre-Tyrrhenian (MIS6)	GGSCi	48	Abbazzi et Masini, 1998; Boscato et Ronchitelli, 2004; Ronchitelli et al., 1998, 2008
Grande Cave, Scario (SA) trench C upper	Pre-Tyrrhenian (MIS6)	GGSCs	25	Abbazzi et Masini, 1998; Boscato et Ronchitelli, 2004; Ronchitelli et al., 1998, 2008
Torre Isolidda 3 (TP) US 15, lower	Pre-Tyrrhenian?	TI3i	42	Mannino, 1962; Martini et al., in press c
Torre Isolidda 3 (TP) US 13, middle	Pre-Tyrrhenian?	TI3m	45	Mannino, 1962; Martini et al., in press c
Torre Isolidda 3 (TP) US 12, upper	Pre-Tyrrhenian?	TI3s	45	Mannino, 1962; Martini et al., in press c

Table III-1: List of samples

### 3. Systematic Palaeontology of *Microtus (Terricola)* from Isolidda 3, Cala Mancina and Oriente caves

**Class:** MAMMALIA

**Order:** Rodentia Bowdich 1821

**Suborder:** Myomorpha Brandt 1855

**Superfamily:** Muroidea Illiger 1811

**Family:** Cricetidae Fischer 1817

**Subfamily:** Arvicolinae Gray 1821

**Genus:** *Microtus* Schrank 1798

**Subgenus:** *Terricola* Fatio, 1867

**Species:** *Microtus (Terricola)* n. sp.

**Holotype:** Specimen 1

**Geographic and stratigraphic distribution:** Sicily (Italy); recovered at Isolidda 3 cave, San Vito Lo Capo (Trapani), in sediments provisionally assigned to late Middle Pleistocene-Late Pleistocene

**Material:**

733 specimen of *Microtus (Terricola)* n. sp. have been recovered: 24 in US 15; 483 in US 13; 226 in US 12; no specimen has been found in Layers 19 and 17. All specimens recovered from US15 have been measured; given the high amount of specimens, only 45 well-preserved specimens have been measured from US13 and US12. In the Isolidda sample, no complete upper tooththrow was found; complete mandibles are present.

**Description:**

**M<sub>1</sub>:** The M<sub>1</sub> is made up of a posterior loop (PL), seven triangles, numbered from the distal to the mesial one (t1-t7) and an anterior cap (AC3). The first three triangles represent the trigonid or posteroconid; the other ones plus AC3 represent the anteroconid (ACC). All the triangles of the trigonid (t1-t3) are not confluent among them. t4 and t5 are widely confluent; this is characteristic of the subgenus *Terricola*; in any other European *Microtus* species these triangles are confluent; only a North American lineage presents this feature, *Microtus (Pitymys)* McMurtrie, 1831. The extend of the opening of these triangles is characteristic of different populations and species. . The pitymyan rhombus (formed by t4-t5) is moderately open and wide. There is a high variability within the sample. t6, t7 and t8 together form the antero-anteroconid (AC2); this is well separated from the pitymyan rhombus. The rhombus formed by t6-t7 is wide, above all in relation to the pitymyan rhombus, and the neck that separates AC3 from t6-t7 is generally narrow, but it is the most variable among the characters and in some specimens (above all it they are old) is larger. At a first sight these teeth look chunky, with a long and wide, well-developed anteroconid,

**M<sup>3</sup>:** it is made up by an anterior loop (AL1), four triangles (t2-t5) and a posterior cap (PC1); PC1 and t5 are widely confluent, so that t5 lost its triangular shape and its distal margin is in most cases in line with the cap profile. t4 is widely confluent with PC, so that only two well-defined labial salient angles are present. Thus, the M<sup>3</sup> can be assigned to the “simplex type”. The second re-entrant lingual angle (LRA2) is very acute and the re-entrance is deep; the distal margin of t3 is almost parallel to the mesial margin of t5. Labial triangles are small, t3 is large.

**Measurements:**

Only 45 specimens from each stratigraphic unit have been measured (Table III-2: descriptive statistical analysis of first lower molars of *Microtus (Terricola)* n. sp. from Isolidda 3. From the analysis, it becomes clear that voles recovered at Isolidda 3 cave display a progressive decrease in size (Table III-3: Mean value of each measurement in different stratigraphic units (US)).

Morphometrical analysis shows that this is a markedly different form than the extant *Microtus (Terricola) savii* living in Sicily and in peninsular Italy and from *M. (T.) subterraneus*. More detailed comparative analysis will be faced in the next paragraphs, in a full discussion of the phylogeography of Sicilian voles.

<i>Microtus (Terricola)</i> n. sp. (Isolidda 3)	L	A	A2	D	E	B	W	C	A/L	A2A	B/W	C/W	E/W	D/W	D/E
Mean	2.68	1.39	0.86	0.25	0.80	0.03	0.90	0.18	51.69	61.68	3.33	20.40	89.51	27.80	31.06
Standard Error	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.15	0.70	0.24	0.36	0.40	0.78	0.91
Median	2.70	1.39	0.86	0.24	0.80	0.02	0.89	0.18	51.51	61.46	2.33	20.57	89.41	27.91	30.19
Mode	2.61	1.36	0.81	0.26	0.80	0.02	0.88	0.19			1.10	20.00	93.10	19.59	23.26
Standard deviation	0.14	0.08	0.12	0.08	0.06	0.02	0.05	0.03	1.68	7.86	2.71	4.10	4.43	8.68	10.01
Sample Variance	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00	2.81	61.79	7.34	16.82	19.60	75.35	100.22
Kurtosis	-0.68	0.14	32.05	0.42	-0.10	8.02	0.00	0.24	1.93	65.07	7.34	-0.10	3.19	0.57	0.74
Skewness	-0.13	-0.28	3.49	0.54	0.17	2.49	-0.08	-0.17	0.20	6.28	2.36	-0.19	0.82	0.59	0.66
Range	0.63	0.43	1.33	0.44	0.29	0.15	0.24	0.18	10.78	101.19	16.30	18.34	30.36	48.56	55.08
Minimum	2.37	1.16	0.46	0.09	0.67	0.00	0.77	0.09	46.47	34.61	0.00	10.23	79.76	9.68	10.59
Maximum	3.00	1.58	1.79	0.53	0.96	0.15	1.01	0.27	57.25	135.81	16.30	28.57	110.13	58.24	65.67
Sum	335.12	174.70	107.80	31.67	98.42	3.83	114.64	23.57	6461.14	7771.71	422.44	2610.73	11009.89	3474.94	3789.30
Count (n)	125	126	126	127	123	130	128	130	125	126	127	128	123	125	122
Confidence Interval (95,0%)	0.03	0.01	0.02	0.01	0.01	0.00	0.01	0.01	0.30	1.39	0.48	0.72	0.79	1.54	1.79

Table III-2: descriptive statistical analysis of first lower molars of *Microtus (Terricola)* n. sp. from Isolidda 3

Us	L	A	A2	D	E	B	W	C	A/L	A2A	B/W	C/W	E/W	D/W	D/E
12	2.59	1.34	0.83	0.25	0.77	0.04	0.87	0.18	51.71	61.55	4.06	20.26	88.58	28.51	32.53
13	2.70	1.40	0.87	0.24	0.81	0.02	0.90	0.17	51.99	62.08	2.38	19.71	90.25	26.29	29.26
15	2.76	1.42	0.87	0.26	0.82	0.03	0.92	0.19	51.30	61.35	3.60	21.34	89.71	28.81	31.61

Table III-3: Mean value of each measurement in different stratigraphic units (US)

### Differential diagnosis:

*Microtus (Terricola)* n. sp. is different from *M. (Terricola) subterraneus* (de Selys-Longchamps, 1836) because  $M^3$  is simplex-type and not complex-type (in complex  $M^3$ , three different triangles are well isolated from AL and PC). The  $M_1$  from Isolidda 3 cave are generally more robust, while in *M. (T.) subterraneus*  $M_1$  is slender. The two species share a long anteroconid and antero-anteroconid, narrow neck between AC3 and t6-t7, and almost complete separation between pitemyan rhombus and ACC.

It differs from recent *M. (T.) savii* (de Selys-Longchamps, 1836) from Sicily for having a very long ACC and AC2. On average, AC3 is less confluent with distal triangles (despite there being a high variability in this character in Isolidda 3 sample). Compared to *M. (T.) savii* the new species as a large t6-t7, and low confluence between pitemyan rhombus and AC2. They both have simplex  $M^3$ .

### *Microtus (Terricola) savii*

**Material:** 1712 dental remains from Cala Mancina cave and 278 from Oriente cave. Given the multitude of remains recovered, only a representative sample has been measured and used for multivariate analysis.



## Cala Mancina cave and Oriente cave

Overall, the dental pattern is the same of *M. (T.) n. sp.*, but some differences occur in the morphological arrangements of triangles. The triangles themselves are larger; the anterior cap is less constricted, the anteroconid is shorter and looks more squat and asymmetric. Descriptive statistical analysis are reported in Table III-4 and Table III-5.

<i>Microtus (Terricola) savii</i> Cala Mancina cave	A2	A	L	W	B	E	D	C	4	5	WT	AL	A2A	BW	EW	DW	CW	DE	L45
Mean	0.83	1.41	2.82	0.92	0.04	0.77	0.34	0.20	1.49	1.81	1.04	0.50	0.59	0.05	0.83	0.37	0.22	0.45	0.82
Standard Error	0.01	0.01	0.02	0.01	0.00	0.01	0.01	0.00	0.01	0.01	0.01	0.00	0.01	0.00	0.01	0.01	0.01	0.02	0.00
Median	0.84	1.43	2.84	0.92	0.03	0.77	0.32	0.20	1.49	1.80	1.04	0.50	0.59	0.03	0.83	0.36	0.22	0.45	0.82
Mode	0.83	1.47	2.89	0.95	0.03	0.78	0.24	0.21	1.50	1.82	1.13								
Standard deviation	0.09	0.09	0.14	0.05	0.03	0.04	0.10	0.04	0.08	0.10	0.05	0.02	0.04	0.03	0.04	0.09	0.04	0.12	0.02
Sample Variance	0.01	0.01	0.02	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00
Kurtosis	2.68	1.71	0.68	-0.42	7.83	-0.31	0.63	0.29	-0.05	-0.16	-0.62	1.80	1.85	6.08	1.44	-0.57	0.84	-1.03	-0.45
Skewness	-0.95	-0.85	-0.66	0.14	2.46	-0.29	-0.41	-0.02	0.02	-0.09	-0.19	-0.67	-0.93	2.25	-0.05	-0.03	0.32	-0.05	-0.09
Range	0.52	0.50	0.60	0.19	0.15	0.17	0.50	0.17	0.36	0.43	0.20	0.09	0.18	0.16	0.21	0.38	0.22	0.45	0.10
Minimum	0.51	1.10	2.46	0.82	0.01	0.68	0.02	0.11	1.29	1.59	0.93	0.44	0.46	0.01	0.73	0.17	0.11	0.21	0.77
Maximum	1.03	1.60	3.06	1.01	0.16	0.84	0.52	0.28	1.64	2.02	1.13	0.54	0.65	0.17	0.93	0.55	0.33	0.66	0.87
Sum	39.94	67.62	121.11	46.82	2.32	32.21	17.98	11.74	69.96	83.40	47.65	21.53	28.30	2.23	34.14	17.51	11.23	18.10	37.82
Count (n)	48	48	43	51	57	42	53	59	47	46	46	43	48	49	41	47	51	40	46
Confidence Interval (95,0%)	0.03	0.03	0.04	0.01	0.01	0.01	0.03	0.01	0.02	0.03	0.02	0.01	0.01	0.01	0.01	0.03	0.01	0.04	0.01

Table III-4: descriptive statistical analysis of *Microtus (Terricola) savii* from Cala Mancina cave

<i>Microtus (Terricola) savii</i> Oriente cave	A2	A	L	W	B	E	D	C	4	5	WT	AL	A2A	BW	EW	DW	CW	DE	L45
Mean	0.82	1.37	2.74	0.89	0.04	0.76	0.31	0.20	1.45	1.75	0.99	0.50	0.60	0.05	0.85	0.35	0.22	0.42	0.83
Standard Error	0.01	0.02	0.03	0.01	0.00	0.01	0.02	0.01	0.01	0.02	0.01	0.00	0.00	0.00	0.01	0.02	0.01	0.03	0.01
Median	0.80	1.37	2.74	0.90	0.04	0.76	0.33	0.20	1.45	1.75	1.00	0.50	0.60	0.04	0.85	0.36	0.22	0.44	0.83
Mode	0.76	1.37		0.92	0.03	0.74	0.38	0.20	1.45	1.73	1.02								
Standard deviation	0.07	0.09	0.14	0.06	0.02	0.05	0.12	0.04	0.07	0.09	0.07	0.02	0.02	0.03	0.03	0.13	0.04	0.15	0.03
Sample Variance	0.01	0.01	0.02	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.02	0.00	0.02	0.00
Kurtosis	0.33	-0.20	0.32	3.03	3.38	-0.41	-0.77	-0.11	0.27	0.75	1.32	2.29	-0.92	3.07	-0.23	-0.84	0.44	-0.82	-0.20
Skewness	0.91	0.31	-0.47	-1.44	1.61	-0.50	-0.41	0.08	-0.27	-0.33	-0.92	0.41	-0.15	1.51	0.27	-0.31	-0.06	-0.38	0.36
Range	0.29	0.37	0.58	0.30	0.11	0.21	0.45	0.17	0.33	0.40	0.34	0.08	0.09	0.12	0.14	0.48	0.18	0.54	0.11
Minimum	0.74	1.22	2.38	0.69	0.00	0.63	0.08	0.11	1.26	1.51	0.78	0.47	0.55	0.00	0.78	0.09	0.12	0.11	0.78
Maximum	1.03	1.59	2.97	0.99	0.12	0.84	0.53	0.28	1.60	1.90	1.13	0.55	0.65	0.13	0.92	0.57	0.30	0.65	0.89
Sum	25.49	42.62	76.64	31.26	1.70	25.75	10.92	7.41	45.03	50.89	32.54	14.11	18.53	1.63	27.27	10.75	7.25	13.29	23.99
Count (n)	31	31	28	35	41	34	35	38	31	29	33	28	31	35	32	31	33	32	29
Confidence Interval (95,0%)	0.03	0.03	0.05	0.02	0.01	0.02	0.04	0.01	0.03	0.03	0.03	0.01	0.01	0.01	0.01	0.05	0.01	0.06	0.01

Table III-5: descriptive statistical analysis of  $M_1$  of *Microtus (Terricola) savii* from Oriente cave

## 4. Results

### 4.1 Size variation

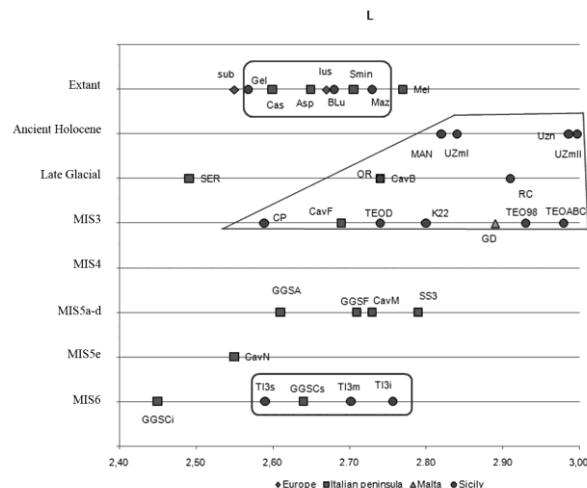


Figure III-3: scatter plot of  $M_1$  length variation with time (MIS)

Figure III-3 shows the variation in size related both to time and to geography inferred by the length of  $M_1$ . Most of the fossil Sicilian populations are on the average bigger than the continental ones. The largest sizes were reached during MIS3 (San Teodoro trench 03-04 and square A B C, TEO0304ABC), the Late Glacial (Castello Shelter - RC) and especially in the ancient Holocene (Uzzo Mesolithic II and Neolithic levels, UZmII - UZn). However,

also very small sized or “normal” sized samples (namely Contrada Pianetti, Oriente Cave and San Teodoro square D) occur among the fossil Sicilian voles of these time slices. In older samples, the size difference between insular populations (Isolidda 3) and continental ones (Cavallo cave, Grotta Grande di Scario) seems to be less, even though Sicilian samples are already slightly larger.

## 4.2 Morphological variation

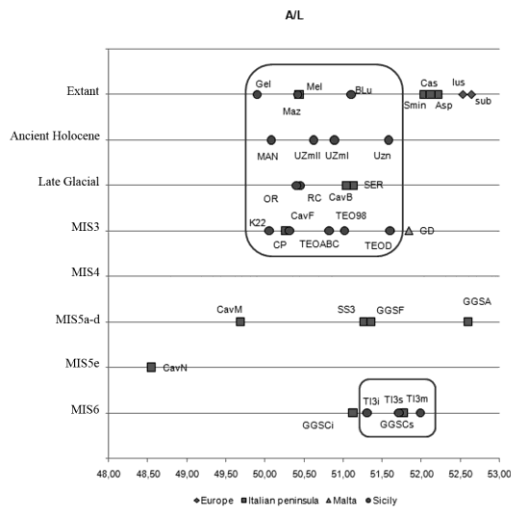


Figure III-4: scatter diagram of the variation of A/L ratio with time (MIS)

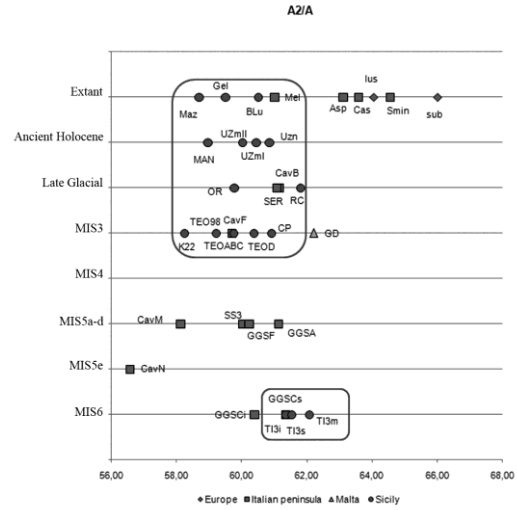


Figure III-5: scatter diagram of the variation of A2/A ratio with time (MIS)

The relative proportions of the anteroconid (ACC, the anterior portion of the first lower molar, Figure III-4 and Figure III-5) respect to the total length of  $M_1$  have been plotted using the indices, A/L and A/2A.

There is a difference between insular and continental populations (Figure III-4 and 5); the latter ones have longer anteroconid complex (A) and anterior cap (A2) relative to the Sicilian Savi voles. Notably, the extant Savi sample from Melendugno, in the Salento peninsula, is closer to Sicilian populations than to peninsular ones.

As the ACC represents the most variable part of the first lower molar, this part of the teeth is particularly important for the taxonomy of the group and its morphology has been investigated more in the details. In order to analyze the degree of constriction of the triangles, three parameters (D, E, W) and their indices have been used (Figure III-6 and Figure III-7).

The variable D measures the degree of constriction of the anterior cap; E describes the width of the triangles T6 and T7 that in the maximum development shapes a rhombus (Figure III-2); W conveys the width of the next pair of triangles (T5-T4), the so-called pitymyan rhombus, a particular feature for the morphology of *Microtus (Terricola)*. Again, peninsular populations are well separated from insular ones, with the oldest Sicilian (Isolidda 3) and peninsular (Scario) samples closer to each other.

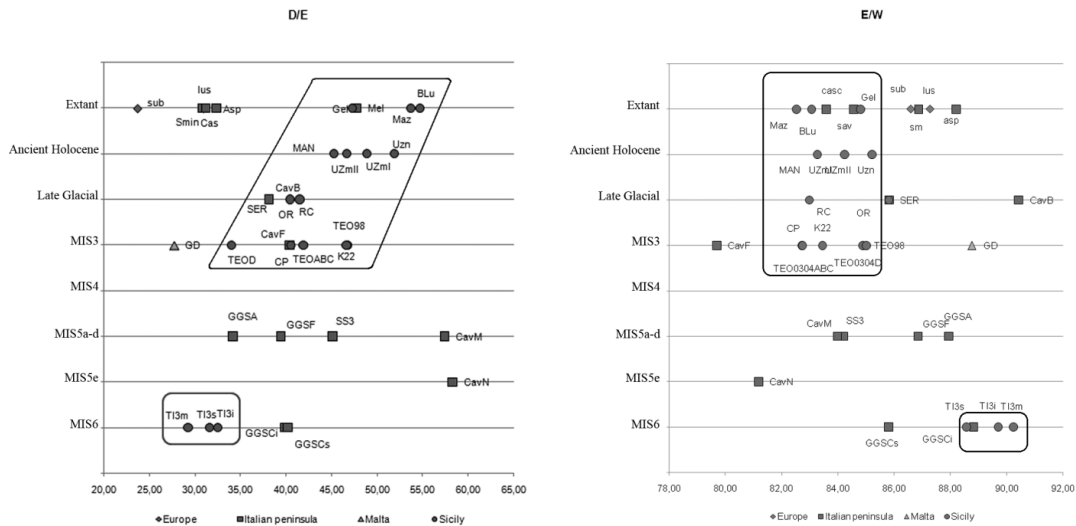


Figure III-6: scatter diagram of the variation of E/W ratio with time (MIS)

Figure III-7: scatter diagram of the variation of D/E ratio with time (MIS)

From MIS3 to Holocene, all Sicilian populations are very homogeneous in the E/W diagram (Figure III-6), showing slight variation as the living ones, but having smaller values (t6-t7 rhombus relatively smaller with respect to the pitymyan rhombus than in the continental populations). On the other hand, the anterior complex of Sicilian populations since MIS3 undergoes an opening (DE index), with the higher value found in the recent populations, thus increasing the distance with the northern samples that maintain rather small values. Considering all samples at the same time, E/W doesn't show a great variation (standard deviation of the mean values of E/W of each sample is 2.64), but D/E is highly variable (8.85) and extant northern populations are clearly separated from the Sicilian ones. Again, the recent Apulian population from Melendugno plots with the Sicilian samples, while the Aspromonte *Microtus (Terricola) brachycercus* is always within the *multiplex-subterraneus* group and the two Central Italy Savi populations.

A different pattern is shown by pre-Tyrrhenian samples. The Isolidda 3 populations are close to the contemporary continental samples from Grotta Grande di Scario, both in the E/W and in D/E diagrams. Fossil Apulian populations from levels M and N of Cavallo cave are well isolated from all the other ones in showing plesiomorphic features (namely, high values of D/E and low values of E/W).

### 4.3 PCA

In the PCA Figure III-8, we have considered the first two components that account for 75% of total variance (47,14% and 28,17% respectively, Table III-6).

Interpretation of the morphological meaning of components 1 and 2 is not particularly straight because most variables are correlated to both axes (see factor loadings Table III-7).



Thus, the PCA confirms the previous results. Populations of the same area and the same age tend to plot together in the PC1-2 diagram, with the exception of the Apulian samples. With regard to extant populations, samples from Calabria and Central Italy are clearly separated from those from Sicilian localities and from Apulia. The first are close to the *multiplex-subterraneus* voles, while the others tend to disperse on the opposite side. Fossil samples from Isolidda 3 are rather homogeneous and disperse close to Calabrian, Central Italian and *subterraneus* voles. Fossil samples from Grotta Grande di Scario are more scattered; they plot rather close to Isolidda 3 and the peninsular samples. The Sicilian populations of younger age (MIS2-3) are rather isolated (indicating high degree of endemism), plotting along the positive part of the Axis 1 (47,14% variance) and negative part of Axis 2; the sample of *Microtus (Terricola)* from Malta stands isolated in the same square and is characterized by extremely negative values of Component 2. The fossil sample for the Hyblean Plateau (Contrada Pianetti) is also apart from the other Sicilian samples, falling very close to the continental fossil populations. Apulian samples from Cavallo cave are the most scattered, even though they come from a single geographic location. In particular, there is a great difference between the ancient populations (CavM and CavN), which show very marked “*savimorph*” characters, and the more recent ones (CavF and CavB), which seem to be closer to the peninsular samples. San Sidero 3 plots in an intermediate position among extant Apulian *Terricola*, fossil Savi vole from Grotta Grande di Scario and the less “endemic” Würmian Sicilian samples.

## **5. Discussion**

The morphometric study of Southern Italian fossil *Microtus (Terricola)* revealed distinctive patterns, which give rise to a series of questions.

### **5.1 Size variation**

The comparison of the length of the first lower molar (Figure III-3) gives an immediate idea of the body size variation occurring in Sicilian samples and in the southern peninsula ones. Mammals in a “normal” continental regime may reduce or increase their size, always at a slight extent, mainly in relation to variation of climatic and environmental conditions (Bergmann rule), while on islands body size usually varies in one direction only and its variation is ruled mainly by several ecological factors typical of the island environment (e.g. area of the island, availability of resources, reduced predatory pressure etc.; Lomolino, 2005). By and large, according to the so-called “island rule” (Foster, 1964; Van Valen, 1973; Sondaar, 1977) geographic isolation on islands is expected to produce “giant” small mammals and “dwarfed” large mammals, i.e. small mammals should acquire a larger size respect to their mainland counterparts, while the reverse is expected in large mammals. The increase in size of small mammals may be explained by competitive interactions, that is by the benefit that a larger size gives in the individual exploitation of food supply in consideration of the small area of the island; the bigger they are, the best they prevail in the competition within the populations of the same species and/or with individuals of the other species. Sicily, indeed, is a sort of limited case for this rule, as it is a large island (the largest in the Mediterranean Sea) and it is separated from the mainland only by a sea corridor, the Strait of Messina. This particular geographical and geological configuration made the isolation unstable, at least from the Late Middle Pleistocene onwards, thus reducing the above mentioned effects on the faunal association and the body size variation.

Considering the mean value of the length (L) of each sample, Sicilian Savi vole are on average some 5% (computed on the mean L of each sample) larger than the peninsular populations of *Terricola*, but a distinction has to be made for samples of different age. The extant Sicilian populations are rather variable in size, but they are quite small, about the same size as the extant mainland ones. This homogeneity between insular and mainland populations could be due to frequent human and faunal exchanges between the island and the mainland, and to the influence of men on the insular mammals ecology (with the introduction of foreign taxa, terrestrial predators, habitat fragmentation for agriculture purposes and domestication) that has reduced, perhaps annulled, the insular condition and consequently the endemic evolutionary pressure (Sarà, 1998; Petruso et al., in press). A rather different situation can be observed in populations of the Early Holocene, when the Sicilian *Microtus (Terricola)* reached its maximum size, and in samples from Late Glacial and MIS3, where the difference with the coeval peninsular samples is nearly 8% (computed again among the means of L of each sample). Such a large size is in accordance with the general trend of size increase predicted for insular small mammals by the “island rule”. Even if we are not facing a true gigantism episode, the increment in size is conspicuous and is likely to be the result of isolation, perhaps of the reduced interspecific competitive pressure, since small mammal community is poor and other species of arvicolids are absent on the island. It should be noted, however, that the MIS3 time slice includes also two smaller-sized populations, from San Teodoro D (dated older than 33 ka) and, even more so, from Contrada Pianetti, which are in the range of extant populations of the Savi vole from Sicily and from the peninsula. We are inclined to exclude a climatic effect on the size variation for several reasons. First of all, extant samples from Tuscany are of the same size as those from Sicily, even though climatic conditions are different. Secondly, samples from MIS3 (younger levels of San Teodoro cave) and samples from the early Holocene at Uzzo Cave (UZ mII, UZ nI), have more or less the same size, even though climatic conditions are expected to be very different. Furthermore, a direct correlation between climate and body size has been excluded also by Piras et al. (2010), based on the study of extant populations. On the other hand, one should note that, even in peninsular populations, a very high variation in size occurs between samples from different geographical locations (e.g. Serratura Cave, Campania on the Tyrrhenian side, and Cavallo Cave layer B, Southern Salento, at the Ionian Sea), confirming that different ecological conditions may influence body size.

When considering the older samples (MIS5 a-d, MIS5e and MIS6) one can observe that the Sicilian samples from Isolidda 3 (TI3), here tentatively referred to MIS6, are smaller than those of MIS3 - Early Holocene, and have roughly the same size of extant Sicilian and peninsular Savi voles. When compared to samples of the same age, they are close to or even smaller than the peninsular ones (Grotta Grande di Scario). At Isolidda 3 the vole occurs after the disappearance of the endemic dormouse *Leithia* sp., but still together with very endemic small mammals such as *Maltamys* and *Crocidura esuae*, forming a poorly diversified assemblage, that suggests isolated conditions. In such a context, the small “normal” size of the vole might suggest the absence of endemism, and is a clue that Isolidda populations were rather close in time to the dispersal event of this species on the island, and therefore they had not yet achieved endemic features.

## 5.2 Morphological variation

The morphology of the anteroconid allows recognizing two distinct groups among the extant samples; according to Petruso (2003), they can be named as “savimorph” (from the Savi vole) and “subterraneomorph” (from the common pine vole). Even if almost all the *Microtus (Terricola)* here considered, except *Microtus (Terricola) lusitanicus*, and *Microtus (Terricola) subterraneus*, are referred to as *M. (T.)* ex gr. *savii* (i.e. they have a simplex M<sup>3</sup>, Chaline and Graf, 1988), the

anterior portion of the first lower molar shows a remarkable degree of variation that justifies such morphological distinction. In “subterraneomorph” populations, the anterior cap is more constricted (lower B and D, as can be seen in DE diagram of Figure III-6 and III-7) and the anteroconid is more elongated and articulated (higher A, A2 and E in III-4 and III-5); conversely, in the “savimorph” populations the anterior cap is less constricted, the anteroconid is shorter and looks more squat and asymmetric. This means that samples belonging to the first group plot closer to the *M. (T.) subterraneus* and *M. (T.) lusitanicus* populations, while the other ones plot on the opposite side in our PC1-2. The populations from Tuscany (San Miniato – Smin - and Cascina – Casc), and the one from Aspromonte (Calabria), are part of the subterraneomorph group, while all the Sicilian populations and the one from Meldendugno (Mel – Apulia), belong to the savimorph group. These observations, although based on a small number of samples (n=7), support the conclusions of Nappi et al. (2006) and Castiglia et al. (2008), who found a differentiation among Northern - Central and Southern Italy populations, more than the claim of Piras et al. (2010), who denied such differences. On the other hand, as already reported by Petruso (2003), the sample from Aspromonte is fairly distinct from the savimorph M<sub>1s</sub>. It is close to the Central Italy samples as well as to *M. (T.) lusitanicus* and *M. (T.) subterraneus* and must be referred to the species *M. (T.) brachycercus*. The occurrence of morphological distinction of *M. (T.) brachycercus* with respect to the other southern *Microtus (Terricola)* populations apparently does not support the conclusions of Nappi et al. (2005), while it has been recently confirmed by Piras (2010).

Considering the Early Holocene, Late Glacial and MIS3 time slices, one can observe that the savimorph group is still visible, particularly in plots which report the ACC elongations (AL and A2A). The savimorphs are also identifiable considering the width of t6-t7 complex (index E/W), with the exception of CavB, which displays, for this feature only, subterraneomorph values. On the other hand, considering the width of the anterior cap (index D/E), even though the two morpho-groups are still distinguishable, one can note in the savimorph populations a trend towards enlargement of the anterior cap in younger samples.

The Sicilian fossil populations from Oriente cave, Uzzo cave, Cala Mancina, K22, Castello Shelter, San Teodoro cave as well as the extant Sicilian samples can be clearly assigned to the savimorph group, notwithstanding the aforementioned differences in size in some of them. The Salento (Apulia) sample of Cavallo F (MIS2 in age) and the Serratura sample (Campania, Late Glacial) belong to this group as well, while sample CavB (Late Glacial) is distinguished by a very wide t6-t7, a feature that could denote a drift due to isolation or, perhaps, the phenotypic effects of migrations from central - north Italian peninsula.

When considering also the older time slices, the results are less straightforward.

The samples from Grotta Grande di Scario are rather homogenous and show intermediate characters between the two morpho-groups, fairly closer to the subterraneomorph group. The tooth looks quite elongated, but not as much as the extant Central Italy ones. It should be noted that the younger sample from the Serratura cave (SER) is close to Grotta Grande di Scario, but it has the smallest size.

The three samples from the oldest Sicilian deposit of Isolidda 3 are clearly distinct from the younger Sicilian samples. They are close to the extant subterraneomorph populations from Central Italy and to Grotta Grande di Scario samples (pre- and post-Tyrrhenian in age). They definitely cannot be included in the savimorph group and apparently they are not even very suitable ancestors to the later Sicilian Savi vole. The similarity with the continental Scario voles

coupled with the aforementioned “normal” size may be a further confirm that the Isolidda 3 vole is not much modified by the endemic evolution.

In this respect also the vole from Contrada Pianetti (MIS3) is somewhat distinct from the other Sicilian MIS3-Holocene populations, being smaller sized and morphologically closer to the Grotta Grande di Scario southern peninsular samples, thus suggesting a low degree of endemism.

The vole samples from Cavallo cave represent a remarkable case, as some of them show peculiar characters that cannot be found in any other sample. Firstly, there is a great difference among samples of different age. While younger samples (CavF – MIS3 and CavB – MIS2) are more similar to those coeval from the peninsula (see in AL, A2A and DE diagrams of Figure III-4, Figure III-5, Figure III-7 respectively), the oldest ones (CavN – MIS5e and CavM – MIS5d-a) are noticeably different from any other population in having a rather shorter ACC-AC2 and the widest neck of AC2 (D, D/E). Curcio et al. (2005) already noticed a peculiarity in the Apulian populations, which they linked to the possible role of glacial refuge assumed by this area during cold climatic oscillations. However, the most distinct morphology is shown by the sample from the “warm” Eemian layer N from Cavallo cave deposit. It has to be stressed that Cavallo cave is located at the extreme south of the Salento peninsula, and therefore it is peripheral respect to the species geographical range. The observed morphological divergence could be interpreted as the result of geographic isolation during the Eemian interglacial, while the minor divergence observed in the younger sample CavM is possibly the result of contacts with population from the peninsula that migrated southwards in response to the cooler climatic fluctuations of isotopic stage 5. As already mentioned, the Late Glacial vole from Cavallo cave (CavB) is distinct from the other savimorphs for having a wide t6-t7 rhombus, a feature which can denote contacts with more northern populations. On the other hand, the sample from the MIS5a-d Apulia site San Sidero 3 (SS3) has typical savimorph characters and is indistinguishable from smaller sized Sicilian samples and is also very close to the extant populations of Savi vole from Apulia (Mel).

*Microtus (Terricola) melitensis* from the Maltese site of Ghar Dalam (GD) is different from *Microtus (Terricola) savii* in having some strong subterraneomorph features (like the high E/W and the low D/E values, Figure III-6 and Figure III-7) coupled to a shorter ACC (AL and A2A in Figure III-4 and Figure III-5) and a wide constriction between the t6-t7 and the pitymyan rhombuses (high B and B/W). It is of a fairly large size, comparable with the bigger M<sub>1</sub> from the Sicilian sites, indicative of its endemic status, and is characterized by poorly differentiated enamel walls of the dental triangles, a feature that is primitive within genus *Microtus* (Martin, 1987; Petruso, 2003). Its M<sup>3</sup> is of the simplex type, as in the *savii* group (Petruso, 2003). Thus, the Ghar Dhalam sample displays a mixture of characters, some primitive and others more derived. The most parsimonious hypothesis is that the Maltese species derives from some primitive Sicilian populations belonging to the *savii* group – the Isolidda vole could be a suitable ancestor - that underwent a genetic drift resulting from a long isolation condition in a small island such as Malta, and bringing to the very conspicuous size recognized in the analysis (Figure III-3). Unfortunately, the age of such dispersal phase is unknown as no absolute dating but a relative chronological attribution to the Würmian, provided by Storch (1974) is available for this taxon, thus placing the Maltese taxon coeval with the Sicilian Savi vole, and opening several phylogenetic and paleogeographic problems.

### 5.3 The role of the climate



In the attempt of determining the factors acting on the variation of the tooth size and morphology, we cannot avoid to consider the role that climatic and environmental fluctuations could have played in generating such variation. As usual in the continental record of mammals, our sample does not allow to correlate finely the frequent and short climatic variations of the Middle - Late Pleistocene with the modifications in dental structure, as the palaeontological documentation is fragmentary in time (for example we miss populations of the MIS4) and space (we don't have samples of every area for every period) and the precise dating of the deposits is not always feasible. Nevertheless, it is possible to concentrate only on the major climatic events for checking evidences that support or contradict a big climatic influence on the characters analyzed.

If the morphological variation of the anteroconid of *Microtus (Terricola)* was correlated to environmental factors (change in temperature and humidity for instance), we should have found a high variation of measurements and indices in conformity with the major climatic fluctuations of the last glacial cycle, but considering the A/L, A2/A and E/W indices (Figure III-4, Figure III-5, Figure III-7) for the Sicilian samples during MIS3, Late Glacial and the ancient Holocene (a time span characterized by a dramatic climatic change), we do not find any significant variation. Furthermore, even if D/E index displays a strong difference between MIS3 and ancient Holocene, this difference is even stronger in living Sicilian populations and the variation is linear (a continuous increase) and so difficult to associate to climatic variations (ancient Holocene had dramatically different climatic conditions than LGM, Late Glacial and nowadays, with a strong increase in the mean temperature and humidity). This supports the hypothesis of a morphological stasis in extinct populations of *Microtus (Terricola)*, as suggested by Maul et al. (1998) and Piras et al. (2009).

According to Masini et al. (2008), climate affects insular biodiversity mainly as a promoter of dispersals from the mainland, and seems to have a minor impact on the evolution of the resident endemic species. Therefore, insular species can, in strongly isolated systems, last for a long time with minor, or no morphological modifications. In the samples analyzed and in the characters considered, we can't detect the effects of climate. This does not mean at all that morphology is not susceptible to environmental changes, but its influence cannot be read in our dataset, maybe because other factors are affecting stronger the variables analyzed. In our samples, the variation seems to be more correlated to phylogenetic factors, that is to the history of each population and their ancestors, at least on a finer scale.

Quite ironically, it is possible to detect traces of the climate molding in similarities among populations which are well separated in time and space. For example, the similarities between some extant and fossil Apulian samples (Mel, SS3, CavM) with the Sicilian ones is rather hard to be explained by a very strict phyletic link. It could be better explained as a homoplasy due to parallel evolution, likely as a response to quite similar environmental conditions between Sicily and the Salento peninsula.

Furthermore, it is possible to detect a north-south trend, with northern samples characterized by elongated teeth with constricted anteroconid, and southern samples (with the exception of the Calabrian population, that has been also assigned to a different species), whose anteroconid is shorter, compressed and made up of highly confluent triangles. These characters are the same pointed out by Nappi et al. (2006) and seem to be related to the geography of the area. Thus, if at a local scale it is not possible to correlate the variation of these features to environmental factors, traces of this relation are recognizable at a regional scale.

## 5.4 Dispersals to Sicily

Our data suggest that *M. (Terricola)* voles underwent at least two different dispersal events from Italian peninsula to Sicilian island (Figure III-9) during the Middle and Late Pleistocene.

This hypothesis is supported by the marked difference occurring among the older Sicilian samples from site Isolidda 3 and the younger Würmian (MIS3) populations, which resemble recent and fossil populations of Savi vole from the southern Italian peninsula. Although the occurrence of a gap in the documentation between Isolidda 3 and the younger samples requires caution, we feel that the hypothesis of a direct phyletic link between Isolidda 3 and the younger voles would imply the development of an amount of homoplasies, due to parallel evolution on the island and on the mainland, that is rather improbable. Furthermore, some smaller sized Würmian populations such as those from Contrada Pianetti or San Teodoro square D are suitable to be considered as new arrivals and ancestors of the endemic Savi vole populations of the island. Eventually, the dispersals of several taxa to the island during the Würmian render the hypothesis of the evolution in isolated conditions since the last-but-one glacial (MIS6) even more unlikely.

This leads to the following interpretation. The ancestor of the vole from Isolidda 3 first reached the island during an ancient low stand phase of the sea level, presumably during MIS6. The absence in Isolidda 3 samples of southern savimorph feature, their close similarity with the peninsular populations from the site of Grotta Grande di Scario (GGSC attributed to MIS6, as well as their small size, support the hypothesis of such an old dispersal for this vole, and that the age of Isolidda should be rather close to that of the dispersal event. The second dispersal from the peninsula involved *Microtus (Terricola) savii* populations already characterized by well developed “southern” savimorph features. Such dispersal might have occurred during the low stand phase related to the glacial peak of MIS4. Possibly MIS3, characterized by alternating cool and relatively warmer fluctuations, may have been a period of partial isolation for the Sicilian populations, allowing the voles to develop a large size. It is difficult to assess if the climate deterioration of MIS2 and the following Late Glacial. The probable connection with the mainland introduced the Epi-Paleolithic man onto the island, and consequently affected the evolution of the Sicilian voles by the introduction of continental populations or groups of individuals from the mainland. Actually, if it was so, such contacts did not influence the voles’ size, which are still large in the Late Glacial sites and particularly so in the ancient Holocene.

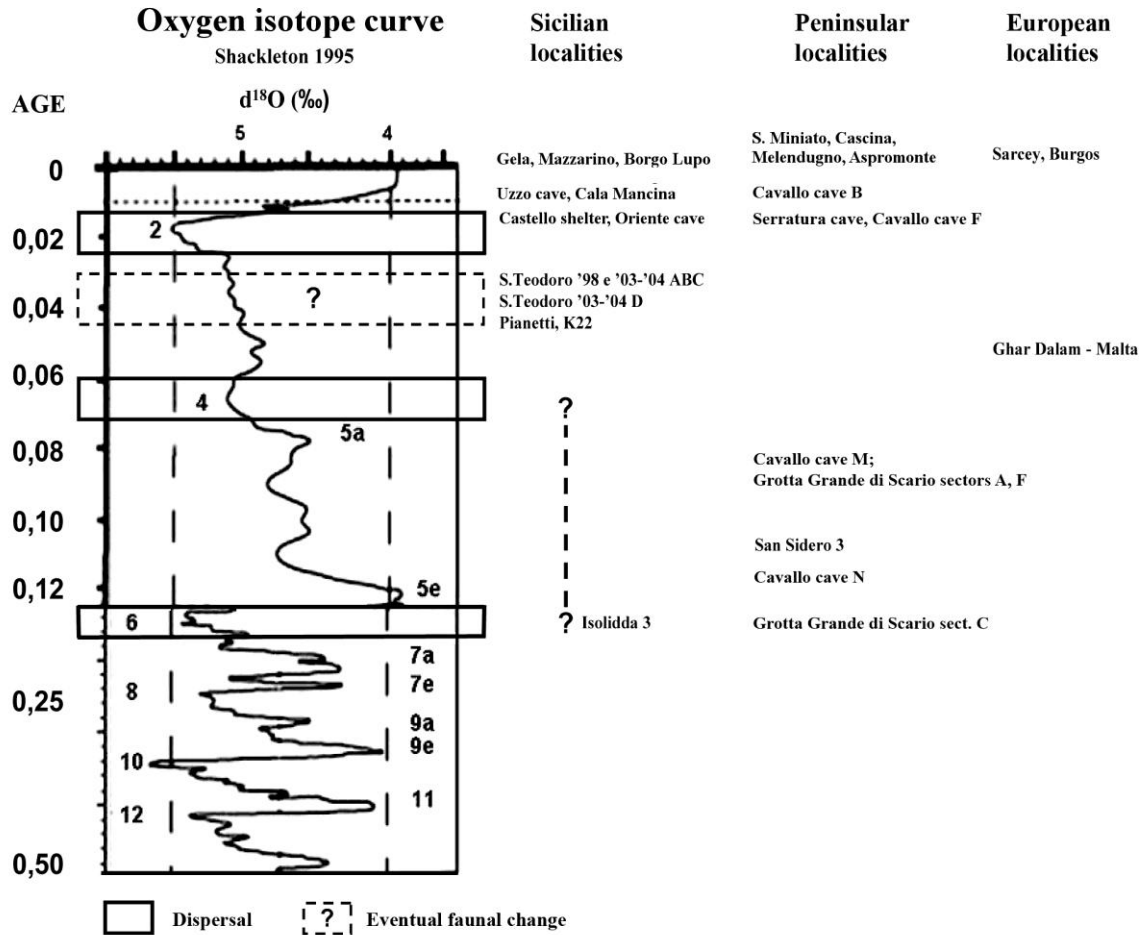


Figure III-9: temporal attribution of the samples and identification of eventual fauna changes and dispersal events

### Remarks

Before the discovery of Isolidda3 cave, no vole had been described in association with a strongly endemic fauna in Sicily. The oldest voles were recovered at K22, in association with newcomers from the mainland (*Apodemus* sp. and *Cervus elaphus* cf. *siciliae*), in “blocks” layer; Deeper and older deposits of the same site (“orange lens” and “red horizon”), are rich in endemics, among which giant dormice (*Leithia* ex gr. *melitenis-cartei* and *Maltamys* aff. *wiedincitensis*), but did not yield any remains of *M. (T.) savii* (Di Maggio et al., 1999). The latter deposits have been dated late Middle Pleistocene- Late Pleistocene; the blocks layer is considered Pleniglacial. At Isolidda 3, voles are found in association with *Crocidura esuae* and *Maltamys wiedincitensis*, elephant remains, but without *Leithia melitensis*. This layer documents an intermediate phase between the two faunas recorded at K22, since *Apodemus* had not reached the island yet while the endemics were still present (among which elephant remains). Whilst *M. (T.) savii* from Pleniglacial layer of K22 in the multivariate analysis plots with other Sicilian samples, *M. (T.)* recovered at Isolidda 3 is completely different and cannot be related to this species (see discussion below). Consequently, these deposits attest a previous arrival of the vole on the island, and since

it does not come alone (in the same US 15 we record the first occurrences in the site of *Sus Scrofa* and *Cervus elaphus siciliae*) we can hypothesize a faunal change with the mainland at the end of Middle Pleistocene during a phase of sea level low. Analysing the faunal succession at Isolidda3, we do not notice any sudden faunal change: *Leithia melitensis* is scarce in US19 and in US 17 is already disappeared; *Maltamys wiedincitensis* progressively decreases in relative abundance; *M. (T.) n. sp.* appears in US15 in a very low percentage (2.78%) and increases abruptly only later. This gradual transformation suggests a progressive change in the faunal succession, and discards the possibility of important gaps in the fossil documentation. Since even the uppermost layer (US12) records the contemporary presence of elephants and *M. wiedincitensis*, even the most recent layers seem to attest a quite ancient phase of the Late Pleistocene in Sicily, still referable to the *Elephas mnaidrensis* Faunal Complex.

## 6. Conclusions

The morphometric analysis of the first lower molars of *Microtus (Terricola)* from Sicily, Malta, peninsular Italy, France and Spain proved to be helpful in the attempt to reconstruct the phylogenetic relationships between Sicilian Savi vole and the peninsular ones as well as to detect the dispersal events from the mainland to the island.

The following points can be drawn.

1 – The analysis allows identifying, within the Savi vole sensu lato, two main morphotypes or morpho-groups that we call “subterraneomorph” – for the affinity with the common pine vole morphology - and “savimorph” – from the southern Savi vole populations.

2 – In the extant populations, we found a clear separation between Sicilian *Microtus (Terricola) savii* and the central peninsular populations (which show subterraneomorph features). These results are in agreement with Nappi et al. (2006) and Castiglia et al. (2008), but dissent with Piras et al. (2010). The Apulia population is close to Sicilian ones, in agreement with the occurrence of a “southern” group of Savi voles as affirmed by Nappi et al. (2006). The small size of the extant Savi vole of the island is likely due to the anthropogenic impact that reduces or cancels the effects of geographic isolation. As a by-product, although based on few samples, the morphological distinction of the Calabrian vole referred to *M. (T.) brachycercus*, already noticed by Petruso (2003), is supported by our analysis, in agreement also with Piras et al. (2010).

3 – Since the MIS3 till the early Holocene, the morphology of the fossil Sicilian Savi vole is close to the Southern Italy populations. Several Sicilian populations, however, show markedly larger size than continental ones, while few others are of the same size as the continental voles. Larger size is interpreted as an effect of geographic isolation. This would suggest that voles of the *savii* group during the Würmian glaciation dispersed from the mainland, and then became isolated, developing endemic features during the late part of the glaciation (Figure III-9). The possibility that some exchanges with the mainland repeatedly occurred during the cooler phases cannot be ruled out. This reconstruction is apparently in contrast with Castiglia et al. (2008), who suggested a species status for the Sicilian vole based on the divergence evidenced by molecular data. Indeed, one may suggest that isolation and drift may have played an important role in determine such a high divergence.

4 - Pre-Tyrrhenian Sicilian populations from the site Isolidda 3, referable to the last-but-one glaciation (MIS6), are distinctly different from post-MIS4 populations, and are closer to coeval population from the Tyrrhenian side of the peninsula, thus suggesting that they originate from an older dispersal event that took place during the sea - level low stand of MIS6 (Figure III-9).

5 - The *M. (T.) melitensis* sample from Ghar Dalam (Malta) is a mosaic of subterraneomorph and savimorph features, and occupies an isolate position. The result of our comparisons, as well as the primitive enamel pattern of the M<sub>1</sub>, apparently rules out its derivation from a Late Pleistocene Savi vole dispersed from Sicily, and support the hypothesis of an older dispersal.

6 – Climatic changes do not seem to have a direct effect on size and morphology of the insular voles, while dispersals from the mainland, likely stimulated by climatic driven environmental changes and facilitated by the eustatic effects of climatic changes, are the responsible of species substitution in the island.

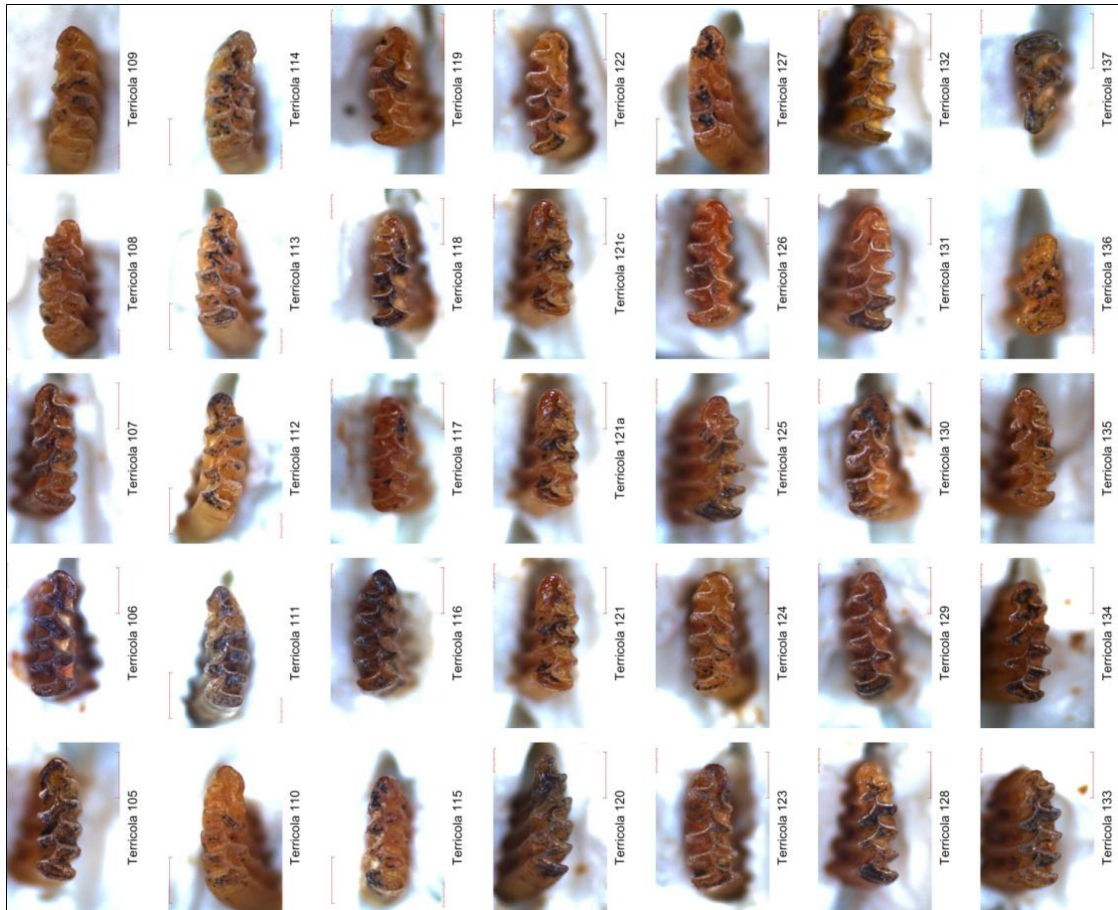
In summary, the work provides a large amount of original information regarding the Sicilian voles, and a new piece of information to the reconstruction of the evolutionary history of *Microtus (Terricola)* in the Southern Italian regions. It stresses that fossil evidence can provide valuable information in solving taxonomic puzzles, and that in order to fully comprehend the history of a group, all types of evidence need to be considered. Further studies, regarding both extant and fossil populations could help in unraveling the problems that are still open.



## Appendix Chapter III







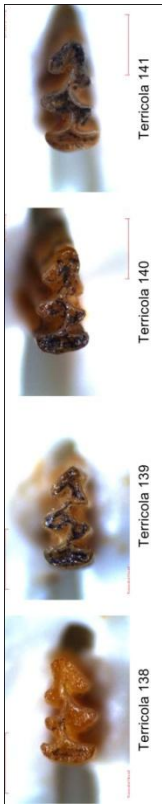


Plate 1: *Microtus (Terricola) n. sp.* From Isolidda 3 cave (all specimens)

Plate 2: *Microtus (Terricola) savii*, from Oriente cave

Plate 3: *Microtus (Terricola) savii*, Cala Mancina cave



ID	Us	L	A	A2	D	E	B	W	C	A/L	A2A	B/W	C/W	EW	D/W	D/E	L4	L5	WT	L45	
1	15	2.89	1.45	0.87	0.28	0.91	0.06	0.96	0.23	50.03	59.94	6.25	23.96	94.79	29.17	30.77	1.42	1.83	0.99	77.58	
2	15	2.80	1.45	0.94	0.12	0.83	0.01	0.91	0.18	51.60	64.62	1.10	19.78	91.21	13.19	14.46	1.37	1.71	1.03	80.05	
3	15	2.97	1.46	0.81	0.38	0.96	0.03	1.01	0.23	49.28	55.57	2.97	22.77	95.05	37.62	39.58	1.45	1.82	1.08	79.57	
4	15	2.82	1.50	0.96	0.24	0.90	0.03	0.96	0.17	53.35	63.63	3.13	17.71	93.75	25.00	26.67	1.43	1.74	1.09	81.94	
5	15	2.73	1.35	0.80	0.44	0.84	0.02	0.91	0.25	49.29	59.24	2.20	27.47	92.31	48.35	52.38					
6	15	2.79	1.48	0.88	0.30	0.76	0.03	0.89	0.17	52.97	59.32	3.37	19.10	85.39	33.71	39.47	1.48	1.74	1.01	84.98	
7	15	2.59	1.32	0.87	0.31	0.75	0.09	0.87	0.23	50.98	65.76	10.34	26.44	86.21	35.63	41.33	1.34	1.62	0.94	82.64	
8	15	2.77	1.45	0.88	0.19	0.85	0.01	0.97	0.15	52.35	60.97	1.03	15.46	87.63	19.59	22.35	1.35	1.71	1.08	78.56	
9	15	2.72	1.44	0.93	0.15	0.85	0.03	0.94	0.17	52.75	64.86	3.19	18.09	90.43	15.96	17.65	1.24	1.62	1.00	76.63	
10	15	2.85	1.45	0.89	0.31	0.80	0.05	0.92	0.18	50.93	61.43	5.43	19.57	86.96	33.70	38.75	1.44	1.80	1.08	80.12	
11	15	2.70	1.44	0.87	0.24	0.96	0.04	0.97	0.18	53.30	60.64	4.12	18.56	98.97	24.74	25.00	1.34	1.63	1.02	82.18	
12	15	2.76	1.46	0.94	0.25	0.78	0.03	0.88	0.21	52.75	64.79	3.41	23.86	88.64	28.41	32.05	1.37	1.67		82.06	
13	15	2.88	1.48	0.90	0.29	0.89	0.01	1.00	0.20	51.14	60.95	1.00	20.00	89.00	29.00	32.58	1.45	1.84	1.07	78.85	
14	15	1.51	0.93	0.30	0.81	0.03	0.86	0.23		61.73	3.49	26.74	94.19	34.88	37.04					0.96	
15	15	2.93	1.48	0.86	0.30	0.81	0.03	0.93	0.17	50.58	58.23	3.23	18.28	87.10	32.26	37.04				1.05	
16	15	2.89	1.45	0.87	0.32	0.76	0.03	0.85	0.21	50.22	59.68	3.53	24.71	89.41	37.65	42.11	1.44	1.78	1.00	81.26	
17	15	2.76	1.44	0.94	0.28	0.73	0.09	0.89	0.25	52.12	65.35	10.11	28.09	82.02	31.46	38.36	1.40	1.63	1.00	85.49	
18	15	2.68	1.38	0.85	0.36	0.75	0.02	0.88	0.20	51.38	61.76	2.27	22.73	85.23	40.91	48.00	1.31	1.73	0.96	76.13	
19	15	2.62	1.37	0.88	0.19	0.80	0.14	0.88	0.19	52.14	64.76	15.91	21.59	90.91	21.59	23.75	1.33	1.64	0.94	81.54	
20	15	2.86	1.33	0.70	0.53	0.85	0.02	0.91	0.26	46.47	52.22	2.20	28.57	93.41	58.24	62.35				1.04	
21	15				0.22			0.03													
22	15	2.48	1.28	0.76	0.12	0.72	0.02	0.86	0.15	51.43	59.69	2.33	17.44	83.72	13.95	16.67	1.25	1.46	0.96	85.71	
23	15	2.82	1.49	0.98	0.22	0.80	0.03	0.93	0.15	52.98	65.84	3.23	16.13	86.02	23.66	27.50	1.39	1.73	1.02	79.98	
24	15	2.92	1.56	0.94	0.32		0.02	1.00	0.20	53.48	60.26	2.00	20.00		32.00		1.41	1.70	1.05	82.82	
25	15				0.09	0.85	0.03	0.93	0.10			3.23	10.75	91.40	9.68	10.59				0.95	
26	15	2.84	1.47	0.91	0.16	0.84	0.02	0.97	0.19	51.80	61.67	2.06	19.59	86.60	16.49	19.05	1.38	1.77	1.07	77.77	
27	15						0.04	0.87	0.22			4.60	25.29				1.37	1.70	0.91	80.47	
28	15	2.76	1.43	0.89	0.24	0.85	0.03	0.93	0.22	51.98	61.83	3.23	23.66	91.40	25.81	28.24	1.37	1.71	0.99	79.95	
29	15							0.96	0.20			20.83					1.45	1.77	1.01	81.87	
30	15	2.62	1.39	0.91	0.25	0.81	0.05	0.87	0.22	53.29	64.99	5.75	25.29	93.10	28.74	30.86	1.27	1.54	0.97	82.30	
31	15	2.59	1.36	0.87	0.31	0.73	0.04	0.86	0.22	52.29	63.86	4.65	25.58	84.88	36.05	42.47	1.27	1.63	0.95	78.34	
32	15	2.73	1.45	0.90	0.21	0.87	0.02	0.90	0.14	53.25	62.16	2.22	15.56	96.67	23.33	24.14	1.37	1.72	0.99	79.62	
33	15	2.61	1.34	0.86	0.18	0.76	0.01	0.91	0.19	51.36	64.00	1.10	20.88	83.52	19.78	23.68	1.28	1.67	0.96	76.75	
34	15	3.00	1.58	1.02	0.19	0.89	0.01	0.92	0.16	52.82	64.54	1.09	17.39	96.74	20.65	21.35	1.45	1.79	1.01	81.05	
35	15	2.74	1.39	0.84	0.33	0.81	0.02	0.95	0.20	50.58	60.59	2.11	21.05	85.26	34.74	40.74	1.30	1.68	1.01	77.59	
36	15	2.80	1.39	0.87				0.91	0.20	49.61	62.46										
38	15	2.81	1.43	0.88	0.20	0.86	0.02	0.96	0.27	50.80	61.48	2.08	28.13	89.58	20.83	23.26	1.42	1.80	1.04	78.71	
39	15	2.77	1.45	0.85	0.20	0.83	0.02	0.97	0.19	52.49	63.39	2.06	19.59	85.57	20.93	26.10	1.47	1.77	1.01	83.13	
40	15	2.81	1.40	0.83	0.28	0.82	0.04	0.89	0.21	49.80	58.15	4.49	23.60	92.13	31.46	34.15	1.37	1.70	1.04	80.41	
41	15	2.49	1.16	0.59			0.04			20.00	46.50	30.61									
42	15	2.53	1.25	0.81	0.20	0.77	0.01	0.85	0.14	49.54	64.91	1.18	16.47	90.59	23.53	25.97	1.25	1.59		78.62	
43	15	2.71	1.37	0.83	0.40		0.01	0.92	0.20	50.59	60.56	1.09	21.74		43.48		1.32	1.64	1.01	80.33	

Table III-8: measurements of M1 from Isolidda 3 cave – US 15

ID	Us	L	A	A2	D	E	B	W	C	A/L	A2A	B/W	C/W	EW	D/W	D/E	L4	L5	WT	L45
46	13	2.88	1.48	0.92	0.20	0.86	0.01	0.95	0.19	51.28	61.91	1.05	20.00	90.53	21.05	23.26	1.42	1.85	1.04	76.51
47	13	2.60	1.38	0.87	0.38	0.75	0.04	0.86	0.20	53.25	62.91	4.65	23.26	87.21	44.19	50.67	1.33	1.64	0.96	81.27
48	13	2.62	1.37	0.90	0.26	0.83	0.01	0.89	0.13	52.12	65.47	1.12	16.85	93.26	29.21	31.33	1.24	1.63	0.98	76.32
49	13	2.73	1.42	0.82	0.29	0.80	0.01	0.90	0.18	52.13	57.99	1.11	20.00	88.89	32.22	36.25	1.34	1.73	0.99	77.42
50	13	2.72	1.42	0.86	0.25	0.80	0.01	0.88	0.19	52.30	60.52	4.55	15.59	90.91	28.41	31.25	1.39	1.73	0.96	80.24
51	13	2.77	1.42	0.84	0.20	0.84	0.01	0.88	0.17	51.21	59.53	1.14	19.32	95.45	22.73	23.81	1.25	1.75	1.02	76.81
52	13	2.71	1.41	0.84	0.21	0.74	0.01	0.81	0.20	51.77	59.72	1.23	24.69	91.36	25.93	28.38	1.42	1.65	0.90	86.09
53	13	2.80	1.48	0.95	0.24	0.82	0.01	0.86	0.16	53.00	64.10	1.16	18.60	95.35	27.91	29.27	1.40	1.75	0.98	80.25
54	13	2.76	1.40	0.80	0.20	0.86	0.01	0.91	0.17	50.85	56.66	1.10	18.68	94.51	21.98	23.26	1.41	1.70	0.96	82.72
55	13	2.72	1.32	1.19	0.20	0.83	0.02	0.90	0.16	48.55	135.81	2.22	17.78	92.22	22.22	24.10	1.41	1.64	0.98	86.26
56	13	2.55	1.30	0.78	0.17	0.76	0.01	0.88	0.09	51.04	59.88	1.14	10.23	86.36	19.32	22.37	1.31	1.66	0.96	78.63
57	13	2.61	1.39	0.88	0.23	0.74	0.03	0.78	0.20	53.02	63.47	3.85	25.64	94.87	29.49	31.08				
58	13	2.55	1.30	0.81	0.22	0.80	0.02	0.91	0.14	50.80	62.68	2.20	15.38	87.91	24.18	27.50	1.30	1.63	0.96	79.99
59	13	2.67	1.36	0.79	0.38	0.82	0.02	0.90	0.20	51.13	57.59	2.22	22.22	91.11	42.22	46.34	1.39	1.72	0.99	80.85
60	13	2.70	1.39	0.56	0.13	0.77	0.01	0.86	0.21	51.42	39.93	1.16	24.42	89.53	15.12	16.88	1.40	1.65	1.01	84.75
61	13	2.37	1.33	0.46	0.10	0.87	0.05	0.79	0.15	56.15	34.61	6.33	18.99	110.13	12.66	11.49	1.12	1.41	0.80	79.28
62	13	2.81	1.48	0.93	0.28	0.76	0.02	0.88	0.16	52.74	62.91	2.27	18.18	86.56	31.82	36.84	1.38	1.71	0.96	80.55
63	13	2.74	1.39	0.84	0.28	0.77	0.01	0.91	0.20	50.57	60.36	1.10	21.98	84.62	30.77	36.36	1.50	1.70	1.05	88.01
64	13	2.50	1.29	0.79	0.16	0.76	0.02	0.85	0.13	51.70	61.16	2.35	15.29	89.41	18.82	21.05	1.31	1.63	0.92	80.11
65	13	2.81	1.52	0.92	0.18	0.86	0.01	0.97	0.19	54.17	60.39	1.03	19.59	88.66	18.56	20.93	1.36	1.78	1.00	76.34
66	13	2.92	1.57	1.02	0.24	0.86	0.01	1.01	0.18	53.68	64.86	0.99	17.82	85.15	23.76	27.91	1.44	1.80	1.02	80.16
67	13	2.67	1.40	0.83																

ID	Us	L	A	A2	D	E	B	W	C	A/L	A2/A	B/W	C/W	EW	DW	DE	L4	L5	WT	L45	
91	12	2.50	1.40	0.92	0.16	0.77	0.03	0.88	0.19	55.87	65.62	3.41	21.59	87.50	18.18	20.78	1.25	1.53	0.94	82.18	
92	12	2.59	1.33	0.83	0.29	0.76	0.07	0.87	0.18	51.24	62.22	8.05	20.69	87.36	33.33	38.16	1.36	1.66	0.87	81.74	
93	12	2.63	1.35	0.74	0.32	0.77	0.04	0.86	0.19	51.47	54.70	4.65	22.09	89.53	37.21	41.56	1.33	1.65	0.93	80.63	
94	12																				
95	12	2.39	1.20	0.74	0.18	0.67	0.05	0.79	0.13	50.46	61.30	6.33	16.46	84.81	20.25	23.88	1.21	1.52	0.83	79.61	
96	12	2.51	1.19	0.67	0.44	0.67	0.03	0.84	0.17	47.50	55.88	3.57	20.24	79.76	52.38	65.67	1.37	1.73	0.96	79.48	
97	12	2.54	1.29	0.81	0.18	0.79	0.02	0.89	0.12	50.89	62.65	2.25	13.48	88.76	20.22	23.78	1.27	1.63	0.94	77.98	
98	12	2.65	1.45	0.95	0.16	0.78	0.01	0.90	0.14	54.55	65.47	1.11	15.56	86.67	17.78	20.51	1.26	1.60	0.97	79.04	
99	12	2.48	1.26	0.76	0.18	0.75	0.03	0.87	0.16	50.79	60.24	3.45	18.39	86.21	20.69	24.00	1.27	1.57	0.94	80.85	
100	12	2.39	1.37	0.80	0.30	0.87	0.07	0.98	0.21	57.25	58.57	7.14	21.43	88.78	30.61	34.48	1.37	1.74	1.09	78.71	
101	12	2.48	1.29	0.83	0.18	0.73	0.04	0.77	0.17	51.98	64.41	5.19	22.08	94.81	23.38	24.66	1.27	1.53	0.91	82.86	
102	12	2.60	1.36	0.82	0.26	0.75	0.00	0.84	0.17	52.09	60.10	0.00	20.24	89.29	30.95	34.67	1.35	1.64	0.92	82.30	
103	12	2.60	1.31	0.81	0.33	0.78	0.10	0.89	0.22	50.42	62.04	11.24	24.72	87.64	37.08	42.31	1.37	1.69	0.96	80.76	
104	12	2.58	1.38	0.81	0.39	0.77	0.01	0.88	0.14	53.51	58.44	1.14	15.91	87.50	44.32	50.65	1.34	1.64	0.96	81.25	
105	12	2.65	1.37	0.86	0.32	0.72	0.05	0.87	0.17	51.51	62.84	5.75	19.54	82.76	36.78	44.44	1.34	1.68	1.00	79.86	
106	12	2.80	1.47	0.91	0.25	0.75	0.05	0.84	0.24	52.47	62.06	5.95	28.57	89.29	29.76	33.33	1.41	1.74	0.98	80.82	
107	12	2.71	1.40	0.86	0.17	0.81	0.04	0.87	0.18	51.55	61.60	4.60	20.69	93.10	19.54	20.99	1.37	1.65	1.01	83.05	
108	12	2.55	1.27	0.76	0.16	0.85	0.02	0.94	0.16	49.86	59.51	2.13	17.02	90.43	17.02	18.82	1.32	1.67	1.02	78.67	
109	12	2.68	1.36	0.84	0.25	0.75	0.01	0.83	0.17	50.54	61.85	1.20	20.48	90.36	30.12	33.33	1.40	1.71	0.93	81.77	
110	12	2.62	1.34	0.85	0.28	0.85	0.04	0.88	0.16	51.14	63.34	4.55	18.18	96.59	31.82	32.94	1.34	1.64	1.00	81.90	
111	12	2.62	1.34	0.82	0.19					0.02	0.85	0.20	51.40	60.71	2.35	23.53		1.38	1.74	0.98	79.57
112	12	2.55	1.37	0.89	0.14	0.81	0.02	0.87	0.18	53.91	64.89	2.30	20.69	93.10	16.09	17.28	1.23	1.60	0.95	76.94	
113	12	2.54	1.38	0.87	0.18	0.75	0.02	0.91	0.19	54.13	63.35	2.20	20.88	82.42	19.78	24.00	1.31	1.65	0.99	79.28	
114	12	2.60	1.36	0.83	0.31	0.79	0.03	0.91	0.19	52.28	60.97	3.30	20.88	86.81	34.07	39.24	1.38	1.58	1.02	86.99	
115	12	2.49	1.25	0.72	0.39					0.17	50.06	57.30									
116	12	2.65	1.38	0.98	0.21	0.83	0.03	0.88	0.19	52.15	70.80	3.41	21.59	94.32	23.86	25.30	1.34	1.61	1.00	83.10	
117	12									0.29	0.68	0.05	0.79	0.19							
118	12	2.38	1.19	0.71	0.27	0.72	0.02	0.78	0.17	49.98	59.46	2.56	21.79	92.31	34.62	37.50	1.28	1.55	1.00	82.11	
119	12	2.57	1.36	0.90	0.38	0.75	0.15	0.92	0.21	52.84	66.67	16.30	22.83	81.52	41.30	50.67	1.32	1.62	0.95	81.50	
120	12	2.61	1.33	0.84	0.20	0.75	0.01	0.88	0.20	51.13	63.17	1.14	22.73	85.23	22.73	26.67	1.30	1.66	0.95	78.70	
121	12	2.53	1.25	0.73	0.32	0.79	0.03	0.92	0.16	49.50	58.08	3.26	17.39	85.87	34.78	40.51	1.35	1.62	0.93	83.23	
122	12	2.76	1.40	0.82	0.20	0.73	0.02	0.84	0.22	50.65	58.67	2.38	26.19	86.90	23.81	27.40	1.41	1.76	0.93	80.15	
123	12	2.72	1.44	0.97	0.27	0.90	0.04	0.96	0.13	52.83	67.62	4.17	13.54	93.75	28.13	30.00	1.31	1.54	1.04	85.03	
124	12	2.61	1.29	0.80	0.28	0.77	0.02	0.85	0.23	49.29	62.10	2.35	27.06	90.59	22.96	26.36	1.38	1.68	0.96	82.30	
125	12	2.71	1.41	0.87	0.31	0.84	0.02	0.92	0.18	51.99	61.91	2.17	19.57	91.30	33.70	36.90	1.33	1.68	0.96	78.97	
126	12	2.74	1.39	0.86	0.21	0.77	0.02	0.87	0.22	50.82	61.48	2.30	25.29	88.51	24.14	27.27	1.45	1.75	1.00	82.58	
127	12	2.57	1.31	0.81	0.26	0.73	0.07	0.89	0.20	50.86	61.54	7.87	22.47	82.02	29.21	35.62	1.26	1.58	0.97	80.19	
128	12	2.62	1.33	0.81	0.13	0.80	0.01	0.87	0.11	50.78	61.04	1.15	12.64	91.95	14.94	16.25	1.37	1.65	0.92	83.25	
129	12	2.46	1.36	0.85	0.38	0.77	0.03	0.85	0.18	55.54	61.95	3.53	21.18	90.59	44.71	49.35	1.30	1.61	0.93	80.81	
130	12	2.67	1.37	0.80		0.73	0.08	0.80	0.20	51.20	58.20	10.00	25.00	91.25			1.41	1.77	0.91	79.78	
131	12	2.72	1.36	0.83	0.19	0.85	0.02	0.97	0.12	50.09	61.14	2.06	12.37	87.63	19.59	22.35	1.31	1.73	1.06	75.72	
132	12	2.81	1.43	0.86	0.19	0.79	0.02	0.99	0.17	50.07	60.15	2.02	17.17	79.80	19.19	24.05	1.43	1.77	1.05	80.71	
133	12	2.52	1.29	0.77	0.23	0.80	0.01	0.87	0.09	51.03	59.88	1.15	10.34	91.95	26.44	28.75	1.32	1.59	0.97	83.41	
134	12	2.52	1.39	0.84	0.21	0.79	0.02	0.88	0.25	54.92	60.72	2.27	28.41	89.77	23.86	25.58	1.35	1.65	1.01	81.93	
135	12	2.57	1.31	0.80	0.36	0.80	0.07	0.88	0.17	50.91	61.47	7.95	19.32	90.91	40.91	45.00	1.31	1.68	0.96	77.80	

Table III-10: measurements of M1 from Isolidda 3 cave – US 12

ID	A2	A	L	W	B	E	D	C	s	WT	A/L	A2/A	B/W	EW	DW	CW	DE	L45	
1	0.78	1.39	2.67	0.92	0.02	0.78	0.27	0.20	1.89	1.67	1.02	0.52	0.56	0.02	0.85	0.40	0.22	0.47	0.83
2	0.80	1.37	2.67	0.82	0.03	0.67	0.25	0.20	1.41	1.65	0.96	0.51	0.59	0.03	0.82	0.31	0.24	0.38	0.85
3	0.88	1.50	2.90	0.92	0.05	0.83	0.38	0.19	1.51	1.78	1.02	0.52	0.59	0.05	0.90	0.41	0.20	0.46	0.85
4	0.89	1.46	2.83	0.93	0.12	0.82	0.45	0.23	1.45	1.77	1.02	0.52	0.61	0.13	0.88	0.49	0.24	0.55	0.82
5	0.76	1.32	2.83		0.01	0.76		0.21	1.60		1.03	0.47	0.57						
6	0.76	1.37		0.90	0.07	0.71	0.46	0.20		0.96		0.55	0.08	0.78	0.51	0.22	0.45		
7	0.92	1.49	2.97	0.91	0.04	0.78	0.40	0.20	1.57	1.90	1.01	0.50	0.62	0.04	0.85	0.44	0.22	0.51	0.83
8				0.90	0.04	0.75	0.38	0.14		1.02			0.04	0.83	0.42	0.16	0.51		
9	0.74	1.24	2.38	0.69	0.04	0.63	0.09	0.15	1.26	1.51	0.78	0.52	0.60	0.06	0.92	0.14	0.22	0.15	0.84
10				0.88	0.03		0.19	1.39	1.71	0.97							0.21		0.81
11	0.89	1.43	2.78	0.95	0.03	0.82	0.44	0.23	1.45	1.76	1.03	0.51	0.62	0.03	0.86	0.46	0.24	0.53	0.82
12	0.85	1.41	2.75	0.90	0.03	0.80	0.33	0.21	1.45	1.78	1.03	0.51	0.60	0.04	0.89	0.36	0.23	0.41	0.81
13	0.75	1.22		0.77	0.03	0.68	0.11	0.15		0.86		0.62	0.03	0.88	0.15	0.19	0.17		
14	0.77	1.35	2.72	0.92	0.06	0.84	0.53	0.25	1.44	1.73	1.00	0.50	0.57	0.06	0.91	0.57	0.25	0.43	0.83
15				0.92	0.03	0.84	0.18	0.11		1.00			0.03	0.91	0.18	0.12	0.21		
16	0.78	1.30	2.66	0.86	0.03	0.73	0.40	0.17	1.45	1.71	0.95	0.49	0.60	0.04	0.85	0.47	0.19	0.55	0.85
17	0.89	1.43	2.85	0.95	0.05	0.79	0.22	0.20	1.48	1.89	1.06	0.50	0.62	0.03	0.83	0.23	0.21	0.28	0.78
18	0.76	1.25	2.52	0.90	0.02	0.74	0.26	0.14	1.34	1.70	1.00	0.50	0.61	0.02	0.83	0.29	0.16	0.35	0.79
19	0.74	1.31	2.68		0.03	0.37	0.16	0.36		0.49	0.56								
20	0.77	1.28	2.59	0.87	0.07	0.69	0.30	0.20	1.40	1.69	0.86	0.49	0.60	0					

ID	A2	A	L	W	B	E	D	C	4	ξ	WT	AL	A2A	BW	EW	DW	CW	DE	L4ξ
1	0.79	1.44	2.93	0.93	0.03	0.78	0.49	0.20	1.52	1.94	1.08	0.49	0.55	0.03	0.84	0.53	0.21	0.63	0.79
2	0.83	1.47	2.89	0.93	0.02	0.77	0.30	0.22	1.46	1.79	1.10	0.51	0.57	0.02	0.83	0.33	0.23	0.40	0.82
3					0.03		0.52	0.25											
4				1.00	0.04		0.39	0.18		1.13				0.04		0.39	0.18		
5	0.76	1.33	2.66	0.91	0.01	0.78	0.45	0.11	1.42			0.50	0.57						0.57
6	0.93	1.52	2.92	0.91	0.03	0.80	0.31	0.18	1.41	1.76	1.09	0.52	0.61	0.03	0.88	0.34	0.20	0.39	0.80
7	0.75	1.22	2.46	0.88	0.05		0.24	0.13	1.29	1.59		0.50	0.62	0.05		0.27	0.15		0.81
8	0.98	1.59	3.05	0.93	0.02	0.75	0.19	0.17	1.64	1.95	1.09	0.52	0.62	0.02	0.81	0.20	0.18	0.25	0.85
9	0.86	1.40	2.80	0.86	0.04		0.31	0.19	1.43	1.76	1.08	0.50	0.61	0.05		0.36	0.23		0.81
10	0.96	1.48	2.77	0.83	0.04	0.78	0.28	0.21	1.39	1.71	0.98	0.53	0.65	0.05	0.93	0.33	0.25	0.36	0.81
11	0.88	1.40	2.79	0.90	0.03	0.76	0.29	0.17	1.45	1.78	0.95	0.50	0.63	0.03	0.84	0.33	0.19	0.39	0.81
12	0.92	1.52	2.95	0.95	0.02	0.76	0.36	0.20	1.50	1.86	1.05	0.51	0.61	0.02	0.80	0.38	0.21	0.47	0.80
13	0.90	1.46	2.88	0.88	0.03	0.77	0.29	0.18	1.52	1.79	1.01	0.51	0.62	0.03	0.87	0.33	0.21	0.38	0.85
14	0.71	1.29	2.69	0.92	0.02	0.76	0.51	0.21	1.51	1.80	1.08	0.48	0.56	0.02	0.83	0.55	0.22	0.66	0.84
15	0.83	1.46		0.97	0.02	0.76	0.33	0.21			1.08		0.57	0.02	0.78	0.34	0.22	0.44	
16				0.93	0.06	0.68	0.40	0.20	1.51	1.80	1.02			0.06	0.73	0.43	0.21	0.60	0.84
17	0.75	1.34	2.75		0.03		0.16	1.50	1.82			0.49	0.56						0.82
18	0.71	1.30		0.89	0.05		0.43	0.22			1.01		0.55	0.06		0.49	0.25		
19	0.94	1.45	2.72	0.85	0.03	0.71	0.30	0.19	1.38	1.61	0.94	0.54	0.65	0.03	0.83	0.36	0.22	0.43	0.85
20				0.97			0.26	1.61	2.02								0.27		0.80
21	0.86	1.44	2.91	0.91	0.04	0.74	0.48	0.23	1.55	1.92	1.04	0.49	0.59	0.04	0.81	0.52	0.26	0.64	0.81
22	0.85	1.48	2.86	0.91	0.02	0.72	0.16	0.20	1.45	1.84	1.01	0.52	0.58	0.02	0.80	0.17	0.22	0.21	0.79
23	0.83	1.37	2.68	0.88	0.05	0.73	0.41	0.23	1.44	1.72	1.01	0.51	0.60	0.05	0.82	0.47	0.25	0.57	0.84
24				0.92	0.02	0.78	0.36	0.20	1.57	1.84	1.01			0.02	0.85	0.39	0.22	0.46	0.85
25	0.51	1.10	2.47	0.86	0.03		0.15	1.45	1.77	0.99	0.44	0.46	0.03				0.17		0.82
26	0.81	1.40		0.92			0.15						0.58						
27	0.83	1.39	2.75	0.94	0.03	0.78	0.35	0.16	1.45	1.72		0.50	0.60	0.03	0.83	0.37	0.17	0.45	0.84
28	0.81	1.38	2.78	0.91	0.02	0.71	0.32	0.25	1.48	1.76	1.04	0.50	0.58	0.03	0.78	0.35	0.27	0.45	0.84
29				0.95	0.05		0.33	0.21	1.44	1.65									0.87
30				0.95	0.11	0.74	0.47	0.22			1.04			0.11	0.77	0.49	0.23	0.64	
31	0.69	1.21	2.57		0.03		0.26	0.18	1.37	1.70	0.93	0.47	0.57						0.81
32	0.89	1.45	2.85	0.96	0.06	0.79	0.30	0.17	1.48	1.79	1.06	0.51	0.61	0.06	0.83	0.31	0.18	0.38	0.83
33	0.78	1.45	2.92	0.93	0.05	0.79	0.47	0.27	1.60	1.90	1.07	0.50	0.54	0.06	0.85	0.51	0.29	0.60	0.84
34	0.82	1.43	2.85	0.93	0.05	0.77	0.37	0.19	1.49	1.92	1.01	0.50	0.57	0.06	0.83	0.40	0.21	0.48	0.78
35	0.80	1.42	2.87	0.93	0.06	0.81	0.41	0.28	1.53	1.85	1.06	0.50	0.56	0.06	0.87	0.43	0.30	0.50	0.83
36	0.90	1.47	2.84	0.96	0.03	0.81	0.28	0.23	1.42	1.83	1.04	0.52	0.62	0.03	0.84	0.30	0.24	0.35	0.77
37				0.26															
38				0.04			0.02	0.17											
39	0.82	1.41	2.85	0.96			0.24	1.51	1.75			0.50	0.58						0.87
40	0.64	1.27	2.66	0.82	0.01		0.31	0.28	1.49	1.77		0.48	0.50	0.01		0.37	0.33		0.84
41	0.86	1.42	2.81	0.89	0.03	0.78	0.23	0.18	1.47	1.82	1.06	0.50	0.61	0.03	0.87	0.26	0.20	0.30	0.81
42	0.84	1.45	2.96	1.01	0.03	0.82	0.46	0.22	1.59	1.92	1.08	0.49	0.57	0.03	0.81	0.46	0.22	0.56	0.83
43	0.87	1.54	3.06	1.01	0.04	0.82	0.42	0.19	1.64	2.00	1.12	0.50	0.57	0.04	0.81	0.42	0.19	0.51	0.82
44	0.91	1.45	2.89	0.97	0.02	0.77	0.26	0.18	1.52	1.93	1.04	0.50	0.62	0.02	0.80	0.26	0.19	0.33	0.79
45	1.03	1.60	3.03	0.97	0.16	0.81	0.38	0.20	1.61	1.93	1.07	0.53	0.64	0.17	0.84	0.39	0.20	0.47	0.83
46				0.93	0.03	0.84	0.25	0.23		1.09			0.03	0.91	0.27	0.25	0.30		
47				0.93	0.09		0.38	0.20		1.00			0.09		0.41	0.22			
48	0.74	1.32	2.81	0.88	0.03	0.73	0.42	0.18	1.53	1.89	1.03	0.47	0.56	0.04	0.83	0.48	0.20	0.58	0.81
49	0.88	1.45		0.90	0.02	0.78	0.45	0.19		0.94		0.61	0.03	0.86	0.50	0.21	0.58		
50	0.85	1.34	2.67	0.95	0.03	0.81	0.26	0.11	1.37	1.73		0.50	0.64	0.03	0.85	0.28	0.11	0.33	0.79
51	0.79	1.36	2.83	1.01	0.07	0.82	0.49	0.18	1.47	1.85	1.13	0.48	0.58	0.07	0.81	0.49	0.18	0.60	0.80
52	0.82	1.32		0.85	0.04	0.73	0.28	0.21		0.94		0.62	0.05	0.85	0.33	0.24	0.39		
53				0.88	0.08	0.71		0.19		1.00			0.09	0.81		0.21			
54	0.85	1.41	2.91	0.90	0.02		0.31	0.21	1.49	1.80		0.49	0.60	0.02		0.34	0.24		0.83
55	0.94	1.51	3.01	0.98	0.02	0.81	0.29	0.18	1.61	1.90	1.12	0.50	0.62	0.02	0.83	0.30	0.18	0.36	0.85
56	0.78	1.38	2.84	0.89		0.77		0.24	1.56	1.90	1.06	0.49	0.56		0.87		0.27		0.82
57	0.86	1.45	2.83	0.88	0.12	0.71	0.40	0.25	1.55	1.83	0.98	0.51	0.59	0.13	0.81	0.46	0.29	0.57	0.85
58	0.85	1.34	2.69	0.85	0.03	0.76	0.24	0.22	1.41	1.68	1.02	0.50	0.63	0.04	0.89	0.28	0.23	0.31	0.84
59	0.91	1.49	2.89	0.93	0.05		0.32	0.17	1.43	1.78	1.00	0.52	0.61	0.06		0.35	0.18		0.80
60	0.86	1.47	2.79	0.89	0.04	0.74	0.18	0.18	1.47	1.76	0.98	0.53	0.59	0.04	0.83	0.20	0.21	0.24	0.84

Table III-12: measurements of  $M_1$  from Cala Mancina



Sarcey-Rhone (FR)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	5	5	4	5	5	5	5	5	5	5	5	5	4	5	5	5	5	5	5
mean	2.55	1.34	0.9	0.83	0.15	0.02	0.72	0.17	0.93	1.23	1.59	52.64	66.02	2.38	18.3	20.44	86.59	23.67	77.68
SD	0.083	0.076	0.069	0.031	0.016	0.01	0.023	0.047	0.044	0.038	0.067	1.792	1.899	1.124	1.635	5.497	3.988	6.431	2.971
min	2.46	1.28	0.81	0.79	0.13	0.01	0.68	0.11	0.86	1.19	1.52	50.19	63.28	1.22	15.85	13.92	82.76	15.07	72.62
max	2.65	1.45	0.96	0.87	0.17	0.03	0.74	0.23	0.98	1.29	1.68	54.72	67.44	3.53	20	27.06	92.41	31.08	80.26
i.c. 95%	0.07	0.07	0.07	0.03	0.01	0.01	0.02	0.04	0.04	0.03	0.06	1.57	1.86	0.99	1.43	4.82	3.5	5.64	2.6
Lamilla-Burgos (E)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27	27
mean	2.67	1.4	0.9	0.88	0.17	0.03	0.77	0.24	0.95	1.27	1.67	52.53	64.06	3.49	19.34	26.99	87.28	30.91	76.15
SD	0.11	0.08	0.06	0.05	0.03	0.02	0.05	0.04	0.06	0.06	0.07	1.44	1.88	2.47	3.22	4.4	2.32	4.91	2.21
min	2.44	1.27	0.79	0.75	0.11	0.01	0.67	0.12	0.79	1.17	1.53	49.44	60.61	1.11	12.22	15	83.75	17.39	72.47
max	2.94	1.61	1.08	0.97	0.22	0.12	0.86	0.35	1.05	1.42	1.81	54.76	67.36	12.9	24.44	37.63	92.77	43.21	79.88
i.c. 95%	0.04	0.03	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.03	0.54	0.71	0.93	1.21	1.66	0.87	1.85	0.84
Melendugno (LE)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	32	32	32	32	32	32	32	32	32	32	32	32	31	32	32	32	32	32	32
mean	2.77	1.4	0.82	0.89	0.2	0.04	0.74	0.35	1.02	1.4	1.78	50.44	61	4.74	22.17	39.77	83.59	47.75	78.95
SD	0.14	0.09	0.16	0.05	0.03	0.03	0.05	0.09	0.05	0.08	0.07	1.38	2.39	3.15	3.75	10.2	5.47	12.66	2.28
min	2.52	1.21	0	0.77	0.13	0.01	0.65	0.22	0.92	1.29	1.63	48.02	55.56	1.01	13.68	23.66	74.23	28.21	73.77
max	3.01	1.55	0.96	0.99	0.26	0.12	0.84	0.54	1.12	1.56	1.91	53.61	65.97	13.64	28.74	62.07	100	77.14	83.61
i.c. 95%	0.05	0.03	0.06	0.02	0.01	0.01	0.02	0.03	0.02	0.03	0.02	0.48	0.84	1.09	1.3	3.53	1.89	4.39	0.79
San Miniato (PI)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	38	38	38	37	38	38	38	38	38	38	38	38	38	37	37	37	37	38	38
mean	2.71	1.41	0.91	0.89	0.18	0.03	0.77	0.24	0.94	1.34	1.69	52.04	64.5	3.12	20.39	26.36	86.82	30.6	79.4
SD	0.153	0.104	0.068	0.062	0.039	0.012	0.054	0.097	0.069	0.077	0.092	1.46	2.494	1.272	3.864	9.801	3.451	11.94	7.439
min	2.31	1.19	0.78	0.71	0.08	0.02	0.58	0.06	0.76	1.18	1.44	50	57.27	2.05	9.09	8.77	80	10.53	74.44
max	3	1.72	1.09	1.03	0.24	0.08	0.85	0.54	1.08	1.48	1.88	57.89	68.09	8.42	26.47	53.75	93.94	67.19	82.35
i.c. 95%	0.05	0.03	0.02	0.02	0.01	0	0.02	0.03	0.02	0.02	0.03	0.46	0.79	0.41	1.25	3.16	1.11	3.8	0.55
Cascina (PI)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	45	45	45	45	45	45	44	45	45	45	45	45	45	45	45	45	44	44	45
mean	2.6	1.35	0.86	0.86	0.18	0.03	0.72	0.23	0.92	1.29	1.63	52.12	63.58	3.47	21.07	26.42	84.56	31.21	79.38
SD	0.124	0.066	0.056	0.044	0.033	0.019	0.033	0.082	0.055	0.093	0.098	1.364	2.13	2.054	3.766	8.816	3.384	11.085	1.734
min	2.34	1.22	0.78	0.78	0.13	0.02	0.66	0.1	0.8	1.14	1.46	48.3	58.14	2.11	14.49	12.5	75	14.29	76
max	2.91	1.56	1.03	0.95	0.24	0.1	0.8	0.48	1.04	1.64	1.9	54.97	67.42	10.96	28.36	52.05	92.54	63.33	86.32
i.c. 95%	0.04	0.02	0.02	0.01	0.01	0.01	0.01	0.02	0.02	0.03	0.03	0.4	0.62	0.6	1.1	2.58	1	3.28	0.51
Aspromonte (RC)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	30	30	30	27	30	30	28	30	29	30	29	30	30	27	27	27	26	28	29
mean	2.65	1.38	0.87	0.91	0.17	0.05	0.8	0.26	0.98	1.25	1.66	52.22	63.11	5.59	19.65	28.71	88.2	32.38	75.41
SD	0.133	0.083	0.058	0.059	0.042	0.02	0.068	0.071	0.049	0.083	0.084	1.197	1.886	2.032	4.822	7.759	3.908	9.09	3.279
min	2.35	1.23	0.78	0.81	0.07	0.02	0.68	0.15	0.88	1.08	1.44	49.6	58.57	2.22	9.28	15	82.22	17.05	69.32
max	2.84	1.55	1.01	1.02	0.25	0.1	0.9	0.48	1.08	1.44	1.76	54.77	67.38	10	28.4	45.45	94.44	54.05	82.93
i.c. 95%	0.05	0.03	0.02	0.02	0.02	0.01	0.03	0.03	0.02	0.03	0.03	0.43	0.68	0.77	1.82	2.93	1.5	3.37	1.19
Borgo Lupat (IP)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	22	22	22	21	22	22	22	22	21	22	21	22	22	21	21	21	21	22	21
mean	2.68	1.37	0.83	0.87	0.18	0.06	0.73	0.39	0.97	1.31	1.73	51.1	60.52	6.43	21.36	44.53	83.07	53.74	75.66
SD	0.122	0.09	0.076	0.05	0.043	0.03	0.061	0.097	0.057	0.077	0.086	1.765	2.32	3.549	4.952	11.382	4.345	13.996	3.144
min	2.41	1.25	0.7	0.8	0.12	0.02	0.62	0.15	0.84	1.18	1.54	48.45	56	2.13	13.48	16.13	72.94	20	68.6
max	2.95	1.62	1.05	0.97	0.25	0.12	0.8	0.5	1.1	1.42	1.86	54.93	64.81	13.33	28.05	60.98	88.89	75.81	82.93
i.c. 95%	0.05	0.04	0.03	0.02	0.02	0.01	0.03	0.04	0.02	0.03	0.04	0.74	0.97	1.52	2.12	4.87	1.86	5.85	1.34
Piana di Gela (CL)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	26	26	26	26	26	26	26	26	25	26	26	26	26	26	26	26	25	25	26
mean	2.57	1.28	0.76	0.85	0.19	0.07	0.69	0.34	0.97	1.32	1.7	49.9	59.5	8.06	21.96	40.16	84.81	47.32	77.54
SD	0.127	0.08	0.07	0.04	0.04	0.03	0.15	0.09	0.05	0.09	0.08	1.87	2.83	3.82	4.83	11.17	4.94	13.4	2.4
min	2.34	1.1	0.6	0.75	0.06	0.04	0	0.17	0.9	1.16	1.56	45.42	53.91	4.44	7.06	20	77.27	24.64	71.6
max	2.85	1.44	0.84	0.93	0.23	0.16	0.8	0.5	1.1	1.48	1.82	53.06	64.8	18.82	30.67	66.67	94.12	80.65	82.22
i.c. 95%	0.05	0.03	0.03	0.02	0.01	0.01	0.06	0.03	0.02	0.03	0.03	0.72	1.09	1.47	1.86	4.3	1.94	5.25	0.92
Mazzarino (CL)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	11	11	12
mean	2.73	1.38	0.81	0.92	0.18	0.07	0.7	0.42	1.01	1.4	1.79	50.42	58.68	7.98	19.52	45.37	82.53	54.73	78.18
SD	0.18	0.1	0.07	0.05	0.05	0.03	0.23	0.1	0.07	0.11	0.12	1.11	1.49	3.25	5.02	10.35	6.07	15.68	2.88
min	2.45	1.24	0.71	0.82	0.1	0.04	0	0.23	0.88	1.26	1.64	48.04	57.26	4.71	11.11	28.05	74.23	33.33	74.16
max	3	1.5	0.89	1	0.25	0.14	0.9	0.57	1.12	1.54	2	52.19	62.24	15.05	26.88	60.64	92.63	79.17	83.7
i.c. 95%	0.1	0.05	0.04	0.03	0.03	0.02	0.13	0.06	0.04	0.06	0.07	0.63	0.85	1.84	2.84	5.85	3.59	9.27	1.63
Uzzo Cave (IP) I	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n																			

Cala Mancina (TP)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	43	48	48	51	59	57	42	53	46	47	46	43	48	49	51	47	41	40	46
mean	2.82	1.41	0.83	0.92	0.2	0.04	0.77	0.34	1.04	1.49	1.81	50.08	58.95	4.54	22.02	37.27	83.28	45.26	82.22
SD	0.136	0.095	0.09	0.046	0.036	0.027	0.037	0.1	0.053	0.077	0.096	0.018	0.036	0.03	0.04	0.093	0.037	0.124	0.023
min	2.46	1.1	0.51	0.82	0.11	0.01	0.68	0.02	0.93	1.29	1.59	44.28	46.48	1.09	11.45	17.09	72.5	21.41	77.42
max	3.06	1.6	1.03	1.01	0.28	0.16	0.84	0.52	1.13	1.64	2.02	53.52	64.83	16.79	33.45	55.12	93.04	66.32	87.38
i.c.95%	0.04	0.03	0.03	0.01	0.01	0.01	0.01	0.03	0.02	0.02	0.03	0.01	0.01	0.01	0.01	0.03	0.01	0.04	0.01

Castello shelter (PA)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	5	6	6	6	6	6	6	6	5	5	5	5	6	6	6	5	5	6	5
mean	2.91	1.46	0.9	0.94	0.22	0.07	0.79	0.32	1.07	1.56	1.83	50.45	61.81	7.41	23.95	32.94	82.99	40.49	85.34
SD	0.081	0.032	0.035	0.058	0.042	0.021	0.032	0.055	0.033	0.075	0.077	1.263	2.857	1.923	5.267	6.019	5.351	7.887	1.989
min	2.81	1.41	0.86	0.88	0.15	0.04	0.73	0.25	1.04	1.48	1.72	48.45	58.51	4.57	15.38	25.64	76.54	31.25	82.98
max	3.03	1.5	0.94	1.01	0.28	0.1	0.81	0.39	1.12	1.68	1.92	51.61	65.22	9.88	31.43	40	91.43	50	87.5
i.c.95%	0.07	0.03	0.03	0.05	0.03	0.02	0.03	0.04	0.03	0.07	0.07	1.11	2.29	1.54	4.21	5.28	4.69	6.31	1.74

Oriente Cave - Favignana island (TP)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	28	31	31	35	38	41	34	35	33	31	29	28	31	35	33	31	32	32	29
mean	2.74	1.37	0.82	0.89	0.2	0.04	0.76	0.31	0.99	1.45	1.75	50.4	59.77	4.67	21.97	34.68	85.22	41.53	82.73
SD	0.135	0.087	0.072	0.06	0.038	0.023	0.054	0.122	0.071	0.074	0.091	0.015	0.024	0.025	0.04	0.128	0.034	0.154	0.028
min	2.38	1.22	0.74	0.69	0.11	0	0.63	0.08	0.78	1.26	1.51	46.67	55.14	0.44	12.12	9.48	78.1	11.42	77.95
max	2.97	1.59	1.03	0.99	0.28	0.12	0.84	0.53	1.13	1.6	1.9	54.87	64.55	12.69	30.2	57.39	92.02	65.3	89.13
i.c.95%	0.05	0.03	0.03	0.02	0.01	0.01	0.02	0.04	0.02	0.03	0.03	0.01	0.01	0.01	0.01	0.05	0.01	0.05	0.01

Serratura Cave (SA)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	92	96	96	87	96	96	85	93	95	93	92	92	96	87	87	84	81	84	92
mean	2.49	1.27	0.78	0.83	0.18	0.04	0.72	0.28	0.88	1.24	1.59	51.13	61.16	5.15	22.11	32.51	85.82	38.13	78.43
SD	0.118	0.079	0.068	0.048	0.032	0.026	0.05	0.07	0.049	0.056	0.08	1.477	2.497	3.306	4.302	7.57	4.207	9.153	2.031
min	2.16	1.09	0.64	0.7	0.05	0.02	0.6	0.11	0.72	1.08	1.2	47.77	55.13	2.19	5.06	13.04	73.53	14.29	75
max	2.81	1.56	1.03	0.99	0.25	0.14	0.81	0.5	1.04	1.36	1.76	55.56	66.27	16.47	33.33	54.05	95	64.15	90
i.c.95%	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.3	0.5	0.69	0.9	1.62	0.92	1.96	0.42

Cavallo Cave (LE) layer B	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	18	26	26	24	28	29	23	28	26	23	24	18	26	24	24	23	20	23	23
mean	2.74	1.4	0.86	0.82	0.18	0.03	0.72	0.27	0.91	1.38	1.72	51.04	61.06	4.01	21.96	33.06	90.42	38.14	80.07
SD	0.104	0.075	0.066	0.097	0.034	0.019	0.071	0.076	0.098	0.059	0.072	1.009	2.162	2.103	5.599	11.687	12.301	12.82	2.494
min	2.55	1.25	0.74	0.63	0.12	0.01	0.53	0.09	0.7	1.24	1.57	49.02	56.3	1.12	12.5	14.13	76.4	12.5	73.6
max	2.92	1.52	1	0.96	0.24	0.08	0.95	0.4	1.12	1.47	1.85	52.78	65.79	8.22	38.1	57.81	115.85	69.81	85.45
i.c.95%	0.05	0.03	0.03	0.04	0.01	0.01	0.03	0.04	0.04	0.02	0.03	0.47	0.83	0.84	2.24	4.78	5.39	5.24	1.02

K22 (IP)	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	35	35	35	35	35	35	35	34	35	35	35	35	35	35	35	34	35	34	35
mean	2.8	1.4	0.82	0.93	0.2	0.04	0.78	0.37	1.05	1.47	1.82	50.05	58.24	3.97	22.02	38.99	83.46	46.77	81.05
SD	0.13	0.078	0.066	0.055	0.041	0.014	0.054	0.096	0.055	0.098	0.105	1.582	3.082	1.49	4.863	10.057	4.41	12.472	2.573
min	2.58	1.26	0.66	0.84	0.08	0.01	0.67	0.21	0.94	1.29	1.64	46.21	51.56	1.11	8.08	23.08	74.23	26.92	76.84
max	3.16	1.66	1.02	1.06	0.29	0.07	0.92	0.58	1.16	1.64	2.01	53.56	63.97	7.22	30.53	61.7	91.01	81.69	87.23
i.c.95%	0.04	0.03	0.02	0.02	0.01	0	0.02	0.03	0.02	0.03	0.03	0.52	1.02	0.49	1.61	3.38	1.46	4.19	0.85

S.Teodoro Cave (ME) trench 1998	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22
mean	2.93	1.5	0.89	0.99	0.21	0.05	0.84	0.39	1.12	1.49	1.83	51.02	59.22	4.76	20.76	39.61	84.9	46.64	81.38
SD	0.129	0.081	0.07	0.052	0.039	0.019	0.06	0.088	0.054	0.095	0.096	1.492	2.759	1.928	3.76	8.19	29.49	9.467	2.794
min	2.67	1.34	0.73	0.93	0.14	0.02	0.75	0.26	1	1.32	1.62	47.47	51.77	1.96	14.29	26.8	80.41	31.71	73.47
max	3.14	1.66	1.02	1.09	0.3	0.1	0.95	0.55	1.2	1.72	2	52.88	64.08	9.8	29.41	55.79	91.18	67.95	86.96
i.c.95%	0.05	0.03	0.03	0.02	0.02	0.01	0.03	0.04	0.02	0.04	0.04	0.62	1.15	0.81	1.57	3.42	1.23	3.96	1.17

S.Teodoro Cave (ME) trench 2003-04 ABC sectors	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	12	12	12	11	12	11	12	12	11	12	11	12	12	10	11	11	11	12	11
mean	2.98	1.52	0.91	1.05	0.21	0.06	0.87	0.36	1.04	1.57	1.82	50.82	59.76	5.31	19.9	35.33	82.75	41.92	86.73
SD	0.108	0.083	0.073	0.064	0.037	0.018	0.092	0.083	0.1	0.12	0.147	1.723	2.75	1.673	3.916	7.939	8.47	9.1	3.108
min	2.81	1.38	0.75	0.95	0.13	0.03	0.7	0.25	0.75	1.28	1.44	47.37	53.33	3	11.63	27.5	65.12	30.56	80
max	3.19	1.63	1	1.19	0.25	0.09	1.03	0.53	1.12	1.72	2	53.13	63.83	7.89	26.32	55.26	92.11	60	91.49
i.c.95%	0.06	0.05	0.04	0.04	0.02	0.01	0.05	0.05	0.06	0.07	0.09	0.98	1.56	1.04	2.31	4.69	5.01	5.15	1.84

S.Teodoro Cave (ME) trench 2003-04 D sector	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	16	16	16	16	16	14	16	15	16	16	16	16	16	14	16	15	16	15	16
mean	2.75	1.42	0.86	0.93	0.21	0.05	0.79	0.27	0.96	1.46	1.69	51.6	60.37	5.64	21.77	28.63	85.02	34.03	86.26
SD	0.101	0.075	0.077	0.043	0.028	0.017	0.046	0.069	0.059	0.06	0.058	1.949	3.581	1.573	2.986	7.293	3.857	9.35	2.766
min	2.59	1.31	0.72	0.85	0.15	0.04	0.7	0.18	0.84	1.36	1.6	48.84	53.49	4.21	15.79	18.42	78.95	21.21	81.82
max	2.94	1.5																	

Grotta Grande di Scario (SA) trench																			
A	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	16	18	18	17	16	17	16	18	18	16	16	16	18	16	16	17	16	16	16
mean	2.61	1.37	0.84	0.86	0.21	0.04	0.76	0.27	0.91	1.29	1.64	52.6	61.13	4.32	23.87	31.13	87.94	34.19	78.71
SD	0.101	0.057	0.065	0.051	0.038	0.014	0.055	0.078	0.046	0.059	0.072	1.461	3.142	1.712	4.596	8.822	3.587	9.017	1.32
min	2.42	1.3	0.75	0.8	0.13	0.02	0.68	0.13	0.86	1.2	1.5	50.56	55.88	2.35	13.54	15.48	82.35	16.25	76.92
max	2.75	1.5	1	0.96	0.28	0.08	0.85	0.43	1	1.38	1.78	54.55	66.67	9.64	32.94	50.59	95.24	52.56	80.52
i.c. 95%	0.05	0.03	0.03	0.02	0.02	0.01	0.03	0.04	0.02	0.03	0.04	0.72	1.45	0.84	2.25	4.19	1.76	4.42	0.65

Grotta Grande di Scario (SA) trench																			
F	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	24	24	24	20	23	24	22	24	23	23	23	24	24	20	19	20	20	22	23
mean	2.71	1.39	0.84	0.92	0.2	0.05	0.8	0.32	0.95	1.35	1.73	51.36	60.22	4.87	21.55	34.46	86.85	39.49	77.84
SD	0.126	0.089	0.081	0.065	0.033	0.019	0.052	0.076	0.053	0.078	0.088	1.978	3.053	2.069	3.966	7.993	4.615	8.81	2.458
min	2.47	1.25	0.72	0.75	0.13	0	0.73	0.21	0.84	1.2	1.6	48.13	54.76	0	13.16	25	81.08	26.15	74.16
max	2.92	1.59	1.05	1.05	0.28	0.08	0.91	0.5	1.04	1.52	1.94	54.95	67	8.53	30	51.67	96.67	55.17	84.44
i.c. 95%	0.05	0.04	0.03	0.03	0.01	0.01	0.02	0.03	0.02	0.03	0.04	0.79	1.22	0.91	1.78	3.5	2.02	3.68	1

Cavallo Cave (LE)																			
layer M	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	43	45	45	43	45	45	43	45	43	45	43	43	45	43	43	43	42	43	43
mean	2.73	1.35	0.79	0.88	0.2	0.05	0.74	0.35	0.97	1.44	1.77	49.69	58.11	5.4	23.07	40.5	83.98	47.92	81.67
SD	0.136	0.09	0.07	0.063	0.042	0.031	0.057	0.076	0.075	0.07	0.092	1.59	2.574	3.507	5.081	8.14	4.979	10.278	2.486
min	2.33	1.14	0.63	0.7	0.11	0.01	0.57	0.18	0.71	1.26	1.59	45.1	49.61	1.14	12.36	22.47	73.63	25.97	76.53
max	3	1.52	0.9	0.99	0.28	0.17	0.84	0.54	1.11	1.59	1.96	52.78	62.59	18.28	31.51	58.24	98.63	70.13	87.95
i.c. 95%	0.04	0.03	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.03	0.48	0.75	1.05	1.52	2.43	1.51	3.07	0.74

San Sidero 3 (LE)																			
L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5	
n	24	24	24	24	24	24	23	24	24	24	24	24	24	24	24	23	23	24	
mean	2.79	1.43	0.86	0.92	0.21	0.03	0.77	0.35	1.01	1.42	1.79	51.27	60.03	3.38	22.53	37.74	84.21	44.75	79.14
SD	0.127	0.07	0.056	0.052	0.03	0.015	0.047	0.079	0.053	0.093	0.097	1.266	2.838	1.618	3.266	7.342	3.141	8.773	2.559
min	2.55	1.28	0.78	0.81	0.12	0.01	0.68	0.23	0.89	1.21	1.58	48.46	53.79	1.08	12.9	25.84	75.51	30.49	75.58
max	2.97	1.6	1.01	1.01	0.25	0.07	0.86	0.55	1.11	1.63	1.97	53.87	64.96	7.14	27.17	54.46	89.89	63.95	84.27
i.c. 95%	0.05	0.03	0.02	0.02	0.01	0.01	0.02	0.03	0.02	0.04	0.04	0.51	1.14	0.65	1.31	2.94	1.28	3.59	1.02

Cavallo Cave (LE)																			
layer N	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	21	26	29	27	33	33	27	29	27	29	29	20	26	27	27	25	25	26	28
mean	2.55	1.24	0.7	0.81	0.18	0.05	0.65	0.37	0.9	1.34	1.66	48.55	56.56	6.09	21.79	47.08	81.19	58.31	80.32
SD	0.148	0.102	0.085	0.054	0.031	0.029	0.057	0.065	0.083	0.104	0.106	1.953	3.542	3.78	4.339	7.749	8.706	10.124	2.849
min	2.36	1.08	0.53	0.73	0.1	0.02	0.55	0.23	0.64	1.16	1.5	45.76	47.62	2.11	11.36	29.49	63.22	41.82	75.32
max	2.83	1.45	0.85	0.95	0.25	0.12	0.75	0.54	1.08	1.54	1.9	51.81	62.12	14.67	29.76	67.5	98.68	81.82	88.55
i.c. 95%	0.06	0.04	0.03	0.02	0.01	0.01	0.02	0.02	0.03	0.04	0.04	0.86	1.36	1.43	1.64	3.04	3.41	3.89	1.06

Grotta Grande di Scario (SA) trench																			
C lower	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	18	18	18	20	25	25	19	22	22	20	20	18	18	19	19	16	16	19	20
mean	2.45	1.25	0.76	0.86	0.2	0.04	0.77	0.31	0.9	1.25	1.59	51.13	60.38	4.69	23.65	35.74	88.82	40.22	78.69
SD	0.154	0.076	0.086	0.071	0.035	0.018	0.049	0.08	0.077	0.085	0.095	1.502	3.277	2.462	5.117	7.74	4.053	9.749	1.954
min	2.22	1.09	0.58	0.7	0.13	0.02	0.63	0.18	0.72	1.08	1.44	48.81	55.41	2.16	15.15	23.53	80	23.73	75
max	2.69	1.38	0.89	1	0.28	0.1	0.85	0.48	1.06	1.4	1.78	54.67	67.86	12.5	33.85	48.57	98.62	58.46	85.14
i.c. 95%	0.07	0.04	0.04	0.03	0.01	0.01	0.02	0.03	0.03	0.04	0.04	0.69	1.51	1.11	2.3	3.79	1.99	4.38	0.86

Grotta Grande di Scario (SA) trench																			
C upper	L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5
n	37	37	37	46	49	51	46	48	45	38	38	37	37	46	44	44	44	44	38
mean	2.64	1.37	0.84	0.89	0.2	0.03	0.76	0.3	0.92	1.31	1.67	51.78	61.34	3.92	23.32	34.6	85.8	39.86	78.63
SD	0.139	0.091	0.07	0.049	0.028	0.012	0.047	0.061	0.05	0.072	0.091	1.517	2.574	1.392	3.393	6.619	4.74	7.475	1.716
min	2.42	1.19	0.63	0.8	0.15	0.02	0.66	0.19	0.82	1.18	1.48	48.9	56	2.08	16.67	24.24	78.77	25.86	75.27
max	2.88	1.55	0.95	0.98	0.25	0.08	0.85	0.46	1.02	1.46	1.86	54.21	65	8.65	30.3	50.55	98.53	57.5	81.82
i.c. 95%	0.04	0.03	0.02	0.01	0.01	0	0.01	0.02	0.01	0.02	0.03	0.49	0.83	0.4	1	1.96	1.4	2.21	0.55

Torre Isolidda 3 (TP) US 15, lower																			
L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5	
n	37	38	38	39	40	42	35	38	36	34	34	37	38	38	39	37	35	35	34
mean	2.76	1.42	0.87	0.92	0.19	0.03	0.82	0.26	1.01	1.37	1.7	51.3	61.35	3.6	21.34	28.81	89.71	31.61	80.44
SD	0.128	0.08	0.08	0.05	0.04	0.03	0.06	0.09	0.05	0.07	0.09	1.72	3.45	2.96	4.13	10.06	4.24	11.17	2.44
min	2.48	1.16	0.59	0.85	0.1	0.01	0.72	0.09	0.91	1.24	1.46	46.47	50.61	1	10.75	9.68	82.02	10.59	76.13
max	3	1.58	1.02	1.01	0.27	0.14	0.96	0.53	1.09	1.48	1.84	53.48	65.84	15.91	28.57	58.24	98.97	62.35	85.71
i.c. 95%	0.04	0.03	0.02	0.01	0.01	0.01	0.02	0.03	0.02	0.02	0.03	0.55	1.1	0.94	1.3	3.24	1.4	3.7	0.82

Torre Isolidda 3 (TP) US 13, middle																			
L	A	A2	W	C	B	E	D	WT	L4	L5	AL	A2A	BW	CW	DW	EW	DE	L4L5	
n	45	45	45	45	45	45	45	45	44	44	44	45	45	45	45	45	45	45	44
mean	2.7	1.4	0.87	0.9	0.17	0.02	0.81	0.24	0.99	1.36	1.7	51.99	60.4	2.38	19.71	26.29	90.25	29.26	80.17
SD	0.139	0.077	0.171	0.052	0.033	0.013	0.052	0.066	0.074	0.079	0.086	1.34	5.514	1.558	3.915	7.14	4.859	8.168	3.124
min	2.37	1.22	0.46	0.78	0.09	0.01	0.71	0.1	0.8	1.12	1.41	48.55	34.61	0.99	10.23	12.66	81.61	11.49	73.59
max	2.92	1.57	1.79	1.01	0.26	0.07	0.91	0.38	1.31										



# IV. Pleistocene and Holocene remains of *Crocidura esuae* (Kotsakis, 1984) and *Crocidura sicula* (Miller, 1901) in Sicily

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“Then, having identified the nature of geometric axioms, he turned to the question, *Is Euclidian geometry true or is Riemann geometry true?*”

*He answered, The question has no meaning. As well ask whether the metric system is true and the avoirdupois system is false; whether Cartesian coordinates are true and polar coordinates are false. One geometry can not be more true than another; it can only be more convenient. Geometry is not true, it is advantageous.”*

Robert M. Pirsig

## **Introduction**

Kotsakis (1984) described fossil remains from Spinagallo cave (Sicily) (among which 18 mandibular remains), and assigned them to a new species, *Crocidura esuae*. The assemblage in which this species was found belongs to the *Elephas falconeri* faunal complex. Since then many controversies and doubts on the taxonomical status of fossil and living shrews of Sicily have risen. The main unresolved questions are:

Is the living Sicilian shrew, *Crocidura sicula*, a real species or only a subspecies of *Crocidura russula*?

and

Is *Crocidura esuae* really a species, or is it *Crocidura sicula* with differences due to different time and size?

In palaeontology, we cannot be helped by the biological species concept, as it depends on the possibility of interbreeding. As this can obviously not be tested with fossils, the assignment of a specimen (usually a group of specimens) to a different species or subspecies is based on the amount of morphological differences in the skeletal remains. Considering that neontologists who have complete organisms in combination with genetic and ethological data at their disposal have difficulties in deciding the taxonomical status of the living Sicilian shrew, correctly defining the taxonomy of the fossil ones is very challenging.

First, we need to determine which characters are considered to distinguish the living Sicilian shrew from the peninsular one. In other words, which are the available data that support the separation of the *C. sicula* from *C. russula* and other shrews.

Miller (1901) is the first one to state the presence in Sicily of *Crocidura sicula*. However, in the absence of an adequate description, many scholars tried to assign specimens from Sicily to peninsular species (*Crocidura suaveolens*, *Crocidura leucodon*, *Crocidura russula*), not solving the riddle and recognizing in Sicily more than one contemporary species (Toschi, 1959; Pasa, 1959; Niethammer, 1962; van den Brink, 1969; and Vesmanis & Vesmanis, 1982).

Because of this uncertainty, in order to clarify the taxonomical status of the Sicilian shrew, both Contoli et al. (1989) and Vogel et al. (1989) studied thoroughly and independently of one another Sicilian populations of *Crocidura*. Contoli et al. (1989) performed a morphological and morphometrical study of *Crocidura* mandibles and skulls from Sicily and the Italian peninsula. They used: traditional morphometry, with linear measurements of mandibles and skulls; Fourier analysis for the analysis of the shape of mandibles; discriminant analysis, using Fourier amplitude as variables. After admitting that two different hypotheses were plausible (1. in Sicily three different species of *Crocidura* - *C. suaveolens*, *C. leucodon* and *C. russula* - were present; 2. in Sicily only one shrew was present - *Crocidura sicula*), they concluded that the second hypothesis was the most plausible, at the light of the results of the discriminant analysis and the Hotelling  $t^2$  test.

After Vogel et al. (1988) described a new karyotype not shared by other European *Crocidura* species, Vogel et al. (1989) considered all the data collected concerning Sicilian shrews and decided to definitively assign them to a unique species, *Crocidura sicula*, and provide a description of it. The genus *Crocidura* is in fact characterized by high interspecific karyotypic diversity but low intraspecific variation (Zima et al., 1998). Besides the different karyotype - *C. sicula* has a different number of chromosomes ( $2N=36$ ) than *C. leucodon* ( $2N=28$ ), *C. suaveolens* ( $2N=40$ ) and *C. russula* ( $2N=42$ ) -, the multivariate analysis of skull measurements (subsequently published by Sarà et al., 1990) pointed to a unique species in Sicily and the morphological comparisons among samples from the Sicilian islands and Gozo suggested the presence of the same species in the entire area. They noticed considerable size differences among samples from different islands, not associated to a difference in the morphological characters.

Sarà et al. (1990) analyzed the morphometric variation of the insular *Crocidura* of Sicily and surrounding islands. They applied Principal Component Analysis (PCA) and Canonical Variate Analysis (CVA) on mandibles of *Crocidura* in order to test the presence of one or more different species in Sicily and surrounding islands. According to their results, Sicily and islands share the same morphotypes, significantly different from *C. suaveolens*, *C. russula* and *C. leucodon*. The populations from Gozo and Egadi differ in size (they are smaller) but are morphologically similar to *C. sicula*, while shrews from Pantelleria, besides being larger, are more similar to *C. russula*. The evidence of *C. russula* is provisionally explained as result of an invasion by a North African taxon, because of the nearness of this island to Africa and above all the close similarity between this population and a sample from Tunisia.

Hutterer (1991) defined four different subspecies of *Crocidura sicula*: one of them is fossil, *C. s. esuae*; *C. s. sicula* (Sicily); *C. sicula aegatensis* (Egadi Islands); *C. s. calypso* (Gozo) on the basis of cranial and skeletal characters. This classification was subsequently contested by Sarà (1995), who, by means of PCA and CVA applied to morphometrical analysis of skulls and mandibles, ascribes *C. sicula* and *C. canariensis* to the same phyletic group. According to his analysis, three different subspecies of *C. sicula* can be recognized: *C. sicula esuae* (chronospecies); *C. s. sicula* (recent, in Sicily); *C. s. canariensis* (recent, Canary islands). Sarà and Vitturi (1996) extended the morphometric analysis and the karyotype definition to more samples from Sicilian islands and Malta, in order to describe the geographic variation of *Crocidura sicula* on different islands. They found a size decrease in shrews living on small islands around Sicily (the mandibles from Favignana being the smallest), with the exception of Ustica, where shrews are bigger. Apart from that, they recorded a high geographic variation in *Crocidura sicula*, despite the limited geographic area.

Vogel et al. (2003), in order to clarify the taxonomic status and the origin of *Crocidura canariensis* and *Crocidura osorio* from the Canary islands, investigated a fragment of cytochrome *b* gene from all European *Crocidura* species. Since *C. sicula* and *C. canariensis* share the same karyotype ( $2N=36$ ), they were suspected to be monophyletic. Indeed, Vogel et al. found that populations having this karyotype form an independent clade; Sicily and Gozo populations are closely related and conspecific, but Canarian populations are unlikely to be conspecific. According to Fumagalli et al. (1999), the separation of the populations of the

Canary islands from the Siculo-Maltese complex has been dated by the molecular clock to 5 million years. Subsequently, Vogel et al. (2003) assume that *C. sicula* reached Sicily from North Africa during the salinity crisis of the Messinian and there evolved following a vicariance model of speciation. In contrast, the speciation of *C. canariensis* would have followed a dispersal model instead of a vicariant one, and could have reached the archipelago by jump dispersion. Despite that, and new data (Dubney et al. 2008 place the divergence at roughly 4.65 Myr), Rofes and Cuenca-Bescòs (2011) underline the absence of palaeontological data that support this date, making this hypothesis highly speculative. It has also to be considered that no fossil remain of *Crocidura* so old has ever been recovered; nevertheless, this period is poorly documented and shrews remains, considered the dimensions, are difficult to be detected. The only shrew recovered in Sicily in the oldest Faunal Complex described, Monte Pellegrino FC, is *Asoriculus burgioi* and it was about twice as large as the *Asoriculus* representative from the mainland (Bonfiglio et al., 2002). All the small mammals recovered displayed gigantism, but it cannot be discarded that at in the 1970s small faunal remains were not always detected. Above all in shrews, there is a high increase in the material recovered when a specialist in small mammals assist the excavation. For example, the great part of shrews remains from San Teodoro cave have been recovered only when Dr. Daria Petruso joined the fieldwork in the recent excavations.

But, what is the palaeontological record of *Crocidura* in Sicily?

The oldest fossil remains of *Crocidura* were recovered at Spinagallo cave and described by Tassos Kotsakis (1984). The age of Spinagallo cave has as yet not been well defined. At first, an age of 59.000 and 70.000 y BP was calculated by means of amino-acids racemization (Belluomini and Bacchin, 1980; Belluomini, 1981). However, the faunal assemblage was in contradiction with this age and Belluomini and Bada (1985) published an age of 500 ky; this dating was later considered correct in all likelihood, since dating from other sites of similar faunal association gave the same age (Bada et al. 1991). The beginning of the *Elephas falconeri* FC is commonly considered at the beginning of Middle Pleistocene. At Spinagallo cave an endemic faunal association was recovered, with the dwarf *Elephas falconeri*, the giant dormice *Leithia melitensis* and *Leithia cartei*, one small *Vulpes* sp. and many flying animals (both bats and birds). Together with them, more than 70 remains of *Crocidura* were recovered, representing different cranial and skeletal portions. Some characters of these remains made Kotsakis consider them as belonging to a different species from the ones living in Sicily (in 1984 the specific status of *Crocidura sicula* had not been thoroughly studied, yet, and it was generally thought that different species dwelled the island). The new species was called *Crocidura esui* (now *Crocidura esuae*, corrected by Hutterer 1990, according to the rules of the ICZN) and, according to Kotsakis, it was characterized by:

- Large size;
- ratio length/height in the rostrum (lower in *C. esuae*)
- morphology of the symphyseal notch
- Ratio tibia length/femur length (higher in *C. esuae*, related to peculiar swimming capabilities).

*Crocidura esuae* was thought to be present on Malta, too, and to be extinct in the Holocene.

Hutterer (1991), studying the temporal and geographical size variation in *C. sicula*, concluded that the Pleistocene populations from Sicily and Malta were misclassified. They evolved to the present-day populations of Sicily and surrounding islands, sharing the same morphological characters, above all on P<sup>4</sup> (massive and angular parastyle and undulated dorsal edge of the cingulum) and on the condylar process. He did not recognise the relative elongation of the postcranial bones as important, but considered it to be related to the general size reduction of the Sicilian shrews. The detection of conspicuous variation in size (with a maximum of 25%) in living populations supported his hypothesis; the extremities suffered more size

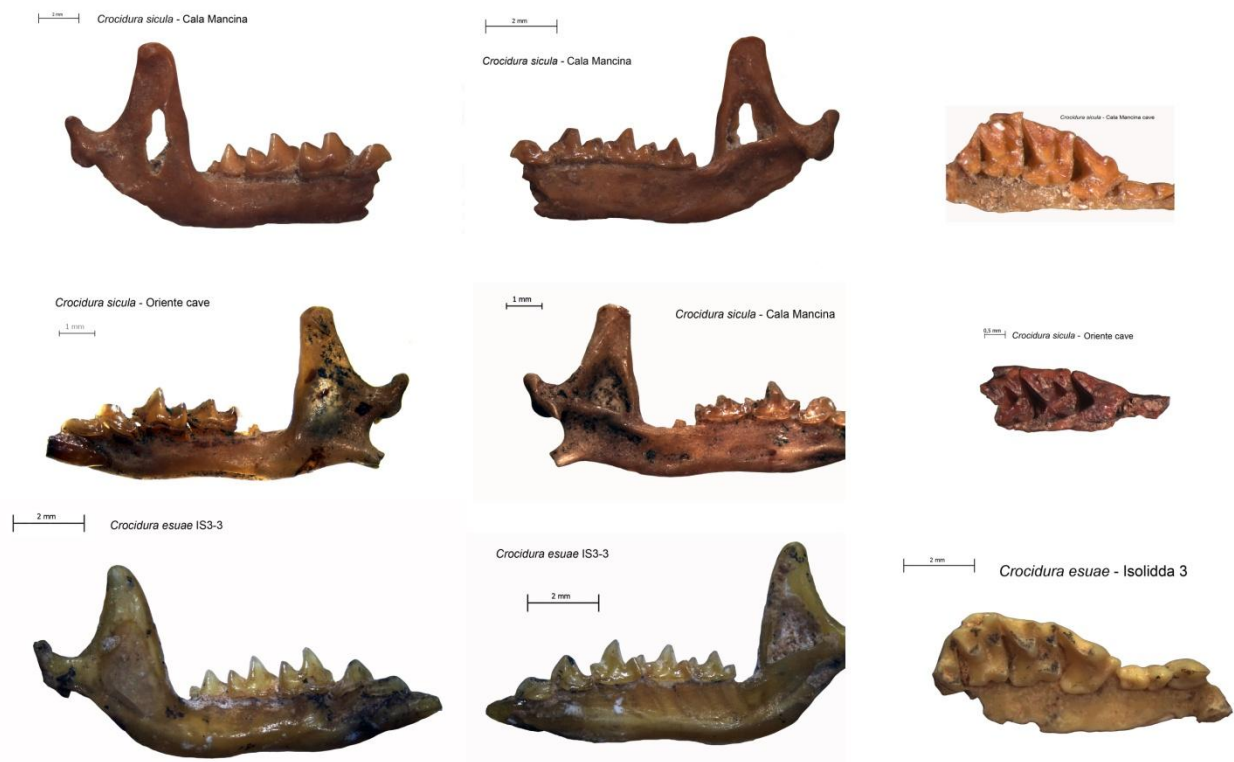
reduction than the skull. In conclusion, he considered the fossil Pleistocenic shrew a subspecies of *C. sicula*, *C. s. esuae*, with the diagnosis “Large shrews with the characters of *C. sicula* and a very long tibia”.

Sarà (1995), taking into account the new dating of Spinagallo cave to 500ky BP and the morphological features of its mandibles and skulls, preferred to regard *C. esuae* a different species, a chronospecies, subsequently replaced by the modern *C. sicula*. In his morphometric analysis, *C. esuae* separates from the other living populations to the same extent that living populations from the islands surrounding Sicily separate from strictly Sicilian populations. Different populations would have been responsible of the colonization of different islands and the evolution of *C. sicula* would have taken place in isolation conditions during Milazziano and Quaternary climatic fluctuations.

This chapter deals with the morphometrical characters of three new populations from Pleistocene and Holocene caves of Sicily: Isoldida 3, Oriente and Cala Mancina caves.

### **Material and methods**

The new material considered in this analysis comes from the Isoldida3, Oriente and Cala Mancina caves (Plate 4)



**Plate 4: lower and upper mandibles of *Crocidura* from Sicily**

Measurements were taken according to Vesmanis (1976) (Figure IV-1). Nomenclature is after Reumer (1984).

Considering the high number of mandibular remains recovered, only a representative sample of the material has been measured in order to carry out the morphometrical analysis. Upper teeth were far fewer than lower ones, thus all the specimens recovered have been measured. Measures have been used to describe and compare the material with other populations reported in literature. Furthermore, it was possible to compare the material from K22 site at the Palermo University and the one from Spinagallo cave at Rome 3 University. Some measurements have been compared with the fossil ones reported in the literature: from Spinagallo cave (Kotsakis, 1984; Sarà, 1995), fossil and recent material from Malta, Gozo, Sicily and Egadi in Hutterer (1991). Measurements of recent material from Sicily, surrounding islands and Gozo, was taken from Sarà et al. (1990).

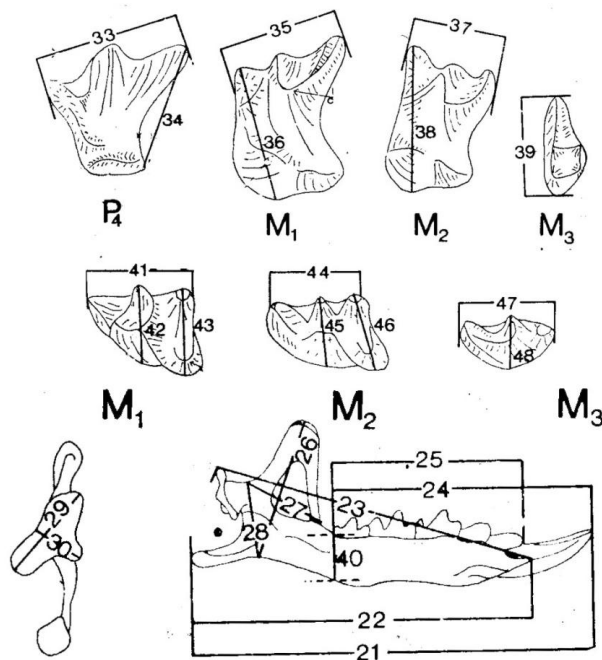


Figure IV-1: plan of measurements (modified after Vesmanis, 1976)

### ***Systematic palaeontology***

**Order:** Insectivora

**Family:** Soricidae, Fischer, 1814

**Subfamily:** Crocidurinae Milne-Edwards, 1874

**Genus:** *Crocidura* Wagler, 1832

*Crocidura esuae* Kotsakis, 1984

**Synonymy:** *Crocidura sicula esuae* Hutterer, 1991

**Holotype:** Anterior cranial fragment, MPUR/N. S. 35/1/1, collected at the University of Rome 3

**Geographic and stratigraphic distribution:** Sicily. Recovered in Middle Pleistocene deposits at Spinagallo cave (Kotsakis, 1984), Contrada Fusco (Kotsakis, 1996), and *Crocidura aff. esuae* from K22 (late Middle Pleistocene, Di Maggio et al., 1999).

**Description:**

**Isolidda 3 cave**

**AA:** A1 is much larger than the other unicuspidates; A2 and A3 are about of the same size, but A3 is slightly bigger. Except for the size, they are all similar in shape. The occlusal surface is roughly oval; the distal border is straight, the mesial one is pointed. A cingulum rounds the tooth and is thick in the distal edges.

**P<sup>4</sup>:** in occlusal view, the parastyle is protruding and separated from the paracone by a valley. A crest connects the parastyle with the protocone, which is located close to the mesio-lingual corner, on the mesial side. A shallow valley separates the protocone from the hypoconal ridge that runs along the lingual margin of the tooth. The hypocone is weak and visible only in few specimens, where the cusps are not much worn. The parastylar crest is absent; the paracone is the highest cusp and a thick and high ridge runs from it to the disto-labial corner. The profile of the lingual edge can be straight or slightly undulated in correspondence of the mesio-lingual corner that is rounded. In labial view, the dorsal edge of the cingulum is undulated, like living specimens of *Crocidura sicula* (Vogel et al; 1989), and thick. The parastyle can be angular or rounded; in both cases it is massif.

**M<sup>1</sup>:** the occlusal outline is squarish with rounded corners; the mesial and labial edges are straight; the distal is arched and the lingual is slightly undulated, with a central concavity. The tooth is made by four main cusps (paracone, protocone, metacone and hypocone), three styler cusps (parastyle, mesostyle and metastyle), and a protoconule. The allocation of the cusps gives to the labial portion of the tooth a W shape. Between labial and lingual cusps, there are two basins; the mesial one, surrounded by the trigon main cusps, is called “trigon basin”; the distal one is the “hypoconal flange”. The metacone is the highest cusp; the protocone is lower than the metacone but higher than the paracone. The hypocone is the less developed cusp; it is low and difficult to distinguish in worn teeth.

**M<sup>2</sup>:** the general structure and allocation of the cusps is the same of M1. It differs from M1 in the development of the labial cusps: whilst in M1 the parastyle the metastyle protrudes distally, in M2 the parastyle is protruding and the metastyle is less developed, making the labial edge of the tooth inclined in the opposite direction. The hypocone and the hypoconal flange is smaller and the protocone, together with the protoconule, is less developed; consequently, the tooth looks slender and rectangular in occlusal view.

**M<sup>3</sup>:** it is far smaller than other upper molars and it is not often preserved. The outline is triangular, with a straight mesial edge and a pointed distal one. The paracone is the best developed cusp; lingually, the protocone and the hypocone are small and low, united into a ridge.

**A<sub>1</sub>:** one low cusp located mesially; smaller than p4. In occlusal view, mesial border is pointed, distal side is notably rounded and hidden by the mesial portion of p4. A thick cingulum surrounds the tooth, both in lingual and labial sides.

**P<sub>4</sub>:** in labial and lingual view, it looks like a cone; one high cusp is located mesially and covers the distal portion of a1. In occlusal view, its outline is triangular, pointed mesially and with rounded corners distally. A thick cingulum is present both in lingual and labial views and is straight.

**M<sub>1</sub>**: in occlusal view, the tooth has a trapezoidal outline. Five cusps form the tooth: a mesio-lingual paraconid, that is the lowest cusp; a labial protoconid that is the highest; a centro-lingual metaconid, aligned on the mesio-labial axe with the protoconid, higher than the paraconid but lower than the labial cusps; distally there are the hypoconid (lingual) and the entoconid (labial). There is an accessory cusp distally to the entoconid, the entostylid. Protoconid is connected to the paraconid by the paralophid; the metalophid connects the protoconid with the paralophid. These three cusps constitute the trigonid, that is V shaped and presents a deep valley between paraconid and metaconid, the “trigonid basin”. Another valley is present distally to the trigonid and separates it from the distal cusps, the “talonid basin”. Hypoconid and entostylid are connected by a crest, the hypolophid. The lingual side of m1 in occlusal view is straighter, while the labial one is rounded in correspondence of the protoconid and paralophid. Talonid and trigonid are about of the same size. In labial view, the cingulum is thick and markedly undulated; in lingual view it is thinner.

**M<sub>2</sub>**: the general structure of m2 is the same of m1. The differences are: the tooth is slightly smaller; the lingual side is usually straighter; the talonid is slightly smaller related to the trigonid; cusps are lower. The labial cingulum is only slightly undulated.

**M<sub>3</sub>**: the outline in occlusal view is semicircular, with a straight lingual side. Four cusps form the tooth: the three of the trigonid (paraconid, protoconid and metaconid) and a distal hypoconid. The cusps are lower than in m2; the labial cingulum is thick; the lingual one is weak.

**Mandible**: The coronoid process is blunt, not high and large at the basis. The coronoid spicule is usually absent. The coronoid process is inclined backward. The external fossa is shallow and its margin is not delimited markedly. The internal temporal fossa is large but not very deep. The mental foramen is located under the distal border of P<sub>4</sub>.

**Measurements**: descriptive statistical analysis of the measurements is reported in Table IV-1 and Table IV-2. The complete list of measurement is in the Appendix.

	25	M <sub>1</sub> -M <sub>3</sub>	23	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
Mean	5.98	4.09	1.72	2.88	4.60	2.37	1.32	1.44	1.40	1.88	0.91	1.48	1.00	1.11	1.19	0.93	1.01	1.21	0.70
Standard Error	0.13	0.03	0.00	0.02	0.03	0.02	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Median	6.01	4.06	1.72	2.88	4.64	2.35	1.31	1.44	1.41	1.90	0.93	1.49	1.00	1.12	1.20	0.94	1.04	1.23	0.72
Mode				2.83	4.45	2.47	1.31	1.60	1.36	1.98	0.96	1.56	1.06	1.15	1.18	0.96	1.06	1.36	0.84
Standard deviation	0.26	0.17		0.22	0.27	0.17	0.15	0.13	0.15	0.15	0.11	0.08	0.10	0.08	0.07	0.09	0.08	0.08	0.10
Sample Variance	0.07	0.03		0.05	0.07	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Kurtosis	1.69	-0.24		0.67	3.99	1.49	0.79	0.31	0.68	1.29	-0.27	1.75	0.21	0.52	-0.36	1.48	2.03	0.47	1.17
Skewness	-0.58	-0.10		-0.28	-1.37	0.29	0.51	0.29	-0.78	-0.98	-0.53	-0.87	-0.03	-0.62	-0.22	-0.60	-1.05	-0.77	-1.01
Range	0.64	0.70	0.00	1.31	1.75	1.14	0.86	0.63	0.80	0.78	0.45	0.48	0.52	0.44	0.35	0.60	0.49	0.38	0.47
Minimum	5.64	3.70	1.72	2.22	3.44	1.83	0.98	1.19	0.88	1.38	0.65	1.16	0.75	0.85	1.01	0.65	0.67	0.98	0.40
Maximum	6.27	4.40	1.72	3.53	5.18	2.97	1.84	1.82	1.68	2.16	1.10	1.64	1.27	1.29	1.36	1.25	1.16	1.36	0.87
Sum	23.92	126.65	1.72	399.71	437.04	286.30	154.66	87.86	189.50	211.06	98.55	189.17	133.45	158.00	158.24	128.92	139.04	77.71	43.84
Count (n)	4	31	1	139	95	121	117	61	135	112	108	128	134	142	133	139	137	64	63
Confidence Interval (95,0%)	0.42	0.06		0.04	0.06	0.03	0.03	0.03	0.03	0.03	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01	0.02

Table IV-1: descriptive statistical analysis of mandibles and lower teeth of *Crocidura esuae* from Isolidda 3 cave

	33	34	35	36	37	38	39
Mean	2.03	1.73	1.62	1.72	1.40	1.96	1.52
Standard Error	0.01	0.04	0.02	0.03	0.04	0.07	0.00
Median	2.04	1.76	1.62	1.73	1.40	1.97	1.52
Mode					1.33		
Standard deviation	0.05	0.14	0.07	0.14	0.11	0.20	
Sample Variance	0.00	0.02	0.01	0.02	0.01	0.04	
Kurtosis	-0.54	-0.43	0.98	-0.13	0.54	-1.49	
Skweness	-0.25	-0.71	0.21	-0.58	0.22	-0.07	
Range	0.19	0.46	0.30	0.49	0.36	0.53	0.00
Minimum	1.93	1.45	1.46	1.42	1.23	1.67	1.52
Maximum	2.12	1.91	1.77	1.91	1.58	2.20	1.52
Sum	32.54	25.99	27.57	29.18	11.18	15.65	1.52
Count (n)	16	15	17	17	8	8	1
Confidence Interval (95,0%)	0.03	0.08	0.04	0.07	0.09	0.17	

Table IV-2 descriptive statistical analysis of upper teeth of *Crocidura esuae* from Isolidda 3 cave

### *Crocidura sicula* (Miller, 1901)

**Synonymy:** *Crocidura caudata* Miller, 1901

**Holotype:** USNM 103301, skin and skull of a young male from Palermo, Sicily, in Miller (1901), Proc. Biol. Soc. Wash. 14:41

Distribution: Sicily, Egadi, Gozo.

### Cala Mancina cave and Oriente cave

The cusps arrangement is the same as *C. esuae* and only few features change in the teeth morphology. Here the differential analysis is presented.

In average, labial cingulum in lower molars is less undulated, above all in Cala Mancina sample and lingual cingulum is rare. In the mandible, the coronoid process does not slopes backwards; the upper sigmoid notch is deeper; despite it is smaller, the height of the mandibular ramus under m2 (AM/2) is about the same or bigger in recent forms; then the ramus is more robust in *C. sicula* than in *C. esuae*.

In upper teeth, the protocone of P4 is more developed in *C. sicula*, so that the valleys which separate this cusp from the hypocone and the parastyle are deeper. In some cases (but not always) the lingual profile in occlusal view presents a concavity in correspondence of the valley between hypocone and protocone in *C. sicula*; *C. esuae*'s lingual and mesial profile is more rounded and almost free of asperity. Nevertheless, it is necessary to keep in mind that upper remains are few and this character could be partly related to wear.

### Measurements

Descriptive statistical analyses of the measurements of samples from Cala Mancina and Oriente caves are reported in Tables IV- 3/5. The complete list of measurement is in the Appendix. The Cala Mancina sample was very rich and only few mandibular specimens have been measured. From Oriente cave only two upper remains have been recovered; thus, the list of the specimens and measures is reported in Table IV-6.



	M <sub>1</sub> -M <sub>3</sub>	23	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
Mean	3.89	10.12	2.70	4.40	2.24	0.67	1.42	1.42	1.79	0.79	1.37	0.99	1.10	1.16	0.90	0.98	1.14	0.66
Standard Error	0.04	0.00	0.03	0.04	0.04	0.02	0.03	0.02	0.05	0.03	0.02	0.01	0.02	0.02	0.03	0.03	0.03	0.03
Median	3.90	10.12	2.70	4.38	2.25	0.66	1.44	1.40	1.82	0.78	1.37	1.00	1.10	1.15	0.95	1.00	1.15	0.69
Mode										0.88		1.00		1.05				
Standard deviation	0.09		0.11	0.13	0.12	0.06	0.09	0.08	0.14	0.08	0.07	0.04	0.06	0.07	0.10	0.09	0.08	0.07
Sample Variance	0.01		0.01	0.02	0.02	0.00	0.01	0.01	0.02	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.01	0.00
Kurtosis	-0.82		-0.69	-1.97	1.67	-0.83	-0.10	-0.29	-0.89	-1.67	0.83	0.68	1.33	-0.38	-1.28	-0.54	-0.82	-0.58
Skewness	-0.30		-0.43	-0.14	0.16	-0.30	-0.36	0.85	-0.46	-0.15	-0.49	0.46	-0.30	-0.02	-0.43	-0.92	-0.62	-1.06
Range	0.25	0.00	0.33	0.33	0.49	0.18	0.27	0.24	0.38	0.19	0.26	0.14	0.23	0.22	0.29	0.26	0.21	0.17
Minimum	3.76	10.12	2.51	4.23	2.01	0.57	1.28	1.34	1.57	0.69	1.22	0.93	0.99	1.05	0.74	0.82	1.01	0.55
Maximum	4.01	10.12	2.84	4.56	2.50	0.75	1.55	1.58	1.95	0.88	1.48	1.07	1.21	1.27	1.03	1.08	1.22	0.72
Sum	23.36	10.12	26.99	39.59	24.69	6.04	9.93	17.09	14.33	5.51	15.05	11.90	13.24	13.88	9.92	11.75	7.97	4.63
Count (n)	6	1	10	9	11	9	7	12	8	7	11	12	12	12	11	12	7	7
Confidence Interval (95,0%)	0.10		0.08	0.10	0.08	0.05	0.08	0.05	0.11	0.07	0.05	0.02	0.04	0.04	0.07	0.06	0.07	0.06

Table IV-3: descriptive statistical analysis of mandibles and lower teeth of *Crocidura sicula* from Cala Mancina cave

	16	33	34	35	36	37	38	39
Mean	4.71	1.90	1.75	1.54	1.69	1.32	1.90	1.18
Standard Error	0.00	0.02	0.02	0.02	0.02	0.03	0.04	0.05
Median	4.70	1.93	1.76	1.57	1.69	1.35	1.93	1.20
Mode		1.84	1.63	1.31	1.69	1.39		
Standard deviation	0.01	0.10	0.11	0.12	0.09	0.10	0.15	0.08
Sample Variance	0.00	0.01	0.01	0.01	0.01	0.01	0.02	0.01
Kurtosis		3.99	0.28	0.86	-0.18	1.38	-0.91	
Skewness	1.29	-1.62	-0.92	-1.23	-0.21	-1.34	-0.28	-1.28
Range	0.01	0.48	0.41	0.44	0.36	0.31	0.46	0.16
Minimum	4.70	1.58	1.49	1.25	1.49	1.11	1.64	1.08
Maximum	4.71	2.06	1.90	1.69	1.85	1.42	2.10	1.24
Sum	14.12	47.59	45.46	40.02	42.34	13.22	24.64	3.53
Count (n)	3	25	26	26	25	10	13	3
Confidence Interval (95,0%)	0.02	0.04	0.04	0.05	0.04	0.07	0.09	0.21

Table IV-4: descriptive statistical analysis of upper teeth of *Crocidura sicula* from Cala Mancina cave

	25	M <sub>1</sub> -M <sub>3</sub>	23	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
Mean	5.94	3.98	9.97	2.74	4.52	2.31	0.66	1.38	1.44	1.86	0.85	1.39	0.96	1.07	1.18	0.91	0.95	1.17	0.70
Standard Error	0.00	0.06	0.39	0.06	0.05	0.13	0.03	0.05	0.03	0.03	0.02	0.03	0.01	0.02	0.01	0.01	0.01	0.02	0.01
Median	5.94	4.03	9.97	2.65	4.56	2.20	0.64	1.46	1.45	1.84	0.86	1.41	0.96	1.09	1.18	0.92	0.96	1.17	0.70
Mode				2.65					1.49		0.86		0.95				0.95		
Standard deviation		0.10	0.56	0.28	0.18	0.55	0.14	0.16	0.12	0.11	0.07	0.12	0.04	0.07	0.06	0.05	0.06	0.05	0.03
Sample Variance		0.01	0.31	0.08	0.03	0.30	0.02	0.03	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kurtosis				9.56	-0.14	14.72	7.09	-0.99	-0.27	-0.37	3.07	3.26	0.08	2.39	-1.15	-0.12	0.65	2.18	2.59
Skewness		-1.72		2.70	-0.49	3.66	1.93	-0.70	-0.09	-0.13	-1.30	-1.56	0.02	-1.42	0.14	-0.45	-0.35	0.65	-1.62
Range	0.00	0.17	0.79	1.31	0.64	2.65	0.75	0.48	0.48	0.42	0.31	0.46	0.17	0.28	0.18	0.18	0.23	0.18	0.10
Minimum	5.94	3.87	9.57	2.42	4.14	1.80	0.40	1.09	1.21	1.62	0.64	1.06	0.88	0.88	1.10	0.81	0.83	1.09	0.62
Maximum	5.94	4.04	10.36	3.73	4.78	4.45	1.15	1.57	1.69	2.05	0.95	1.52	1.05	1.16	1.28	0.99	1.06	1.27	0.73
Sum	5.94	11.95	19.93	51.98	67.82	43.88	13.11	13.81	30.31	31.57	15.34	23.69	16.37	20.35	22.48	16.42	17.15	9.37	5.56
Count (n)	1	3	2	19	15	19	20	10	21	17	18	17	17	19	19	18	18	8	8
Confidence Interval (95,0%)		0.24	5.02	0.13	0.10	0.26	0.07	0.12	0.06	0.06	0.04	0.06	0.02	0.03	0.03	0.02	0.03	0.04	0.03

Table IV-5: : descriptive statistical analysis of mandibles and lower teeth of *Crocidura sicula* from Oriente cave

ID	Strato	33	34	35	36	37	38
s04	7	1.972	1.725	1.529	1.621		
s22	7	1.837	1.46	1.427	1.654	1.412	1.846

Table IV-6: measures (mm) of upper teeth of *Crocidura sicula* from Oriente cave

## Results

Measurements taken on Isolidda 3, Oriente e Cala Mancina samples and recent *Crocidura sicula* from Contrada Sperone Altavilla Milicia (Palermo) have been plotted together and analyzed with Principal Component Analysis with PAST. The results are reported in Figure IV-2 and eigenvalues and variation are reported in Figure IV-3. The PCA was made using mandible measurements.

PCA plots together all the Pleistocene samples from Isolidda 3 caves on the left part of the diagram, while samples from Oriente and Cala Mancina caves plot with the recent sample on the right side. The only determinant component is the first one, that is size related. Then, old *Crocidura esuae* are bigger and separate from the recent ones.

Data have been also compared with measurements published in Kotsakis (1984) and Sarà (1990). Only three measurements on the mandible were comparable ( $M_1$ - $M_3$ ; 30; 26), and the PCA has been built only with them (Figure IV-4 and Figure IV-5).

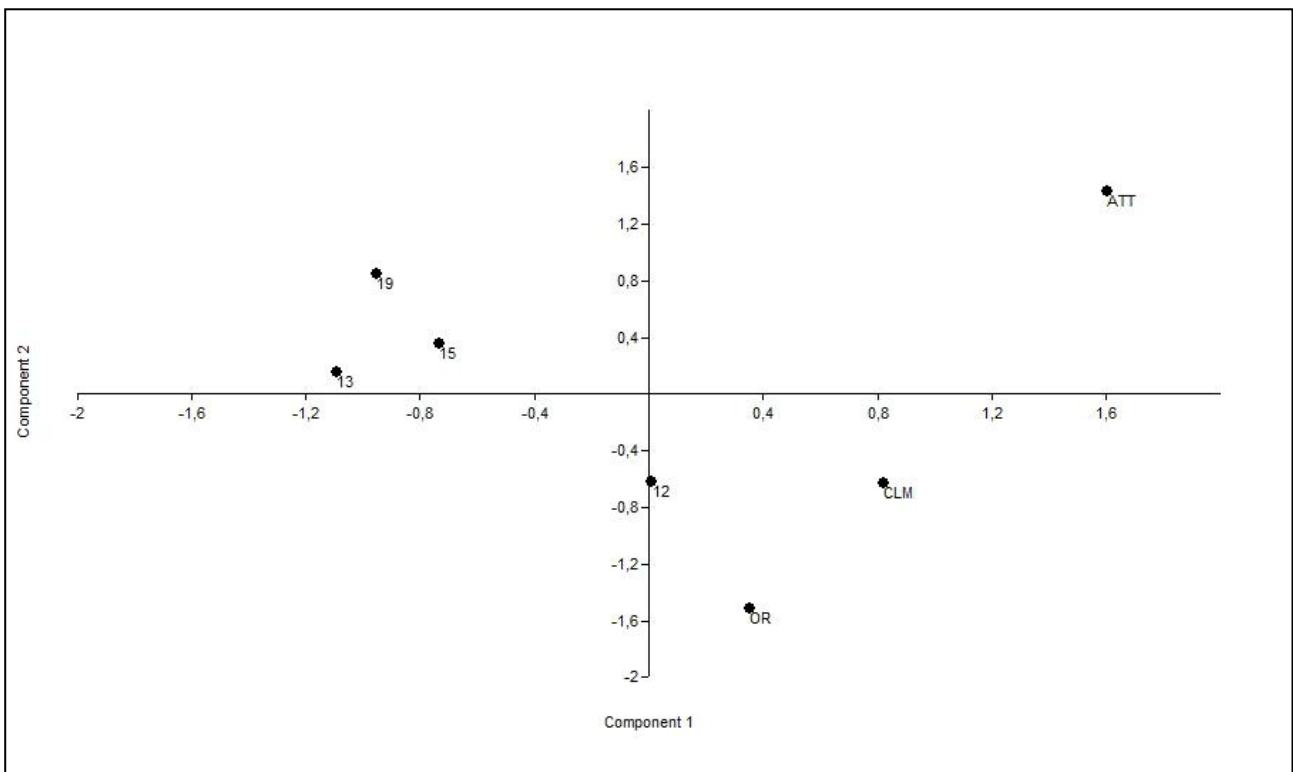


Figure IV-2: PCA of measurements taken on mandibles of new samples

	Axis 1	Axis 2	Axis 3
M/1-M/3	-0,532	0,04047	0,01582
27	-0,4168	0,338	-0,1845
26	-0,5744	-0,488	0,2104
28	-0,1851	-0,05175	0,2089
40	-0,1898	-0,06841	-0,3351
AM/2	0,06923	-0,01071	0,119
29	0,05791	0,3741	0,5836
30	-0,1228	0,1966	0,4899
41	-0,2528	-0,04975	0,09563
42	-0,07653	0,05771	-0,2693
43	-0,06963	0,1303	-0,1506
44	-0,06843	0,0853	0,003973
45	-0,06425	0,2147	-0,09322
46	-0,0769	0,2912	-0,1747
47	-0,1636	0,4796	-0,1467
48	-0,06018	0,2626	0,07531

PC	Eigenvalue	% variance
1	0,0599289	71612
2	0,0141079	16858
3	0,00373377	44616
4	0,00334186	39933
5	0,00199645	23856
6	0,00057709	0,68959
7	5.6001E-27	6.6918E-24
8	1.25533E-61	1.5001E-59

Figure IV-3: PCA factor loadings, eigenvalue and variance. PCA con var-cov; Jolliffe cut-off 0,00367

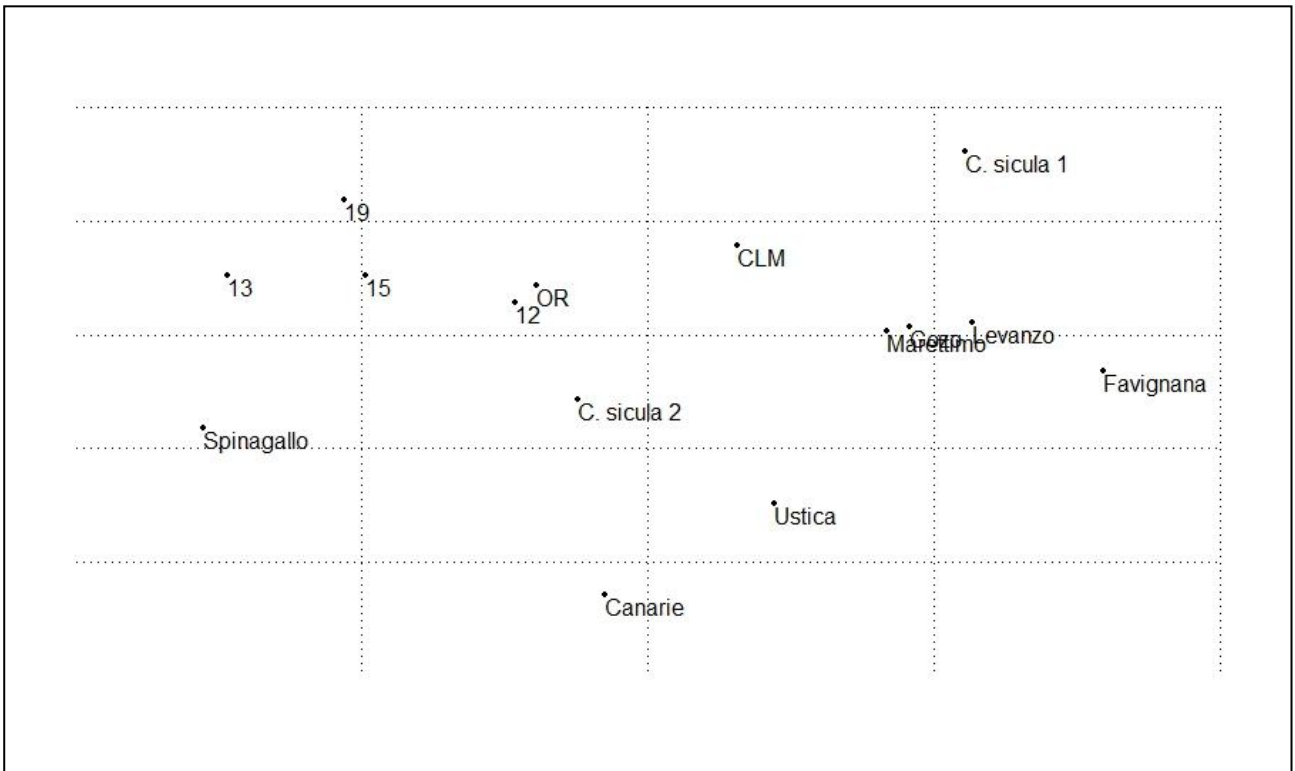


Figure IV-4: PCA of mandible measurements (with samples published in literature). Var-covariance; Jolliffe cut-off.

	Axis 1	Axis 2	Axis 3
Spinagallo	-1555	-0,82668	0,17264
19	-10631	11779	-0,11941
15	-0,9876	0,51855	0,1401
13	-14696	0,5122	0,46089
12	-0,46769	0,27661	-0,10024
CLM	0,30982	0,78407	-18237
OR	-0,38969	0,4346	-0,90666
C. sicula 1	11066	16081	13998
C. sicula 2	-0,24748	-0,57005	-0,45472
Gozo	0,91501	0,062016	10714
Marettimo	0,83285	0,025316	17143
Ustica	0,44329	-14951	0,71857
Favignana	15906	-0,3255	-14107
Levanzo	1133	0,109	-0,89753
Canarie	-0,15098	-22911	0,035285

PC	Eigenvalue	% variance
1	0,0486818	74948
2	0,0144528	22251
3	0,00181955	28013

Figure IV-5 factor loadings, eigenvalue and variance. PCA con var-cov; Jolliffe cut-off 0,0150156

This analysis confirms the result of the PCA performed on the samples investigated previously. Isolidda3 samples plot with Spinagallo one, that is they all belongs to *Crocidura esuae*. *Crocidura sicula* from Cala Mancina and Oriente caves plot with recent *Crocidura sicula*. Nevertheless, recent *Crocidura* from different Sicilian islands shows a degree of variation and occupies all the right portion of the diagram. *Crocidura canariensis* from Canary Islands and *Crocidura* sp. from Ustica are quite isolated from the rest of the group, mainly separated by the component 2.

Upper remains were too scarce to perform a significant Principal Component Analysis. For that reason, only the histogram with the comparison of mean value is shown (Figure IV-6). Isolidda 3 and K22 samples upper molars are bigger, while the recent ones are the smallest.

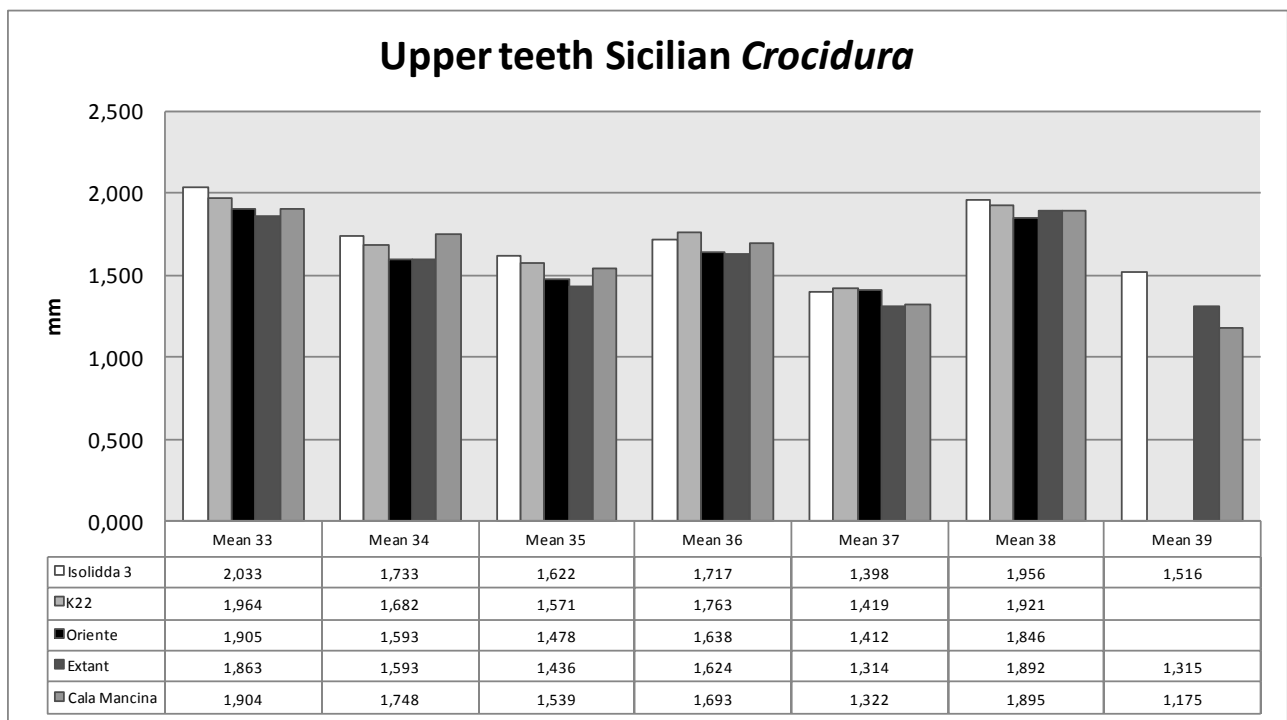


Figure IV-6: comparison among measurements of upper teeth

## **Discussion**

By the morphometric analysis of mandibular and upper maxillary remains of the Sicilian shrew, we can see that ancient remains from Isolidda 3 cave plot with the Spinagallo shrew, *Crocidura esuae* and K22 *Crocidura* aff. *esuae* from the Red layer. Nevertheless, observing the loading diagrams of the PCA analysis, it is clear that the first component, which describes around the 70% of the variance and is the main responsible of the separation, is strictly related to size; other components, far less heavy and morphological related, cannot separate samples of different periods. Morphological characters are not very effective in the separation of the species. Whilst in Cala Mancina and Oriente caves samples morphological characters are quite standardized, in Isolidda 3 cave samples these features seem to be more variable and in recent populations there is high inter-populations variation. Many features seem to be more characteristic of one species instead of the other, but none of these characters is conclusive on its own.

In conclusion, *Crocidura esuae* is an old island endemic, that reached Sicily at the first part of Middle Pleistocene and its first occurrence is recorded at Spinagallo cave, in the *Elephas falconeri* FC. This species is still present in the following *Elephas mnaidriensis* FC (second part of Middle Pleistocene), as attested by its occurrence in the lowest levels of Isolidda 3 cave. In Upper Pleistocene another species dwells the island, *Crocidura sicula*, very similar to the ancient form, but with a reduced size. Entire post-cranial bones, on which diagnostic characters had been detected by Kotsakis (1984), have not been found at Isolidda 3 cave. Considered the strict similarity between these two species, the evolution of *Crocidura sicula* possibly took place on the island, in agreement with Sarà (1995). Shrew remains of Late Pleistocene-Holocene deposits, Cala Mancina and Oriente caves, are already more similar to recent *C. sicula*.

## **Conclusion**

Despite there are not striking morphological differences between *Crocidura esuae* and *Crocidura sicula*, it seems opportune to keep these two species separated because there is a difference in the size (ancient forms are bigger) that on its own allows to separate them, and there is quite a difference in the chronological distributions (chronospecies according to Sarà, 1995). Further analysis that will allow a better quantification of morphological characters (i. e. geometric morphometric analysis of mandibles) could give more support to this hypothesis. In particular, the inclination of the coronoid process could be opportunely checked, as well local enlargements of the mandibular ramus. All the similarities between these two species, the late evolution of *C. sicula* does not seem a product of a succeeding dispersal and isolation episode, but of the local evolution on the island of *C. esuae*.



## **Appendix Chapter IV**

ID	M <sub>1</sub> -M <sub>3</sub>	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
1		2.75	4.89	2.46	1.73		1.44	2.13	0.95	1.45	0.99	1.15	1.08	0.95	1.06		
2	4.28					1.39	1.36			1.54	0.86	1.13	1.12	0.97	0.96	1.27	0.71
3						1.48	0.88						1.22	0.91	1.05	1.30	0.68
4																	
5		2.86	4.59	2.45	1.61			1.91	0.93								
6		3.53															
7							1.62						1.12	0.97	1.07		
8		3.07	4.43	2.21	1.26	1.39	1.98	1.02	1.51	1.05	1.11	1.18	1.01	1.06			
9		2.87	4.51	2.31	1.53			1.89	0.88								
10		2.89	4.51	2.20	1.42			1.87	0.80								
11		3.01		2.20	1.30			1.51	0.71								
12													1.20	0.74	0.91		
13						1.60							1.26	0.71	1.04	1.36	0.63
14		2.82		2.48	1.48			2.08	0.96								
15		2.86		2.27	1.31					1.51	0.95	1.17					
16						1.72	1.68						1.04	0.93	1.06	1.17	0.72
17							1.56					1.12	1.09	0.96	1.07		
18		2.94						1.77	0.99								
19							1.53			1.45	1.12	1.15	1.01	0.95	1.02		
20							1.12						1.24	0.86	1.01		
21																	
22																1.19	0.70
23																	
24	4.13	3.29	4.54	2.49	1.57	1.49	1.32	1.95	0.83	1.48	1.24	1.06	1.07	1.04	1.14	1.26	0.72
25	4.21	3.14				1.19	1.16	1.95	0.94	1.56	1.02	1.13	1.32	0.74	1.06	1.28	0.79
26		2.92	3.99	2.25	1.39			1.74	0.85	1.50	1.11	1.11					
27		3.15	4.79	2.76	1.46		1.41	2.04	1.03	1.58	1.15	1.28	1.24	1.03	1.15		
28		3.00	4.75	2.58	1.39	1.30		2.11					1.11	0.98	1.04		
29		2.59			1.44					1.47	1.22	1.27					
30		2.90	3.66	2.00	1.24			1.38	0.68	1.47	0.95	1.01					
31		2.93						1.80									
32	4.17					1.60	1.57			1.55	1.21	1.23	1.25	1.06	0.99	1.22	0.69
33							1.30			1.53	1.02	1.14	1.17	1.03	1.09		
34													1.14	0.96	1.07		
35		3.05						1.83	1.05	1.39	1.08	1.15					
36		3.17	4.89	2.41	1.31			1.75	0.92								
37		2.83		2.44	1.37					1.52	1.02	1.18					
38		2.74	4.69	2.35	1.84		1.38	1.81	0.67	0.79	0.88	1.15	1.18	1.07	0.89		
39							1.11			1.56	1.27	1.21	1.13	1.25	1.06		
40		3.03	4.64	2.33	1.43			1.88	0.89								
41							1.55						1.21	0.97	1.00		
42										1.42	0.99	1.13					
43																	
44										1.56	1.00	1.17					
45										1.46	0.82	0.97					
46																	
47		3.02	4.77	2.51	1.17			2.03	0.90								
48		2.84					1.56	1.98	0.99	1.42	1.10	1.15	1.08	1.01	1.07		
49		2.85		2.17	1.25			1.78	0.86	1.48	0.95	0.96					
50		3.06	4.45	2.30				2.07	0.98								
51							1.43			1.47	1.06		1.21	0.81	1.09		
52													1.20	0.85	1.01		
53							1.18			1.52	0.90	1.10	1.25	0.89	0.99		
54	3.98					1.39	1.41			1.57	0.97	1.10	1.25	0.94	1.04	1.23	0.72
55							1.26						1.25	1.01	1.06		

Table IV-7: measures (mm) of mandibles of *Crociodura esuae* from Isolidda 3 – US 19



ID	25	M <sub>1</sub> -M <sub>3</sub>	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
56			3.00	4.99	2.54	1.19		1.40	1.99	0.99					0.90	1.03	1.24	0.75
57			3.13		2.43	1.31			1.98	0.85								
58											1.52	1.07	1.10					
59			2.82	4.82	2.50	1.55					1.48	1.06	1.16					
60								1.29			1.61	1.00	1.25	1.22	1.03	1.04		
61								1.61				1.04			1.05	1.07		
62								1.39			1.56	0.92	1.05	1.19	0.92	1.06		
63								1.40					1.17	1.10	0.88	1.06		
64			3.12		2.81	1.48			2.08	0.94								
65											1.46	0.84		1.20		0.99		
66			3.15	5.04	2.62	1.41			1.94									
67							1.36	1.36			1.40	1.15	1.16		0.99	0.97	1.24	0.84
68							1.46	1.39						1.27	1.01	0.89	1.04	0.72
69							1.44	1.46						1.19	0.71	0.87	1.19	0.58
70																		
71																		
72								1.65						1.28	0.98	1.13		
73								1.37			1.45	0.88	0.95					
74							1.40										1.19	0.57
75								1.23						1.27	0.66	1.02		
76							1.60										1.13	0.43
77							1.51	1.59						1.17	0.69	0.97	1.16	0.40
78							1.51	1.55						1.17	0.94	1.08	1.30	0.63
79	6.01	4.08					1.55	1.52			1.45	1.02	1.16	1.20	0.99	0.85	1.25	0.84
80			2.65		2.57	1.58				0.65	1.59	0.89	1.08	1.29	0.99	1.09		
81							1.38	1.34					1.10	1.26	0.97	0.95	1.29	0.72
82								1.53			1.49	1.01	1.00		0.91			
83							1.62	1.55	1.82	0.93				1.20	0.88	1.08	1.27	0.46
84							1.53	1.41						1.14		1.10	1.25	0.63
85		4.23					1.41	1.39			1.56	0.98	1.02	1.21	0.92	0.99	1.17	0.73
86		4.18					1.30	1.38			1.47	0.97	1.04	1.32	0.95	0.90	1.28	0.69
87								1.67			1.54	1.10	1.19	1.25	1.05	1.03		
88											1.49	1.02	1.08					
89			3.02	4.82	2.54	1.45		1.38	2.05	1.02				1.36	0.99	1.10		
90							1.40	1.30				0.81	1.15	1.22	1.00	1.12	1.25	0.70
91											1.49	0.81	1.00					
92								1.52			1.53	1.02	1.04	1.27	0.91	1.01		
93								1.49			1.56	1.01	1.06	1.22	0.93	0.96		
94												0.98	0.90					
95								1.25			1.64	1.03	1.25	1.29	0.86	1.08		
96							1.29	1.05			1.51	1.04	1.12	1.16	0.84	1.04	1.04	0.68
97								1.58						1.17	0.93	1.01		
98			2.90		2.54	1.27		1.43	1.66	1.07	1.56	1.16	1.14	1.13	0.98	1.06		

Table IV-8: measures (mm) of mandibles of *Crocidura esuae* from Isolidda 3 – US 17

ID	25	M <sub>1</sub> -M <sub>3</sub>	23	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
146				2.96	4.95	2.56	1.26		1.38	2.06	0.89	1.59	1.06	1.20	1.05	1.03	0.97		
147				3.00	4.51	2.55	1.29		1.49	1.82	0.82				1.14	0.93	1.06		
148		4.34		2.99		2.42	1.12	1.38	1.13	1.90	0.71	1.50	0.97	1.24	1.23	0.93	1.07	1.30	0.87
150				2.95	4.67	2.20	1.24			1.87	0.96	1.47	0.98	1.11					
151								1.21	1.05			1.48	0.85	1.13	1.16	0.65	1.00	1.34	0.75
152				2.96	4.52	2.17	1.22			1.88	0.99	1.37	1.17	1.28					
153				3.00	4.85	2.41	1.10		1.25	1.95	1.01	1.16	1.05	1.17	1.31	1.05	1.04		
154				2.56			1.27		1.31	1.80	0.97	1.50	0.95	1.14	1.03	0.94			
155				2.97	4.76	2.41	1.23		1.46	1.99	1.04	1.52	0.77	1.16	1.17	0.86	1.06		
156				2.71	4.15	1.95	1.16			1.87		1.50	1.04	1.05					
157				2.84		2.29	1.26	1.29	1.56	1.54	0.67	1.40	0.83	1.02	1.07	0.84	0.93	1.22	0.55
158		4.36				2.84		1.25	1.34	1.94		1.53	0.88	1.09	1.29	0.97	1.13	1.26	0.65
159		4.04		2.57	4.65	2.35		1.20	1.22	1.70	0.82	1.54	1.04	1.05	1.22	0.93	1.04	0.99	0.75
160				3.04	4.75	2.44	1.23			1.85	1.01								
161				3.02	4.58	2.47	1.48			2.00	0.87	1.56	1.20	1.20					
162	6.00	4.02	1.72	2.80				1.82	1.54	2.04	0.96	1.52	0.98	1.12	1.20	0.92	1.02	1.11	0.70
163				2.65	4.35	2.37	1.36			1.92	1.00								
164				2.45	4.71	2.46	1.27		1.34	2.06	0.72				1.24	0.96	1.05		
165				2.71	3.93	2.29	1.23		1.35	1.65	0.74				1.23	0.92	0.93		
166				3.09	4.73	2.58			1.54	2.10	0.99				1.15	0.94	1.08		
167		3.82		2.78		2.16	1.31	1.44	1.41	1.92	0.96	1.51	0.94	0.91	1.19	0.91	0.98	1.14	0.68
168				2.80	4.73	2.24	1.23		1.56	1.96	0.93	1.45	1.08	1.19	1.23	1.02	1.13		
169				2.34	4.39	2.20	1.11					1.62	1.06	1.09					
170				2.88	4.79	2.54	1.46			2.11	1.05	1.37	1.05	1.19					
171				2.87															
172				3.16	4.95	2.61	1.20		1.46			1.38	0.94	1.18	1.22	0.88	1.07		
173		4.06						1.24	1.46			1.54	1.03	1.17	1.11	0.88	0.98	1.27	0.63
174		4.26		3.06	4.48	2.43		1.50	1.48	1.89	0.98	1.33	0.75	1.06	1.15	0.89	1.05	1.30	0.72
175		3.94		2.99	5.18	2.60	1.40	1.65	1.60	2.04	0.94	1.47	1.03	0.94	1.29	1.00	1.12	1.31	0.84
176		3.97		2.77	4.56	2.30	1.35	1.54				1.47	0.91	0.88				1.30	0.77
177				3.07					1.36	1.94	0.84			0.99	1.31	0.86	0.91		
178	6.27	4.06						1.42	1.32			1.50	0.83	1.15	1.28	0.99	0.98	1.28	0.73
179				2.96	4.78	2.49	1.40			1.95		1.50	0.93	1.18					
180				2.83			1.19		1.42			1.20	0.93	1.05	1.22	0.74	1.00		
181				3.21	5.00	2.37	1.38			1.49	0.92								
182				3.18		2.28				1.69	0.78	1.42	0.99	1.11					
183				2.87	4.25	2.32	1.16					1.58	0.95	1.09					
184				2.67	4.60	2.11	0.99		1.46	1.88	0.85	1.47	0.87	1.13	1.05	0.92	1.03		
185				3.00	4.45	2.29	1.06				1.05	1.36	0.93	1.14					
186				3.09	4.63	2.23	1.15		1.13	1.90	0.75			0.98	1.18	0.86	0.98		
187				2.99			1.51			1.78	0.98	1.41	0.99	1.10					
188				3.02		2.35	1.35			1.88	0.84	1.46	1.01	1.17					
189				3.19					1.61			1.53	1.10	1.15	1.23	0.98			
190				3.05	4.76	2.14	1.37		1.61	1.94	1.10	1.37	0.95	1.12	1.19	0.94			
191				3.25	3.44	2.46			1.59	2.16	1.09	1.40	1.06	1.13	1.07	0.94	0.89		

Table IV-9: measures (mm) of mandibles of *Crocidura esuae* from Isoldida 3 – US 15

ID	M <sub>1</sub> -M <sub>3</sub>	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
192		2.71	4.29	2.33	1.26		1.55	1.53	0.98	1.52	1.02	1.12	1.14	0.93	1.05		
193							1.52	1.85		1.40	1.00	1.11	1.31	1.00	1.05		
194		2.80	4.46	2.47	1.40		1.49	1.87	0.96	1.47	1.04	1.22	1.24	1.05	1.13		
195		2.65	4.81	2.35	1.30												
196		2.82	4.90	2.47	1.59			1.99	1.09	1.50	1.02	1.15					
197		2.97	4.67	2.12	0.98		1.37	1.83	0.70				1.26	0.88	0.91		
198		3.09			1.47					1.39	1.01	1.05					
199		2.64	4.68	2.35				1.88	0.95								
200		2.98	4.45	2.43	1.41		1.42		1.06	1.57	1.06	1.19	1.15	1.00	1.06		
201			4.75										1.29	1.02	1.06		
202		3.02	4.64	2.17	1.29					1.51	1.13	1.19					
203		2.96	4.83	2.22	1.28					1.59	1.03	1.20					
204		2.73	4.92	2.51	1.34		1.43	1.82				1.21	1.15	1.05	1.05		
205		2.82	4.83	2.17	1.24												
206		2.96	4.46	2.33	1.17			1.75		1.54	1.14	1.18					
207		2.93		2.34	1.34		1.41		1.05	1.57	1.09	1.14	1.22	1.06	1.06		
208		2.83				1.54	1.60	1.96	0.97			1.23	1.08	1.09	1.15	1.25	0.84
209	4.21					1.48	1.45			1.41	1.06	1.15	1.09	1.08	1.08	1.10	0.87
210		2.80	4.66	2.52	1.60			2.04	1.01								
211		3.07		2.44	1.20				0.93								
212		3.01		2.34	1.14			2.04	0.97					0.99	1.03		
213		2.94	4.69	2.38	1.52			1.95									
214		3.03	4.68	2.38	1.35			1.82	0.71	1.31	1.10	1.18					
215		3.04		2.19	1.22		1.31			1.47	0.85	1.11		1.01	1.15		
216	4.09	2.71	4.38	2.40	1.30	1.46	1.50	1.86	0.91	1.54	1.00	1.12	1.21	0.91	1.05	1.25	0.56
217	4.07	2.61		2.19	1.21	1.46	1.42		0.85	1.53	1.06	1.17	1.16	0.97	0.94	1.24	0.76
218		2.67	4.55	1.35	1.43			2.02	0.98								
219		2.83	4.73	2.44	1.44		1.51	1.92	1.00				1.21	0.94	0.85		
220						1.56	1.48						1.27	0.97	1.08	1.36	0.76
221	4.30						1.44			1.60	1.13	1.08	1.22	0.78	0.98	1.25	0.73
222		2.54	4.37	2.18	1.25			1.79	0.86								
223							1.36			1.46	1.01	1.16	1.19	0.95	1.06		
224						1.55	1.23			1.50	0.99	1.05	1.22	0.88	0.67	1.11	0.45
225		3.11		2.25	1.34			1.95	0.91								
226						1.50	1.14			1.51	1.01	1.19	1.29	0.96	0.90	1.31	0.78
227		2.29						1.88	0.98								
228						1.37	1.50						1.24	0.95	1.00	1.30	0.77
229		3.40					1.58	2.00	1.06			1.01	1.29	0.96	1.07		
230		2.76	4.65	2.47	1.39		1.34	1.92	0.80	1.51	0.87	1.17	1.09	0.81	0.92		
231		3.07			1.26			1.95	1.02		0.94	1.22					
232		2.89	4.59	2.32	1.39		1.36	1.86	0.94	1.53	0.78	1.01	1.21	0.90	0.88		
233		2.96	4.82	2.39	1.14			1.74		1.61	1.05	1.26					
234		3.19	4.91	2.54	1.23			1.98	0.98								
235		2.68		2.24	1.30			1.73	0.89	1.52	0.90	1.08					
236						1.35	1.53			1.42	0.97	1.20		0.98	1.08	1.18	0.78

Table IV-10: measures (mm) of mandibles of *Crocidura esuae* from Isolidda 3 – US 13

ID	25	M <sub>1</sub> -M <sub>3</sub>	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
99		4.06	2.40	4.41	2.25	1.26	1.36	1.38	1.70	0.95	1.48	1.02	1.11	1.12	0.93	0.99	1.18	0.73
100		3.93	2.73	4.42	2.31	1.56	1.41	1.47	1.99	0.90	1.42	1.03	1.08	1.15	0.92	0.99	1.11	0.71
101							1.50	1.48			1.56	1.00	1.16	1.25	0.96	1.07	1.20	0.73
102			2.50	4.68	2.53	1.38	1.24	1.42		0.91	1.38	0.97	1.08	1.08	0.89	1.00	1.15	0.72
103			2.71	4.81	2.37	1.29			2.01	0.94								
104			2.45	4.58	2.29				1.82									
105			2.83				1.29	1.19	1.79	0.81	1.33	1.01	1.09	1.13	0.89	1.05	1.20	0.78
106			2.73	4.67	2.35	1.35			1.83	0.85								
107		3.70					1.42	1.45			1.46	0.87	1.05	1.06	0.85	0.90	1.14	0.61
108								1.37			1.38	1.00	1.05	1.18	0.85	1.01		
109		4.01					1.50	1.52			1.48	1.01	1.14	1.19	0.93	1.04	1.22	0.76
110			2.52		2.23			1.60	1.69	0.90			1.14	1.13	0.92	0.92		
111			2.22	4.61	2.28	1.40												
112			2.77	4.64	2.27	1.31			1.79	0.76								
113			2.84	4.91	2.50	1.57		0.97										
114	5.64	3.80			2.20	1.12	1.37	1.41			1.31	0.97	1.12	1.22	0.77	0.86	1.08	0.71
115		3.93					1.39	1.42			2.23	0.95	1.05	1.21	0.91	1.02	1.23	0.71
116							1.57	1.46					1.18	0.90	1.08	1.31	0.75	
117								1.39			1.40	0.92	1.06	1.18	0.98	1.03		
118								1.36			1.41	0.99	0.85	1.20	0.82	0.95	1.18	
119								1.14			1.39	1.04	1.10	1.27	0.95	1.03		
120								1.59			1.53	1.02	1.20	1.22	1.01	1.12		
121			2.94		2.46	1.37			1.59	0.89								
122							1.61	1.61							0.93	0.94	0.98	0.68
123			2.77	4.58	2.25	1.29				0.80								
124			2.88	4.40	2.22	1.32	1.45	1.60	1.87	0.88			0.92	1.19	0.95	1.05	1.24	0.78
125				4.43	2.97	1.13			1.97	0.88								
126		4.40	3.15	4.82	2.54	1.38	1.34	1.45	2.06	1.08	1.63	1.13	1.29	1.33	0.70	1.16	1.26	0.52
127			2.81	4.60	2.26	1.23	1.37		1.90	0.87							1.14	0.67
128		4.04					1.38	1.30			1.34	0.91	1.06	1.10	0.85	0.97	1.18	0.74
129			2.82	4.68	2.40	1.47				0.82								
130			2.72	4.26	2.15	1.17		1.37	1.89	0.95	1.43	0.96	1.11	1.14	0.88	1.00		
131			2.62		2.52	1.17		1.52	1.94	0.87	1.49	1.07	1.17	1.20	0.98	0.78		
132			2.89		2.41	1.44			1.96	1.05								
133		3.96	2.65	4.38	2.27	1.25	1.50	1.23	1.86	0.88	1.54	1.06	1.16	1.21	0.96	1.05	1.19	0.61
134			2.85		2.22	1.20			1.98	1.02								
135			2.72	4.34	2.26	1.35		1.40	1.96	0.84				1.19	1.02	1.07		
136			2.79	4.44	2.49	1.34			1.91	0.76								
137			2.47	4.26	1.83	1.16					1.49	0.83	1.07					
138								1.24			1.44	0.87	1.05	1.17	0.94	1.02		
139			2.75	4.37	2.46	1.26		1.49	1.48					1.06	0.93	0.87		
140			2.64	4.62	2.44				1.98	0.91	1.45	1.06	1.10					
141								1.06			1.45	0.99	1.04	1.17	0.86	0.97		
142								1.31					0.96	1.17	0.78	1.04		
143								1.22			1.38	0.92	1.10	1.22	0.91	0.97		
144								1.27			1.38	0.80	0.92	1.10	0.87	0.97		
145								1.33						1.17	0.72	0.84		

Table IV-11: measures (mm) of mandibles of *Crocidura esuae* from Isolidda 3 – US 13

ID	25	M <sub>1</sub> -M <sub>3</sub>	23	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
1			9.57	3.73	4.14	2.03	1.15	1.31	1.42	1.62	0.75	1.31	0.98	1.07					
2				2.65	4.36	2.13	0.4	1.22		1.93	0.82								
3				2.63	4.61	2.2	0.71			2.05	0.9								
5				2.82	4.63	2.31	0.55			1.84	0.87								
6				2.78	4.56	2.24	0.55	1.49	1.29	1.95	0.86			0.88	1.18	0.87	0.96	1.16	0.72
7				2.44		1.8	0.57			1.77	0.89	1.28	0.88	1.02					
8								1.2	1.31						1.26	0.87	0.89	1.09	0.7
9									1.52			1.45	0.96	1.14	1.19		1.04		
10												1.52	1.05	0.98	1.11				
11				2.65	4.4	2.18	0.59			1.84	0.82								
12				2.74		2.12	0.69		1.37	1.82	0.95	1.41		1.11	1.2	0.96	0.96		
13								1.09	1.35			1.48	0.95	1.08	1.16	0.9	0.95	1.18	0.62
14									1.53			1.5	0.9	1.13	1.19	0.92	0.83		
15								1.53	1.51			1.5	0.97	0.98	1.23	0.93	1	1.17	0.7
16				2.99	4.58	2.2	0.73		1.52	1.73	0.86	1.29	1.02	1.16	1.27	0.96	1.06		
17				2.61	4.29	2.22	0.67		1.53	1.76	0.64								
18																			
19								1.48	1.49						1.28	0.9	0.91	1.18	0.67
20				2.65		2.02	0.61		1.34	1.82	0.83				1.18	0.87	0.97		
21									1.24			1.41	0.92	1.06	1.12	0.92	0.94		
23				2.42	4.54	2.08	0.73		1.43	1.9	0.85	1.48	0.94	1.09	1.1	0.91	0.97		
24				2.57	4.78	2.23	0.55			1.85	0.81								
25				2.56	4.47	2.2	0.63		1.45			1.06	0.98	1.09	1.1	0.95	0.95		
26		4.034						1.48	1.49			1.48	1	1.13	1.25	0.94	0.99	1.19	0.71
27				2.73		2.19	0.64		1.54	1.75	0.84	1.39	1.01	1.12	1.16	0.98	0.98		
28				2.88	4.76	2.29	0.58		1.69			1.38	0.94	1.05		0.92	0.93		
29	5.9	3.87	10.4	2.65	4.73	2.29	0.62	1.57	1.63	1.94	0.94		0.95	1.09	1.16	0.99	0.86	1.27	0.73
30							0.74			2.01	0.91								
31				2.74	4.39	2.72	0.75				0.86	1.32	0.95	1.09					
32		4.043		2.74	4.6	4.45	0.67	1.44	1.44	2.01	0.95	1.42	0.98	1.1	1.24	0.81	0.96	1.14	0.72
33																			
34																			
35																			
36									1.21						1.11	0.83			

Table IV-12: measures (mm) of mandibles of *Crocidura sicula* from Oriente cave

ID	M <sub>1</sub> -M <sub>3</sub>	23	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
1	4.007		2.77	4.26	2.2	0.75	1.55	1.45	1.87	0.78	1.45	1	1.15	1.23	0.96	1.05	1.21	0.55
2	3.961		2.66		2.18	0.65	1.28	1.36	1.8	0.77	1.37	0.96	1.09	1.27	0.96	1	1.22	0.72
3		10.12	2.68	4.53	2.33	0.62		1.53	1.94		1.34	1.03	1.21	1.17	1.03	1.08		
4	3.86		2.51	4.56	2.3		1.41	1.45			1.37	0.93	1.13	1.14	1.02	1.05	1.2	0.69
5	3.932		2.56	4.53	2.19		1.33	1.34			1.22	0.99	1.09	1.16		1.01	1.1	0.67
6	3.838		2.65	4.38	2.25	0.7	1.47	1.4		0.83	1.38	1.01	1.08	1.13	0.98	1	1.08	0.71
7			2.71	4.36	2.5	0.74		1.58	1.95	0.88	1.37	1.07	1.11	1.22	0.81	1.04		
8			2.78	4.23	2.01	0.74		1.5	1.84	0.7		0.98	1.12	1.2	0.95	0.83		
9			2.84	4.5	2.28	0.66		1.38	1.7	0.88	1.43	0.95	1.04	1.12	0.88	0.95		
10			2.83	4.26	2.31	0.57			1.67									
11								1.4			1.48	1	1.15	1.05	0.84	1.06		
12	3.758				2.15	0.64	1.45	1.36	1.57	0.69	1.31	0.97	1.09	1.13	0.75	0.88	1.01	0.7
13							1.44	1.37			1.33	1.02	0.99	1.05	0.74	0.82	1.15	0.58

Table IV-13: measures (mm) of mandibles of *Crocidura sicula* from Cala Mancina cave

ID	24	25	M <sub>1</sub> -M <sub>3</sub>	23	27	26	28	ES	40	AM <sub>2</sub>	29	30	41	42	43	44	45	46	47	48
1	7.72		3.814	9.713	2.54	4.23	2.12	0.73	1.18	1.14	1.95	0.87	1.34	0.96	1.06	1.15	0.92	1	1.17	0.74
2	8.01	5.74	3.771	10.28	2.72	3.44	2.32	0.59	1.36	1.56	2.05	0.9	1.41	0.92	1.13	1.14	0.98	1.05	1.2	0.75
3	7.69	5.81	3.873		2.93	4.82	2.32	0.66	1.51	1.8	2.1	0.94	1.37	1.01	1.14	1.19	0.96	1.05		0.72
4	7.8	5.74	3.808	9.718	2.54	4.27	2.15	0.63	1.21	1.31	1.87	0.85	1.16	0.95	1.06	1.14	0.86	0.9	1.19	0.64

Table IV-14: measures (mm) of mandibles of extant *Crocidura sicula* from Contrada Sperone Altavilla (Palermo)

US	ID	33	34	35	36	37	38	39
12	s01	2.01	1.714	1.55	1.732			
	13							
	s02							
	s03	1.931	1.634	1.464	1.67			
	s04			1.575	1.77			
	s05	2.094	1.728					
	s06	2		1.577	1.821			
	s07			1.757	1.856			
	s08	2.121	1.912	1.765	1.877			
	s09	2.088	1.813					
	s10			1.605	1.905			
	s11							
	s12			1.613	1.76			
	s13			1.663	1.706	1.466	2.049	
	s14	2.06	1.84	1.681	1.523	1.228	1.888	
	s15	2.002	1.6					
	s16	1.964	1.453					
	s17	1.968	1.852					
	s18					1.329	2.192	
	s19			1.603	1.619			
	s20	2.029	1.893					
	s21			1.624	1.666	1.449	2.057	
	s22			1.615	1.604	1.383	1.812	
	s23	2.042	1.763					
	s24	2.051	1.85					
15	s25			1.674	1.861			
	s26	2.09	1.494					
	s27			1.616	1.795			
	s28					1.584	2.202	
	s29							
	s30	2.062	1.799	1.563	1.416	1.412	1.783	
	s31	2.023	1.646	1.623	1.6	1.329	1.668	1.516

Table IV-15: measures (mm) of upper teeth of *Crocidura esuae* from Isolidda 3

ID	33	34	35	36	37	38
Re21			1.477	2.108		
Re38						
Re8	1.897	1.551	1.575	1.699		
Rt5	1.918	1.816	1.505	1.76		
SR2-3	1.934	1.639	1.411	1.522		
SR2-4						
SR2-5	1.962					
SR2-6					1.428	1.767
Sr2-7			1.389	1.92		
SR4-27			1.376	1.978		
SR4-29			1.605	1.783		
SR5-18	2.04	1.733	1.666	1.717	1.444	2.019
SR5-19						
SR5-42	2.055	1.799	1.619	1.953		
SR5-46			1.845	1.876	1.475	2.084
SR5-47			1.653	1.691		
SR6-14	1.979	1.631				
SR7-3						

Table IV-16: measures (mm) of upper teeth of *Crocidura aff. esuae* from K22

ID	Strato	16	33	34	35	36	37	38	39
01	3C								
02	3C								
03	3C	4.703	1.877	1.788	1.309	1.787	1.111	1.987	1.243
04	3C	4.7	1.831	1.832	1.488	1.677	1.263	2.083	1.081
05	3C		1.715	1.608	1.309	1.491	1.328	1.776	
06	3C	4.712	1.791	1.889	1.667	1.712	1.223	1.692	1.202
07	3C								
08	3C								
09	3C		1.576	1.747	1.249	1.659		1.64	
10	3C		1.954	1.855	1.544	1.777			
11	3C		1.843	1.805	1.323	1.679			
12	3C						1.419	1.926	
13	3D		1.959	1.772	1.517	1.842	1.346	2.016	
14	3D		1.902	1.896	1.497	1.64	1.393	1.993	
15	3D								
16	3D				1.625	1.693			
17	3D		1.95	1.813					
18	3D		2.056	1.783					
19	3D		2.039	1.629	1.638	1.675		1.82	
20	3D				1.542	1.562			
21	3D				1.605	1.693			
22	3D				1.693	1.75			
23	3D		1.94	1.539					
24	3D		1.843	1.489	1.598		1.393	1.825	
25	3D		1.927	1.756	1.538	1.601			
26	3D		1.908	1.743	1.61	1.615			
27	3D		1.966	1.839					
28	3B				1.619	1.798			
29	3E		1.957	1.744	1.576	1.791		1.818	
30	3E								
31	3E								
32	3E				1.589	1.736			
33	3E			1.84	1.587	1.69	1.388	1.958	
34	sotto 3E		1.894	1.716	1.605	1.595			
35	2/3		1.95	1.815	1.555	1.733			
36	3F								
37	3F		2.004	1.756	1.68	1.579			
38	3B		1.919	1.629					
39	3B		1.942	1.824	1.505	1.853	1.359	2.103	
40	3B		1.92	1.612	1.55	1.707			
41	3A		1.93	1.737					

Table IV-17: measures (mm) of upper teeth of *Crocidura sicula* from Cala Mancina cave

Locality	ID	16	33	34	35	36	37	38	39
Contrada Sperone Altavilla Milicia (Palermo)	5			1.874	1.417	1.453	1.634	1.34	1.923
Contrada Sperone Altavilla Milicia (Palermo)	6	4.475	1.648	1.576	1.376	1.548	1.303	1.863	1.295
Contrada Sperone Altavilla Milicia (Palermo)	7	4.919	1.928	1.739	1.489	1.691	1.265	1.898	1.338
Vignazze (Palermo)			1.916	1.593	1.427	1.623	1.349	1.885	1.313
Gibilrossa Belmonte Mezzagno (Palermo)			1.949	1.64					

Table IV-18: measures (mm) of upper teeth of extant *Crocidura sicula*





IV-7 Isolidda 3 cave, upper teeth of *Crocidura esuae*

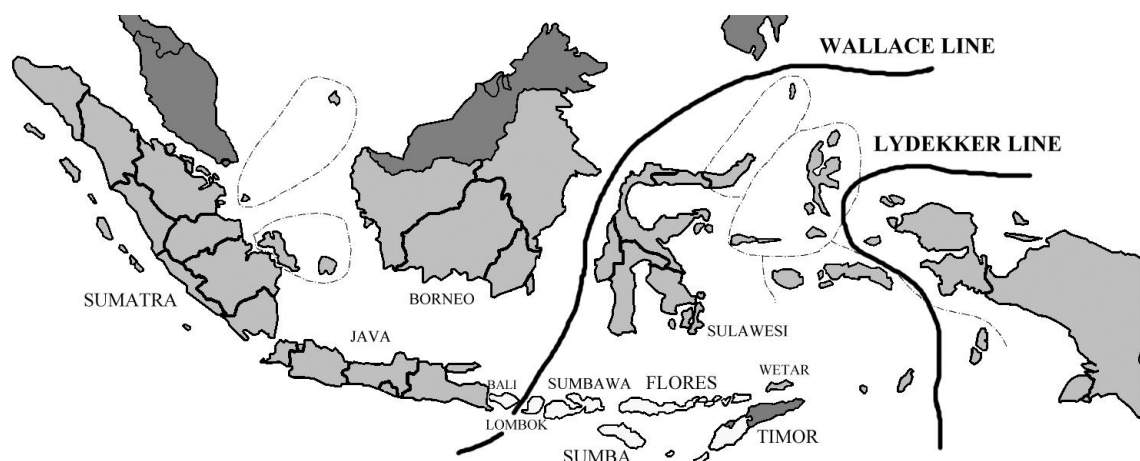


## PART 2: FLORES

### V. Liang Bua cave

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Flores is an oceanic island of Lesser Sunda Islands (the whole chain from Bali to Wetar and few more islands), midway between Sunda and Sahul. It is about 400km long and has an area of about 14000 km<sup>2</sup> (Figure V-1). It is situated east of the Wallace's Line/Huxley's Line, which is one of the main biogeographic barriers all over the world.



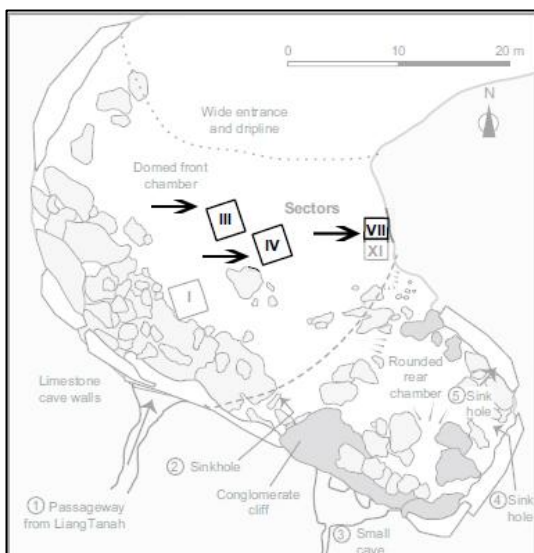
**Figure V-1: Map of Lesser Sunda islands, with the Wallace and Lydekker lines.**

Seven different biogeographic lines have been drawn in this area (Simpson, 1977). It is not so easy to trace conclusive biogeographic lines that unequivocally separate faunal groups of different origin, because it depends a lot on the method used to separate different faunas (maximal diversity between contiguous faunas, percentage of animals from different zoogeographical areas, etc and on the faunal group considered. Wallace's Line, located between Lombok and Bali, is the best known and most widely used among the lines that separate Flores from the Asian group on the east; Huxley's Line modifies it, extending it northward. This line forms the boundary of the Asian zoogeographical region. The Lydekker's Line, which separates the Australian region from the Austro-Malayan region, runs between K. Kai and K. Aru and leaves Ceram on the west and the Irian Jaya occidentale on the East. The area in the middle, called Wallacea or Indo-Malayan region, is, according to Simpson (1977), not a proper transitional zone between these different regions from a faunal point of view and is even not homogeneous in faunal composition. Because of this, every oceanic island has to be considered independently and not as a part of a big zoogeographical region. In this paper I will use Wallacea only as a geographic name, to indicate the area between Huxley's Line and Lydekker's Line, and not as a zoogeographical region.

In order to reach Flores from the west, it is necessary to cross at least two sea barriers: the first between Bali and Lombok (25km) and the second between Sumbawa and Flores (9km). Since very strong currents pass by there, the crossing of these barriers is very challenging and even during periods of major sea level lows crossing the strait was very difficult if not impossible for the greater part of terrestrial animals (van den Bergh, 1999). As a consequence, all Pleistocene faunas east of the Wallace's Line have an impoverished fauna. To the east, Flores is separated from the Australian region by the Lydekker's Line; in between are Timor and many small islands. To the north, Flores is separated from Sulawesi and smaller islands by the Flores Sea, which in the area between Flores and Sulawesi can reach a depth of 5140m. Between Flores and Sulawesi are only some very small volcanic islands. According to van den Bergh (1999), the connection between Flores and Sulawesi would require a sea level drop of at least 1000m, allowing only an indirect connection via Java Sea. This means that during the Pleistocene there was no connection between either Flores and Sulawesi or Flores and the Sunda Shelf.

### ***History of research***

Research at Liang Bua cave began when the Dutch priest and archeologist Father Theodor Verhoeven carried out excavations at many archaeological sites in Flores, both in caves and at open fossil sites (Morwood et al., 2009). He made a first survey of the cave in 1950, when the cave was still used by an elementary school and made a test-trench. He came back in 1965 to make more extensive excavation, and recovered six Neolithic and Proto-Metallic burials, associated with stone artifacts and faunal remains. Later, excavations were resumed by Prof. R. P. Soejono of the Indonesian Centre of Archaeology and in more than ten years (1978-1989) he investigated ten squares (I-X) down to a maximum depth of 4.2m, recovering material dating up to 10,000 years. Further excavations were carried on by an international team, headed by Prof. M. J. Morwood of the University of Wollongong, Australia, since 2001 as part of a multi-disciplinary project "Astride the Wallace Line" of the University of New England. This project allowed extensive excavations, going deeper in sectors already investigated by previous teams and opening a new sector, Sector XI. The planimetry of the cave, with the indication of the sectors investigated, is illustrated in Figure V-2.



**Figure V-2: planimetry of Liang Bua cave, modified after Westaway et al. (2009a). Sectors investigated in this thesis are indicated by the arrows**

The material recovered was studied by an international team, involving many institutions all over the world. The study of vertebrate remains has been headed by Dr. Gert van den Bergh (NCB Naturalis, Indonesian Centre of Archaeology and University of Wollongong), who is expert in Indonesian vertebrate deposits, and particularly in elephantoid evolution (Van der Bergh, 1999; Van der Bergh et al, 2009). Birds remains were studied by Dr. Hanneke Meijer (Smithsonian Institution and NCB Naturalis) and Rokus Due Awe (Indonesian Centre for Archaeology) (Meijer

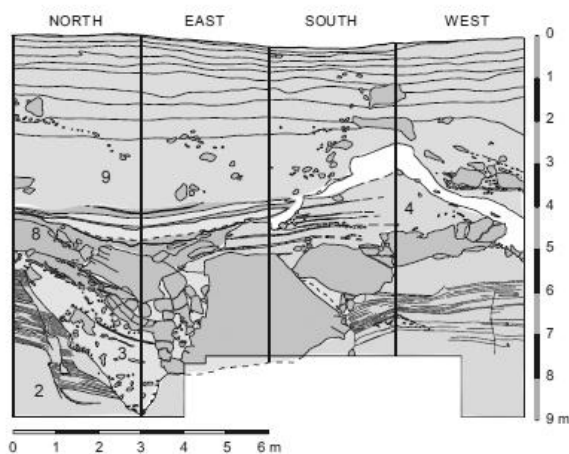
et al., 2010), insectivores by Dr. Lars van den Hoek Ostende (NCB Naturalis) (Van den Hoek Ostende et al., 2007), bats are under study by the same and rodents will be analyzed in this thesis.

### **The cave**

Liang Bua cave is located in West Flores, 7 km northwest of Ruteng. It is a large limestone cave located at an altitude of 500 m above sea level and 30 km from the recent margin of north and south coasts. The material discussed in this thesis comes from Sector IV (all the material collected since the 70's), part of Sector III (spits 27-48; 10) and Sector VII (30-70), collected in the 2001-2004 excavations. Excavations were carried on by 10cm spits or stratigraphic units. Therefore, the spit number indicates the depth at which remains have been recovered (for instance, spit 16 = 150-160 cm deep).

### **Sector IV**

Sector IV is 3x3 m square; it was excavated down to a depth of 4.3 m by Prof. Soejono between 1978 and 1985 and by Morwood and Soejono between 2001 and 2004, reaching a maximum depth of 9.0 m. The stratigraphy is illustrated in V-3.



**Figure V-3: stratigraphy of Sector IV (after Westaway et al., 2009b)**

This sector is the most extensively dated, with a total of thirteen <sup>14</sup>C, two coupled ESR/U-series dating, a single U-series age and seven TL estimates (Roberts et al., 2009). The <sup>14</sup>C chronology spans the entire Holocene and the terminal Pleistocene. The uppermost layers (from 1 to 4 m) are clayey

silts and sandy silts and contain evidence of young occupations (Neolithic pottery burials and artifacts) (Unit 9). Extensive layers of volcanic material were found in this sector and provide a good stratigraphic marker (Unit 8). It is possible to distinguish black volcanic sand (or black tuffaceous sand or BTS) and fine layers with tephra (white tuffaceous silt of WTS). Westaway et al. (2009), in the analysis of the sediments, conclude that these deposits represent an airfall tephra that settled on the land surface and was later washed into the cave. The sloping relief in the cave affected the deposit, causing increased accumulations to a thickness of 80 cm in the northeastern corner of Sector IV. Since deposits referable to Units 7-5 have been eroded in this sector, there is a big chronological gap under the volcanic sediments. Under volcanic Unit 8, Unit 4 represents an occupational level, very rich in stone artifacts, endemic vertebrate remains (among which *Stegodon florensis insularis*) and seven bones of *Homo floresiensis*. The material has been deposited here along a natural sloping and thin layers of flowstone suggest that water was the main responsible for the material accumulation. This Unit should have an age of 61-74ka and material up to spit 50 can be referred to this Unit. The lowest Unit 3 represents collapse material that fills the scoured channels of the underlying Unit 2. These two units are mainly sterile, with



only some stone artifacts in Unit 1. They are dated to 95-100ka (Unit 3) and 100-130 ka (Unit 2) (Roberts et al. 2009).

### Sector III

Of this Sector, only central Units have been investigated (spits 27-48; 10), since the material from other spits is still at the Jakarta Centre for Archeology. Down to 3.6 m (Layer 1-3; Unit 9) only modern human and extant animals have been recovered; Neolithic evidence begins at a depth of 1.7m (Morwood et al., 2009).

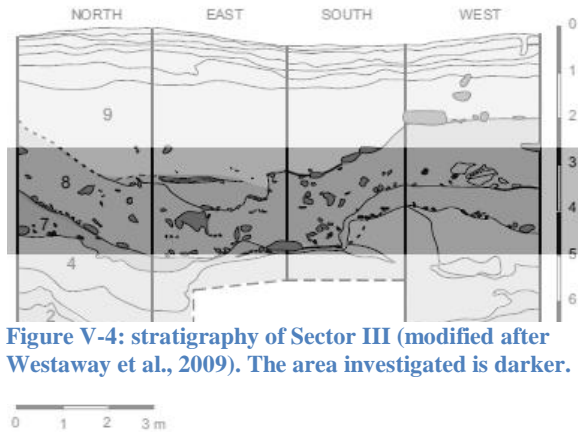


Figure V-4: stratigraphy of Sector III (modified after Westaway et al., 2009). The area investigated is darker.

The earliest evidence of hominine occupation and faunal remains comes from the base of Layer 5 (Unit 4) (among which two teeth of *Homo floresiensis* at spits 48 and 51 and *Stegodon floresiensis insularis* remains, Morwood and Jungers, 2009). A similar association has been recovered from overlying clay (Layer 4, Unit 8). Only two <sup>14</sup>C dating has been made in this sector: the upper one from the base of Unit 9 (3.63m) has an age of 1.82-0.94 ka; the lower one, at

the base of Unit 8/7(4.46 m) is 17.1-15.7ka. One U-series dating was made, but it was carried out on a fallen slab of flowstone, that is it only indicates that the flowstone fell into the deposit within the last 140±4ka. TL dating at a depth of 4.91-4.96m and 7.40-7.45m gave respectively ages of 69±12 and 106±31ka, respectively (Roberts et al., 2009).

### Sector VII

This is the Sector that yielded the famous partial hominine skeleton of *Homo floresiensis* (LB1), found in 2003 excavations (Morwood et al., 2004). In this thesis only the material excavated in 2003, from a depth of 3m down to 7m (Unit 8 and 7), is studied. We do not have the material from upper spits, collected during Soejono excavations, and the material recovered in next years. In fact, in 2004 excavations went on, with the deepening down to 11 m of the excavation in Sector VII and the opening of a new sector close to this one, with the purpose of finding the lacking parts

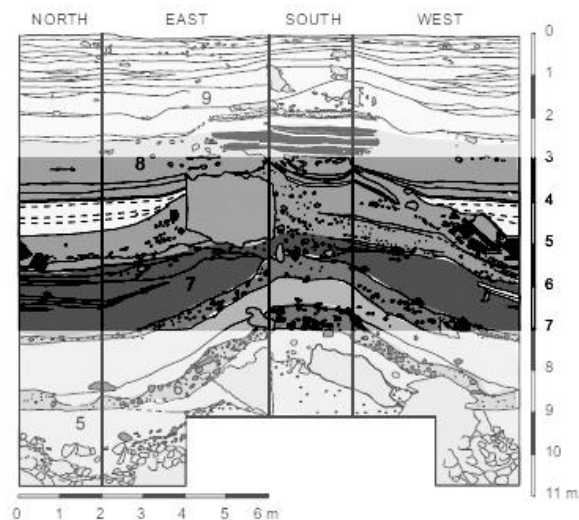


Figure V-5: stratigraphy of Sector VII (modified after Westaway et al., 2009). The area investigated is darker.

of the skeleton recovered (and eventually at least 14 individuals were recovered there; Morwood et al., 2009a). Stone artifacts and endemic animal remains (*Stegodon floresiensis insularis*, *Varanus komodoensis*) were concentrated between ca. 5-3 m in depth (Unit 8). Unit 7 represents a pool deposit during a phase of intensive occupation. Many datings have been carried out in this Sector.

Five  $^{14}\text{C}$  datings gave an age of 13.4-12.7 for the uppermost one (4.5-5.6m deep) and an age ranging 17.9-19.8ka for the deepest ones (5.88-6.70m), indicating that the deposits stem from the Late Glacial.

### ***Homo floresiensis***

This cave is well known for the find of a small sized hominine, *Homo floresiensis*, nicknamed “the Hobbit”. Since 2004 many fossils have been attributed to this species, and in 2009 a list of 79 remains attributed to *H. floresiensis* has been published (Morwood and Jungers, 2009).

There is no general consensus on the taxonomical status of this species, with hypotheses ranging from a relict Australopithecine form (Falk et al., 2009; Brown and Maeda, 2009) to human affected by microcephaly (Martin, 2006), Laron Syndrome (Hershkovitz et al., 2007), cretinism (Obendorf et al., 2008), or microcephalic osteodysplastic primordial dwarfism type II (MOPD II) (Hall et al., 2004; Rauch et al., 2008). It is remarkable to notice how much debate these relatively numerous findings have caused, compared to the general specific acceptance of fossil species in palaeo-anthropology on the basis of few (sometimes unique) remains. Then, why is *Homo floresiensis* so particular? The main points concern age, size and morphology.

1. AGE: *Homo sapiens* has always been considered the only human survivor of last glaciation. No other human species was known after the extinction of *Homo neanderthalensis* around 27ka BP.
2. SIZE: the estimation of stature of *Homo floresiensis* is 106-109 cm (Morwood et al., 2005) and its brain capacity is 417cc; it is the smallest hominine ever found;
3. MORPHOLOGY: the analysis of morphological characters of teeth, skulls and post-cranial bones show a mosaic of characters that can be alternatively (and in some cases without consensus of opinions) referred to *Homo habilis* (Morwood et al., 2005; Tocheri et al., 2007; Argue et al. 2009; Brown and Maeda, 2009; Jungers et al., 2009), *Homo erectus* (Lyras et al., 2008), pigmy *Homo sapiens* or *Homo sapiens* affected by many different kinds of diseases; some finds in the peculiarities of the morphological characters the proof for the evolution in insular environment (Niven et al., 2007a and b), some others the refusal (Köhler et al., 2008).

I am not an anthropologist and I cannot and I do not want to give any conclusive hypothesis about the taxonomical status of *Homo floresiensis*. In stead, this thesis focuses on the pristine fauna of the island, as knowing the environment of a species is vital for understanding its evolution.

### ***Vertebrate assemblage***

Vertebrate evolution on Flores is documented by few sites located in two main areas: Ola Bula formation and Liang Bua cave. Quaternary vertebrate documentation can be group in three Pleistocene groups plus the Holocene faunal association, product of the introduction in the island of cosmopolitan species.

The oldest documentation of Quaternary vertebrate presence in Flores comes from the Ola Bula formation, dated to the Early Pleistocene. Two different faunal associations were recovered there. Fauna A (Tangi Talo) with *Stegodon sondaari* and three reptiles (*Varanus komodoensis*, Crocodile sp. and *Geochelone* sp.) (van den Bergh et al., 2001a). In the following Fauna B (Dhoso Dhalo, Boa Leza, Ola Bula, Mata Menge) the last two reptiles disappear, *Stegodon sondaari* is replaced by *Stegodon florensis*, the first endemic rodent is found (*Hooijeromys nusatenggara*) and the occurrence of artifacts implies the presence of man, likely *Homo erectus* (van den Bergh et al., 2001; Meijer et al., 2010). Only 100 ka separate these faunal successions: the older is dated to 0.9 Ma and the younger to 0.8-0.7Ma. Before the discovery of deeper layers of Liang Bua, the following faunal succession known came from Holocene cave deposits, like Liang Toge (Musser, 1981). The discovery of Liang Bua has not filled completely the gap, since more 500 ka still separates Mata Menge from Liang Bua, but important data have been found. In particular, the species present in older spits shows a high degree of continuity with the Early Pleistocene fauna B; the elephantoid recovered belongs to a different sub-species, *Stegodon florensis insularis*; many rodents are strictly related to *Hooijeromys nusatenggara* (*Papagomys* species, *Paulamys naso*, *Komodomyx rintjanus*); the giant lizard is still present (*Varanus komodoensis*). Important changes coincide with the volcanic events during Late Glacial (extinction of *Homo floresiensis* and *S. f. insularis*) and with the occurrence of the first Neolithic evidence since around 4ka BP. Together with pottery and agriculture, man introduced animals, and in particular large mammals (*Macaca fascicularis*, *Hystrix javanica*, *Paradoxurus hermaphrodites*, *Sus scrofa*) (van den Bergh et al., 2009), but also rodents such as *Rattus exulans*. These introductions changed the composition of the small mammal fauna. Therefore, the fossils from Liang Bua are now the main source for reconstruction the pristine insular environment of Flores, and the changes therein over time.

In the following chapters I will take into account the rodent succession at Liang Bua.

Flores Island a hot-spot for the biodiversity, also thanks to the presence of some endemics. Among small mammals, only rats, mice and two shrews are living there now and the great part of them are commensal species, with a wide distribution and were introduced to Flores during Holocene by modern humans: *Rattus exulans*, *Rattus norvegicus*, *Rattus rattus*, *Rattus argentiventer*, *Mus musculus* and *Mus caroli*. Besides these, one shrew (*Suncus mertensi*) three endemic rats dwell the island, *Rattus hainaldi*, *Paulamys naso* and *Papagomys armandvillei*. The former is a small rat (about the same size of *Rattus exulans*) that was discovered by Kitchener et al. in 1991 (Kitchener et al., 1991a). It already inhabited the island during the Late Pleistocene, as documented by the material recovered at Liang Bua. *Paulamys naso* is a middle size murid, described for the first time by Musser (1981) on the basis of four subfossil mandibular remains recovered in the Holocene site of Liang Toge, Flores. It was initially described as *Floresomys naso*, but its generic name turned out to be pre-occupied.



# VI. Small rats: evidence of the Neolithic introduction of *Rattus exulans*

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*“Organisms are not billiard balls, propelled by simple and measurable external forces to predictable new positions on life's pool table. Sufficiently complex systems have greater richness. Organisms have a history that constrains their future in myriad, subtle ways.”*

*S. J. Gould*

Excavations at Liang Bua Cave have yielded a large amount of micromammals remains, the major part of which are Murids. In this chapter the small size ones will be discussed. They can be referred to two species: *Rattus hainaldi* Kitchener, 1991 and *Rattus exulans* Peale, 1848, the former endemic to Flores and the latter known to be spread all over the South-Eastern Asia, Australia and the other Pacific Islands with Polynesian populations (Matisoo-Smith and Robins, 2004). *Rattus hainaldi* results to be a very old element of the Flores fauna, already present in the most ancient deposits, in association with endemic fauna like *Stegodon florensis insularis* (van den Bergh et al., 2008) and *Varanus komodoensis* (van den Bergh et al., 2009), since 95ka. It was found in 1990 (Kitchener et al., 1991a), thus it didn't get extinct, but specimens referable to this species become very rare from spit 13, when *R. exulans* was recovered for the first time, supporting the spread with the Neolithic population around 4ka ago. The morphological differences between lower and upper molars of these two species will be discussed.

## **Introduction**

The distribution of species is largely influenced by Man. Especially in historical times, introductions had a devastating effect on the endemic faunas of islands all over the world. Although the number of recorded extinctions has reached alarming numbers over the last centuries, the process began already in Neolithic times, as early farmers brought their life stock with them on their explorations. This led for instance to the extinction of the local faunas in the Mediterranean, such as the dwarfed goat *Myotragus* on Mallorca (Bover and Alcover, 2003), and the insular deer *Candiacervus* on Crete and Karpathos (De Vos, 2006).

Not all introductions were intentional. The clearest example of these are the rodents, and more in particular the rats. As Europeans set out to explore the world, ship rats (*Rattus rattus*) set shore on many islands, and these highly adaptable creatures turned out to be disastrous for the unbalanced insular ecosystems. Even before that time, *Rattus exulans* accompanied the Polynesians on their travels across the Pacific, making it one of the most wide-spread mammal species on Earth today (Matisoo-Smith et al., 1998). Presumably, this species, whose divergence from *R. rattus* and *R. tanezumi* has been dated at ca. 2.2 Mya (Robins et al., 2008), was native to one of the Lesser Sunda Island (Schwarz and Schwarz, 1967; Roberts, 1991). The expansion of *R. exulans* in archaeological sites in Oceania has been extensively studied by Matisoo-Smith (Matisoo-Smith et al., 1998; Matisoo-Smith and Allen, 2001; Matisoo-Smith and Robins, 2004).

Excavations in Liang Bua (Ruteng district, Flores, Indonesia) have yielded numerous murid remains. Among these are many mandibles and maxillaries which are of similar size as those of *R. exulans*, a species that is now numerous on the island. However, Flores is also home to a native rat, which is morphologically very close, *R. hainaldi*. This species seems to be a rare component of the fauna; at first it was known exclusively by one specimen recovered on the island in 1990 and another one tentatively attributed to this species (Kitchener et al., 1991a). Later it was found to have survived in undisturbed forest habitats (Kitchener & Yani, 1998; Maryanto et al., 2009)

The well-dated sections from Liang Bua now offer a unique opportunity to study the effect of the introduction of *Rattus exulans* on the local fauna, and in particular on the endemic species which are of similar size. In this paper we describe the remains of the smaller rats from the Liang Bua excavations, in order to find dental characteristics which can distinguish between the two species. Thus, we will be able to determine the moment of arrival of *R. exulans* and to track the replacement of the local species.

Liang Bua Cave is a key site for the recovery and description of the Late Pleistocene and Holocene endemic fauna of Flores. Large vertebrates, like the new subspecies *Stegodon florensis florensis* (van den Bergh, 2008) or *Leptoptilos robustus*, a giant marabou stork (Meijer and Due, 2010), and small mammals, like two species of shrew (van den Hoek Ostende et al., 2007), had never been recorded in other fossil sites on Flores. The large amount of fossil remains recovered also allowed to demonstrate the extinction of the Verhoeven's giant rat (Zijlstra et al., 2008), despite claims the species still survived (Suyanto & Watts, 2002). This site is also crucial for the identification of small rats because of the large amount of mandibles and various maxillary remains belonging to these species, allowing a morphological description and characterization of *Rattus hainaldi* and a distinction with *R. exulans* remains. This can enrich the understanding of ancient human behaviour, as the latter one results to be clearly introduced together with the arrival of Neolithic culture in the island.

## **Material and methods**

The sample comes from the Soejono excavations in 1978, 1980, 1981, 1982, and the ones under direction of Morwood in 2001, 2002, 2003. The sections were excavated in 10 cm spits, thus allowing the specimens location.

At Liang Bua Cave 236 mandibles of *Rattus hainaldi* from Sector III, IV and VII and 52 of *Rattus exulans* from the upper spits of Sector IV were recovered, as well as 23 maxillaries with molars (7 referable to *exulans*, 16 to *hainaldi*). In addition, 16 isolated teeth, 71 mandibles with unidentified teeth and 167 edentulous mandibles of similar size were recovered. These could not be identified with certainty and have not been taken into account in our analyses.

The nomenclature used in this paper for the description of the teeth is the one developed by Musser (1981).

For each molar the length and width were recorded. Before measuring, teeth were aligned along their axis as shown in Figure VI-1. In lower molars the axis of the tooth passes the middle of the primary cusps of the first two laminae, in upper ones in the middle of the central cusps of the first two rows. Subsequently, the maximum length, and maximum width were measured.

The fossil material has been compared to recent *Rattus exulans* specimens from Indonesia in the collections of the Netherlands Centre for Biodiversity, Naturalis in Leiden . We had no original material of *Rattus hainaldi* at our disposition, since the species is known only from few specimens collected in recent expeditions (Kitchener et al., 1991a, Kitchener et Yani, 1998). Thus, our identifications are based on the pictures and description of the holotype from Kitchener et al. (1991a).

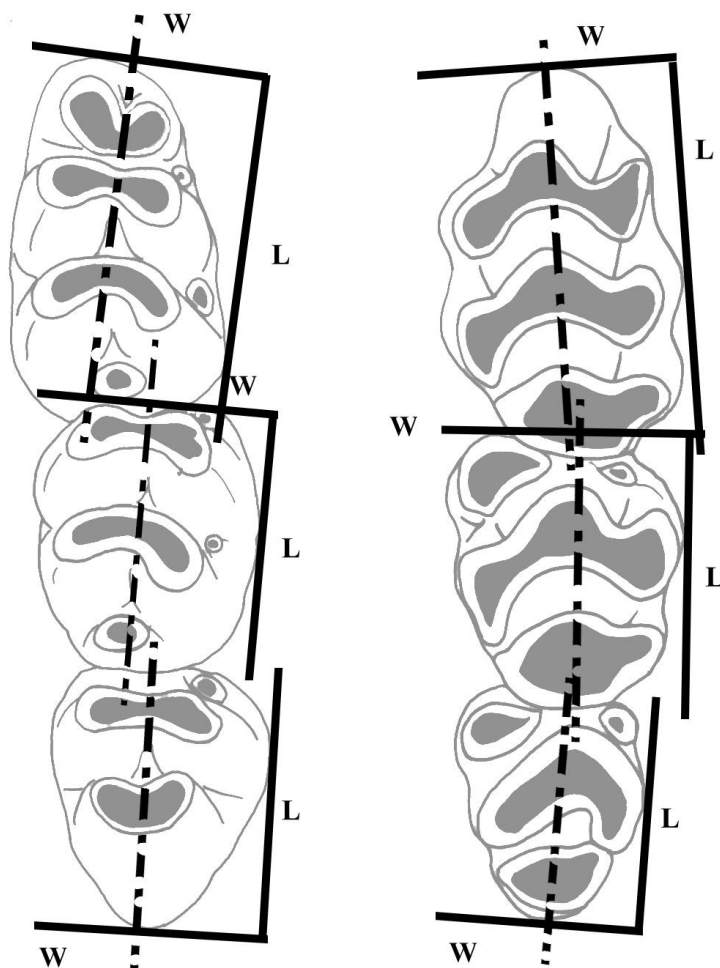


Figure VI-1: plan of measurement

## Systematic Palaeontology

**Class:** Mammalia Linnaeus, 1758

**Order:** Rodentia Bowdich, 1821

**Suborder:** Muridae Illiger, 1811

**Genus:** *Rattus* Fischer, 1803

*Rattus hainaldi* Kitchener, How & Maharadatunkamsi, 1991

**Original reference** - *Rattus hainaldi* Kitchener et al. (1991a)

**Holotype** – WAM M32877 at Western Australian Museum

### Measurements

see Table VI-2

<i>Rattus hainaldi</i>	$LM_1$	$WM_1$	$LM_2$	$WM_2$	$LM_3$	$WM_3$	$WM_2/WM_1$	$WM_3/WM_1$	$WM_3/WM_2$
<b>Mean</b>	2.38	1.47	1.72	1.53	1.50	1.32	104.03	89.89	86.38
<b>Standard Error</b>	0.01	0.01	0.01	0.00	0.01	0.01	0.31	0.50	0.31
<b>Median</b>	2.38	1.48	1.71	1.53	1.51	1.32	103.97	89.71	86.52
<b>Mode</b>	2.36	1.52	1.66	1.49	1.55	1.36	100.00	87.50	87.18
<b>Standard deviation</b>	0.10	0.07	0.08	0.06	0.09	0.06	3.65	4.68	2.98
<b>Sample Variance</b>	0.01	0.01	0.01	0.00	0.01	0.00	13.29	21.88	8.89
<b>Kurtosis</b>	-0.11	-0.23	0.24	0.48	0.17	0.64	9.88	6.04	0.02
<b>Skweness</b>	-0.13	-0.31	0.64	-0.15	-0.34	-0.12	1.63	1.55	-0.30
<b>Range</b>	0.50	0.42	0.39	0.39	0.45	0.38	32.64	30.98	14.04
<b>Minimum</b>	2.08	1.24	1.56	1.33	1.25	1.13	93.98	81.93	78.48
<b>Maximum</b>	2.58	1.66	1.95	1.72	1.70	1.51	126.61	112.90	92.52
<b>Sum</b>	441.02	272.71	306.81	273.55	152.89	134.96	14667.60	7820.07	7860.95
<b>Count (n)</b>	185	186	178	179	102	102	141	87	91
<b>Confidence Interval (95,0%)</b>	0.01	0.01	0.01	0.01	0.02	0.01	0.61	1.00	0.62

**Table VI-1: descriptive statistical analysis of lower molars of *Rattus hainaldi* from Liang Bua**

### Description of the material from Liang Bua Cave

Lower molars: each first lower molar is anchored by four roots. Each second and third lower molar has three roots, two small mesial ones a large distal one.

In both the species the second molar is the widest tooth and the third one the most narrow.

**$M_1$ :** the first lower molar is structured in three laminae, the first corresponding to the anteroconid complex, the second to metaconid and protoconid, the third to hypoconid and entoconid. A small round antero-central cusp is present in 18 % of the specimens. The anteroconid is symmetrical, made up of two large lobe; sometimes the anterlingual cusp is bigger. In young individuals, with a weak wear, the anteroconid is well separated from the second lamina; in worn teeth, the lingual cusp connects to the metaconid cusp by a thin longitudinal ridge. In the second lamina metaconid is slightly larger; its mesial wall is straight, while the distal one can be straight in young specimens or arched in older ones. The third lamina presents a straight mesial wall in young specimens, that

tends to become arched in teeth. A small accessory cusp (c1 or posterior labial cusp) is always present, and only in much worn specimens merges with the third lamina. The posterior heel can be round (above all in slightly worn teeth) or oval (in worn teeth).

**M<sub>2</sub>**: The second lower molar has a squarish outline. It is made up of two laminae, transverse in young specimens or arched in worn teeth. A small antero-labial cusplet is usually present, in line or slightly protrudent with the first lamina, but it soon merges with the protoconid. A posterior lingual cusplet is also present and in worn teeth it is merged in the second lamina and the labial crest connects the protoconid with the hypoconid. A wide oval heel is present.

**M<sub>3</sub>**: It is formed a straight mesial lamina and a small antero - labial cusplet is present in the 41 % of the specimens. This cusplet is only slightly protrudent. The heel is thin and transverse in slightly worn teeth, but advancing the wear it becomes wider, with a rounded distal profile. The lamina is slightly broader than the distal part of the tooth, thus the outline of the third lower molar is straight mesially and rounded distally.



**Plate 5: Lower and upper molars of *Rattus hainaldi***

Upper molars: Each first molar is anchored by five roots, one large mesial, two small central (one labial and one lingual) and two small distal (one labial and one distal), each second molar has four roots (two mesial and two distal) and each third molar has three roots (two mesial and one distal). The first molar is the widest.

**M<sup>1</sup>**: t1 is cylindrical and placed slightly backwards, is bigger than t3 and forms almost a right angle with t2-t3. The main tubercles, t2, t5 and t8 are voluminous, t3 and t1 are of the same size. The three rows are always well separated. The distal row is made up almost exclusively by t8, t7 is absent, t9 is widely connected to t8 and t12 almost completely integrated in t8. No accessory cusplet is present.

**M<sup>2</sup>:** t1 is voluminous, cylindrical and well separated from t2, except in worn teeth when an enamel crest connects them. t3 is very small, sometimes it is reduced to a mere enamel fold. t4 and t6 are around of the same size, but t4 is located slightly backwards. t8 is wide and widely connected to t9.

**M<sup>3</sup>:** The third upper molar has a wide, drop shaped, lingual tubercle (t1) and a very small cylindrical labial one (t3). Distally to these cusps is a row, made by the confluence of t4 (lingual), t5 (central) and t6 (small and labial). All these cusps are largely merged since the first stages of wear into a “boomerang-shaped structure”. t8 is wide, elliptical in section and can be widely labially connected to t6.

*Rattus exulans* Peale, 1848

**Original reference** – *Mus exulans* Peale, 1848

**Lectotype** – U.S.N.M. No. 3730 Tahiti, Society Island (Selected by Stone, 1917, p. 258, from several animals from a number of islands listed by Peale under his description of *exulans*) in Tate 1935

**Measurements** – see Table VI-2

<i>Rattus exulans</i>	<i>LM<sub>1</sub></i>	<i>WM<sub>1</sub></i>	<i>LM<sub>2</sub></i>	<i>WM<sub>2</sub></i>	<i>LM<sub>3</sub></i>	<i>WM<sub>3</sub></i>	<i>WM<sub>2</sub>/WM<sub>1</sub></i>	<i>WM<sub>3</sub>/WM<sub>1</sub></i>	<i>WM<sub>3</sub>/WM<sub>2</sub></i>
<b>Mean</b>	2.19	1.30	1.61	1.39	1.41	1.20	105.84	91.79	86.53
<b>Standard Error</b>	0.01	0.01	0.01	0.01	0.01	0.01	0.33	0.60	0.55
<b>Median</b>	2.20	1.31	1.61	1.40	1.42	1.19	105.97	91.14	85.97
<b>Mode</b>	2.14	1.32	1.63	1.40	1.40	1.16	106.87	90.98	82.86
<b>Standard deviation</b>	0.07	0.05	0.08	0.06	0.08	0.06	2.05	2.95	2.78
<b>Sample Variance</b>	0.01	0.00	0.01	0.00	0.01	0.00	4.20	8.71	7.75
<b>Kurtosis</b>	-0.49	-0.39	1.38	-0.83	0.37	-0.38	-0.45	-0.07	-1.00
<b>Skweness</b>	0.16	0.26	0.23	-0.12	0.20	0.44	-0.06	0.13	0.22
<b>Range</b>	0.28	0.21	0.39	0.20	0.34	0.21	7.98	12.77	9.61
<b>Minimum</b>	2.05	1.22	1.42	1.29	1.27	1.11	102.10	85.61	81.69
<b>Maximum</b>	2.33	1.43	1.81	1.49	1.61	1.32	110.08	98.37	91.30
<b>Sum</b>	100.79	60.00	69.30	59.66	40.91	34.77	4127.81	2202.97	2249.74
<b>Count (n)</b>	46	46	43	43	29	29	39	24	26
<b>Confidence Interval (95,0%)</b>	0.02	0.02	0.02	0.02	0.03	0.02	0.66	1.25	1.12

**Table VI-2: descriptive statistical analysis of lower molars of *Rattus exulans* from Liang Bua**

**Description of the material from Liang Bua Cave**

Lowe molars

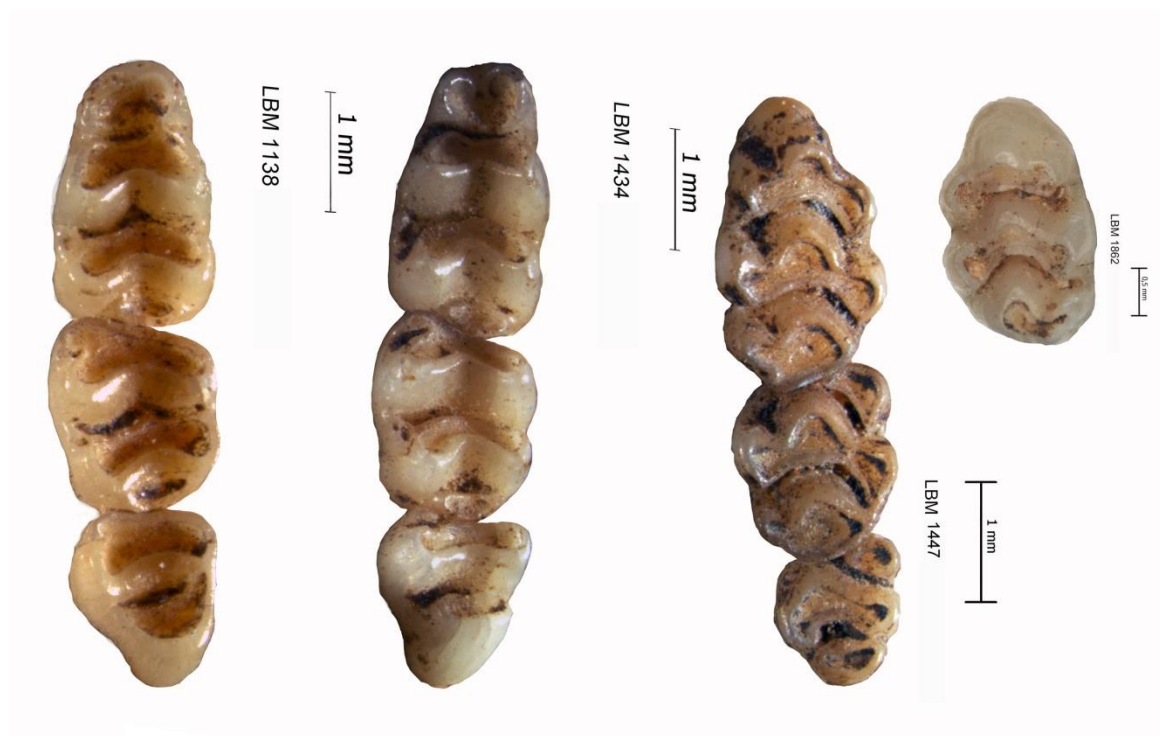
Each first lower molar is anchored by four roots. Each second and third lower molar has three roots, two small mesial ones a large distal one.

**M<sub>1</sub>:** the cusps of each first lower molar are arranged in three laminae. The first lamina (the anteroconid) is symmetrical, made up of two cusps, an anterolingual cusp, sometimes slightly larger, and an anterolabial cusp. An additional small anteroconid cusp is present only in one specimen (LBM 1304). The second lamina is symmetrical, transverse and bilobated, made up of two main cusps, the metaconid and the protoconid. In few cases and in early stages of wear, there

is a small anterolabial cusplet, that disappears with the wear and gives rise to an enamel connection between the anteroconid complex and the second lamina. When the tooth is not worn, the third lamina is made up of two drop-shaped cusped (entoconid and hypoconid) that meet along the midline; with the wear the dentine field widens and the lamina becomes arched-shaped. The posterolabial (c1) cusplet is small and slightly mesial to the third lamina. A posterior-cingulum is thin and elliptical in cross section.

**M<sub>2</sub>**: In the second molar the protoconid and the metaconid form a transverse or arched lamina, sometimes connected to a small cylindrical anterolabial cusplet. The second lamina is arched, made up of entoconid and hypoconid. A posterior labial cusplet is generally present. The posterior-cingulum, located at the center of the distal margin, is large and oblong in cross section.

**M<sub>3</sub>**: The anterolabial cusplet is often present (74%) is quite big and highly protruding the mesial border of the tooth., that assume an inclined profile. Protoconid and metaconid are about of the same size and the distal wall of the lamina is arched.



**Plate 6: *Rattus exulans*; lower and upper molars**

Upper molars

**M<sup>1</sup>**: In each first molar tubercles are aligned in order to form three rows. The central and main tubercles (t2, t5 and t8) are large and circular in cross section. t1 is placed distally to t2-t3; t3 is far smaller than t1 and t2. . The second row is symmetrical; the distal wall can be arched, or straight in proximity of t5-t6 and veer of 90° in proximity of t4. The third row consists of a large central tubercle (t8) merged with a small labial one (t9), and t12.



**M<sup>2</sup>:** t1 is large, protruding and semicircular or drop shaped in cross section. t3 is cylindrical and gets larger with the wear. t4 is placed slightly distally to t4-t5, whilst the latter two are rounded, it looks triangular. t8 is large and widely connected labially to a very small and cylindrical t9.

**M<sup>3</sup>:** The third upper molar has a wide, drop shaped, lingual cusp (t1) and a very small cylindrical labial one (t3). Distally to these cusps is a wide row, made by the confluence of t4 (lingual), t5 (central) and t6 (small and labial). All these cusps are largely merged since the first stages of wear into a “boomerang-shaped structure”. The distal row has an elliptical or circular section. The outline of this tooth is triangular

The upper molars are few compared to the amount of lower remains; despite this, it’s possible to detect some differences between *Rattus exulans* and *Rattus hainaldi*.

### Remarks on the smaller murids from Liang Bua

The material described here was provisionally classified as ‘small murid’. The first indication that this encompassed more than one species was the size variation. Checking the standards of Freudenthal and Martin Suarez (1990), V’ was too large for it to represent a single species:

LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>
14,87	19,84	20,51	18,62	24,60	20,92

This suspicion was confirmed, when Lisa Matisoo-Smith sampled ‘small murid’ mandibles of different spits for her research on *Rattus exulans*. Several mandibles were indeed referable to this species, but other fossils yielded unknown DNA of a second species (Matisoo-Smith, personal communication).

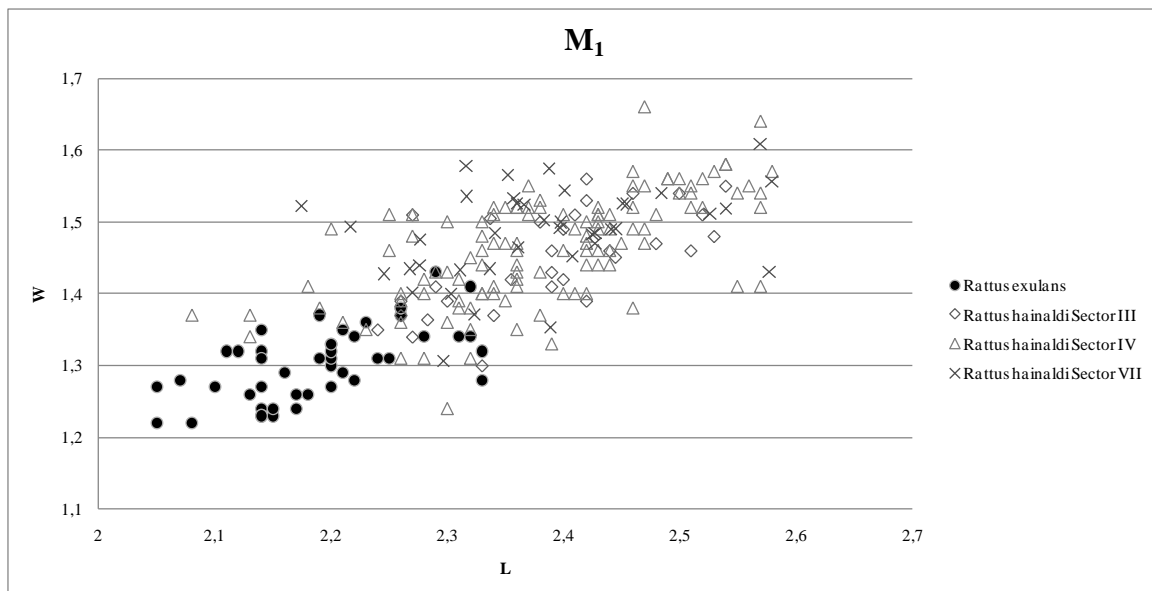


Figure VI-2: Scatter diagram of measurements of M<sub>1</sub> from Liang Bua



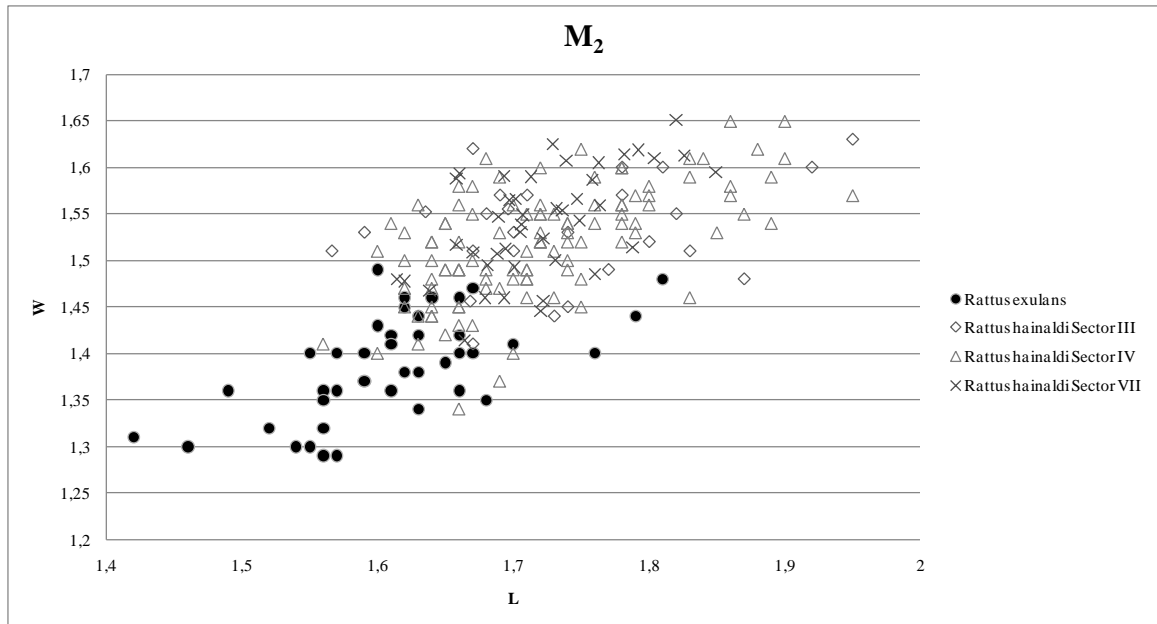


Figure VI-3: Scatter diagram of measurements of  $M_2$  from Liang Bua

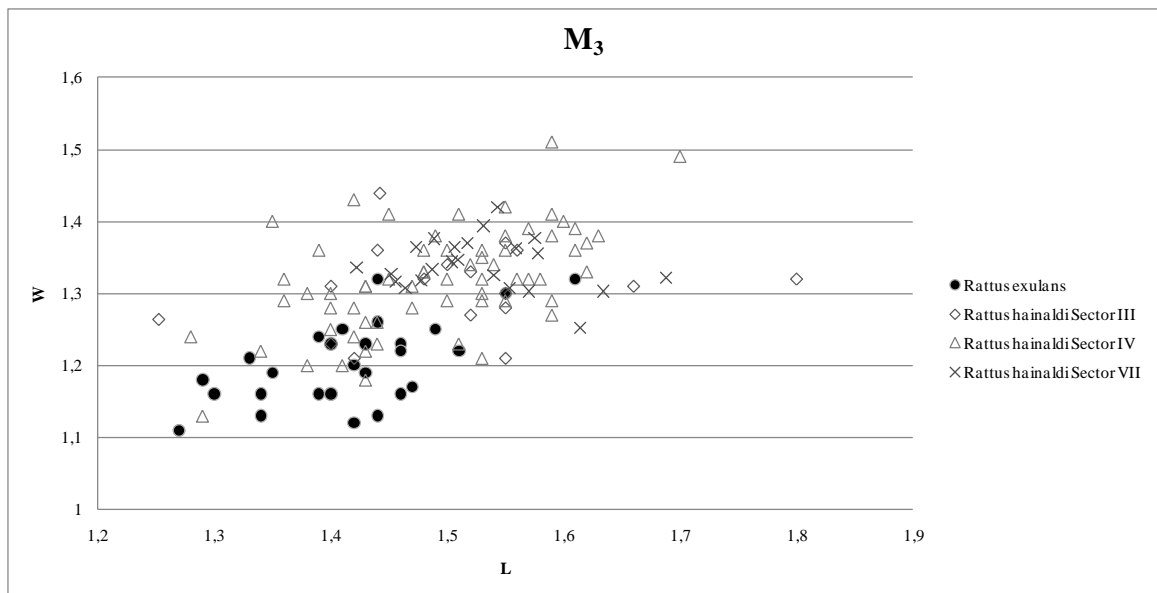


Figure VI-4: Scatter diagram of measurements of  $M_3$  from Liang Bua

Close examination of the material revealed slight but consistent morphological differences, confirming the presence of a second species beside *Rattus exulans*. Comparison with the illustrations of Kitchener et al. (1991a) showed that, as was to be expected, the other species was *Rattus hainaldi*, the smallest of the endemic Flores rats.

Surprisingly, differences between the two species are most clear in the mandibles, which can be identified with a great degree of certainty. Usually in murids, upper molars are more diagnostic. In our sample, different morphotypes can be recognized and assigned to the two species, but differences are certainly less clear than in the mandibles.

*Rattus hainaldi* is overall larger than *Rattus exulans*, both in lower and upper tooth rows (Table VI-1, Table VI-2, Figure VI-2, Figure VI-3, Figure VI-4, Figure VI-5), but there is a significant overlap in the measurements. The relative proportions among the width of the teeth are similar.

The two species show important significant differences in the morphology of the occlusal surface as well (the occlusal configurations of the upper and lower molars are illustrated in Plate 5 and Plate 6).

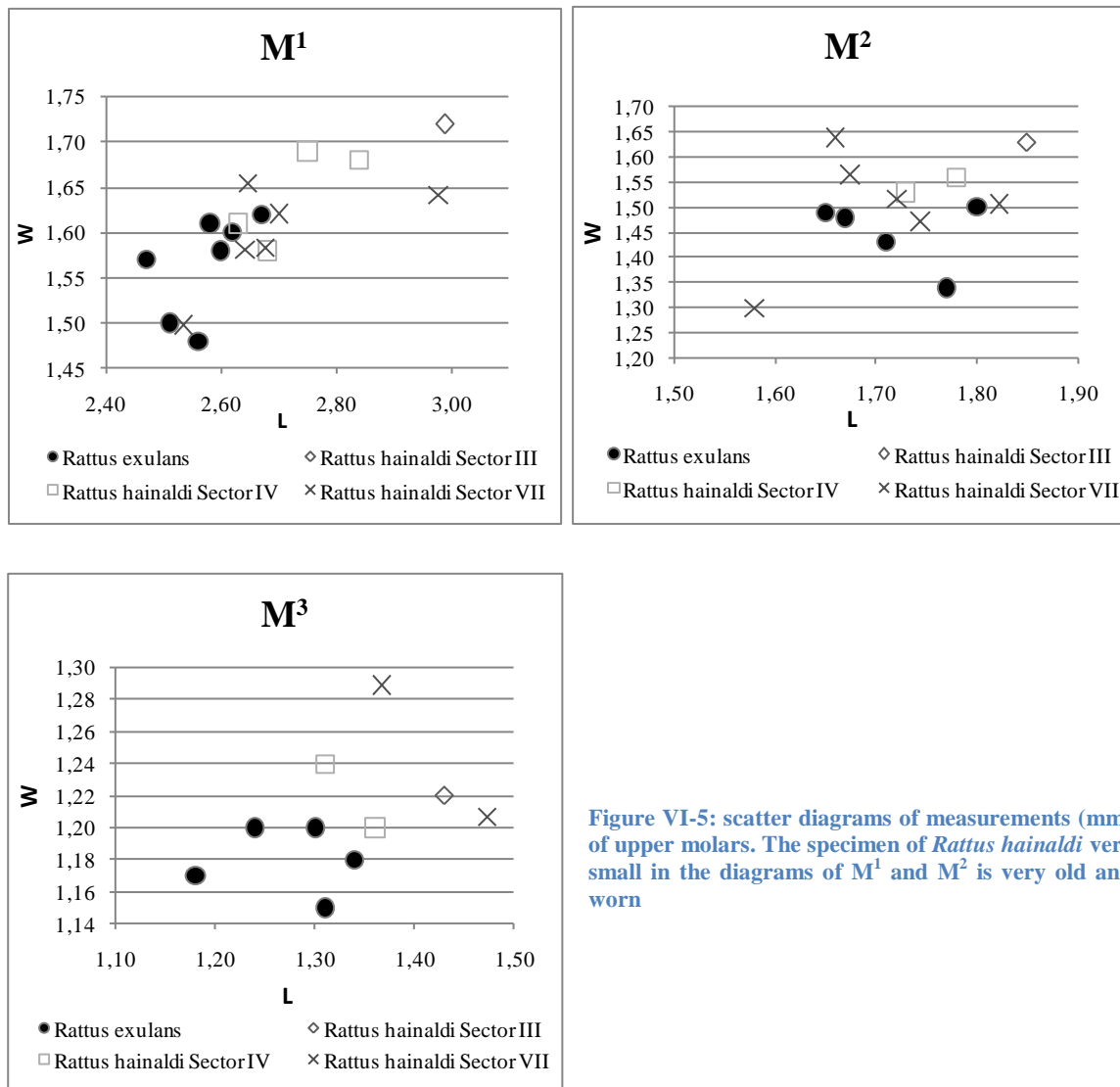


Figure VI-5: scatter diagrams of measurements (mm) of upper molars. The specimen of *Rattus hainaldi* very small in the diagrams of M<sup>1</sup> and M<sup>2</sup> is very old and worn

The two species present some differences in the lower tooth row. While in *Rattus exulans* teeth cusps are higher and more inclined, the tooth appears instead more robust in *Rattus hainaldi*, and dentine wear folds look wider in *Rattus exulans* at the same wear stage. Furthermore, in *R. exulans* the anterior lingual and labial cusps are widely confluent, even when the tooth is scantily worn, while in *Rattus hainaldi* they are partly separated. Finally, in *R. hainaldi* the first lower molar sometimes possesses an anterocentral cusp (18%), present in only one specimen of the other species.

The second lower molar is the most distinct tooth between the two species, above all for the strongly different dislocation of the anterolabial cusp; in *Rattus exulans* it is very protruding, thus being located labially to the posterior cingulum of the first lower molar; in *Rattus hainaldi* it is aligned with the protoconid and the metaconid or slightly protruding. Both species have a posterolabial cusplet, that is more aligned with the transverse lamina in *Rattus hainaldi* and more protruding mesially in *Rattus exulans*, but it's a variable character. Whilst in *Rattus hainaldi* the tooth has a squarish occlusal outline, in *Rattus exulans* the first transverse lamina is slightly wider than the second one, suggesting a trapezoidal shape.

The third molar is the most difficult to distinguish, because wear can easily delete the distinctive characteristics. It is more robust in *Rattus hainaldi*, with a wider entoconid, while the difference between the first and the second row is more accentuated in *Rattus exulans*, resulting in a more triangular outline. While the anterolabial cusp is mostly present (74%) and strongly protruding in young individuals of *Rattus exulans*, it is more often absent (56%) and is slightly protruding in *Rattus hainaldi*.

In *R. hainaldi* the cusps of the first row of the first upper molar are more aligned, while in *Rattus exulans* they're more arched and form a sharper angle; this configuration can be ascribed to a greater dislocation of the t1. t3 is generally smaller in *Rattus exulans*. The cusps of *R. exulans*, in particular the ones of the second row, are circular in section and keep this shape even when they're worn, while the region of confluence among the cusps in *Rattus hainaldi* is wider, thus making the row more transverse.

Small differences can be detected in the second upper molars as well. T3 is smaller in *R. hainaldi* and is easily confluent with the first row, while in *R. exulans* it is bigger, cylindrical and stands apart. t1 is better separated from the first row in *R. exulans*. The first row shows the same differences detected in the second row of the first upper molar.

The third upper molar is very similar in the two species; despite this, the outline of the tooth tends to be more triangular in *R. exulans*, because the difference in the width between the first row (t4, t5 and t6) and the posterior cingulum is more accentuated in the latter.

## **Discussion**

Given all the attention that gigantism among insular rodents has received over the last decades, it seems almost a paradox to have a paper on small-sized murids from an island. Neither *Rattus exulans* nor *R. hainaldi* were recognised in the work of Musser (1981) on the Flores rodents, the latter species not even having been named at the time. With a body weight of 81g for *R. hainaldi* (Kitchener et al. 1991a) and 40 to 80 g for *R. exulans* (Kitchener, 1991a), the species are minute compared to the extant giant rat of Flores, *Papagomys armandvillei*. Still, the presence on islands of small rodents which apparently do not respond to the 'Island Rule', is a quite normal phenomenon. New genera of insular oryzomyines in the West Indies, for instance, are of similar or even smaller size than their counterparts from the mainland (Zijlstra et al., 2010, submitted). The Miocene palaeo-island of Gargano is known for giant forms as the murid *Mikrotia* (Freudenthal, 1976; Freudenthal, 2006), the dormouse *Stertomys* (Daams & Freudenthal, 1985; Rinaldi & Masini, 2009) and the galericine *Deinogalerix* (Freudenthal, 1973; Butler, 1980). Yet, the smaller counterparts of these, partly still undescribed, are far more numerous than the insular giants (van den Hoek Ostende, pers. obv.). The observation made by Foster (1963) that island

rodents have a tendency to increase in size was first termed a ‘rule’ (including the quotation marks) by Van Valen (1973). Still, as insular rodents tend to occupy a variety of niches, including those for small-sized species, the ‘Island Rule’ does certainly not imply that each and every small mammal on an island shows an increase in size. The Flores endemic *Rattus hainaldi* clearly exemplifies this.

Having two species nearly identical in size and very similar in morphology, makes the Liang Bua sample unique. In common palaeontological practice, such a close resemblance would be considered unrealistic, as two species that similar would have outcompeted one another in a short period, which is generally speaking not recordable. As we aim to demonstrate in this paper, this competition is exactly what occurred in the case of Liang Bua, and is only traceable because of the excellent time control in the section.

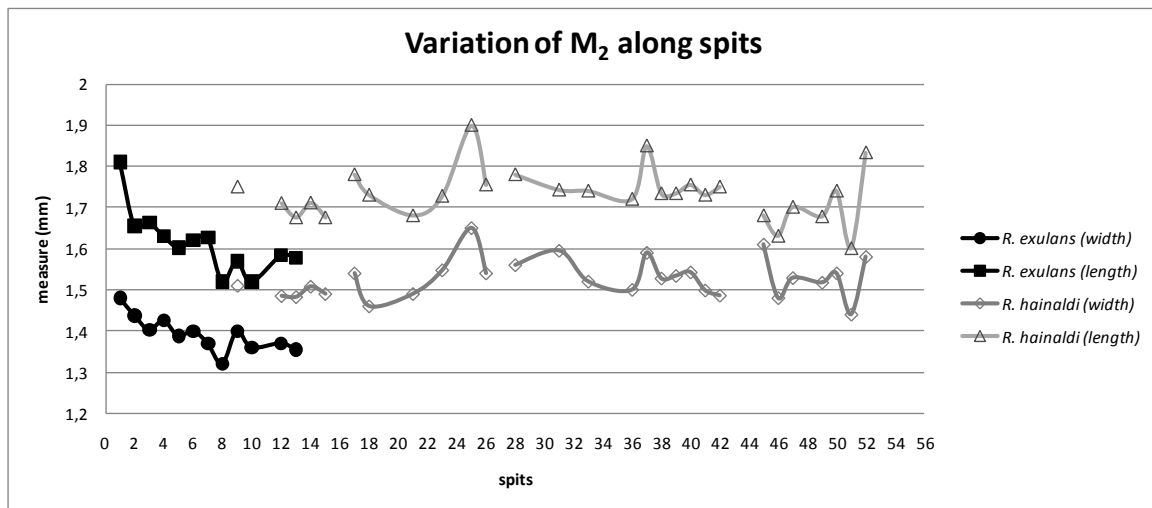


Figure VI-6: variation of measurements of second lower molar along spits of Sector IV.

As we noted above, the differences between the dentitions of *Rattus hainaldi* and *R. exulans* are slight, albeit consistent. This accounts for the strong competition and rapid take over by the latter species. However, it also raises a number of questions.

The first indication for the presence of two species was the high variation, as expressed by the  $V'$  (Freudenthal et al. 1990). Having separated the two species, the  $V'$  for *Rattus hainaldi* is hardly less than that of the combined assemblage, whereas *R. exulans* shows a value for  $V'$  which is quite normal. We assume that the lessening of constraints in the insular environment (no predators, less competitors) lead to a wider range of variation in *R. hainaldi*.

The second question is whether or not the close resemblance indicates a close relationship. If so, *Rattus hainaldi* would be the only non-volant endemic mammal from Flores which has its closest relatives in the west. However, we found no reference to studies dealing with the genome of *R. hainaldi*. Solely based on dental morphology, we would consider both small-sized murids from Liang Bua to be closely related. However, this needs to be confirmed on the basis of molecular data. Should these place *hainaldi* indeed closer to the other Flores endemics, the resemblance with *exulans* must be considered a case of parallel evolution, and even the assignment of the species to *Rattus* would be untenable. On the other hand, the ancestor of *Rattus exulans* is still unknown and it is thought to be originated on the Lesser Sunda Islands. The origin of *Rattus exulans* from *Rattus hainaldi* (at least the populations recovered at Liang Bua) sounds unlikely because its morphological change should have occurred in a very short time. Furthermore, *Rattus exulans* first

recovery in the sequence dates to ~4ka ago, in spit 13, when many other other taxa make their appearance, like the Masked palm civet (*Paradoxurus hermaphrodites*) and the Long-tailed macaque (*Macaca fascicularis*), together with all the hallmarks of the Neolithic, ground adzes and pottery (van den Bergh et al., 2009). As a matter of fact, Glover (1986) noticed the appearance of the same faunal association together with the first pottery findings at Uai Bobo (East Timor) since around 4000 y BP and Groves (1984) showed evidence that *Macaca*, *Paradoxurus* and *Viverra* were transported widely. Fragments of the crab-eating macaque, a pig, and Javan porcupine were found in cave deposits on Liang Toge (Hooijer, 1967b). Musser thought that many of the animals living on Flores had been introduced, inadvertently or intentionally by humans, among which the crab-eating macaque and the palm civet. He also retained significant that the macaque, civet are even now kept by villagers and townspeople either for food or for the pleasures that pets provide and then they could have been transported and introduced by the first prehistoric agriculturists.

Grayson (2001) formulated three conditions that had to be met in order to claim that species were deliberately introduced by humans: i) it is necessary to demonstrate that the animal was not present on the island prior to human colonization; ii) its arrival must coincide with or have occurred after human arrival; iii) the species should be highly unlikely to have gotten there on its own. On Flores, before the appearance of Neolithic culture only *Rattus hainaldi* was present on the island. The first record of *Rattus exulans* at Liang Bua (spit 13) is very close to the first recovery of Neolithic pottery and tools (spit 17), and finally, ecological studies on *R. exulans* (Spenneman and Rapp, 1989) showed that this species cannot swim or be dispersed in the ocean. Since Flores has always been separated from the mainland (Heaney, 1986), we can conclude that in all likelihood *R. exulans* has been introduced.

Motokawa et al. (2004) also indicated that *Rattus exulans* was introduced onto Flores by humans. They came to this conclusion from studying the morphometrical variation in *Rattus exulans* skulls from southeast Asia. The very limited divergence among island populations in southeast Asia indicates interbreeding between populations. This, in turn, can only be explained but the movements with man. In fact, there were no land bridge formations in the Late Pleistocene between Flores and the mainland (Heaney, 1986).

The chronology and the general picture of the faunal association could support the spread of Neolithic cultures through the Southeast Asia made by Spriggs (1989), who detected a rapid spread but spotty distribution of the Neolithic, from Taiwan to Timor, before 4100 BP. Neolithic agriculturists presumably brought animals with them for their own pleasure, as food item or other uses. All evidence suggests that *Rattus exulans* was introduced at that time, but we cannot tell if its introduction was intentional or accidental. The wide spread of this species all over Southeast Asia till the remote Polynesia shows that in either case, the species was highly successful.

The ecological effect of this introduction appears to have been devastating for *Rattus hainaldi*. Since the first phases of the human occupation at Liang Bua – and probably long before that - it had been an important element of the faunal association. In some spits it represents up to 50% of the relative abundance among the small mammals. *Rattus hainaldi* underwent a first strong reduction in concomitance with the arrival of modern humans on the island, around spit 30, and after 4 ka ago it completely disappeared from the section.

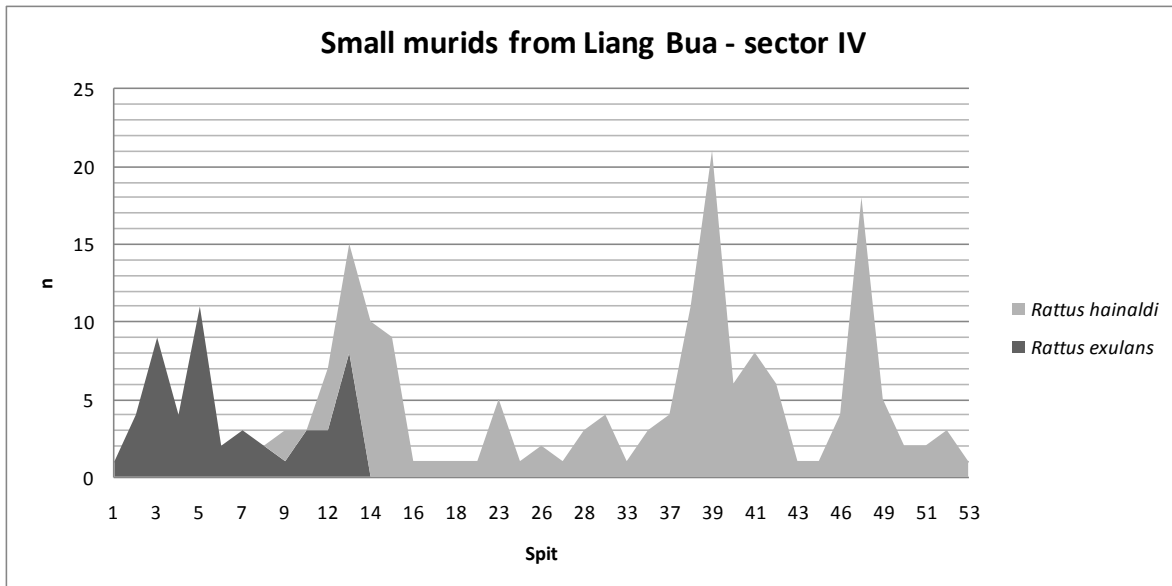


Figure VI-7: cumulative digram of the amount of specimens of *Rattus exulans* and *Rattus hainaldi* ercovered in each spit

Environmental change, related to climatic oscillations during the Holocene, could have influenced its relative abundance in the sequence. But as climate shifts were only minor, they cannot explain the complete disappearance of a species in the Late Holocene. A far more plausible scenario would be that interspecific competition with a rat of around the same size (*R. exulans*) and habitat disturbance introduced by Neolithic agriculturists lead to the demise of *Rattus hainaldi*. We need to be cautious to apply this scenario for all of Flores, as even today it is unclear to what extend *R. hainaldi* still survives on the island. As the animal show a strong resemblance to *R. exulans*, only a careful inventory can clarify its current status. But the Liang Bua sections do show that in the vicinity of humans, the take-over by the commensal *R. exulans* was swift and (nearly) complete.

## Conclusions

Our analysis shows that two different species of small rats were and are present at Liang Bua: *Rattus hainaldi* and *R. exulans*. Even though the dentitions are similar, consistent differences provide sufficient distinction to allow identification. The two species seems to be in competition, since with the appearance of the Polynesian rat the endemic forms underwent a strong reduction in their relative abundance among the small mammals.

The first occurrence of *Rattus exulans* and the subsequent demise of *R. hainaldi* in our sections is closely associated to the first evidence of Neolithic man in Liang Bua, both from ceramics and other introduced species, such as *Paradoxurus hermaphroditus*, *Sus scrofa*, *Hystrix javanicus* and *Macaca fascicularis*.

*Rattus hainaldi* is a member of the ancient faunal pool of Flores island together with other better known autochthonous forms, like the two giants rats *Papagomys armandvillei* and *Papagomys theodorverhoeveni*, or the middle size *Paulamys floresiensis* and *Komodomyx rijntianus*. In contrast, *Rattus exulans* is a commensal form, well spread all over the Southeast Asia and the Oceania. Most likely, it was introduced, either accidentally or purposefully by Neolithic

agriculturists. Thus Liang Bua is not only a key site for human palaeoanthropology , for the striking discovery of the insular *Homo floresiensis*, but also contributes to the understanding of the behaviour of Neolithic people in South East Asia.

## Appendix Chapter VI

nr	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>
LBM 547	29	<i>Rattus hainaldi</i>	2,30	1,39	1,77	1,49	1,50	1,34
LBM 548	29	<i>Rattus exulans</i>	2,26	1,39	1,67	1,41	1,42	1,21
LBM 553	31	<i>Rattus hainaldi</i>	2,27	1,34	1,73	1,44	1,55	1,21
LBM 554	31	<i>Rattus hainaldi</i>			1,87	1,48		
LBM 557	31	<i>Rattus hainaldi</i>	2,52	1,51				
LBM 566	32	<i>Rattus hainaldi</i>	2,42	1,53	1,78	1,60		
LBM 567	32	<i>Rattus hainaldi</i>	2,40	1,42				
LBM 570	32	<i>Rattus hainaldi</i>	2,33	1,30				
LBM 580	34	<i>Rattus hainaldi</i>	2,27	1,51	1,70	1,53		
LBM 581	34	<i>Rattus hainaldi</i>	2,42	1,39				
LBM 586	35	<i>Rattus hainaldi</i>	2,34	1,37		1,33		
LBM 587	35	<i>Rattus hainaldi</i>	2,48	1,47	1,67	1,51	1,52	1,27
LBM 589	35	<i>Rattus hainaldi</i>	2,46	1,54				
LBM 590	35	<i>Rattus hainaldi</i>	2,38	1,50	1,67	1,62	1,48	1,32
LBM 607	36	<i>Rattus hainaldi</i>	2,51	1,46	1,74	1,53	1,55	1,30
LBM 608	36	<i>Rattus hainaldi</i>	2,39	1,43	1,78	1,57	1,52	1,33
LBM 609	36	<i>Rattus hainaldi</i>	2,39	1,46	1,68	1,55		
LBM 610	36	<i>Rattus hainaldi</i>	2,24	1,35	1,59	1,53		
LBM 617	36	<i>Rattus hainaldi</i>	2,40	1,49	1,71	1,57	1,56	1,36
LBM 654	37	<i>Rattus hainaldi</i>	2,41	1,51	1,69	1,57	1,66	1,31
LBM 659	37	<i>Rattus hainaldi</i>	2,54	1,55				
LBM 660	37	<i>Rattus exulans</i>			1,83	1,51	1,80	1,32
LBM 664	38	<i>Rattus hainaldi</i>	2,42	1,56	1,95	1,63	1,55	1,28
LBM 665	38	<i>Rattus hainaldi</i>	2,53	1,48	1,81	1,60	1,44	1,36
LBM 682	40	<i>Rattus hainaldi</i>	2,50	1,54	1,92	1,60	1,55	1,37
LBM 683	40	<i>Rattus hainaldi</i>	2,29	1,41			1,40	1,23
LBM 689	40	<i>Rattus hainaldi</i>	2,44	1,46	1,82	1,55		
LBM 690	40	<i>Rattus hainaldi</i>	2,39	1,41				
LBM 693	40	<i>Rattus hainaldi</i>			1,80	1,52		
LBM 711	41	<i>Rattus hainaldi</i>			1,70	1,51	1,40	1,31
LBM 714	41	<i>Rattus hainaldi</i>	2,26	1,37	1,74	1,45		
LBM 737	42	<i>Rattus hainaldi</i>	2,34	1,51	1,57	1,51	1,25	1,26
LBM 738	42	<i>Rattus hainaldi</i>	2,36	1,42	1,67	1,46		
LBM 742	42	<i>Rattus hainaldi</i>			1,64	1,55		
LBM 748	42	<i>Rattus hainaldi</i>	2,28	1,36				
LBM 756	43	<i>Rattus hainaldi</i>	2,45	1,45	1,70	1,56	1,44	1,44

Table VI-3: measurements (mm) of lower molars from Sector III



nr	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>
LBM 0009	26	<i>Rattus hainaldi</i>	2,34	1,51	1,72	1,55		
LBM 0011	26	<i>Rattus hainaldi</i>	2,36	1,52	1,79	1,53		
LBM 0022	27	<i>Rattus hainaldi</i>	2,26	1,31				
LBM 0032	28	<i>Rattus hainaldi</i>	2,33	1,5				
LBM 0033	28	<i>Rattus hainaldi</i>			1,78	1,56		
LBM 0034	28	<i>Rattus hainaldi</i>					1,5	1,32
LBM 0049	31	<i>Rattus hainaldi</i>	2,5	1,56	1,78	1,71	1,42	1,43
LBM 0050	31	<i>Rattus hainaldi</i>	2,53	1,57	1,8	1,57	1,45	1,41
LBM 0051	31	<i>Rattus hainaldi</i>	2,43	1,51	1,67	1,58		
LBM 0052	31	<i>Rattus hainaldi</i>			1,72	1,52		
LBM 0144	33	<i>Rattus hainaldi</i>			1,74	1,52		
LBM 0174	36	<i>Rattus hainaldi</i>			1,8	1,56	1,62	1,33
LBM 0183	36	<i>Rattus hainaldi</i>	2,33	1,44				
LBM 0184	36	<i>Rattus hainaldi</i>			1,64	1,44		
LBM 0189	37	<i>Rattus hainaldi</i>	2,54	1,58	1,84	1,61		
LBM 0190	37	<i>Rattus hainaldi</i>	2,57	1,52	1,86	1,57	1,61	1,39
LBM 0194	37	<i>Rattus hainaldi</i>	2,43	1,5				
LBM 0195	37	<i>Rattus hainaldi</i>					1,63	1,38
LBM 0218	38	<i>Rattus hainaldi</i>	2,38	1,52			1,55	1,38
LBM 0219	38	<i>Rattus hainaldi</i>	2,33	1,48	1,72	1,52	1,42	1,28
LBM 0220	38	<i>Rattus hainaldi</i>	2,37	1,52	1,71	1,49	1,48	1,33
LBM 0221	38	<i>Rattus hainaldi</i>	2,25	1,46	1,64	1,52	1,57	1,39
LBM 0222	38	<i>Rattus hainaldi</i>			1,71	1,48		
LBM 0223	38	<i>Rattus hainaldi</i>	2,47	1,47				
LBM 0227	38	<i>Rattus hainaldi</i>	2,47	1,49	1,76	1,56	1,53	1,36
LBM 0230	38	<i>Rattus hainaldi</i>	2,34	1,41	1,74	1,53	1,58	1,32
LBM 0231	38	<i>Rattus hainaldi</i>			1,79	1,54		
LBM 0232	38	<i>Rattus hainaldi</i>			1,8	1,58		
LBM 0233	38	<i>Rattus hainaldi</i>					1,55	1,42
LBM 0250	39	<i>Rattus hainaldi</i>	2,52	1,52				
LBM 0251	39	<i>Rattus hainaldi</i>	2,23	1,35				
LBM 0252	39	<i>Rattus hainaldi</i>	2,43	1,44	1,87	1,55		
LBM 0253	39	<i>Rattus hainaldi</i>			1,67	1,5		
LBM 0259	40	<i>Rattus hainaldi</i>	2,29	1,43	1,68	1,48	1,45	1,32
LBM 0260	40	<i>Rattus hainaldi</i>	2,43	1,52	1,86	1,65		
LBM 0261	40	<i>Rattus hainaldi</i>			1,74	1,54		
LBM 0268	41	<i>Rattus hainaldi</i>	2,4	1,51	1,72	1,53	1,38	1,3
LBM 0269	41	<i>Rattus hainaldi</i>	2,42	1,48	1,72	1,56	1,59	1,41
LBM 0271	41	<i>Rattus hainaldi</i>	2,57	1,54	1,83	1,59		
LBM 0272	41	<i>Rattus hainaldi</i>	2,33	1,46	1,78	1,52		
LBM 0273	41	<i>Rattus hainaldi</i>	2,58	1,57				
LBM 0274	41	<i>Rattus hainaldi</i>	2,13	1,34	1,66	1,34		
LBM 0278	41	<i>Rattus hainaldi</i>	2,36	1,46	1,71	1,48	1,48	1,36
LBM 0280	41	<i>Rattus hainaldi</i>	2,28	1,42	1,69	1,47		
LBM 0291	42	<i>Rattus hainaldi</i>	2,36	1,41	1,7	1,49	1,47	1,28
LBM 0292	42	<i>Rattus hainaldi</i>	2,45	1,47	1,74	1,49	1,36	1,29
LBM 0296	42	<i>Rattus hainaldi</i>	2,28	1,31	1,67	1,43		
LBM 0297	42	<i>Rattus hainaldi</i>			1,75	1,48		
LBM 0305	42	<i>Rattus hainaldi</i>					1,36	1,32
LBM 0306	42	<i>Rattus hainaldi</i>	2,38	1,43	1,89	1,54		
LBM 0312	43	<i>Rattus hainaldi</i>	2,36	1,35				

Table VI-4: measurements (mm) of lower molars of *Rattus hainaldi* from Sector IV (1)

nr	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>
LBM 0325	45	<i>Rattus hainaldi</i>	2,49	1,56	1,68	1,61		
LBM 0333	46	<i>Rattus hainaldi</i>	2,44	1,49	1,61	1,54	1,44	1,26
LBM 0335	46	<i>Rattus hainaldi</i>	2,26	1,36	1,65	1,42	1,38	1,2
LBM 0340	46	<i>Rattus hainaldi</i>	2,55	1,41				
LBM 0341	46	<i>Rattus hainaldi</i>	2,42	1,4				
LBM 0369	47	<i>Rattus hainaldi</i>	2,48	1,51	1,72	1,52	1,53	1,3
LBM 0370	47	<i>Rattus hainaldi</i>	2,36	1,43	1,66	1,49	1,47	1,31
LBM 0371	47	<i>Rattus hainaldi</i>	2,44	1,51	1,66	1,58	1,42	1,24
LBM 0372	47	<i>Rattus hainaldi</i>	2,3	1,24	1,79	1,57	1,6	1,4
LBM 0373	47	<i>Rattus hainaldi</i>	2,46	1,38	1,64	1,48		
LBM 0374	47	<i>Rattus hainaldi</i>	2,57	1,41				
LBM 0375	47	<i>Rattus hainaldi</i>	2,31	1,42	1,66	1,49	1,59	1,29
LBM 0376	47	<i>Rattus hainaldi</i>			1,75	1,62		
LBM 0377	47	<i>Rattus hainaldi</i>	2,32	1,45	1,71	1,55	1,54	1,34
LBM 0378	47	<i>Rattus hainaldi</i>	2,27	1,48	1,66	1,52		
LBM 0379	47	<i>Rattus hainaldi</i>	2,51	1,55	1,78	1,6		
LBM 0380	47	<i>Rattus hainaldi</i>	2,3	1,5	1,66	1,49	1,28	1,24
LBM 0381	47	<i>Rattus hainaldi</i>	2,37	1,51	1,73	1,55	1,59	1,38
LBM 0382	47	<i>Rattus hainaldi</i>	2,32	1,38	1,7	1,48		
LBM 0383	47	<i>Rattus hainaldi</i>	2,38	1,37	1,71	1,46		
LBM 0384	47	<i>Rattus hainaldi</i>	2,36	1,47				
LBM 0385	47	<i>Rattus hainaldi</i>			1,6	1,51		
LBM 0387	47	<i>Rattus hainaldi</i>			1,78	1,55		
LBM 0419	49	<i>Rattus hainaldi</i>			1,68	1,47		
LBM 0420	49	<i>Rattus hainaldi</i>	2,3	1,36	1,62	1,47	1,43	1,31
LBM 0421	49	<i>Rattus hainaldi</i>	2,42	1,47	1,76	1,59		
LBM 0423	49	<i>Rattus hainaldi</i>					1,59	1,51
LBM 0430	49	<i>Rattus hainaldi</i>	2,44	1,44	1,65	1,54	1,57	1,32
LBM 0443	50	<i>Rattus hainaldi</i>	2,33	1,4	1,74	1,54		
LBM 0445	50	<i>Rattus hainaldi</i>	2,44	1,46				
LBM 0455	51	<i>Rattus hainaldi</i>	2,08	1,37	1,56	1,41	1,29	1,13
LBM 0456	51	<i>Rattus hainaldi</i>	2,31	1,38	1,64	1,47	1,5	1,36
LBM 0460	52	<i>Rattus hainaldi</i>	2,5	1,54	1,88	1,62		
LBM 0461	52	<i>Rattus hainaldi</i>			1,67	1,55	1,49	1,38
LBM 0462	52	<i>Rattus hainaldi</i>			1,95	1,57		
LBM 0472	53	<i>Rattus hainaldi</i>	2,4	1,46				
LBM 0836	40	<i>Rattus hainaldi</i>	2,36	1,52				
LBM 0837	40	<i>Rattus hainaldi</i>			1,74	1,5		
LBM 0838	40	<i>Rattus hainaldi</i>					1,55	1,36
LBM 0841	39	<i>Rattus hainaldi</i>	2,42	1,46	1,7	1,56	1,53	1,29
LBM 0842	39	<i>Rattus hainaldi</i>	2,57	1,64	1,79	1,72	1,7	1,49
LBM 0843	39	<i>Rattus hainaldi</i>	2,43	1,49	1,64	1,52	1,4	1,28
LBM 0844	39	<i>Rattus hainaldi</i>	2,42	1,44	1,73	1,51		
LBM 0845	39	<i>Rattus hainaldi</i>	2,27	1,51	1,62	1,53		
LBM 0847	39	<i>Rattus hainaldi</i>	2,34	1,4	1,7	1,4		
LBM 0850	39	<i>Rattus hainaldi</i>	2,41	1,49				
LBM 0853	39	<i>Rattus hainaldi</i>	2,35	1,47	1,65	1,49	1,51	1,23
LBM 0854	39	<i>Rattus hainaldi</i>	2,52	1,56	1,9	1,61	1,62	1,37
LBM 0855	39	<i>Rattus hainaldi</i>			1,89	1,59	1,59	1,27
LBM 0859	39	<i>Rattus hainaldi</i>	2,55	1,54				
LBM 0862	39	<i>Rattus hainaldi</i>			1,75	1,52		

Table VI-5: measurements (mm) of lower molars of *Rattus hainaldi* from Sector IV (2)

nr	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>
LBM 0863	39	<i>Rattus hainaldi</i>					1,4	1,3
LBM 0867	39	<i>Rattus hainaldi</i>	2,4	1,4				
LBM 0868	39	<i>Rattus hainaldi</i>			1,63	1,44		
LBM 0869	39	<i>Rattus hainaldi</i>					1,41	1,2
LBM 0870	39	<i>Rattus hainaldi</i>					1,43	1,31
LBM 0889	25	<i>Rattus hainaldi</i>	2,56	1,55	1,9	1,65		
LBM 0950	23	<i>Rattus hainaldi</i>			1,65	1,54		
LBM 0951	23	<i>Rattus hainaldi</i>	2,54	1,58	1,83	1,61		
LBM 0968	23	<i>Rattus hainaldi</i>	2,34	1,47	1,71	1,49	1,56	1,32
LBM 0970	23	<i>Rattus hainaldi</i>	2,42	1,5	1,72	1,55	1,61	1,36
LBM 0971	23	<i>Rattus hainaldi</i>	2,35	1,39				
LBM 0981	21	<i>Rattus hainaldi</i>	2,26	1,4	1,68	1,49		
LBM 0998	18	<i>Rattus hainaldi</i>	2,31	1,39	1,73	1,46		
LBM 1008	17	<i>Rattus hainaldi</i>	2,37	1,55	1,78	1,54		
LBM 1019	16	<i>Rattus hainaldi</i>	2,43	1,46				
LBM 1026	15	<i>Rattus hainaldi</i>	2,39	1,33	1,66	1,45	1,44	1,23
LBM 1027	15	<i>Rattus hainaldi</i>	2,2	1,49	1,64	1,5	1,48	1,33
LBM 1029	15	<i>Rattus hainaldi</i>	2,18	1,41	1,6	1,4	1,4	1,25
LBM 1030	15	<i>Rattus hainaldi</i>	2,47	1,66	1,63	1,56	1,39	1,36
LBM 1031	15	<i>Rattus hainaldi</i>	2,25	1,51	1,62	1,5		
LBM 1032	15	<i>Rattus hainaldi</i>	2,26	1,39	1,64	1,45	1,53	1,21
LBM 1036	15	<i>Rattus hainaldi</i>	2,41	1,4	1,83	1,46		
LBM 1039	15	<i>Rattus hainaldi</i>						
LBM 1042	15	<i>Rattus hainaldi</i>	2,46	1,57	1,78	1,6		
LBM 1046	14	<i>Rattus hainaldi</i>	2,47	1,55	1,78	1,56		
LBM 1050	14	<i>Rattus hainaldi</i>			1,69	1,37		
LBM 1051	14	<i>Rattus hainaldi</i>	2,21	1,36	1,62	1,45	1,34	1,22
LBM 1052	14	<i>Rattus hainaldi</i>			1,75	1,45		
LBM 1054	14	<i>Rattus hainaldi</i>	2,35	1,52	1,66	1,56	1,35	1,4
LBM 1057	14	<i>Rattus hainaldi</i>	2,28	1,4	1,63	1,41	1,43	1,22
LBM 1058	14	<i>Rattus hainaldi</i>	2,49	1,56	1,86	1,58	1,52	1,34
LBM 1059	14	<i>Rattus hainaldi</i>	2,51	1,54	1,72	1,6	1,51	1,41
LBM 1067	14	<i>Rattus hainaldi</i>	2,43	1,51	1,69	1,59		
LBM 1068	14	<i>Rattus hainaldi</i>	2,32	1,31				
LBM 1101	13	<i>Rattus hainaldi</i>	2,36	1,42				
LBM 1122	13	<i>Rattus hainaldi</i>	2,33	1,4	1,66	1,45	1,43	1,18
LBM 1135	13	<i>Rattus hainaldi</i>	2,32	1,35				
LBM 1139	13	<i>Rattus hainaldi</i>	2,3	1,43	1,71	1,51	1,53	1,35
LBM 1140	13	<i>Rattus hainaldi</i>	2,46	1,55				
LBM 1141	13	<i>Rattus hainaldi</i>	2,34	1,52	1,69	1,53		
LBM 1145	13	<i>Rattus hainaldi</i>	2,19	1,38	1,64	1,44		
LBM 1196	12	<i>Rattus hainaldi</i>	2,46	1,52				
LBM 1200	12	<i>Rattus hainaldi</i>	2,51	1,52				
LBM 1202	12	<i>Rattus hainaldi</i>	2,13	1,37	1,66	1,43	1,55	1,29
LBM 1247	12	<i>Rattus hainaldi</i>	2,38	1,53	1,76	1,54	1,53	1,32
LBM 1309	9	<i>Rattus hainaldi</i>	2,46	1,49	1,85	1,53	1,5	1,29
LBM 1310	9	<i>Rattus hainaldi</i>	2,36	1,44	1,65	1,49	1,43	1,26

Table VI-6: measurements (mm) of lower molars of *Rattus hainaldi* from Sector IV (3)

nr	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>
LBM 1100	13	<i>Rattus exulans</i>					1,51	1,22
LBM 1116	13	<i>Rattus exulans</i>	2,17	1,24	1,54	1,3	1,29	1,18
LBM 1118	13	<i>Rattus exulans</i>			1,66	1,46	1,61	1,32
LBM 1123	13	<i>Rattus exulans</i>	2,05	1,27	1,56	1,36		
LBM 1136	13	<i>Rattus exulans</i>	2,15	1,23	1,56	1,35	1,33	1,21
LBM 1138	13	<i>Rattus exulans</i>	2,14	1,24	1,56	1,32	1,42	1,12
LBM 1146	13	<i>Rattus exulans</i>	2,08	1,22	1,42	1,31	1,27	1,11
LBM 1171	13	<i>Rattus exulans</i>	2,15	1,24	1,68	1,35	1,3	1,16
LBM 1172	13	<i>Rattus exulans</i>	2,14	1,35	1,65	1,39		
LBM 1195	12	<i>Rattus exulans</i>	2,05	1,22	1,57	1,29	1,27	1,11
LBM 1246	12	<i>Rattus exulans</i>	2,28	1,34	1,63	1,42	1,35	1,19
LBM 1252	12	<i>Rattus exulans</i>	2,2	1,3	1,55	1,4	1,43	1,23
LBM 1284	10	<i>Rattus exulans</i>	2,11	1,32	1,49	1,36	1,34	1,13
LBM 1293	10	<i>Rattus exulans</i>	2,14	1,23	1,46	1,3		
LBM 1299	10	<i>Rattus exulans</i>	2,16	1,29	1,61	1,42	1,34	1,16
LBM 1304	9	<i>Rattus exulans</i>	2,25	1,31	1,57	1,4	1,4	1,16
LBM 1327	8	<i>Rattus exulans</i>	2,22	1,28	1,52	1,32	1,42	1,2
LBM 1328	8	<i>Rattus exulans</i>	2,2	1,33				
LBM 1341	7	<i>Rattus exulans</i>	2,2	1,31	1,63	1,34	1,47	1,17
LBM 1342	7	<i>Rattus exulans</i>	2,19	1,31	1,59	1,37		
LBM 1349	7	<i>Rattus exulans</i>	2,24	1,31	1,66	1,4	1,43	1,19
LBM 1350	6	<i>Rattus exulans</i>	2,14	1,32	1,61	1,36	1,46	1,16
LBM 1351	6	<i>Rattus exulans</i>	2,21	1,35	1,63	1,44	1,4	1,23
LBM 1355	5	<i>Rattus exulans</i>	2,2	1,32	1,62	1,38	1,44	1,26
LBM 1356	5	<i>Rattus exulans</i>	2,26	1,37	1,63	1,44		
LBM 1357	5	<i>Rattus exulans</i>	2,13	1,26	1,55	1,3		
LBM 1360	5	<i>Rattus exulans</i>	2,18	1,26	1,59	1,37		
LBM 1361	5	<i>Rattus exulans</i>	2,17	1,26	1,56	1,29		
LBM 1362	5	<i>Rattus exulans</i>	2,14	1,23				
LBM 1363	5	<i>Rattus exulans</i>	2,19	1,37	1,62	1,45		
LBM 1364	5	<i>Rattus exulans</i>	2,29	1,43	1,64	1,46		
LBM 1365	5	<i>Rattus exulans</i>	2,1	1,27				
LBM 1366	5	<i>Rattus exulans</i>					1,39	1,16
LBM 1367	5	<i>Rattus exulans</i>	2,2	1,33	1,61	1,41		
LBM 1377	4	<i>Rattus exulans</i>	2,2	1,27				
LBM 1380	4	<i>Rattus exulans</i>	2,26	1,38	1,6	1,49		
LBM 1383	4	<i>Rattus exulans</i>	2,21	1,29	1,66	1,36		
LBM 1384	4	<i>Rattus exulans</i>	2,32	1,34				
LBM 1396	3	<i>Rattus exulans</i>	2,22	1,34	1,7	1,41	1,49	1,25
LBM 1397	3	<i>Rattus exulans</i>			1,63	1,38		
LBM 1403	3	<i>Rattus exulans</i>	2,12	1,32	1,6	1,43	1,46	1,23
LBM 1404	3	<i>Rattus exulans</i>	2,33	1,32	1,76	1,4		
LBM 1415	3	<i>Rattus exulans</i>	2,14	1,27			1,44	1,13
LBM 1416	3	<i>Rattus exulans</i>	2,33	1,28				
LBM 1417	3	<i>Rattus exulans</i>	2,07	1,28	1,57	1,36		
LBM 1419	3	<i>Rattus exulans</i>	2,14	1,31	1,59	1,4		
LBM 1421	3	<i>Rattus exulans</i>			1,79	1,44	1,46	1,22
LBM 1434	2	<i>Rattus exulans</i>	2,31	1,34	1,66	1,42	1,41	1,25
LBM 1435	2	<i>Rattus exulans</i>	2,23	1,36	1,62	1,46	1,39	1,24
LBM 1436	2	<i>Rattus exulans</i>	2,26	1,38	1,67	1,47	1,44	1,32
LBM 1445	2	<i>Rattus exulans</i>			1,67	1,4	1,4	1,16
LBM 1457	1	<i>Rattus exulans</i>	2,32	1,41	1,81	1,48	1,55	1,3

Table VI-7: measurements (mm) of lower molars of *Rattus exulans* from Sector IV

nr	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>
LBM 1560	63	<i>Rattus hainaldi</i>		1,563	1,713	1,59	1,559	1,363
LBM 1570	60	<i>Rattus hainaldi</i>	2,425	1,483				
LBM 1610	57	<i>Rattus hainaldi</i>	2,276	1,44	1,664	1,414	1,614	1,252
LBM 1613	57	<i>Rattus hainaldi</i>	2,341	1,485	1,702	1,566		
LBM 1625	56	<i>Rattus hainaldi</i>	2,217	1,494	1,693	1,591	1,543	1,42
LBM 1630	56	<i>Rattus hainaldi</i>	2,451	1,526	1,849	1,595		
LBM 1645	54	<i>Rattus hainaldi</i>	2,401	1,544	1,732	1,556	1,422	1,336
LBM 1650	54	<i>Rattus hainaldi</i>			1,707	1,549		
LBM 1652	54	<i>Rattus hainaldi</i>	2,427	1,485				
LBM 1653	54	<i>Rattus hainaldi</i>			1,681	1,495	1,464	1,308
LBM 1654	54	<i>Rattus hainaldi</i>						
LBM 1658	54	<i>Rattus hainaldi</i>	2,54	1,519	1,804	1,61	1,531	1,394
LBM 1685	53	<i>Rattus hainaldi</i>	2,268	1,435	1,688	1,507	1,554	1,307
LBM 1690	53	<i>Rattus hainaldi</i>	2,484	1,54	1,739	1,607	1,509	1,347
LBM 1691	53	<i>Rattus hainaldi</i>	2,445	1,491				
LBM 1698	53	<i>Rattus exulans</i>	2,337	1,435	1,694	1,513	1,575	1,377
LBM 1713	52	<i>Rattus hainaldi</i>	2,577	1,431				
LBM 1722	51	<i>Rattus hainaldi</i>	2,408	1,452	1,638	1,468		
LBM 1737	50	<i>Rattus hainaldi</i>	2,526	1,512	1,826	1,613		
LBM 1738	50	<i>Rattus hainaldi</i>						
LBM 1739	50	<i>Rattus hainaldi</i>			1,689	1,547		
LBM 1745	49	<i>Rattus hainaldi</i>	2,246	1,428	1,614	1,48	1,456	1,316
LBM 1746	49	<i>Rattus hainaldi</i>	2,311	1,433	1,693	1,46		
LBM 1754	48	<i>Rattus hainaldi</i>	2,569	1,609	1,82	1,651		
LBM 1766	48	<i>Rattus hainaldi</i>	2,389	1,353	1,722	1,524	1,489	1,376
LBM 1768	48	<i>Rattus hainaldi</i>			1,736	1,554	1,54	1,325
LBM 1769	48	<i>Rattus hainaldi</i>			1,62	1,478		
LBM 1777	48	<i>Rattus hainaldi</i>	2,297	1,306				
LBM 1778	48	<i>Rattus hainaldi</i>			1,763	1,605		
LBM 1787	47	<i>Rattus hainaldi</i>	2,317	1,536				
LBM 1788	47	<i>Rattus hainaldi</i>	2,316	1,578	1,749	1,543		
LBM 1790	47	<i>Rattus hainaldi</i>	2,398	1,5	1,697	1,565	1,473	1,365
LBM 1794	46	<i>Rattus hainaldi</i>	2,397	1,492	1,658	1,588	1,452	1,327
LBM 1795	46	<i>Rattus hainaldi</i>			1,758	1,587		
LBM 1804	45	<i>Rattus hainaldi</i>	2,388	1,574	1,658	1,517	1,504	1,344
LBM 1805	44	<i>Rattus hainaldi</i>	2,579	1,557	1,792	1,619	1,506	1,364
LBM 1806	44	<i>Rattus hainaldi</i>	2,352	1,566	1,729	1,625		
LBM 1808	44	<i>Rattus hainaldi</i>	2,175	1,522				
LBM 1810	44	<i>Rattus hainaldi</i>	2,383	1,503	1,705	1,531		
LBM 1811	44	<i>Rattus hainaldi</i>	2,36	1,526	1,67	1,509	1,478	1,318
LBM 1813	44	<i>Rattus hainaldi</i>	2,357	1,533	1,66	1,594		
LBM 1815	44	<i>Rattus hainaldi</i>	2,454	1,525	1,782	1,614	1,578	1,356
LBM 1832	43	<i>Rattus hainaldi</i>	2,366	1,524	1,764	1,559	1,517	1,37
LBM 1834	43	<i>Rattus hainaldi</i>	2,27	1,402	1,679	1,46		
LBM 1836	43	<i>Rattus hainaldi</i>	2,277	1,475	1,701	1,493	1,634	1,303
LBM 1837	43	<i>Rattus hainaldi</i>			1,747	1,566		
LBM 1838	43	<i>Rattus hainaldi</i>	2,323	1,371	1,72	1,446		
LBM 1839	43	<i>Rattus hainaldi</i>	2,303	1,4	1,722	1,457	1,57	1,303
LBM 1840	43	<i>Rattus hainaldi</i>	2,441	1,49	1,788	1,514	1,688	1,322
LBM 1843	43	<i>Rattus hainaldi</i>			1,706	1,539		
LBM 1848	42	<i>Rattus hainaldi</i>	2,427	1,47	1,76	1,485	1,487	1,333
LBM 1849	42	<i>Rattus hainaldi</i>			1,731	1,5		
LBM 1854	31	<i>Rattus hainaldi</i>	2,361	1,465				

Table VI-8:measurements (mm) of lower molars from Sector VII

nr	sector	spit	ID	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
LBM 0182	IV	36	<i>Rattus hainaldi</i>	2,75	1,69				
LBM 0285	IV	41	<i>Rattus hainaldi</i>	2,84	1,68				
LBM 0286	IV	41	<i>Rattus hainaldi</i>			1,78	1,56		
LBM 0309	IV	42	<i>Rattus hainaldi</i>				1,5	1,31	1,24
LBM 0327	IV	45	<i>Rattus hainaldi</i>	2,68	1,58				
LBM 0604	III	35	<i>Rattus hainaldi</i>	2,99	1,72	1,85	1,63	1,43	1,22
LBM 1083	IV	14	<i>Rattus hainaldi</i>	2,63	1,61	1,73	1,53	1,36	1,2
LBM 1155	IV	13	<i>Rattus exulans</i>	2,47	1,57	1,65	1,49	1,31	1,15
LBM 1224	IV	12	<i>Rattus exulans</i>	2,6	1,58	1,8	1,5	1,34	1,18
LBM 1227	IV	12	<i>Rattus exulans</i>	2,62	1,6	1,67	1,48	1,3	1,2
LBM 1370	IV	5	<i>Rattus exulans</i>	2,67	1,62				
LBM 1424	IV	3	<i>Rattus exulans</i>	2,58	1,61	1,77	1,34	1,24	1,2
LBM 1430	IV	3	<i>Rattus exulans</i>	2,51	1,5				
LBM 1447	IV	2	<i>Rattus exulans</i>	2,56	1,48	1,71	1,43	1,18	1,17
LBM 1673	VII	53	<i>Rattus hainaldi</i>	2,701	1,621				
LBM 1676	VII	53	<i>Rattus hainaldi</i>			1,674	1,565		
LBM 1677	VII	53	<i>Rattus hainaldi</i>	2,977	1,642	1,822	1,507	1,473	1,207
LBM 1701	VII	53	<i>Rattus hainaldi</i>	2,535	1,498	1,579	1,299		
LBM 1824	VII	44	<i>Rattus hainaldi</i>	2,678	1,583	1,744	1,472		
LBM 1825	VII	44	<i>Rattus hainaldi</i>	2,641	1,581	1,721	1,517		
LBM 1862	VII	43	<i>Rattus hainaldi</i>	2,646	1,655				
LBM 1863	VII	43	<i>Rattus hainaldi</i>			1,66	1,64		
LBM 1864	VII	43	<i>Rattus hainaldi</i>					1,367	1,289

Table VI-9: measurements (mm) of upper molars of small murids from Liang Bua cave

## VII. Middle size murids: insular endemics, human introductions and palaeoenvironment

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*“Della conoscenza mitica degli astri egli capta solo qualche stanco  
barlume; della conoscenza scientifica, gli echi divulgati dai giornali; di ciò  
che sa diffida; ciò che ignora tiene il suo animo sospeso. Soverchiato,  
insicuro, s’innervosisce sulle mappe celesti come su orari ferroviari  
scartabellati in cerca d’una coincidenza.”*

*Italo Calvino*

### **Introduction**

Middle size murids were recovered at Liang Bua, Flores, Indonesia. Every island of the Indonesian archipelago hosts some endemic species of Muridae, and Flores wasn't the exception. One of the species described (*Paulamys naso*) was found to be still living (Kitchener, 1991b) ; a new small rat, about the same size of *Rattus exulans* was discovered (*Rattus hainaldi*, Kitchener, 1991a). In this chapter I will deal with the new findings in the archeological deposit of Liang Bua (Flores, Indonesia).

This study will focus on middle size murids, that is murids around the same size of *Rattus rattus*. At Liang Bua were found two endemic species, *Komodomys rintjanus* Sody, 1941 and *Paulamys naso* Musser, 1981, present since the oldest phases of the occupation of the cave, and two commensal species, *Rattus rattus* and *Rattus argentiventer*, that reached the island only in the latest phases. The prominent part of this work consists in the description and analysis of the former two, for which this deposit represents the richest documentation. Originally described on the basis of a few mandibles only (Musser, 1981), we can now extent our knowledge to the upper dentitions as well, and get a reliable picture of the variation. Apart from these endemics, we shall also describe fossils of the introduced species that appear in the upper part of the sections.

## ***Previous work on the fossil rodents of Flores***

The first fossil rodents from Flores were collected by Father Verhoeven and studied by Hooijer (1967). Apart from giant rats, Hooijer recognized five fragments of middle-sized murids, which he identified as *Rattus rattus*, with incertitude about the subspecies (*argentiventer* or *diardi*). In his research on rats from Sumba, Musser (1972) suggested that the Flores finds could be classified as *Rattus rattus sumbae*. However, in a review of the fossil material from Liang Toge (Musser, 1981), he recognized that the material was not referable *Rattus rattus*, but instead represented two different species. One of these was identified as *Komodomys rintjanus*, a rat endemic to off shore islands near Flores. For the other species a separate genus and species were erected: *Floresomys naso*. As the generic name was pre-occupied, Musser et al. (1986) changed it into *Paulamys*, and in that occasion described more fossil material determined as *P. naso* from Liang Toge and two other caves, Liang Bua and Soki. In 1989, during an expedition of the Western Australian Museum and Museum Zoological Bugoriense, a modern murid very similar to *P. naso* was trapped and was assigned to *Paulamys* sp. cf. *P. naso* (Kitchener et al., 1991b). According to Kitchener et al. (1991b, p. 187), *Paulamys* and *Bunomys* were so similar that: “On the basis of our rather limited material we can determine no reliable characters that enable us to distinguish *Paulamys* from *Bunomys*.” Indeed, they later placed the Flores species in the Sulawesi genus *Bunomys* (Kitchener et al., 1998). Musser and Carlton (2005), however, maintained a separate generic status for the Flores taxon.

*Komodomys rintjanus* is an extant species, but its distribution is now limited to two other islands near Flores, Rinca and Padar. Shrew remains from Liang Bua were not referable to any of the soricids currently inhabiting the island, and presumably represent extinct species (Van den Hoek Ostende et al., 2007). The connections between the faunas of Flores and Komodo Islands is not confined to only this species; because their closeness and the geomorphological characteristics of the area, these islands share among the others also the Komodo Dragon, *Varanus komodoensis*, and the Flores Giant Rat, *Papagomys armandvillei*. The first report of *Komodomys rintjanus* dates to 1941, when Sody (1941), studying the rats from the Indo-Malayan and Indo-Australian regions, described a new species, *Rattus rintjanus*. Unfortunately, he only found an old individual, so he didn't have enough evidence for a new genus, but recognized its peculiarity when he wrote “It seems probable that a new genus shall have to be created for this species”. And he was right, because in 1980 Musser & Boeadi made the description of a new species, *Komodomys rintjanus*, on the basis of 16 extant individuals collected at Rinca and Padar. The year later, in his review of the rats of Flores, Musser (1981) described the fifth middle size murid specimen of the ones collected by Verhoeven at Liang Toge as *Komodomys rintjanus*.

## ***Material and Methods***

The material described in this paper was excavated in the Liang Bua Cave (Ruteng District, Flores, Indonesia).



The material has been measured with the same method explained in Chapter VI, paragraph “Materials and methods” and represented in Figure VI-1. The list of the identified specimens and measurements are reported in VII-1.

The material has been compared to fossil and recent specimens collected at NCB Naturalis (Leiden). In particular, it was possible to use the holotype of *Komodomys rintjanus* (RMNH 9801) and the fossil one from Liang Toge (RGM 629511) and the fossil material of *Paulamys naso* from Liang Toge (the holotype RGM 629507 and the other three specimens RGM 629508-629510).

## ***Systematic Palaeontology***

**Class:** Mammalia Linnaeus, 1758

**Order:** Rodentia Bowdich, 1821

**Suborder:** Muridae Illiger, 1811

### ***Komodomys rintjanus* (Sody 1941)**

#### **Synonymy**

*Rattus rintjanus* Sody 1941

*Rattus rattus* from Liang Toge Hooijer 1957

*Rattus rattus sumbae* from Liang Toge Musser 1972

*Komodomys rintjanus* Musser and Boedi, 1980; Musser, 1981

**Holotype:** adult male, Lohoboeaja, Indonesia, RMNH 9801 at Netherlands Centre for Biodiversity, Naturalis, Leiden, The Netherlands

**Measurements:** measurements of the teeth are reported in the Appendix. The results of the descriptive statistical analysis are reported in Table VII-1 and Table VII-2

<i>Komodomys rintjanus</i>	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	Ratio M <sub>1</sub>	Ratio M <sub>2</sub>	Ratio M <sub>3</sub>	WM <sub>2</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>2</sub>
<b>Mean</b>	3,23	2,17	2,42	2,39	2,49	2,22	99,07	67,48	89,60	110,70	102,20	92,71
<b>Standard Error</b>	0,02	0,01	0,01	0,01	0,02	0,01	0,52	0,34	0,97	0,42	0,60	0,37
<b>Median</b>	3,22	2,18	2,41	2,38	2,51	2,22	99,16	67,47	87,92	110,09	101,60	92,24
<b>Mode</b>	3,20	2,19	2,38	2,38	2,57	2,23	100,00	68,90	81,27	114,01	100,00	93,80
<b>Standard deviation</b>	0,19	0,13	0,15	0,12	0,22	0,12	5,15	3,55	8,78	4,00	5,09	3,26
<b>Sample Variance</b>	0,04	0,02	0,02	0,02	0,05	0,02	26,54	12,62	77,03	16,03	25,88	10,62
<b>Kurtosis</b>	-0,61	-0,65	0,34	-0,53	1,27	-0,08	0,06	0,49	2,12	1,06	2,80	-0,10
<b>Skweness</b>	-0,01	-0,06	0,19	0,19	-0,73	0,34	0,10	0,07	1,30	0,76	1,07	0,42
<b>Range</b>	0,85	0,57	0,85	0,56	1,20	0,58	26,33	20,86	44,37	21,19	30,40	14,75
<b>Minimum</b>	2,78	1,89	2,03	2,12	1,74	1,96	87,50	56,73	75,67	102,25	92,92	86,12
<b>Maximum</b>	3,63	2,46	2,88	2,68	2,94	2,54	113,83	77,60	120,03	123,44	123,32	100,88
<b>Sum</b>	354,77	239,05	242,31	241,79	204,26	181,74	9906,91	7422,53	7347,36	9962,66	7358,21	7138,55
<b>Count (n)</b>	110	110	100	101	82	82	100	110	82	90	72	77
<b>Confidence Interval (95,0%)</b>	0,04	0,02	0,03	0,02	0,05	0,03	1,02	0,67	1,93	0,84	1,20	0,74

**Table VII-1: descriptive statistical analysis of lower teeth of *Komodomys rintjanus***

	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
Mean	4.11	2.67	2.55	2.57	2.13	2.01
Standard Error	0.04	0.02	0.03	0.03	0.05	0.04
Median	4.18	2.68	2.59	2.60	2.14	2.04
Mode	4.18	2.52	2.59	2.50	2.05	2.05
Standard deviation	0.24	0.14	0.18	0.15	0.20	0.17
Sample Variance	0.06	0.02	0.03	0.02	0.04	0.03
Kurtosis	0.79	2.39	1.87	4.84	0.31	2.15
Skewness	-0.46	-0.93	0.25	-1.49	-0.43	-1.23
Range	1.23	0.76	0.91	0.82	0.79	0.71
Minimum	3.46	2.17	2.16	2.00	1.68	1.55
Maximum	4.69	2.93	3.07	2.82	2.47	2.26
Sum	160.21	103.94	81.69	82.14	40.52	38.12
Count (n)	39	39	32	32	19	19
Confidence Interval (95,0%)	0.08	0.05	0.06	0.06	0.10	0.08

Table VII-2: descriptive statistical analysis of upper teeth of *Komodomys rintjanus*

### Description of the material from Liang Bua:

**M<sub>1</sub>**: it is structured in three laminae. The first one represents the anteroconid and is made up of two cusps, anterolabial and anterolingual. When the wear is not accentuated, the first lamina looks symmetrical, made up of two cusps of about the same size. In older individuals or in individuals with more worn teeth, first the cusps merge abundantly, the a-ling is bigger and the lamina looks inclined; with more wear the lamina merges with the metaconid. Thus, the connection between the first and the second lamina is not central (except for few cases) but lingual. The anteroconid cusplet is absent. The second lamina is symmetrical, transverse and formed by metaconid and protoconid. The cusps are about the same size of the anteroconid ones. As the cusps merge early, the lamina looks bilobated. In few specimens an accessory anterolabial cusplet is present (less than 3%). The last lamina is made up by the entoconid and the hypoconid. The mesial wall is straight, the distal wall is arched. In young specimens, the cusps are drop shaped and there is only a point of contact in the middle of the lamina. In older specimens, the hypoconid looks bigger, rounded and is located slightly distally to the entoconid, that is more elongated. Then, the lamina hardly looks bilobated, but often in the mesial wall there is a concavity in correspondence of the hypoconid. Usually, a posteriolabial cusplet is present (around 65%), located slightly mesially to the hypoconid, that merges early with the third lamina and in old specimens accentuates the arch. The posterior cingulum is small, oval and in worn teeth is not always detectable.

**M<sub>2</sub>**: This tooth is characterized by a squarish outline, with length and width of around the same value (mean ratio Width/Length is 99, 16%). The first lamina, formed by protoconid (pd) and metaconid (md), is transverse. The mesial wall is straight and oblique, while the distal one can be arched or straight in older individuals. The anteriolabial cusp (a-lab), mesial to the pd, can be very small or reach around half of the size of the other main cusps, and merges very early with the lamina. Thus, the labial portion of this lamina is generally wider than the lingual one. The second lamina is formed by entoconid (ed) and hypoconid (hd). The cusps are drop shaped and meet in the middle of the lamina. A cylindrical posteriolabial cusplet (plc) is located at the side of the hd. The wear makes the cusps and the cusplet merge and the lamina assumes the shape of a wave, with a straighter lingual portion and a more curved labial one, with the complete fusion of the plc. The posterior cingulum (pc) is elliptical in cross section and is well separated from the second lamina.

**M<sub>3</sub>**: it is formed by two laminae. The first one, made up of metaconid and protoconid, is transverse and straight. In few cases an antero-labial cusp (a-lab) is present, and merges soon with the lamina. The second lamina, formed almost exclusively by the entoconid, is transverse and thin in young individuals; as the wear of the tooth increases, it is characterized by a straight mesial wall and a half circular distal one. Small traces of hypoconid are detectable in few cases as a tiny cusp.



**Plate 7: lower and upper tooth rows of *Komodomys rintjanus***

**M<sup>1</sup>**: The median cusps are large and cylindrical. The first row is made constituted by three tubercles and is quite symmetrical. Despite that, the lingual cusp (t1) is slightly dislocated distally and it is better separated from t2 compared to t3. The second row (t4, t5 and t6) has the same internal organization of the first row, but in this case the labial cusp, t6, is located slightly distally. t4 is robust and cylindrical. The last row is formed by t8 and t9. t9 is merged with t8 and a small distal protrusion suggest that also the posterior cingulum (pc) has been incorporated t7 is absent.

**M<sup>2</sup>**: the outline of the tooth is triangular. t1 is cylindrical, large and well separated from the posterior row. t3 is absent. The row formed by t4, t5 and t6 is organize in the same way of the second row in the first molar, with a large median cusp, two slightly smaller lateral cusps, with the lingual one (t4) more cylindrical, placed against the central one but still well separated from it. The distal row, formed by t8 and t9, is narrower than the others, with the tiny t9 emerging labially from the wide and elliptical shaped t8. M<sup>2</sup> wears earlier than M<sup>1</sup>.

**M<sup>3</sup>**: this tooth is robust, with an almost circular outline. t1 is large and cylindrical, well separated by the median row. t3 is absent. The second row is transverse, in young specimen it is thin but t4, t5 and t6 are already merged since the first phases of wear. The distal row is semicircular in cross section.

*Paulamys Musser 1981*

***Paulamys naso* (Musser 1981)**

**Original reference:** *Floresomys naso*, Musser 1981

Replaced by *Paulamys naso* in Musser (1986)

**Synonymy**

*Rattus rattus* from Liang Toge in Hooijer 1957

*Rattus rattus sumbae* specimen 5 from Liang Toge in Musser 1972)

*Paulamys naso* from Liang Toge in Musser (1981)

**Holotype:** specimen 1 from Liang Toge, stored at the Netherlands Centre for Biodiversity

**Measurements:** measurements of the teeth are given in the Appendix. The results of the descriptive statistical analysis are given in Table VII-3 and Table VII-4.

<i>Paulamys naso</i>	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	Ratio M <sub>1</sub>	Ratio M <sub>2</sub>	Ratio M <sub>3</sub>	WM <sub>2</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>2</sub>
<b>Mean</b>	3,14	2,02	2,47	2,20	2,23	1,90	89,03	64,42	85,40	108,84	95,17	87,46
<b>Standard Error</b>	0,02	0,02	0,02	0,02	0,03	0,02	0,50	0,33	0,93	0,64	0,97	0,53
<b>Median</b>	3,14	1,99	2,46	2,19	2,23	1,89	89,00	64,45	86,16	109,09	96,91	87,76
<b>Mode</b>	3,14	1,99	2,49	2,14	2,27	1,81	89,21	65,63			96,98	
<b>Standard deviation</b>	0,16	0,12	0,17	0,14	0,19	0,11	3,70	2,62	5,57	4,56	5,55	3,14
<b>Sample Variance</b>	0,03	0,01	0,03	0,02	0,04	0,01	13,69	6,87	30,98	20,76	30,78	9,89
<b>Kurtosis</b>	1,22	0,05	0,94	0,96	0,03	0,36	-0,78	-0,56	0,48	-0,14	-0,71	0,49
<b>Skweness</b>	0,68	0,73	0,73	0,63	0,20	0,20	0,16	0,04	-0,73	-0,03	-0,06	0,53
<b>Range</b>	0,84	0,52	0,80	0,68	0,88	0,48	15,70	10,82	23,63	21,66	22,21	13,74
<b>Minimum</b>	2,77	1,84	2,14	1,90	1,84	1,64	81,63	59,01	70,96	98,13	84,36	82,61
<b>Maximum</b>	3,61	2,36	2,94	2,58	2,72	2,12	97,33	69,82	94,58	119,79	106,57	96,35
<b>Sum</b>	198,10	127,56	133,41	118,61	80,21	68,22	4807,56	4058,59	3074,28	5441,99	3140,46	3061,25
<b>Count (n)</b>	63	63	54	54	36	36	54	63	36	50	33	35
<b>Confidence Interval (95,0%)</b>	0,04	0,03	0,05	0,04	0,06	0,04	1,01	0,66	1,88	1,29	1,97	1,08

**Table VII-3: descriptive statistical analysis of lower teeth of *Paulamys naso***

	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
<b>Mean</b>	4.08	2.65	2.61	2.56	2.22	2.04
<b>Standard Error</b>	0.08	0.06	0.06	0.06	0.12	0.07
<b>Median</b>	4.15	2.70	2.61	2.61	2.18	2.06
<b>Mode</b>	4.21	2.82	2.57	2.75		
<b>Standard deviation</b>	0.32	0.24	0.24	0.22	0.35	0.21
<b>Sample Variance</b>	0.10	0.06	0.06	0.05	0.12	0.04
<b>Kurtosis</b>	0.44	-0.39	0.01	0.87	-0.73	-0.15
<b>Skweness</b>	-0.71	-0.52	-0.13	-0.99	0.13	-0.79
<b>Range</b>	1.19	0.85	0.88	0.82	1.06	0.64
<b>Minimum</b>	3.32	2.17	2.16	2.06	1.74	1.66
<b>Maximum</b>	4.51	3.02	3.04	2.88	2.80	2.30
<b>Sum</b>	69.41	45.13	36.52	35.90	20.02	18.32
<b>Count (n)</b>	17	17	14	14	9	9
<b>Confidence Interval (95,0%)</b>	0.16	0.12	0.14	0.13	0.27	0.16

**Table VII-4: descriptive statistical analysis of upper teeth of *Paulamys naso***

**Description of the material from Liang Bua cave:**

**M<sub>1</sub>:** The first lamina is formed symmetrical, formed by a-ling and a-lab cusps of around the same size and scantily separated, so that the lamina generally is heart-shaped. Going on with wear, the lamina usually meets the second lamina in the midline. The a-cen is absent. The second lamina is transverse and chunky, with a wide connection between pd and md. The third lamina is chunky and arched, and the plc is generally present. When the tooth is worn, the plc merges completely with the other cusps. pc is cylindrical and well developed.

**M<sub>2</sub>:** The outline of this tooth is generally rectangular. pd is bigger than md; a-lab is generally present semicircular in cross section, with the straight wall placed against the pd. The second lamina (hd and ed) is arched, symmetrical and the plc, of the same size as a-lab, is placed against hd. pc is cylindrical and well developed.

**M<sub>3</sub>:** The occlusal outline of this molar is sub-triangular. The first lamina is transverse and symmetrical. A tiny a-lab is present in few specimens, and merges with the lamina in early stages of wear.



**Plate 8: lower and upper molars of *Paulamys naso***

**M<sup>1</sup>:** The first row is quite transverse, but t1, that is cylindrical and bigger than t3, is placed slightly distally to the other cusps. All the cusps are wide confluent, but t1 merges later than the other two cusps (t2 and t3). The pattern of the second row is the same as the first, but this one is more arched and t4 is more robust. The distal row is formed by a wide central t8 merged with a smaller labial t9. t7 is absent.

**M<sup>2</sup>:** t1 is very robust and cylindrical, well separated from the first row. t3 is absent. t4 is cylindrical and separated from or slightly confluent with t5 and t6, that merged early and widely. The distal row is formed exclusively by a large t8 and a tiny t9.

**M<sup>3</sup>:** t1 is cylindrical and well separated from the row, so that also in cases of advanced wear it doesn't merge with t4-5. t4 is small, and t4, t5 and t6 merge in the first stages of wear. In young individuals, the row is transverse, wider in the part formed by t5-6; in worn teeth the row becomes arched and merges early with the distal cusp. The latter is formed by t8 and t9, the row is thin and transverse.

### **Remarks on the endemic middle-sized murids of Liang Bua cave**

*Komodomys rintjanus* (Sody, 1941) is an endemic species, currently restricted to the isles of Rinca, Padar, Lomblen and Pantar (Wilson and Reeder, 2005). One subfossil fragment from Flores ("specimen 5") was described by Musser (1981). It had been recovered at Liang Toge, in sediments dating to 3000-4000 BP. At Liang Bua the most ancient specimen attributed to this species was recovered in sector IV spit 82, older than 95ky (Roberts et al., 2009) and in association with endemic fauna. After that, it was abundantly recovered from spit 59 upwards. Surveys meant to record the presence of this species on Flores have been carried out, but to date no living specimen was found (Aplin et al., 2008). The island where the species has been found, Rinca and Padar to the west and Lomblen and Pantar to the east, are separated from Flores by relatively shallow water, and would have been part of one large island during the Late Pleistocene. Assuming that the species is really extirpated on Flores, the Holocene isolation of the islands may have preserved this old faunal elements, in much the same way as the survival of Komodo dragons on the island of Komodo. However, there are also indications that its ecological preference may have played a role in its current distribution (see below).

Whereas *Komodomys* was first described from extant material, of which later fossils were found, exactly the reverse holds true for *Paulamys*. The original description of *P. naso* (Musser, 1981, there as *Floresomys naso*) based on four fossil mandibles recovered at Liang Toge (Flores, Indonesia), a deposit dated to 3550 ± 525 years BP.

At first sight, the dentitions of *Komodomys rintjanus* and *Paulamys naso* are very similar. Furthermore, the two species show an enormous overlap in size. It is noteworthy that the metrical variation of either species is very large, an phenomenon which is also noted for the endemic small-sized murid *Rattus hainaldi*. The differences between the two middle-sized species were already discussed by Musser (1981). However, that was based on a very small sample, and therefore it is useful to reiterate on the morphological differences now that we have a sample of dozens of mandibles for each species from Liang Bua. Furthermore, Musser (1981) did not have any upper dentitions available, which are now present for both *Komodomys* and *Paulamys*.

Lower dentition: the main difference are in the general aspect of the tooth row, which looks slender in *Paulamys naso* and more robust in *Komodomys rintjanus*. In fact, as can be seen in table X, the ratio between width and teeth of each tooth is higher in *K. rintjanus* than in *P. naso*, above all in M<sub>2</sub>. Besides, the laminae of *Paulamys naso* are chunkier, while in *K. rintjanus* the area of connection between the labial and lingual cusps is narrower and the cusps are more inclined. In M<sub>1</sub>, the first lamina generally merges with the second from a middle position in *Paulamys naso*, while in *K. rintjanus* the point of merger is more often located lingually. The

second lower molar is the one that carries the biggest difference, above all because of the difference in the average ratio between width and length (around 10%). The outline of this element is generally squarish in *K. rintjanus* and rectangular in *P. naso*, the laminae in the latter are chunkier. The third lower molar is slender compared to the other two on *P. naso*.

Upper dentition: The upper dentition of *Paulamys naso* was unknown till 1991, when Kitchener et al. described a recent specimen that they tentatively assigned to this species. In *P. naso*, the rows are thicker, the cusps more aligned and cylindrical. The size difference between the lateral and the centrals cusps is less pronounced.

### ***Rattus* Fischer 1803**

*Rattus* sp.

Measurements are reported in the Appendix. The results of the descriptive statistical analysis are reported in Table VII-5

<i>Rattus</i> sp.	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	Ratio M <sub>1</sub>	Ratio M <sub>2</sub>	Ratio M <sub>3</sub>	WM <sub>2</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>2</sub>
<b>Mean</b>	2,96	1,88	2,23	1,99	2,16	1,82	89,20	63,33	84,37	106,80	97,44	90,44
<b>Standard Error</b>	0,03	0,03	0,04	0,03	0,05	0,05	0,98	0,84	1,30	0,99	1,47	1,10
<b>Median</b>	2,93	1,86	2,24	1,98	2,16	1,81	89,23	63,95	83,54	107,59	99,18	91,59
<b>Mode</b>	3,09	1,86	2,32	1,97		1,81						#N/D
<b>Standard deviation</b>	0,13	0,13	0,15	0,13	0,20	0,18	4,14	3,75	5,02	3,97	5,51	4,12
<b>Sample Variance</b>	0,02	0,02	0,02	0,02	0,04	0,03	17,17	14,10	25,19	15,77	30,34	16,94
<b>Kurtosis</b>	-0,66	2,06	0,01	0,76	-0,95	2,08	-0,59	0,57	-1,11	-0,51	-0,92	1,02
<b>Skweness</b>	0,49	0,38	0,02	0,60	0,39	-0,17	-0,19	-0,31	-0,05	-0,20	0,12	-1,15
<b>Range</b>	0,46	0,60	0,59	0,55	0,64	0,79	14,13	16,02	15,41	13,76	18,30	14,99
<b>Minimum</b>	2,77	1,57	1,96	1,76	1,88	1,42	81,11	54,90	75,53	98,92	89,50	80,68
<b>Maximum</b>	3,23	2,17	2,55	2,31	2,52	2,21	95,24	70,92	90,95	112,68	107,80	95,67
<b>Sum</b>	59,24	37,50	40,13	35,75	32,46	27,36	1605,55	1266,62	1265,50	1708,85	1364,13	1266,21
<b>Count (n)</b>	20	20	18	18	15	15	18	20	15	16	14	14
<b>Confidence Interval (95,0%)</b>	0,06	0,06	0,08	0,07	0,11	0,10	2,06	1,76	2,78	2,12	3,18	2,38

**Table VII-5: descriptive statistical analysis of *Rattus* sp.**

**M<sub>1</sub>:** the first lamina is asymmetrical, a-ling is much bigger than a-lab, the a-ling is connected to md. Traces of a very small a-cen and a small alc is generally present. The second lamina, made by md and pd, is transverse and bilobated or arched; md is large and cylindrical in cross section. The third lamina is narrower than the others; it is arched and a cylindrical plc is located against its labial wall. The plc is oval in cross section.

**M<sub>2</sub>:** it is made of two laminae. The first one is slightly arched, md and pd are around the size size and there is always a a-lab cusp, usually merged with the lamina. The second lamina is arched, and a small plc is present. The pc is oval in cross section

**M<sub>3</sub>:** there is usually a small a-lab cusplet in front of the pd; the lamina is transverse. The second lamina is thick and transverse. The tooth has a triangular outline.

The small mandibles of *Rattus* sp., even if few, show internal variation, that can't be explained by one species. It seems that at least two different species are present here, and they seem to be referable to *Rattus argentiventer* and *Rattus rattus*. They can be tentatively attributed to one species or the other, by comparison with recent material from Flores and near islands. Despite



that, because of the low difference in the tooth morphology between these two species (Musser, 1981) and the high internal variation inside the species *Rattus rattus* (also testified by the high number of sub-species recognized), the right assignment on the solely basis of toothrow morphometric seems unachievable. For this reason, all these specimens are here referred as *Rattus* sp.

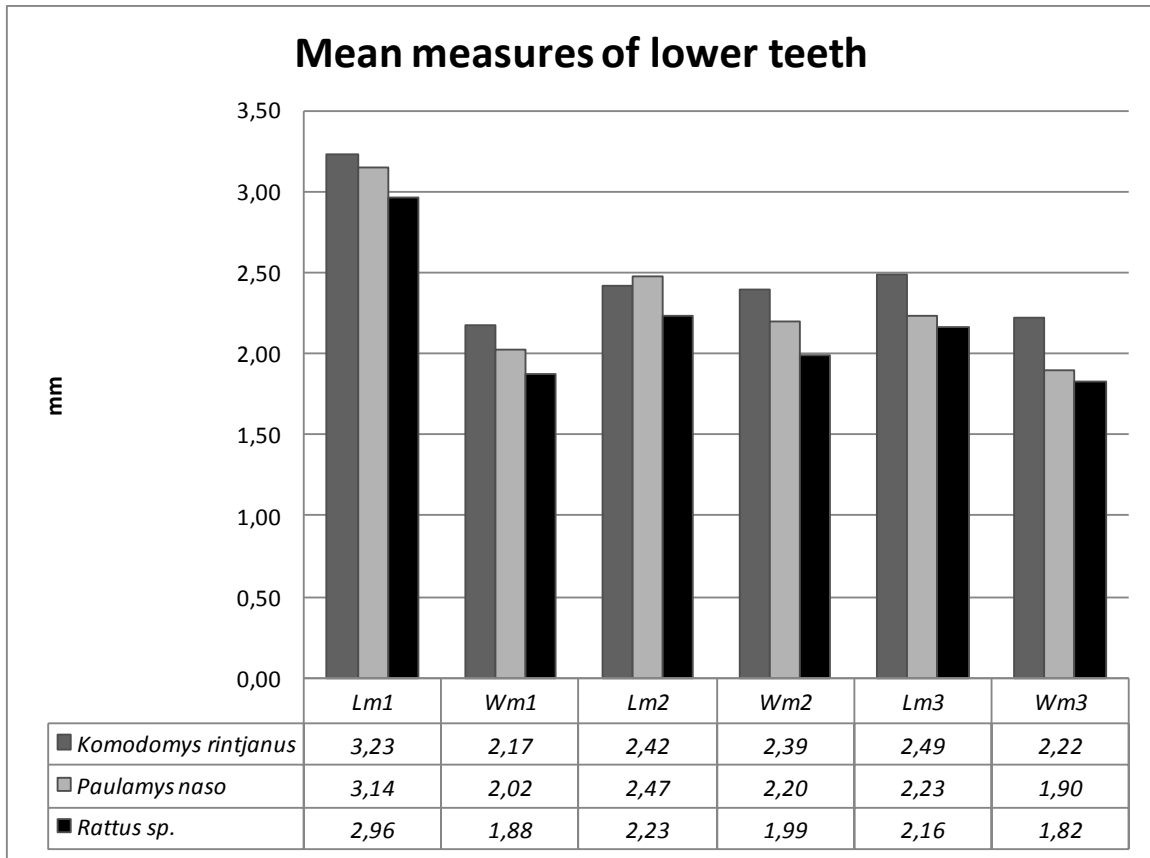


Figure VII-1: comparison of mean values of lower teeth measurements of middle size murids



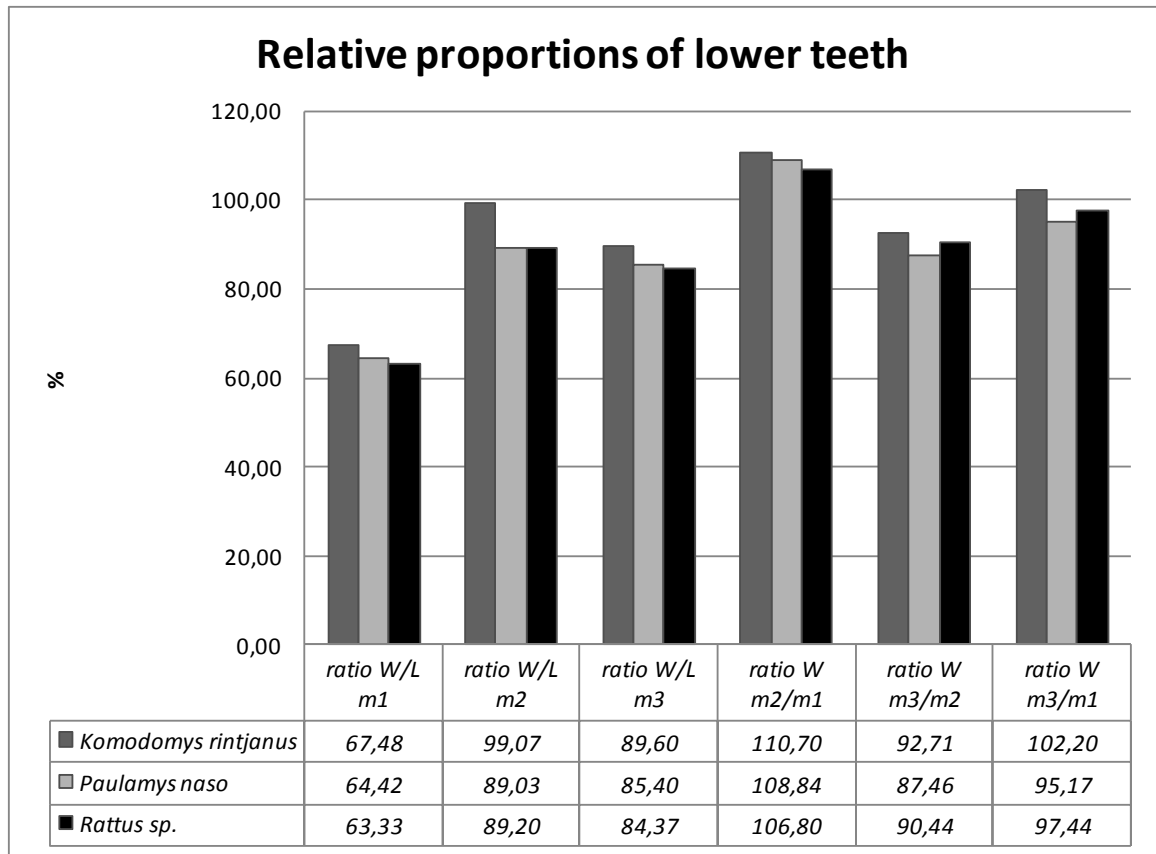


Figure VII-2: comparison of mean values of ratios among measurements of lower teeth of middle size murids

Although the specimen could represent a rare endemic not found elsewhere in the section, it is noteworthy that spit 13 is exactly the same spit in which for the first time *Rattus exulans* has been found. It is also near the first appearance of other introduced mammals, such as the civet *Paradoxurus hermaphrodites* and the porcupine *Hystrix javanica*, which came to the island with the Neolithic occupation. Given its absence in the older part of Sector IV and in the material from the other sectors, it is therefore likely to also represent an immigrant. Possibly it represents an introduction from another island, but in order to establish this, more material is needed to determine the identity of this species.

It is necessary to spend some words about the mandibles of the species here described. In the first descriptions of fossil middle sized murid from Flores, Musser noticed differences in the morphology of the dentaries of *Komodomys rintjanus* and *Paulamys naso*. Describing the former species (Musser, 1980), he noted small differences in the mandible configuration with other species of *Rattus*, in particular in the coronoid processes (that are smaller in *K. rintjanus*) and in the angular processes (longer and more slender). The dentary behind the toothrow of the fossil mandible described in Musser (1983) wasn't preserved, but the anterior portion was still present and different from that described for *P. naso*. *Paulamys naso* (Musser, 1983) has a very distinctive dentary, characterized by slim incisor set in a long and gently curved dentary, with masseteric ridges high and prominent. These features were related to the presence of a long rostrum and were confirmed in Musser et al. (1986), and then found again in Kitchener in the living exemplar collected at Kelimutu.

The great part of these features have been found in Liang Bua material as well, but here, because of the large amount of specimens retrieved, the variability in some characters is higher. In particular, the prominence of the masseteric ridges seem to vary a lot among specimens, as well as the size, and the age could play an important role in this variation. Also the length of the diastema is high variable, but as a matter of fact the longest diastemas are the ones of *P. naso* specimens. There are few samples of *K. rintjanus* with long diastema, but in those cases mandibles are very large in absolute. From around spit 14, *K. rintjanus* mandibles are bigger in average, with higher dentaries and robust diastema, while the smallest mandibles retrieved are in Pleistocene strata (41-42). In *Rattus* sp. mandibles, the toothrow is far smaller and thinner related to the size of the mandible, that is in general only slightly smaller than the endemics' ones.

## **Discussion**

### **Morphology**

*Rattus* sp. specimens are significantly smaller than the previous species and have slender toothrow. The first lamina of m1 is more asymmetrical and provided with a small a-cen. The crown of the teeth is less high and the cusps are less inclined than in *K. rintjanus* and *P. naso*.

Some specimens of large dimension (similar to *P. naso* or *K. rintjanus*), but with a morphology more similar to the genus *Rattus* have been recovered. In particular, they display an organization of the cusps similar to genus *Komodomys* or *Rattus*, but with quite narrow m<sub>2</sub>. Usually the a-lab cusp of the m<sub>2</sub> is located quite mesially, is bigger than in *Paulamys* and *Komodomys*, and rounded. The cusps are less thick than in *K. rintjanus* or *P. naso*.

All the peculiar specimens and the *Rattus* sp. specimens were recovered over spit 14, after 3,62 ky, an area of the stratigraphy with many anthropological and faunal changes: first Neolithic evidence and mammals introductions, among which the Polynesian rat *Rattus exulans*, the palm civet *Paradoxuros hermaphrodites*, the pig *Sus scrofa* and *Macaca fascicularis* (van den Bergh et al., 2009)

Comparing the measurements of the species recovered with the ones of other sub-fossil specimens of *P. naso* and *K. rintjanus* and the living species of Flores reported in Musser (1981) and Musser et al. (1986) (Figure VII-1 and Figure VII-2), we have that the mean value of the measurements are similar, but the variation in the sample is higher. That can be partly assigned to the size of the sample, that is far smaller than the one used in those articles; partly can be assigned to the wider chronological frame from which our specimens come; partly can be also attributed to an increase in the internal variation as adaptation to ecological niches available at that time.

Subfossil remains from *Paulamys naso* are known from Holocene sites on Flores island (Musser, 1981; Musser et al., 1986). Only one living species of *Paulamys* sp. has been described till now (Kitchener et al., 1991b).

From the comparison of the specimens from Liang Bua and the other published (Figure VII-3 and Figure VII-4), it results that the sample studied in this paper has in the average larger, but the general structure of the tooththrow, expressed by the ratios of the breadth, is around the same.

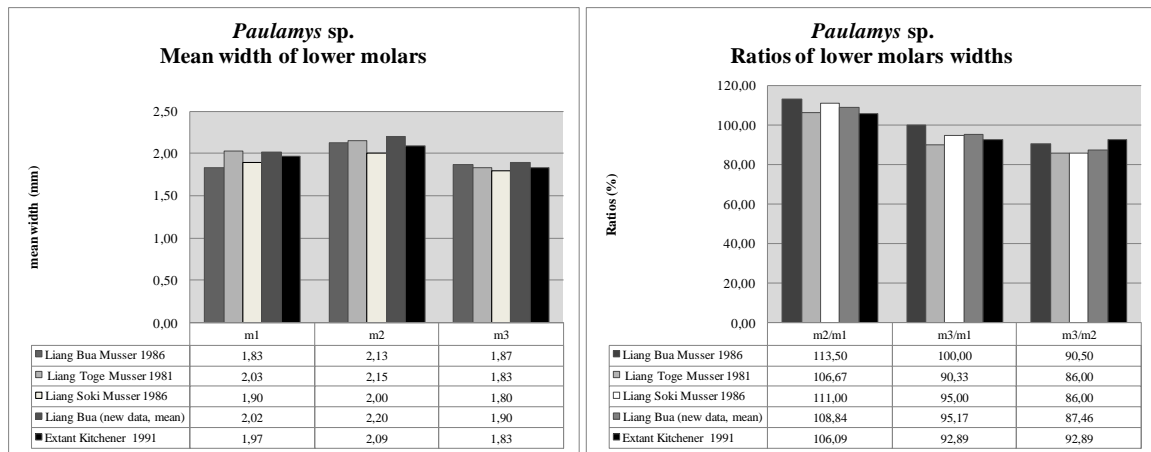


Figure VII-3: comparison of the mean value of measurements of the published specimens of *Paulamys sp.*

Figure VII-4: comparison of the ratios among mean values of relative proportion of lower teeth of the published specimens of *Paulamys sp.*

*Komodomy's rintjanus* is known only by seven living specimens from Rinca (Musser, 1980) and one specimen from Liang Toge (Musser, 1981); thus, comparisons are not easy to be carried on, as the sample is not big enough to catch the variability of the species.

However, by the comparison with these eight specimens, it seems that the fossil *Komodomy's rintjanus* from Liang Bua was larger, but the ratios among the teeth was around the same. The only specimen from Liang Toge had a larger  $m_2$  in relation with  $m_1$ , but it is necessary to consider that it was only one specimen and it falls within the variation found at Liang Bua.

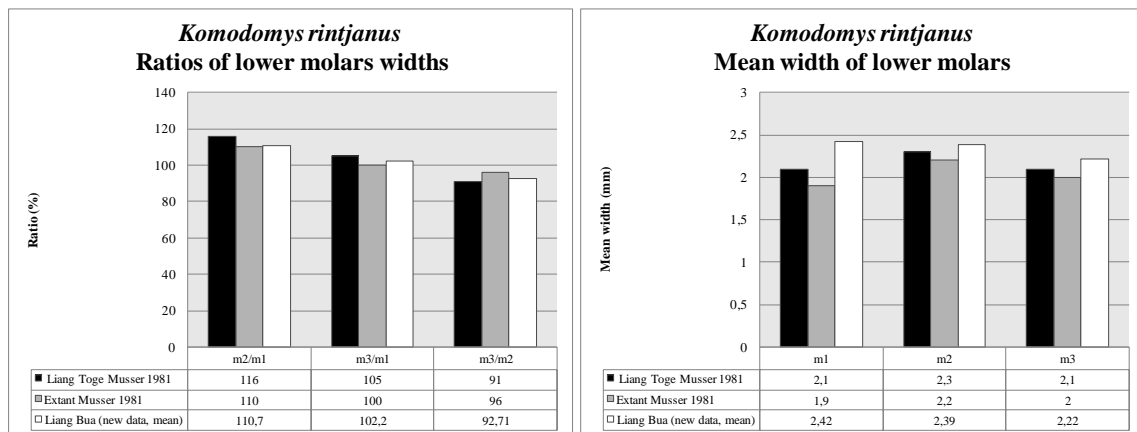


Figure VII-5: comparison of the mean value of measurements of the published specimens of *Komodomy's rintjanus*

Figure VII-6: comparison of the ratios among mean values of relative proportion of lower teeth of the published specimens of *Komodomy's rintjanus*

*Rattus* fossil specimens from Liang Bua cave have never been described. Compared to extant specimens, the one from Liang Bua are larger, but the same condition has been found in the other species with fossil remains (i.e. *Komodomys rintjanus*, *Paulamys naso*, *Rattus exulans* and *Rattus hainaldi*).

## Ecology

Living specimens of these two species show a different ecological adaptation, and thus occupy different niches. According to Aplin et al. (2008), *Komodomys rintjanus* seems to be adapted to dry, thorny scrub habitats, despite the fact that only few specimens have been collected. This habitat is not very represented on Flores and the current distribution of this species (Rinca, Komodo and Padar) seems to be a relict *Paulamys naso* seems to be more adapted to montane forest (Musser and Carlton, 2005), that is wetter environments than the former. Thus, the former can be considered as an indicator of dryer climate, the latter moister (related to the general climate present on Flores).

Looking at the variation of these species along the stratigraphical sequence, we can notice that their relative abundance change in correspondence of the main climatic events of Pleistocene and Holocene (Figure VII-7) According to Roberts et al. (2009) and by C<sup>14</sup> dating, the first 5 spits have less than 500 years, spit 15 can be dated to 3,62 ka, spit 22 dates to 6,37 ka, spit 31 is 11,3 ka, spit 48 is 16,6 ka. Deeper sectors have been dated by uranium-series, luminescence, and electron spin resonance, with ages that cover the last 95ka. Sector IV has been object of erosional or collapse processes that took away part of the sediments and gave rise to a temporal gap in the stratigraphy (Westaway et al., 2009). Remains located under spit 50 can date to the first phases of the human occupation of the cave, around 100 ka ago.

In the figure, it is possible to notice that, while in the most ancient phases (unit 2-3 according to Westaway et al., 2009; around 100ka) *Komodomys rintjanus* was more common, since the the Lateglacial took place a change in the relative abundance of species, and a phase dominated by *Paulamys naso* began. Because of the low numbers of specimen per spit, it is impossible to make more precise palaeoenvironmental inductions in ancient spits. At the beginning of the Lateglacial deposits, *Komodomys rintjanus* is still dominant, but soon after *Paulamys naso* becomes predominant. Around spit 15 it begins the reduction of *Paulamys naso*, in correspondence with the first appearance of *Rattus* sp. around 4ka BP and the commensal rats become common in the uppermost part of Sector IV. The dispersal of *Rattus* cannot be considered natural, as in that same moments major changes likely driven by man took place, like the appearance in the sequence of suids, *Macaca fascicularis*, the palm civet *Paradoxurus hermaphrodites* and *Hystrix javanica*, with the first Neolithic traces (van den Bergh et al., 2009).



but only by means of overseas dispersal, because of the lack of other species in common between the islands, with the exception of recently introduced species. But Watt and Baverstock (1994), analyzing the relationships among Murinae of South-east Asia by means of microcomplement fixation of Albumin, found a strict relationship among *Komodomys rijntianus*, *Bunomys chrysocomys* and *Rattus timorensis*, to the extent that the generic distinction between *Komodomys* and *Bunomys* was questioned. The strong morphological similarity among other murids dwelling the islands had already been considered. According to Musser (1981), *Papagomys* and *Lenomys* and *Eropeplus* are very similar:

*“The striking similarities in derived cranial characters between Lenomys and Eropeplus on one hand and between those two and Papagomys on the other, as well as the derived resemblances in molar structure between Eropeplus and Papagomys and in some dental features between Lenomys and Papagomys, along with the dental link between Lenomys and the Sundanese Lenothrix, suggest that the Sulawesi genera and Papagomys with its Floresian allies were derived from a common ancestral stock that once occurred on the Sunda Shelf, Sulawesi, and Flores at a time when these areas were either once continuous or separated only by narrow water gaps.” (pag. 165)*

For the morphological characters of fossil mandibles and maxillaries, endemic rats from Flores studied by Musser (1981), with the exception of *Spelaeomys florensis*, looked to be more related among them than to any other rat, so that to imagine a common ancestor, likely advisable in *Hooijeromys nusatenggara* Musser 1981, the only Murid species recorded in the fossil documentation of Flores in the late Early Pleistocene. But, on the other hand, according to Watt and Baverstock (1995) and to Kitchener et al. (1991b), both *Komodomys* and *Paulamys* are more related to *Bunomys* than to *Papagomys*, despite the fact that they all belong to a clade of *Rattus*-like species. Then the relation has to be reconsidered, not discarding an eventual contact between the fauna from Sulawesi and Flores in the Middle Pleistocene. The Pleistocene faunal association of Liang Bua is entirely formed by species that are in phylogenetic continuity with the old species dwelling the island in Early Pleistocene (Meijer et al., 2010), but because of the big gap in the fossil documentation between 0,7 and 0,1 Ma many aspects of the faunal succession on the island are still unclear. Furthermore, finds of small mammals from before 95 ka are restricted to *Hooijeromys nusatenggara*. Since Flores was never connected to the Sunda Shelf, and, in order to reach the island, species had to cross the Wallace’s Line, any dispersal from the western islands has to be considered unlikely. The similarities in some of the Late Pleistocene murids of Flores and Sulawesi can’t exclude the possibility that at least a brief and temporary exchange between these two islands, took place. However, all the obstacles considered (distance and sea depth) it was only a chance event of faunal oversea dispersal and not a stable connection.

## **Conclusion**

Middle size murids recovered at Liang Bua Cave (Flores, Indonesia) could be assigned to at least three different species. Two of them were endemic, *Paulamys naso* and *Komodomys rintjanus*, were present since the earliest phases of human occupation documented at the cave and seem to undergo abundance changes along the sequence in correspondence of major climatic oscillation of Quaternary. The wideness of the study to the other sectors of the cave could increase the number of specimens per spit and thus the statistical confidence of palaeoenvironmental reconstructions. Since the recent Holocene, around 4 ka ago, first specimens of *Rattus* sp. made their first appearance, and their relative number increases till the most recent phases of the occupation. The presence of this species is likely to be due to an accidental or deliberate introduction by Neolithic people.

All the species show a very high internal variation in size and morphology.





## Appendix Chapter VII

nr	sector	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	Ratio M <sub>1</sub>	Ratio M <sub>2</sub>	Ratio M <sub>3</sub>	WM <sub>2</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>2</sub>
LBM 0001	IV	23	<i>Komodomys rintjanus</i>	3,07	2,22	2,55	2,27	2,46	2,23	89,02	72,31	90,65	102,25	100,45	98,24
LBM 0048	IV	31	<i>Komodomys rintjanus</i>			2,27	2,15	2,38	1,96	94,71		82,35			91,16
LBM 0265	IV	41	<i>Komodomys rintjanus</i>	3,01	2,03	2,37	2,23	2,49	2,11	94,09	67,44	84,74	109,85	103,94	94,62
LBM 0267	IV	41	<i>Komodomys rintjanus</i>	2,89	1,95	2,26	2,25			99,56	67,47		115,38		
LBM 0289	IV	42	<i>Komodomys rintjanus</i>	3,37	2,19	2,56	2,41	2,62	2,35	94,14	64,99	89,69	110,05	107,31	97,51
LBM 0316	IV	44	<i>Komodomys rintjanus</i>	3,36	2,18	2,76	2,59			93,84	64,88		118,81		
LBM 0365	IV	47	<i>Komodomys rintjanus</i>	3,1	2,19						70,65				
LBM 0368	IV	47	<i>Komodomys rintjanus</i>	2,78	1,89	2,2	2,17	2,06	2,06	98,64	67,99	100,00	114,81	108,99	94,93
LBM 0417	IV	49	<i>Komodomys rintjanus</i>	2,92	1,97	2,14	2,12			99,07	67,47		107,61		
LBM 0422	IV	49	<i>Komodomys rintjanus</i>			2,21	2,21			100,00					
LBM 0434	IV	49	<i>Komodomys rintjanus</i>	3,15	2,07						65,71				
LBM 0452	IV	51	<i>Komodomys rintjanus</i>	3,5	2,28						65,14				
LBM 0457	IV	51	<i>Komodomys rintjanus</i>	2,81	2,12	2,21	2,21	2,42	2,06	100,00	75,44	85,12	104,25	97,17	93,21
LBM 0476	IV	54	<i>Komodomys rintjanus</i>	3,31	2,32						70,09				
LBM 0477	IV	54	<i>Komodomys rintjanus</i>			2,35	2,59		110,21						
LBM 0480	IV	54	<i>Komodomys rintjanus</i>	3,14	2,09						66,56				
LBM 0481	IV	54	<i>Komodomys rintjanus</i>	3,26	2,23	2,54	2,5		98,43	68,40		112,11			
LBM 0487	IV	54	<i>Komodomys rintjanus</i>					2,27	2,31			101,76			
LBM 0489	IV	55	<i>Komodomys rintjanus</i>	3,37	2,46						73,00				
LBM 0499	IV	56	<i>Komodomys rintjanus</i>	3,63	2,32	2,4	2,53			105,42	63,91		109,05		
LBM 0505	IV	57	<i>Komodomys rintjanus</i>	3,2	1,93	2,6	2,38	2,44	2,38	91,54	60,31	97,54	123,32	123,32	100,00
LBM 0506	IV	57	<i>Komodomys rintjanus</i>	3,49	2,36	2,6	2,68			103,08	67,62		113,56		
LBM 0510	IV	59	<i>Komodomys rintjanus</i>	3,57	2,19						61,34				
LBM 0831	IV	82	<i>Komodomys rintjanus</i>	3,52	2,31	2,56	2,49	2,75	2,34	97,27	65,63	85,09	107,79	101,30	93,98
LBM 0861	IV	39	<i>Komodomys rintjanus</i>	3,03	2,11	2,3	2,28	2,41	2,09	99,13	69,64	86,72	108,06	99,05	91,67
LBM 1034	IV	15	<i>Komodomys rintjanus</i>	3,2	2,02	2,52	2,25	2,63	1,99	89,29	63,13	75,67	111,39	98,51	88,44
LBM 1053	IV	14	<i>Komodomys rintjanus</i>	3,14	2,15	2,36	2,34	2,32	2,13	99,15	68,47	91,81	108,84	99,07	91,03
LBM 1081	IV	14	<i>Komodomys rintjanus</i>	3,05	2,05	2,38	2,27	2,43	2,17	95,38	67,21	89,30	110,73	105,85	95,59
LBM 1090	IV	13	<i>Komodomys rintjanus</i>	3,3	2,13	2,59	2,39	2,61	2,23	92,28	64,55	85,44	112,21	104,69	93,31
LBM 1091	IV	13	<i>Komodomys rintjanus</i>	3,16	2,04	2,4	2,38	2,16	2,2	99,17	64,56	101,85	116,67	107,84	92,44
LBM 1092	IV	13	<i>Komodomys rintjanus</i>	3,32	2,03	2,5	2,32	2,67	2,14	92,80	61,14	80,15	114,29	105,42	92,24
LBM 1093	IV	13	<i>Komodomys rintjanus</i>	3,03	2,03	2,19	2,25	2,31	2,16	102,74	67,00	93,51	110,84	106,40	96,00
LBM 1094	IV	13	<i>Komodomys rintjanus</i>	3,05	2,09	2,48	2,36	2,65	2,27	95,16	68,52	85,66	112,92	108,61	96,19
LBM 1096	IV	13	<i>Komodomys rintjanus</i>	3,2	2,14	2,46	2,38	2,75	2,24	96,75	66,88	81,45	111,21	104,67	94,12
LBM 1097	IV	13	<i>Komodomys rintjanus</i>	3,11	2,07	2,63	2,33	2,48	2,18	88,59	66,56	87,90	112,56	105,31	93,56
LBM 1099	IV	13	<i>Komodomys rintjanus</i>	3,18	2,18						68,55				
LBM 1103	IV	13	<i>Komodomys rintjanus</i>	3,24	2,15	2,4	2,45	2,09	2,11	102,08	66,36	100,96	113,95	98,14	86,12
LBM 1105	IV	13	<i>Komodomys rintjanus</i>	3,02	2,07	2,24	2,27	2,35	2,15	101,34	68,54	91,49	109,66	103,86	94,71
LBM 1106	IV	13	<i>Komodomys rintjanus</i>	3,54	2,2	2,36	2,42	2,52	2,23	102,54	62,15	88,49	110,00	101,36	92,15
LBM 1107	IV	13	<i>Komodomys rintjanus</i>	3,44	2,37	2,79	2,56	2,48	2,32	91,76	68,90	93,55	108,02	97,89	90,63
LBM 1108	IV	13	<i>Komodomys rintjanus</i>	3,31	2,17	2,38	2,38	2,57	2,11	100,00	65,56	82,10	109,68	97,24	88,66
LBM 1109	IV	13	<i>Komodomys rintjanus</i>	3,21	2,32	2,46	2,42	2,73	2,27	98,37	72,27	83,15	104,31	97,84	93,80
LBM 1110	IV	13	<i>Komodomys rintjanus</i>	3,14	1,96	2,31	2,26	2,28	1,96	97,84	62,42	85,96	115,31	100,00	86,73
LBM 1111	IV	13	<i>Komodomys rintjanus</i>	3,22	2,09	2,52	2,37	2	2,19	94,05	64,91	109,50	113,40	104,78	92,41
LBM 1112	IV	13	<i>Komodomys rintjanus</i>	3,13	2,26	2,25	2,38	2,7	2,12	105,78	72,20	78,52	105,31	93,81	89,08
LBM 1142	IV	13	<i>Komodomys rintjanus</i>	3,18	2,17	2,33	2,32	2,62	2,09	99,57	68,24	79,77	106,91	96,31	90,09
LBM 1143	IV	13	<i>Komodomys rintjanus</i>	3,46	2,26	2,88	2,52			87,50	65,32		111,50		
LBM 1144	IV	13	<i>Komodomys rintjanus</i>	3,28	2,21	2,62	2,37	2,32	2,22	90,46	67,38	95,69	107,24	100,45	93,67
LBM 1168	IV	13	<i>Komodomys rintjanus</i>	3,27	2,25	2,36	2,56	2,49	2,22	108,47	68,81	89,16	113,78	98,67	86,72
LBM 1169	IV	13	<i>Komodomys rintjanus</i>	3,3	2,4	2,31	2,48	2,69	2,23	107,36	72,73	82,90	103,33	92,92	89,92
LBM 1174	IV	13	<i>Komodomys rintjanus</i>	3,03	2,07	2,3	2,36	2,52	2,13	102,61	68,32	84,52	114,01	102,90	90,25
LBM 1175	IV	13	<i>Komodomys rintjanus</i>	2,93	2,02	2,28	2,27	2,38	2,07	99,56	68,94	86,97	112,38	102,48	91,19
LBM 1179	IV	13	<i>Komodomys rintjanus</i>	3,28	2,1	2,33	2,29	2,35	2,18	98,28	64,02	92,77	109,05	103,81	95,20
LBM 1189	IV	12	<i>Komodomys rintjanus</i>	2,96	2,07	2,28	2,3	2,55	2,05	100,88	69,93	80,39	111,11	99,03	89,13
LBM 1191	IV	12	<i>Komodomys rintjanus</i>	3,53	2,36	2,49	2,55	2,57	2,31	102,41	66,86	89,88	108,05	97,88	90,59
LBM 1193	IV	12	<i>Komodomys rintjanus</i>	3,29	2,19	2,52	2,36			93,65	66,57		107,76		
LBM 1194	IV	12	<i>Komodomys rintjanus</i>	3,45	2,16						62,61				
LBM 1199	IV	12	<i>Komodomys rintjanus</i>	2,99	1,91	2,35	2,19	2,31	2	93,19	63,88	86,58	114,66	104,71	91,32
LBM 1208	IV	12	<i>Komodomys rintjanus</i>	2,95	2,084	2,032	2,313	1,937	2,269	113,83	70,64	117,14	110,99	108,88	98,10
LBM 1209	IV	12	<i>Komodomys rintjanus</i>	3,54	2,3	2,56	2,46	2,92	2,36	96,09	64,97	80,82	106,96	102,61	95,93

nr	sector	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	Ratio M <sub>1</sub>	Ratio M <sub>2</sub>	Ratio M <sub>3</sub>	WM <sub>2</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>2</sub>
LBM 1218	IV	12	<i>Komodomys rintjanus</i>	3,08	2,06	2,39	2,27	2,39	2,19	94,98	66,88	91,63	110,19	106,31	96,48
LBM 1219	IV	12	<i>Komodomys rintjanus</i>	3,27	2,1						64,22				
LBM 1220	IV	12	<i>Komodomys rintjanus</i>	3,12	1,92	2,51	2,37			94,42	61,54		123,44		
LBM 1237	IV	12	<i>Komodomys rintjanus</i>	3,09	2,08	2,17	2,28	2,49	2,3	105,07	67,31	92,37	109,62	110,58	100,88
LBM 1240	IV	12	<i>Komodomys rintjanus</i>	3,06	2,19	2,33	2,38	2,56	2,23	102,15	71,57	87,11	108,68	101,83	93,70
LBM 1241	IV	12	<i>Komodomys rintjanus</i>			2,34	2,42	2,57	2,26	103,42		87,94			93,39
LBM 1242	IV	12	<i>Komodomys rintjanus</i>			2,28	2,37	2,53	2,1	103,95		83,00			88,61
LBM 1243	IV	12	<i>Komodomys rintjanus</i>			2,46	2,53			102,85					
LBM 1248	IV	12	<i>Komodomys rintjanus</i>	3,17	2,19	2,42	2,38	2,4	2,18	98,35	69,09	90,83	108,68	99,54	91,60
LBM 1250	IV	12	<i>Komodomys rintjanus</i>	3,5	2,2						62,86				
LBM 1257	IV	11	<i>Komodomys rintjanus</i>	3,2	2,26	2,38	2,43	2,6	2,35	102,10	70,63	90,38	107,52	103,98	96,71
LBM 1258	IV	11	<i>Komodomys rintjanus</i>	3,23	2,28	2,54	2,42	2,81	2,27	95,28	70,59	80,78	106,14	99,56	93,80
LBM 1259	IV	11	<i>Komodomys rintjanus</i>	3,47	2,15	2,37	2,38	2,43	2,19	100,42	61,96	90,12	110,70	101,86	92,02
LBM 1260	IV	11	<i>Komodomys rintjanus</i>	3,35	2,07	2,39	2,36	2,67	2,17	98,74	61,79	81,27	114,01	104,83	91,95
LBM 1263	IV	11	<i>Komodomys rintjanus</i>	3,25	2,15			2,63	2,09		66,15	79,47		97,21	
LBM 1264	IV	11	<i>Komodomys rintjanus</i>	3,49	1,98	2,41	2,33	2,39	2,1	96,68	56,73	87,87	117,68	106,06	90,13
LBM 1276	IV	11	<i>Komodomys rintjanus</i>	3,12	2,27	2,39	2,48	2,57	2,24	103,77	72,76	87,16	109,25	98,68	90,32
LBM 1279	IV	11	<i>Komodomys rintjanus</i>	3,35	2,08	2,41	2,31	2,5	2,08	95,85	62,09	83,20	111,06	100,00	90,04
LBM 1280	IV	11	<i>Komodomys rintjanus</i>			2,34	2,4	2,67	2,17	102,56		81,27			90,42
LBM 1292	IV	10	<i>Komodomys rintjanus</i>	3,51	2,25						64,10				
LBM 1294	IV	10	<i>Komodomys rintjanus</i>	3,38	2,25	2,49	2,43	2,72	2,45	97,59	66,57	90,07	108,00	108,89	100,82
LBM 1295	IV	10	<i>Komodomys rintjanus</i>	3,22	2,12	2,38	2,36	2,3	2,11	99,16	65,84	91,74	111,32	99,53	89,41
LBM 1302	IV	10	<i>Komodomys rintjanus</i>	2,961	2,131	2,269	2,314			101,98	71,97		108,59		
LBM 1307	IV	9	<i>Komodomys rintjanus</i>	3,51	2,26	2,61	2,54			97,32	64,39		112,39		
LBM 1311	IV	9	<i>Komodomys rintjanus</i>	3,04	2,08	2,45	2,33	2,64	2,21	95,10	68,42	83,71	112,02	106,25	94,85
LBM 1312	IV	9	<i>Komodomys rintjanus</i>	3,44	2,37	2,63	2,61	2,94	2,37	99,24	68,90	80,61	110,13	100,00	90,80
LBM 1325	IV	8	<i>Komodomys rintjanus</i>	3,37	2,3	2,54	2,52	2,57	2,29	99,21	68,25	89,11	109,57	99,57	90,87
LBM 1326	IV	8	<i>Komodomys rintjanus</i>	3,3	2,15						65,15				
LBM 1330	IV	8	<i>Komodomys rintjanus</i>	3,22	2,18	2,45	2,32	2,35	2,06	94,69	67,70	87,66	106,42	94,50	88,79
LBM 1332	IV	7	<i>Komodomys rintjanus</i>	3,22	2,08						64,60				
LBM 1335	IV	7	<i>Komodomys rintjanus</i>	3,31	2,33	2,62	2,53	2,87	2,43	96,56	70,39	84,67	108,58	104,29	96,05
LBM 1336	IV	7	<i>Komodomys rintjanus</i>	3,08	2,39	2,5	2,54	2,67	2,33	101,60	77,60	87,27	106,28	97,49	91,73
LBM 1344	IV	7	<i>Komodomys rintjanus</i>	3,16	2,25	2,51	2,49	2,69	2,22	99,20	71,20	82,53	110,67	98,67	89,16
LBM 1345	IV	7	<i>Komodomys rintjanus</i>	3,41	2,33	2,55	2,5	2,46	2,25	98,04	68,33	91,46	107,30	96,57	90,00
LBM 1346	IV	7	<i>Komodomys rintjanus</i>	3,55	2,34	2,63	2,52			95,82	65,92		107,69		
LBM 1347	IV	7	<i>Komodomys rintjanus</i>	3,34	2,27	2,43	2,45			100,82	67,96		107,93		
LBM 1379	IV	4	<i>Komodomys rintjanus</i>	3,34	2,26	2,41	2,46			102,07	67,66		108,85		
LBM 1388	IV	3	<i>Komodomys rintjanus</i>	3,48	2,31	2,48	2,66	2,59	2,48	107,26	66,38	95,75	115,15	107,36	93,23
LBM 1391	IV	3	<i>Komodomys rintjanus</i>	3,18	2,24	2,44	2,44	2,69	2,15	100,00	70,44	79,93	108,93	95,98	88,11
LBM 1392	IV	3	<i>Komodomys rintjanus</i>	2,99	2,08	2,26	2,26	2,33	2,17	100,00	69,57	93,13	108,65	104,33	96,02
LBM 1409	IV	3	<i>Komodomys rintjanus</i>	3,24	2,3						70,99				
LBM 1439	IV	2	<i>Komodomys rintjanus</i>	3,56	2,39	2,52	2,66	2,54	2,44	105,56	67,13	96,06	111,30	102,09	91,73
LBM 1446	IV	2	<i>Komodomys rintjanus</i>	3,29	2,3	2,61	2,43			93,10	69,91		105,65		
LBM 1503	VII	70	<i>Komodomys rintjanus</i>					2,643	2,536			95,95			
LBM 1506	VII	70	<i>Komodomys rintjanus</i>	3,329	2,176	2,459	2,556			103,94	65,36		117,46		
LBM 1548	VII	68	<i>Komodomys rintjanus</i>	3,016	2,038	2,252	2,408			106,93	67,57		118,16		
LBM 1552	VII	68	<i>Komodomys rintjanus</i>			2,523	2,545	2,332	2,418	100,87		103,69			95,01
LBM 1556	VII	68	<i>Komodomys rintjanus</i>	3,24	2,235	2,398	2,601	2,313	2,508	108,47	68,98	108,43	116,38	112,21	96,42
LBM 1557	VII	68	<i>Komodomys rintjanus</i>			2,528	2,535	2,547	2,389	100,28		93,80			94,24
LBM 1563	VII	63	<i>Komodomys rintjanus</i>	3,334	2,319						69,56				
LBM 1565	VII	62	<i>Komodomys rintjanus</i>	3,239	2,266						69,96				
LBM 1567	VII	62	<i>Komodomys rintjanus</i>	3,244	2,413	2,47	2,597	2,443	2,361	105,14	74,38	96,64	107,63	97,85	90,91
LBM 1609	VII	57	<i>Komodomys rintjanus</i>												
LBM 1628	VII	56	<i>Komodomys rintjanus</i>												
LBM 1646	VII	54	<i>Komodomys rintjanus</i>	2,988	2,101	2,444	2,386	2,486	2,222	97,63	70,31	89,38	113,56	105,76	93,13
LBM 1720	VII	52	<i>Komodomys rintjanus</i>			2,16	2,298			106,39					
LBM 1721	VII	52	<i>Komodomys rintjanus</i>					2,012	2,273			112,97			
LBM 1752	VII	48	<i>Komodomys rintjanus</i>	3,034	2,315	2,211	2,41	2,279	2,243	109,00	76,30	98,42	104,10	96,89	93,07
LBM 611	III	36	<i>Komodomys rintjanus</i>	3,18	2	2,43	2,25	2,59	2,22	92,59	62,89	85,71	112,50	111,00	98,67
LBM 637	III	37	<i>Komodomys rintjanus</i>	2,94	1,96	2,38	2,31			97,06	66,67		117,86		
LBM 712	III	41	<i>Komodomys rintjanus</i>	2,99	2,12						70,90				
LBM 755	III	43	<i>Komodomys rintjanus</i>	2,839	2,106	2,21	2,27	1,737	2,085	102,71	74,18	120,03	107,79	99,00	91,85
LBM 759	III	43	<i>Komodomys rintjanus</i>				2,199								

Table VII-6: measurements (mm) of lower molars of *Komodomys rintjanus*

nr	sector	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	Ratio M <sub>1</sub>	Ratio M <sub>2</sub>	Ratio M <sub>3</sub>	WM <sub>2</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>2</sub>
LBM 0012	IV	26	<i>Paulamys naso</i>			2,61	2,19	2,21	1,87	83,91		84,62			85,39
LBM 0013	IV	26	<i>Paulamys naso</i>	3,23	2,12	2,49	2,18	2,23	1,84	87,55	65,63	82,51	102,83	86,79	84,40
LBM 0047	IV	31	<i>Paulamys naso</i>	3,3	2,1	2,43	2,13	2,05	1,81	87,65	63,64	88,29	101,43	86,19	84,98
LBM 0127	IV	33	<i>Paulamys naso</i>	3,14	2,07	2,49	2,22			89,16	65,92		107,25		
LBM 0128	IV	33	<i>Paulamys naso</i>	3,28	2,02						61,59				
LBM 0192	IV	37	<i>Paulamys naso</i>	3,22	1,9						59,01				
LBM 0214	IV	38	<i>Paulamys naso</i>	2,99	1,98	2,25	2,19	2,27	2,11	97,33	66,22	92,95	110,61	106,57	96,35
LBM 0226	IV	38	<i>Paulamys naso</i>	3,1	2,03						65,48				
LBM 0229	IV	38	<i>Paulamys naso</i>			2,44	2,11			86,48					
LBM 0266	IV	41	<i>Paulamys naso</i>	3,07	1,93	2,5	2,12			84,80	62,87		109,84		
LBM 0290	IV	42	<i>Paulamys naso</i>	3,15	1,9	2,29	2,14	2,09	1,91	93,45	60,32	91,39	112,63	100,53	89,25
LBM 0321	IV	45	<i>Paulamys naso</i>	3,38	2,36	2,9	2,53			87,24	69,82		107,20		
LBM 0322	IV	45	<i>Paulamys naso</i>	3,51	2,27						64,67				
LBM 0323	IV	45	<i>Paulamys naso</i>	2,98	1,96	2,2	2,03	1,95	1,74	92,27	65,77	89,23	103,57	88,78	85,71
LBM 0415	IV	49	<i>Paulamys naso</i>	3,22	2,15	2,52	2,37			94,05	66,77		110,23		
LBM 0416	IV	49	<i>Paulamys naso</i>	2,98	1,99						66,78				
LBM 0497	IV	56	<i>Paulamys naso</i>	3,32	2,24	2,77	2,5			90,25	67,47		111,61		
LBM 0501	IV	56	<i>Paulamys naso</i>	3,6	2,24						62,22				
LBM 0834	IV	51	<i>Paulamys naso</i>	3,61	2,29	2,93	2,58			88,05	63,43		112,66		
LBM 0922	IV	24	<i>Paulamys naso</i>	3,03	2,11	2,26	2,14	2,08	1,78	94,69	69,64	85,58	101,42	84,36	83,18
LBM 0925	IV	24	<i>Paulamys naso</i>	3,25	2,21	2,67	2,32	2,39	2,04	86,89	68,00	85,36	104,98	92,31	87,93
LBM 0926	IV	24	<i>Paulamys naso</i>	3,24	2,13	2,42	2,29	2,32	2,08	94,63	65,74	89,66	107,51	97,65	90,83
LBM 0956	IV	23	<i>Paulamys naso</i>	3,19	2,08	2,41	2,15	2,3	1,88	89,21	65,20	81,74	103,37	90,38	87,44
LBM 0982	IV	21	<i>Paulamys naso</i>	3,12	1,95			2,31	1,9		62,50	82,25		97,44	
LBM 0983	IV	20	<i>Paulamys naso</i>	3,18	1,95	2,49	2,13	2,22	1,92	85,54	61,32	86,49	109,23	98,46	90,14
LBM 0990	IV	18	<i>Paulamys naso</i>	3,27	2,09	2,41	2,15	2,42	1,89	89,21	63,91	78,10	102,87	90,43	87,91
LBM 1020	IV	15	<i>Paulamys naso</i>	3,14	1,97	2,33	2,14			91,85	62,74		108,63		
LBM 1062	IV	14	<i>Paulamys naso</i>	3,02	1,94	2,55	2,21	2,27	1,99	86,67	64,24	87,67	113,92	102,58	90,05
LBM 1063	IV	14	<i>Paulamys naso</i>	3,06	1,99	2,47	2,32	2,72	1,93	93,93	65,03	70,96	116,58	96,98	83,19
LBM 1095	IV	13	<i>Paulamys naso</i>	3,13	1,85	2,38	2,04	2,16	1,81	85,71	59,11	83,80	110,27	97,84	88,73
LBM 1102	IV	13	<i>Paulamys naso</i>			2,43	2,18	1,96	1,81	89,71		92,35			83,03
LBM 1104	IV	13	<i>Paulamys naso</i>	3,03	2,04	2,37	2,27	2,47	2,12	95,78	67,33	85,83	111,27	103,92	93,39
LBM 1114	IV	13	<i>Paulamys naso</i>	3,52	2,19	2,94	2,4			81,63	62,22		109,59		
LBM 1124	IV	13	<i>Paulamys naso</i>	3,02	1,98	2,59	2,22			85,71	65,56		112,12		
LBM 1126	IV	13	<i>Paulamys naso</i>	2,97	2,02						68,01				
LBM 1148	IV	13	<i>Paulamys naso</i>	3,02	1,94	2,51	2,09	2,13	1,88	83,27	64,24	88,26	107,73	96,91	89,95
LBM 1149	IV	13	<i>Paulamys naso</i>	3,01	1,94						64,45				
LBM 1176	IV	13	<i>Paulamys naso</i>	2,95	1,89	2,33	2,07	1,95	1,83	88,84	64,07	93,85	109,52	96,83	88,41
LBM 1178	IV	13	<i>Paulamys naso</i>	3,08	2	2,36	2,07	2,06	1,81	87,71	64,94	87,86	103,50	90,50	87,44
LBM 1190	IV	12	<i>Paulamys naso</i>	3,01	1,87	2,31	2,14	2,03	1,92	92,64	62,13	94,58	114,44	102,67	89,72
LBM 1192	IV	12	<i>Paulamys naso</i>	3,14	2,05	2,55	2,21			86,67	65,29		107,80		
LBM 1212	IV	12	<i>Paulamys naso</i>	3,23	2,12	2,58	2,43			94,19	65,63		114,62		
LBM 1215	IV	12	<i>Paulamys naso</i>	3,12	2,04						65,38				
LBM 1238	IV	12	<i>Paulamys naso</i>	3,16	2,14	2,52	2,1	2,14	1,88	83,33	67,72	87,85	98,13	87,85	89,52
LBM 1275	IV	11	<i>Paulamys naso</i>	2,95	1,87	2,22	2,07	2,04	1,84	93,24	63,39	90,20	110,70	98,40	88,89
LBM 1278	IV	11	<i>Paulamys naso</i>	3,21	2,2	2,6	2,37	2,49	2,08	91,15	68,54	83,53	107,73	94,55	87,76
LBM 1321	IV	8	<i>Paulamys naso</i>	2,97	1,87	2,31	1,94	2,37	1,71	83,98	62,96	72,15	103,74	91,44	88,14
LBM 1354	IV	6	<i>Paulamys naso</i>	3,07	1,99	2,47	2,24			90,69	64,82		112,56		
LBM 1359	IV	5	<i>Paulamys naso</i>	2,99	1,87	2,19	1,9			86,76	62,54		101,60		
LBM 1372	IV	4	<i>Paulamys naso</i>	3,13	1,9	2,4	2,07			86,25	60,70		108,95		
LBM 1373	IV	4	<i>Paulamys naso</i>	3,17	1,93						60,88				
LBM 1571	VII	60	<i>Paulamys naso</i>	2,848	1,98	2,327	2,081			89,43	69,52		105,10		
LBM 525	III	10	<i>Paulamys naso</i>	3,14	1,99	2,41	2,16	2,49	1,93	89,63	63,38	77,51	108,54	96,98	89,35
LBM 543	III	29	<i>Paulamys naso</i>	3,31	2,03	2,53	2,31	2,37	2	91,30	61,33	84,39	113,79	98,52	86,58
LBM 544	III	29	<i>Paulamys naso</i>	3,05	1,87	2,4	2,19	2,3	1,82	91,25	61,31	79,13	117,11	97,33	83,11
LBM 545	III	29	<i>Paulamys naso</i>	3,24	2,03	2,58	2,25	2,17	1,92	87,21	62,65	88,48	110,84	94,58	85,33
LBM 579	III	33	<i>Paulamys naso</i>	3,22	2,18						67,70				
LBM 584	III	35	<i>Paulamys naso</i>	3,14	2,03	2,4	2,18	2,15	1,87	90,83	64,65	86,98	107,39	92,12	85,78
LBM 612	III	36	<i>Paulamys naso</i>	3,18	2,03	2,62	2,2			83,97	63,84		108,37		
LBM 651	III	37	<i>Paulamys naso</i>			2,55	2,2	2,34	1,87	86,27		79,91			85,00
LBM 663	III	38	<i>Paulamys naso</i>	3,14	2,1	2,37	2,21	2,41	1,91	93,25	66,88	79,25	105,24	90,95	86,43
LBM 667	III	38	<i>Paulamys naso</i>	3,27	1,96	2,66	2,26			84,96	59,94		115,31		
LBM 685	III	40	<i>Paulamys naso</i>	3,06	1,92	2,6	2,3	2,12	1,9	88,46	62,75	89,62	119,79	98,96	82,61
LBM 692	III	40	<i>Paulamys naso</i>	3,26	1,99	2,6	2,2			84,62	61,04		110,55		
LBM 710	III	41	<i>Paulamys naso</i>	2,87	1,95	2,33	2,16	2,39	1,98	92,70	67,94	82,85	110,77	101,54	91,67
LBM 735	III	42	<i>Paulamys naso</i>	3,14	1,99						63,38				
LBM 736	III	42	<i>Paulamys naso</i>	2,77	1,84	2,14	1,96	1,84	1,64	91,59	66,43	89,13	106,52	89,13	83,67

Table VII-7: measurements (mm) of lower molars of *Paulamys naso*

nr	sector	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	Ratio M <sub>1</sub>	Ratio M <sub>2</sub>	Ratio M <sub>3</sub>	WM <sub>2</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>1</sub>	WM <sub>3</sub> /WM <sub>2</sub>
LBM 1117	IV	13	<i>Rattus</i> sp.	2,86	1,57	2,17	1,76	1,88	1,42	81,11	54,90	75,53	112,10	90,45	80,68
LBM 1198	IV	12	<i>Rattus</i> sp.	2,89	1,84	2,32	2,07	2,19	1,89	89,22	63,67	86,30	112,50	102,72	91,30
LBM 1320	IV	8	<i>Rattus</i> sp.	3,2	1,89	2,37	2,05	2,4	1,93	86,50	59,06	80,42	108,47	102,12	94,15
LBM 1324	IV	8	<i>Rattus</i> sp.	3,09	1,83	2,32	1,97	2,24	1,81	84,91	59,22	80,80	107,65	98,91	91,88
LBM 1334	IV	7	<i>Rattus</i> sp.	3,01	2,05	2,44	2,31	2,43	2,21	94,67	68,11	90,95	112,68	107,80	95,67
LBM 1358	IV	5	<i>Rattus</i> sp.	3,23	1,86						57,59				
LBM 1382	IV	4	<i>Rattus</i> sp.	2,84	1,81	2,12	1,88	2	1,62	88,68	63,73	81,00	103,87	89,50	86,17
LBM 1389	IV	3	<i>Rattus</i> sp.	2,88	1,86	2,07	1,84	1,97	1,7	88,89	64,58	86,29	98,92	91,40	92,39
LBM 1390	IV	3	<i>Rattus</i> sp.	3,02	1,94	2,28	2,11	2,37	1,98	92,54	64,24	83,54	108,76	102,06	93,84
LBM 1393	IV	3	<i>Rattus</i> sp.			2,34	2,09	2,16	1,78	89,32		82,41			85,17
LBM 1394	IV	3	<i>Rattus</i> sp.	2,77	1,79	1,96	1,85			94,39	64,62		103,35		
LBM 1395	IV	3	<i>Rattus</i> sp.			2,27	1,89			83,26					
LBM 1398	IV	3	<i>Rattus</i> sp.	2,9	1,86	2,1	2	1,94	1,76	95,24	64,14	90,72	107,53	94,62	88,00
LBM 1399	IV	3	<i>Rattus</i> sp.	3,08	1,88	2,23	2	2,06	1,87	89,69	61,04	90,78	106,38	99,47	93,50
LBM 1400	IV	3	<i>Rattus</i> sp.	2,81	1,82	2,16	1,96	2,08	1,81	90,74	64,77	87,02	107,69	99,45	92,35
LBM 1401	IV	3	<i>Rattus</i> sp.	2,87	1,83			2,02	1,83		63,76	90,59		100,00	
LBM 1418	IV	3	<i>Rattus</i> sp.	2,8	1,78	1,96	1,86			94,90	63,57		104,49		
LBM 1437	IV	2	<i>Rattus</i> sp.	3	1,93	2,23	1,99	2,2	1,79	89,24	64,33	81,36	103,11	92,75	89,95
LBM 1438	IV	2	<i>Rattus</i> sp.	2,88	1,88						65,28				
LBM 1452	IV	1	<i>Rattus</i> sp.	2,96	1,8	2,24	1,97			87,95	60,81		109,44		
LBM 1455	IV	1	<i>Rattus</i> sp.	3,06	2,17						70,92				
LBM 1456	IV	1	<i>Rattus</i> sp.	3,09	2,11	2,55	2,15	2,52	1,96	84,31	68,28	77,78	101,90	92,89	91,16

Table VII-8: measurements (mm) of lower molars of *Rattus* sp.

ID	Sector	Spit	Species	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
LBM 1041	IV	15	<i>Komodomys rintjanus</i>	4,18	2,52	2,51	2,37	1,92	2,05
LBM 1047	IV	14	<i>Komodomys rintjanus</i>	3,86	2,51			2,15	2,11
LBM 1048	IV	14	<i>Komodomys rintjanus</i>	4,06	2,52				
LBM 1085	IV	14	<i>Komodomys rintjanus</i>	4,22	2,82	2,43	2,69		
LBM 1088	IV	14	<i>Komodomys rintjanus</i>	4,19	2,77	2,48	2,62		
LBM 1089	IV	14	<i>Komodomys rintjanus</i>	4,27	2,65	2,61	2,62	2,02	2,07
LBM 1130	IV	13	<i>Komodomys rintjanus</i>	4,11	2,59	2,59	2,5	2,11	1,95
LBM 1150	IV	13	<i>Komodomys rintjanus</i>	3,83	2,52	2,59	2,6	2,05	2,17
LBM 1151	IV	13	<i>Komodomys rintjanus</i>			2,44	2,5	2,05	1,93
LBM 1152	IV	13	<i>Komodomys rintjanus</i>					2,14	1,95
LBM 1153	IV	13	<i>Komodomys rintjanus</i>	4,01	2,61	2,66	2,46	2,1	1,94
LBM 1156	IV	13	<i>Komodomys rintjanus</i>	3,74	2,52				
LBM 1157	IV	13	<i>Komodomys rintjanus</i>	3,79	2,52	2,16	2,36	2,21	1,94
LBM 1230	IV	12	<i>Komodomys rintjanus</i>	4,29	2,76				
LBM 1231	IV	12	<i>Komodomys rintjanus</i>	3,99	2,68	2,58	2,52	2,23	2,07
LBM 1233	IV	12	<i>Komodomys rintjanus</i>	4,18	2,63	2,63	2,51	2,32	2,05
LBM 1267	IV	11	<i>Komodomys rintjanus</i>	3,81	2,57	2,23	2,48	2,24	2,01
LBM 1268	IV	11	<i>Komodomys rintjanus</i>	4,21	2,63	2,87	2,59		
LBM 1269	IV	11	<i>Komodomys rintjanus</i>			2,5	2,6		
LBM 1271	IV	11	<i>Komodomys rintjanus</i>			2,46	2,82		
LBM 1289	IV	10	<i>Komodomys rintjanus</i>	3,96	2,64	2,38	2,68		
LBM 1306	IV	9	<i>Komodomys rintjanus</i>	4,23	2,65	2,66	2,5	2,23	2,04
LBM 1368	IV	5	<i>Komodomys rintjanus</i>	4,06	2,6	2,44	2,48	2	1,99
LBM 1385	IV	4	<i>Komodomys rintjanus</i>	4,19	2,77	2,59	2,64	2,41	2,26
LBM 1386	IV	4	<i>Komodomys rintjanus</i>	4,17	2,69	2,59	2,62	2,47	2,23
LBM 1387	IV	4	<i>Komodomys rintjanus</i>	4,38	2,78	2,7	2,6		
LBM 1406	IV	3	<i>Komodomys rintjanus</i>	3,46	2,17	2,24	2	1,68	1,55
LBM 1407	IV	3	<i>Komodomys rintjanus</i>	4,18	2,53	2,62	2,5		
LBM 1411	IV	3	<i>Komodomys rintjanus</i>	4,11	2,75				
LBM 1427	IV	3	<i>Komodomys rintjanus</i>						
LBM 1429	IV	3	<i>Komodomys rintjanus</i>					1,83	1,65
LBM 1431	IV	3	<i>Komodomys rintjanus</i>	4,31	2,82	2,67	2,72		
LBM 357	IV	46	<i>Komodomys rintjanus</i>	3,91	2,53	2,39	2,44		
LBM 402	IV	47	<i>Komodomys rintjanus</i>	4,23	2,68				
LBM 403	IV	47	<i>Komodomys rintjanus</i>			2,65	2,68		
LBM 433	IV	49	<i>Komodomys rintjanus</i>	4,31	2,76	2,59	2,71		
LBM 435	IV	49	<i>Komodomys rintjanus</i>	3,67	2,55	2,43	2,56		
LBM 454	IV	51	<i>Komodomys rintjanus</i>	4,18	2,77				
LBM 467	IV	52	<i>Komodomys rintjanus</i>	4,19	2,87				
LBM 468	IV	52	<i>Komodomys rintjanus</i>	3,84	2,74				
LBM 469	IV	52	<i>Komodomys rintjanus</i>			3,07	2,79		
LBM 474	IV	53	<i>Komodomys rintjanus</i>	4,34	2,79	2,62	2,7		
LBM 482	IV	54	<i>Komodomys rintjanus</i>	4,35	2,68	2,63	2,54	2,36	2,16
LBM 488	IV	55	<i>Komodomys rintjanus</i>	4,04	2,8				
LBM 504	IV	57	<i>Komodomys rintjanus</i>	4,24	2,93				
LBM 509	IV	59	<i>Komodomys rintjanus</i>	4,69	2,81				
LBM 513	IV	59	<i>Komodomys rintjanus</i>	4,43	2,81	2,68	2,74		
LBM 1128	IV	13	<i>Paulamys naso</i>	4,15	2,84	2,57	2,75		
LBM 1154	IV	13	<i>Paulamys naso</i>	4,21	2,77				
LBM 1158	IV	13	<i>Paulamys naso</i>	3,72	2,3	2,52	2,29	1,8	1,66
LBM 1159	IV	13	<i>Paulamys naso</i>	3,77	2,36	2,57	2,31	1,74	1,75
LBM 1228	IV	12	<i>Paulamys naso</i>			2,66	2,5	2,12	2,04
LBM 1232	IV	12	<i>Paulamys naso</i>	3,85	2,56	2,64	2,51	2,02	1,99
LBM 401	IV	47	<i>Paulamys naso</i>	4,47	2,66	2,88	2,62		
LBM 436	IV	49	<i>Paulamys naso</i>	3,32	2,17	2,16	2,06		
LBM 470	IV	52	<i>Paulamys naso</i>	4,26	2,82				
LBM 484	IV	54	<i>Paulamys naso</i>	4,38	2,81	2,76	2,67		
LBM 485	IV	54	<i>Paulamys naso</i>	4,47	2,99	3,04	2,88		
LBM 486	IV	54	<i>Paulamys naso</i>	4,51	3,02				
LBM 494	IV	55	<i>Paulamys naso</i>	4,01	2,7	2,66	2,6	2,37	2,18
LBM 495	IV	55	<i>Paulamys naso</i>	4,2	2,57	2,89	2,65	2,18	2,11
LBM 503	IV	56	<i>Paulamys naso</i>	4,21	2,7				
LBM 90	IV	32	<i>Paulamys naso</i>	3,91	2,37				
LBM 1423	IV	3	<i>Rattus sp.</i>	3,28	2,12				
LBM 1426	IV	3	<i>Rattus sp.</i>						
LBM 1459	IV	1	<i>Rattus sp.</i>	3,47	2,12				
LBM 475	IV	53	<i>Rattus sp.</i>	3,74	2,37				

Table VII-9: measurements (mm) of identified upper molars of middle size murids



# VIII. Giant rats from Liang Bua cave...when the Island Rule cannot be broken

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## *Introduction*

Giant rodents, together with dwarf elephants, have always been considered one of the main and first products of insularism. In 1964, when Foster wrote the paper considered one of the manifests of the Island Rule, giant rodents were already alimenting the scientific debate, so much that the first sentence says:

*“Workers in Europe have been debating whether isolation of rodent populations, either on islands or as alpine isolates, results in a tendency toward gigantism, or whether the large size commonly found in these insular populations is the consequence of their being relicts of a once more widely spread large form”.*

Rodentia is the largest order of mammals in terms of number of species (over 40% of mammalian species, more than 2,200 species), and within the order we find considerable differences in size between species. In previous chapters, I dealt with small and middle size murids from Liang Bua. Those were of a common size among living rodents. But Rodentia encompasses very large rodents. The largest living rodent is the capybara (*Hydrochoerus hydrochaeris*) that can weigh up to 65 kg. Among murids, many giant rats are still existing, dwelling islands all over the world, and many of them are in Indonesia.

Giant rats are known from many fossil sites, and among them the largest ever known is *Josephoartigasia monesi* (Rinderknecht and Blanco, 2008), that belongs to the family Dinomyidae. Even if the actual size of this rodent is still debated (with a body mass ranging from 350kg to 1008 kg - Rinderknecht and Blanco, 2008; Millien, 2008), it remains the larger rodent ever described. Notably, this is not an insular form, but a rodent from South America, the continent that yielded the largest rodents. Among Muridae, the largest species come from Indonesia, like the Giant rat of Flores, *Papagomys armandvillei* (Jenkins, 1892) the Giant rats of Sumatra, *Sundamys* Musser, 1983, which still live in the Sunda Shelf, and the extinct *Coryphomys buehleri* Schaub, 1937 from Timor, of which remains have been recently extensively re-described (Aplin and Helgen, 2010).

The first remains of giant rats from Flores have been described by Hooijer (1957), in a paper entitled “Three new Giant Prehistoric rats from Flores Lesser Sunda Islands”. The paper describes fossil remains recovered by Dr. Verhoeven at Liang Toge. Subsequently, Musser (1981) in its monograph, “The Giant rat of Flores and its relatives of Borneo and Bali” extensively describes the morphological characters of giant rats recovered from fossil sites in Flores: *Hooijeromys nusatenggara* Musser, 1981†, *Papagomys armandvillei*, *Papagomys theodorverhoeveni* Musser, 1981† and *Spelaeomys florensis* Hooijer, 1957†. Suyanto and Watts (2002) reported the recovery of a living Giant rat *Papagomys theodorverhoeveni*, a species previously supposed to have been extinct. Later, Zijlstra et al. (2008), with a morphometrical analysis of lower mandibles of *Papagomys theodorverhoeveni* and *Papagomys armandvillei*, demonstrated that the specimen described by Suyanto and Watts is in fact referable to *P. armandvillei*. Thus *P. verhoeveni* has still to be considered extinct. Nevertheless, remains of this species have been found also in the uppermost spits of Liang Bua, which makes the possibility that it is still living plausible.

In this paper, fossil remains of giant rats from Liang Bua cave will be discussed: *Papagomys armandvillei*, *P. verhoeveni* and *Spelaeomys florensis*. *Hooijeromys nusatenggara* has not been found at Liang Bua.

## Material and Methods

544 mandibular and maxillary remains of giant rats were recovered. Among them, 352 are lower remains and 172 are upper ones; 20 are incisive fragments. The list of the number of specimen per species and dental portion is reported in Table VIII-1 and Table VIII-2.

Number of identified teeth	m1	m2	m3	M1	M2	M3
<i>Papagomys armandvillei</i>	87	82	54	47	37	21
<i>Papagomys theodorverhoeveni</i>	88	82	57	56	29	24
<i>Spelaeomys florensis</i>	13	10	7	5	2	
<i>Papagomys</i> sp. Indet.		2				1
<b>Total</b>	188	176	118	108	68	46

Table VIII-1: total number of identified teeth of large murids per species

LOWER	n	Lm1	Wm1	Lm2	Wm2	Lm3	Wm3
<i>Papagomys armandvillei</i>	159	6.10	4.18	4.57	4.46	4.78	4.10
<i>Papagomys theodorverhoeveni</i>	118	5.03	3.45	3.72	3.56	3.70	3.16
<i>Spelaeomys florensis</i>	17	5.72	4.12	4.37	4.17	4.08	3.59
<i>Papagomys</i> sp. Indet.	58			5.56	4.84		
UPPER	n	LM1	WM1	LM2	WM2	LM3	WM3
<i>Papagomys armandvillei</i>	75	7.69	5.04	5.16	4.67	4.59	3.89
<i>Papagomys theodorverhoeveni</i>	69	5.90	3.86	3.94	3.55	3.35	3.10
<i>Spelaeomys florensis</i>	9	6.27	4.25	4.12	4.08		
<i>Papagomys</i> sp. Indet.	19					5.28	4.51

Table VIII-2: total number of remains per species and mean value of measurements. W=width; L=length; minuscule=lower tooth; capitol= upper tooth



Measurements of length and width of all molars have been taken, according to the method used for small and middle size murids (Figure VI-1). Of every measurement, descriptive analysis has been performed, using the Analysis Toolpak of Microsoft Office Excel.

Mean measurements of teeth recovered at Liang Bua have been compared with those of sub-fossil teeth of *Papagomys armandvillei*, *P. theodorverhoeveni* and *Spelaeomys florensis* from Liang Toge and recent of *Papagomys armandvillei* (the only Giant rat still living on Flores). All these measurements are reported in Musser (1981).

On lower tooth rows, PCA has been performed using PAST Software (Hammer et al., 2001). Since complete series are necessary to perform multivariate analysis, only complete tooth rows have been analysed with multivariate analysis. PCA has not been performed on upper tooth rows because of the low number of complete specimens (none of *Spelaeomys florensis* and only 29 of *Papagomys*).

### ***Systematic Palaeontology***

**Class:** Mammalia Linnaeus, 1758

**Order:** Rodentia Bowdich, 1821

**Suborder:** Muridae Illiger, 1811

**Subfamily:** Murinae

**Genus:** *Papagomys* Sody, 1941

*Papagomys armandvillei* Jenkins, 1892

**Synonymy:**

*Mus armandvillei*, Jenkins 1892

*Mallomys armandvillei*, Thomas 1898; Tate 1936

**Holotype:** RMNH 18301, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis)

**Distribution:** Flores, Indonesia. Fossil material has been recovered from Liang Bua (Upper Pleistocene and Holocene) and Liang Toge (Holocene). First occurrence, Liang Bua cave Sector IV spit 60 (Late Pleistocene); last occurrence Sector IV spit 9 (ca.500 years). The species still occurs on Flores today.

**Morphological description:**

Upper tooth row: robust related to maxillary bone; the widest molar is M1, but M2 can be as large as M1; the third is the narrowest. All the cusps are high and slant distally, so that there is overlapping among teeth: M1 covers the mesial part of M2 and the latter covers the mesial part of M3 (characteristic of species without t7).

**I:** massif, curved, with mesial enamels with yellowish/orange pigmentation.

**M<sup>1</sup>:** one large mesial root, two small median ones, a small linguo-distal and a large distal one, for a total of five roots anchoring this tooth. Each tooth has three rows of cusps. All the medial cusps (t2, t5 and t8) are large and circular in occlusal view. The first row, formed by t1, t2 and t3, is almost transversal; only t1 is located a bit distally compared to the other cusps. t1 is circular in cross section and large; t3 is smaller and flattened. The second row is less transverse; the central and the labial cusps (t5 and t6) look like the corresponding ones in the first row, but t4 is not as cylindrical as t1, is more inclined and the shape in cross section is not circular, but elongated toward the first row. The third row, lacking t7, is formed only by a large, almond shaped t8, connected with a vestigial t9.

**M<sup>2</sup>:** it is anchored by four roots, two mesial and two distal ones. It is formed by t1 and two distal rows of cusps. t1 is cylindrical, large or drop shaped; except for a thin connection with t5, this cusp stands apart from the other row. The first row, formed by t4, t5 and t6, is transverse or a bit arched in worn teeth; t3 slants distally. The third row is made by a very large t8; t9 is very small, reduced to a small labial appendix of t8.



**Plate 9:** lower and upper molars of *Papagomys armandvillei*

**M<sup>3</sup>:** it is anchored by three roots, two mesial ones and a large distal one. t1 is large, cylindrical and well separated from the first toothrow. t3 is only a vestigial small mesial protuberance of the first row, which is mainly formed by t4, t5 and t6, arranged in a transverse row (that becomes arched with wear). All the cusps of the first row are about of the same size, with the bigger central

one (t5). The second row is transverse and formed by the confluence of t8 and t9. The molar has a squarish outline.

Lower tooth row: lower molars are wide and the occlusal pattern is simple; subsidiary cusplets are rarely present. The wider molar is the second.

**M<sub>1</sub>:** this tooth is anchored by four roots, a large mesial one, two small central (one lingual and one labial) and a large distal one. The outline of the tooth is rectangular. Cusps are arranged in three laminae. The first lamina is made up of two cusps, the antero-labial cusp (a-lab) and the antero-lingual cusp (a-ling). These cusps are widely confluent; in young individuals the lamina is V shaped, with the cusps merging along the midline; in worn teeth the area of confluence increases and the lamina becomes elliptical. Since a-ling is slightly bigger than a-lab, the lamina looks inclined. The second lamina is formed by two oblong cusps, the protoconid and the metaconid, which merge in the midline. The third lamina is formed by two oblong cusps, hypoconid (hd) and entoconid (ed), which fuse together in the midline. The second and third laminae are very similar and are arched. A massive and cylindrical posterior cingulum is present. Subsidiary cusplets (anterior labial cusplet – alc- and antero-central cusp – a-cen) are present only in few specimens (around 10%), and are poorly developed; a posterior labial cusplet is more frequent (almost 30%).

**M<sub>2</sub>:** this tooth is anchored by three roots, two small mesial and a large distal one. The occlusal outline is squarish, since length and width are about the same. Cusps are arranged in two laminae. The first lamina has a straight mesial margin; the labial and lingual cusps are oblong and merge in the midline, so that distal margin is arched. The protoconid is larger than the metaconid. In around 10% of specimens there is a small a-lab. The second row is made up of two cusps, hypoconid and entoconid, which are oblong and merge in the midline. This lamina is arched, assuming a boomerang shape. A large cylindrical pc is located at the distal margin of the tooth.

**M<sub>3</sub>:** this is the smallest and simplest among molars. It is anchored by three roots, two small mesial ones (labial and lingual) and a large distal one. The occlusal surface is made up by two chunky transverse laminae; the first is straight, the second is oval.

### **Measurements**

Measurements are given in the Appendix. The results of the descriptive statistical analysis are reported in Table VIII-3.

<i>Papagomys armandvillei</i>	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
<b>Mean</b>	6.10	4.18	4.57	4.46	4.78	4.10	7.69	5.04	5.16	4.67	4.63	3.94
<b>Standard Error</b>	0.04	0.03	0.04	0.03	0.07	0.04	0.09	0.04	0.10	0.04	0.06	0.05
<b>Median</b>	6.03	4.12	4.56	4.41	4.84	4.09	7.64	5.03	5.11	4.65	4.68	3.91
<b>Mode</b>	6.25	4.20	4.56	4.28	4.75	4.02	7.65	5.17	5.38	4.64		3.83
<b>Standard deviation</b>	0.35	0.27	0.35	0.28	0.53	0.28	0.60	0.29	0.57	0.25	0.28	0.23
<b>Sample Variance</b>	0.12	0.07	0.13	0.08	0.28	0.08	0.36	0.09	0.33	0.06	0.08	0.05
<b>Kurtosis</b>	-0.59	0.65	0.87	-0.34	-0.41	-0.84	-0.33	-0.05	4.34	4.65	-0.46	0.90
<b>Skweness</b>	0.35	0.70	0.66	0.47	-0.49	-0.02	0.58	0.01	1.54	1.52	-0.49	0.83
<b>Range</b>	1.46	1.39	1.76	1.20	2.01	1.01	2.40	1.40	3.09	1.33	1.01	1.00
<b>Minimum</b>	5.50	3.64	3.93	3.94	3.64	3.59	6.66	4.39	4.18	4.27	4.09	3.52
<b>Maximum</b>	6.96	5.03	5.68	5.14	5.65	4.60	9.06	5.79	7.27	5.60	5.10	4.52
<b>Sum</b>	530.98	359.05	375.06	365.42	258.11	221.15	353.81	236.92	185.70	172.77	97.18	82.77
<b>Count (n)</b>	87	86	82	82	54	54	46	47	36	37	21	21
<b>Confidence Interval (95,0%)</b>	0.07	0.06	0.08	0.06	0.14	0.08	0.18	0.09	0.19	0.08	0.13	0.11

Table VIII-3: descriptive analysis of *Papagomys armandvillei*

*Papagomys theodorverhoeveni* Musser, 1981 †

**Holotype:** RGM 195620, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis)

**Distribution:** Flores, Indonesia. Fossil and sub-fossil remains from Liang Toge and Liang Bua caves. First occurrence at Liang Bua cave, Upper Pleistocene, Sector IV spit 64 (Late Pleistocene). Last occurrence Liang Bua cave, sector IV, spit 1 (sub-recent).

**Morphological description:**

**Upper tooth row:** robust relative to the maxillary bone; the widest molar is M1, but M2 can be as large as M1; the third is the narrowest. All the cusps are high and slant distally, so that the molars overlap: M1 covers the mesial part of M2 and the latter covers the mesial part of M3 (typical of species without t7).

**I:** massif, curved, with mesial enamels with yellowish/orange pigmentation.

**M<sup>1</sup>:** five roots anchor this tooth; one large mesial root, two small medial, a small lingual distal and a large distal one. Each tooth has three rows of cusps. Central cusps (t2, t5 and t8) are large and circular in cross section. The first row, formed by t1, t2 and t3, is straight and transversal in correspondence of t2 and t3, and deviate abruptly with t1 that is linguo-distal to the other cusps. t1 is cylindrical, circular in cross section and large; t3 is smaller and oblong. The second row is arched and formed by triangular cusps in younger specimens and flattened in worn teeth. The third row, lacking t7, is formed only by a large, almond-shaped t8, connected with t9, which is oblong and well defined in young individuals.

**M<sup>2</sup>:** it is anchored by four roots, two mesial and two distal. The M2 is formed by t1 and two distal rows of cusps. t2 sometimes is absent or very small and sometimes cylindrical, well defined, but always far smaller than other cusps. t1 is cylindrical and stout; it is circular or drop shaped. Except for a thin connection with t5, this cusp stands apart from the other row. The first row,

formed by t4, t5 and t6, is transverse or a bit arched in worn teeth; t3 slants distally. The third row is made by a very large t8; t9 is very small, reduced to a small labial appendix of t8.

**M<sup>3</sup>**: it is anchored by three roots, two mesial ones and one large distal. t1 is large, cylindrical; t3 is small, usually connected to the first row. With wear, t1 and t3 merge widely with the first row in a single field. The first row is formed by t4, t5 and t6, arranged in an arched row (that with wear becomes arched). All the cusps of the first row are about of the same size, with the central one (t5) bigger. The second row is transverse and formed by the confluence of t8 and t9. The tooth has a general squarish outline.



**Plate 10: lower and upper teeth of *Papagomys theodorverhoeveni***

**Lower tooth row:** lower molars are wide and the occlusal pattern is simple (few subsidiary cusplets and reduction of cusps). The wider molar is the second.

**M<sub>1</sub>**: this tooth is anchored by four roots, one large mesial, two small central (one lingual and one labial) and a large distal one. Like in *P. armandvillei*, cusps are arranged in three laminae. In the first lamina (a-lab and a-ling) cusps are widely confluent, merging along the axis; in worn teeth the area of confluence increases and the lamina becomes elliptical. Since a-ling is slightly bigger than a-lab, the lamina is asymmetrical. Sometimes (around 20%) a small a-cen is present. The second and third laminae are formed by two oblong cusps (protoconid and metaconid in the second, hypoconid and entoconid in the third one), which merge in the midline. The second and third laminae are very similar and are arcuate. Usually, there is plc standing against hypoconid (around 90% of specimens) and in half of specimens there is also a small alc. A massive and cylindrical posterior cingulum is present.

**M<sub>2</sub>**: this tooth is anchored by three roots, two small mesial and a large distal one. The occlusal outline is squarish, since length and width are about the same. Cusps are arranged in two laminae. The first lamina has a straight mesial margin, often slanting because of the presence of a cylindrical a-lab (around 70%); protoconid and metaconid are oblong and merge in the midline,

so the distal margin of the lamina is arched. protoconid is larger than metaconid. The second row is made by two cusps, hd and ed, which are oblong and merge in the midline. This lamina is arcuate, assuming a boomerang shape. In few cases a plc is visible in young individuals, lying against hd. A large cylindrical posterior cingulum is located at the distal margin of the tooth.

**M<sub>3</sub>**: it is anchored by three roots, two small mesial ones (labial and lingual) and a large distal one. The occlusal surface is made up by two chunky transverse laminae; the first is straight or lobated; in some cases there is a small a-lab against protoconid. The second lamina is oval.

### Measurements

Measurements are given in the Appendix. The results of the descriptive statistical analysis are reported in Table VIII-4

<i>Papagomys theodorverhoeveni</i>	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
Mean	5.03	3.45	3.72	3.56	3.70	3.16	5.90	3.86	3.94	3.55	3.35	3.10
Standard Error	0.04	0.03	0.03	0.03	0.04	0.04	0.07	0.05	0.06	0.05	0.10	0.06
Median	5.03	3.41	3.75	3.56	3.78	3.10	5.97	3.79	3.93	3.55	3.38	3.09
Mode	5.09	3.36	3.67	3.87	3.87	2.92	6.02	3.60	3.93	3.74		3.20
Standard deviation	0.39	0.27	0.24	0.25	0.34	0.30	0.52	0.38	0.33	0.30	0.50	0.28
Sample Variance	0.15	0.07	0.06	0.06	0.12	0.09	0.27	0.14	0.11	0.09	0.25	0.08
Kurtosis	0.26	-0.50	0.67	-0.58	0.29	-0.57	0.58	1.44	-0.85	-0.03	-0.54	0.24
Skweness	0.11	-0.22	0.12	-0.14	-0.46	0.47	-0.96	0.82	0.15	0.36	-0.21	-0.03
Range	2.01	1.09	1.22	1.07	1.65	1.24	2.25	2.09	1.21	1.21	1.89	1.19
Minimum	4.14	2.83	3.17	3.00	2.79	2.55	4.41	3.10	3.35	3.05	2.37	2.54
Maximum	6.15	3.92	4.39	4.07	4.44	3.79	6.66	5.19	4.56	4.26	4.26	3.73
Sum	442.22	299.80	305.37	292.15	211.00	179.98	330.23	216.32	114.13	102.90	80.44	74.30
Count (n)	88	87	82	82	57	57	56	56	29	29	24	24
Confidence Interval (95,0%)	0.08	0.06	0.05	0.05	0.09	0.08	0.14	0.10	0.13	0.11	0.21	0.12

Table VIII-4: descriptive statistical analysis of *Papagomys theodorverhoeveni*

### Differences between *Papagomys armandvillei* and *Papagomys theodorverhoeveni*:

The striking difference between these species is the size: *P. armandvillei* is larger. However, the size variation is gradual, and morphological differences are needed to make the species discrimination stronger.

Musser (1981), on the basis of Liang Toge material, defined the morphological difference between *P. theodorverhoeveni* and *P. armandvillei*. Nevertheless, as it often happens in palaeontology, because of the limited number of specimens retrieved, some differences were not interspecific, but represented local variations in the sample considered. Zijlstra et al. (2008) made an accurate analysis on some mandibular characters that were considered diagnostic by Musser (1981). In particular, they focused on the presence/absence of cusps and subsidiary cusplets on molars, the frequencies in their presence/absence and the relationship between them and wear. Many of these characters resulted to be not diagnostic and to have a certain degree of variation: the presence of a-cen in m1 is not diagnostic at all (only 10% of difference in frequencies between these species); alc on m1 and a-lab on m2 are not determinant if considered alone, but there is

quite a difference in the frequencies (around 50%). The most diagnostic character resulted to be the presence of the plc on m1 (90% in *P. theodorverhoeveni*, 7% in *P. armandvillei*). In general, even if both these species are characterized by a very simple occlusal pattern, *P. theodorverhoeveni* has more subsidiary cusplets and cusps, consequently molars pattern is more elaborate.

Beyond these characters, in upper molars rows are thinner in *P. theodorverhoeveni* than in *P. armandvillei* and cusps have a tendency to look more rounded and circular in *P. armandvillei* and angular or triangular in *P. theodorverhoeveni*.

**Genus:** *Spelaeomys* Hooijer, 1957

*Spelaeomys florensis* Hooijer, 1957 †

**Holotype:** Specimen 1, at the Netherlands Centre for Biodiversity Naturalis (NCB Naturalis)

**Distribution:** Flores, Indonesia. Fossil remains have been recovered from Liang Toge (Holocene) and Liang Bua (Upper Pleistocene; Holocene).

**Morphological description:**

Upper tooth row: teeth pattern is very elaborated, with developed subsidiary cusps and cusplets and a complicated arrangement of main cusps. M1 is the larger tooth. In Liang Bua fossil material, no M3 has been recovered.

**M<sup>1</sup>:** it is anchored by four roots (a large mesial, a small centro-lingual and two small distal ones). Central cusps (t2, t5 and t8) are the biggest and are semicircular or triangular in occlusal view. Lingual cusps (t1, t4 and t7) are oval, labial ones (t3, t6 and t9) are drop-shaped or oblong. Between t1 and t2 and between t1 and t4 there can be two lingual subsidiary cusplets. A small one is present on the labial side between t6 and t9. Cusps are well separated among them; when the tooth is getting worn, distal cusps merge together before mesial ones. Posterior cingulum is



present, but it is small.



Plate 11: lower and upper molars of *Spelaeomys florensis*

**M<sup>2</sup>**: it is anchored by four roots, two mesial and two distal. The outline is squarish. t1 is triangular in occlusal view, pointing lingually. t2 is large and triangular. t3 is smaller and cylindrical. t5 is semicircular, labial and lingual cusps (t4, t6, t7 and t9) are oblong. The posterior cingulum is cylindrical and connected to t8 by the labio-distal corner.

Lower tooth row: m1 is the widest molar, m3 is the narrowest. Lower molars, like upper ones, have an elaborated pattern, with main cups enriched by subsidiary cusplets.

**M<sub>1</sub>**: it is anchored by three roots (large mesial one and two distal ones). Beyond the six main cusps - three lingual (a-ling, md and ed) and three labial (a-lab, pd and hd) - and posterior cingulum, there are many subsidiary cusplets. Main cusps are drop-shaped and meet along the midline of the tooth. The posterior cingulum is triangular in occlusal view. Six subsidiary cusplets are present: one large and circular a-cen; one very small cusplet flanks the mesial margin of a-lab; a cylindrical one flanks the labio-distal margin of a-lab; one large drop shaped alc; a very large oval plc, located mesially to the hypoconid; a cylindrical disto-labial cusplet, opposite to the posterior cingulum.

**M<sub>2</sub>**: its outline is squarish. The cusps pattern is the same of the distal part of m1: protoconid and hypoconid are triangular/semicircular in occlusal view; metaconid and entoconid are oblong and drop shaped. The posterior cingulum is cylindrical. Four subsidiary cusps are present along the labial margin, from the mesial side to the distal: cylindrical a-lab and a smaller cusplet (that merge early); an oval/drop shaped plc and a small cylindrical distal cusp opposite to the posterior cingulum.



**M<sub>3</sub>**: its outline is rectangular and it is anchored by two roots (mesial and distal). There are four main drop-shaped main cusps: metconid, protoconid, entoconid a hypoconid. Beside a-lab, which is semicircular, there are two tiny cylindrical mesial cusplets.

### Measurements

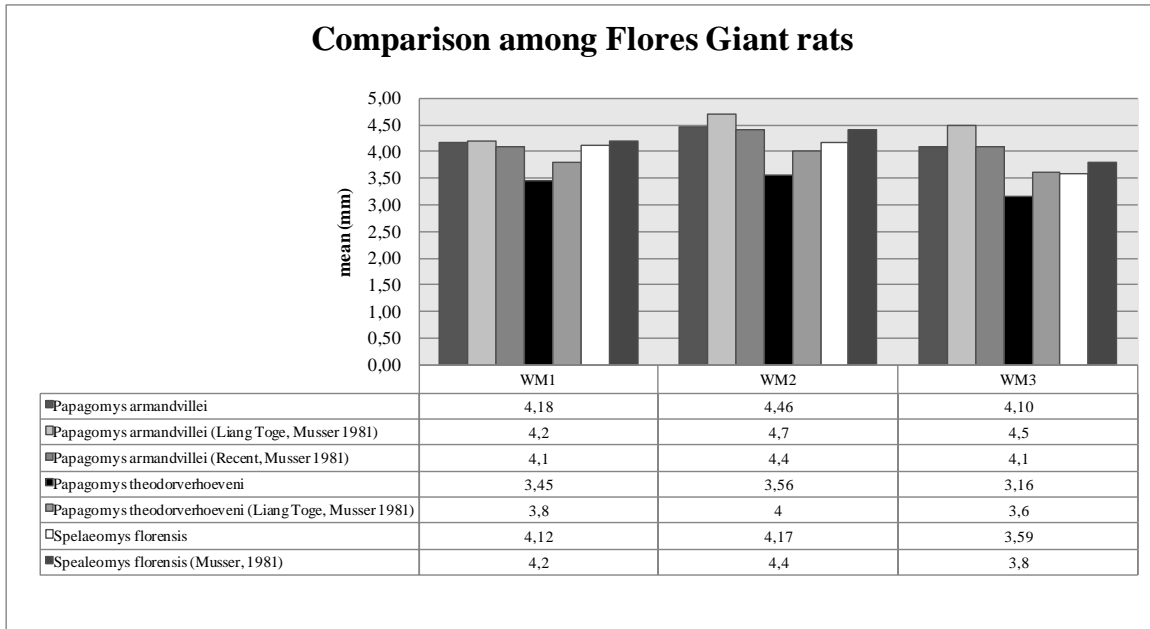
Measurements are given in the Appendix. The results of the descriptive statistical analysis are reported in Table VIII-5.

<i>Spelaeomys florensis</i>	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>
<b>Mean</b>	5.72	4.12	4.37	4.17	4.08	3.59	6.27	4.25	4.12	4.08
<b>Standard Error</b>	0.08	0.06	0.05	0.07	0.03	0.11	0.10	0.04	0.00	0.01
<b>Median</b>	5.64	4.13	4.38	4.19	4.08	3.63	6.30	4.24	4.12	4.08
<b>Mode</b>		4.33								
<b>Standard deviation</b>	0.31	0.20	0.15	0.22	0.08	0.29	0.23	0.08		0.02
<b>Sample Variance</b>	0.09	0.04	0.02	0.05	0.01	0.08	0.05	0.01		0.00
<b>Kurtosis</b>	-0.17	-0.89	1.53	-0.80	-1.14	-1.16	-0.37	0.72		
<b>Skweness</b>	0.59	-0.36	-1.11	-0.29	0.32	-0.18	0.39	0.90		
<b>Range</b>	1.02	0.65	0.51	0.67	0.21	0.77	0.60	0.22	0.00	0.03
<b>Minimum</b>	5.30	3.77	4.04	3.82	3.99	3.18	6.00	4.16	4.12	4.06
<b>Maximum</b>	6.32	4.42	4.55	4.49	4.19	3.95	6.60	4.38	4.12	4.09
<b>Sum</b>	74.41	53.53	43.70	41.74	28.54	25.15	31.34	21.23	4.12	8.15
<b>Count (n)</b>	13	13	10	10	7	7	5	5	1	2
<b>Confidence Interval (95,0%)</b>	0.18	0.12	0.11	0.15	0.07	0.27	0.29	0.10		0.18

Table VIII-5: descriptive statistical analysis of *Spelaeomys florensis*

### Results

Measurements collected fit very well the ones reported in literature (Hooijer, 1957; Musser, 1981).



**Table VIII-6: comparison among measurements taken on Liang Bua large murids and the published material**

In Table VIII-6 that compare the measurements taken on Liang Bua specimens with the ones of recent and fossil material published in Musser (1981), it looks like Liang Toge subfossil specimens were larger, in all the species. Sizes of the same species are comparable, but Liang Bua rats seem to be smaller. On the other hand, recent *Papagomys armandvillei* are smaller than fossil ones. One has to bear in mind, however, that the time span covered by Liang Bua fossil material is much longer. Oscillations in response to climate change could make the intraspecific variation at Liang Bua seem bigger and it could be opportune to consider the size variation in different moments

The results of PCA analysis are reported in Table VIII-7, VIII-8 and Figure VIII-1.

Axis	Eigenvalue	Variation
1	5.3718	89.53
2	0.304875	5.0812
3	0.135038	2.2506
4	0.0898026	1.4967
5	0.0665627	1.1094
6	0.031927	0.53212

**Table VIII-7: Eigenvalues and Variation of PCA applied to large murids from Liang Bua**

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
LM/1	-0.4113	0.1526	-0.6071	0.498	0.4099	0.1512
WM/1	-0.41	0.4018	0.03918	-0.6034	0.3783	-0.4021
LM/2	-0.4149	-0.1921	-0.4386	-0.1531	-0.7146	-0.2542
WM/2	-0.4193	0.2647	0.2485	-0.1812	-0.2194	0.7819
LM/3	-0.3801	-0.8303	0.1849	-0.1299	0.3295	0.08078
WM/3	-0.4125	0.1376	0.5845	0.561	-0.1467	-0.3647

**Table VIII-8: Eigenfactors of PCA**

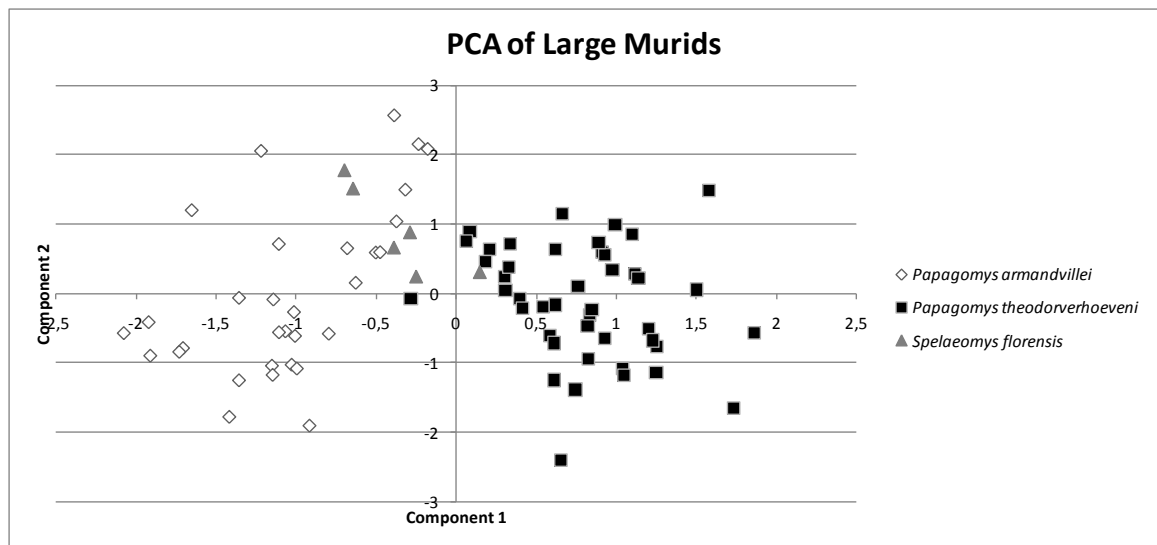


Figure VIII-1: PCA of large murids

The ordination of the PCA successfully separates the different species. The separation is clearest on the first axis, which is mainly related to size variation (all variables are directly correlated, and the first axis describes almost the 90% of the entire variation). This also explains why *Papagomys armandvillei* and *Spelaeomys florensis* result to be closer than the two cogenetic species. On second and third axis there is no separation among different taxa. As already noticed by the morphological analysis, *P. armandvillei* and *P. theodorverhoeveni* are morphometrical very similar, but and can be mostly distinguished on the basis of size differences.

## Discussion

The Giant rats' fossil remains of *Papagomys armandvillei*, *P. theodorverhoeveni* and *Spelaeomys florensis* from Liang Bua cave represent the first fossil occurrence of these species. As the giant rats are already found in the oldest deposits of the cave, and are endemic to the island, we must assume that they had already dwelled the island for a while. It is difficult to establish how long ago they originated, since there is a huge gap in the fossil documentation between the Middle Pleistocene deposit of the Ola Bula Formation and the Liang Bua site. In the passage from one to the other, during 700ky, the faunal composition of the assemblages changed, but not so much if we consider that more than half million years passed (Meijer et al., 2010). The Komodo dragon, *Varanus komodoensis*, survives all the Quaternary climatic variations and is still living today; *Stegodon florensis*, in the passage from one faunal complex to the other, undergoes some modifications, but not even enough to make him earn a new specific status, so that a new subspecific name has been assigned, *Stegodon florensis insularis* (van den Bergh et al., 2008); its extinction is recorded at Liang Bua, at the end of the Pleistocene. The only rodent on the island, recorded before the Liang Bua assemblages is *Hooijeromys nusatenggara* (Musser, 1981). It was a murid of large size, but not so much to be really considered a giant rat. It was larger than *Paulamys naso* and *Komodomys rintjanus*, but smaller than *Papagomys armandvillei*, *P. verhoeveni* and *Spelaeomys florensis*. Only two maxillaries from Ola Bula are known of these

species, plus four isolated molars tentatively associated with *H. nusatenggara* from Boa Leza. The similarities among *Papagomys* sp. and *H. nusatenggara* have been thoroughly analysed by Musser (1981), on the basis of the few remains known. They share the general structure of upper molars, with low cusps in transverse rows, the lack of t7 and posterior cingula and the absence of t3 in M2, beside the number of roots. Stricter similarities have been found among lower teeth that have only been tentatively attributed to the species. Despite some differences in the maxillary bone and arrangement of cusps on upper teeth (that make the oldest species to be assigned to a different genus), it is likely that *Hooijeromys* can represent the ancestor of Late Pleistocene murids of Flores. Thus, the scanty evidence suggests that the phylogenetic continuity between early Middle Pleistocene and Late Pleistocene faunal assemblages from Flores as observed by Meijer et al. (2010) also applies to the giant rodents of the genus *Papagomys*.

The presence of *Spelaeomys florensis* is quite out of the scheme. Whilst all the other native rodents (with the exception of the shrew rat) seem to belong to the same clade and seem to be more related among them than with any other species outside Flores (Musser, 1981), *Spelaeomys florensis* displays more similarities with murids from New Guinea and nearby Timor. From the latter, Quaternary remains of *Coryphomys buehleri* Schaub, 1937 have been recently thoroughly re-described (Aplin and Helgen, 2010). These species share many characters. The mandible shape, that is so different from the ones of the native rats of Flores, with the deepening under the first lower molar; the complex structure of molars; the presence of t7 on upper molars is a feature shared only by few species, together with the presence of a massif posterior cingulum. *Spelaeomys florensis* has many more accessory cusplets than the Timor giant rat, but the morphology of the common ones is very similar. Timor is quite a near island, particularly if we consider the island range directly east of Flores. These islands, which during glacials were probably connected to Flores, have a shortest distance to Timor of about 20 km. Thus, a close phylogenetic relationship between Flores and Timor species is hardly surprising.

Alternatively, could be related to other species dwelling far islands. However, considering the undeniable geographic barriers that characterize the area and the high number of plesiomorphies that characterize murids, it would be more logical to consider morphological subtle difference to be acquired later than to hypothesize a longer route. In this case, it is quite easy for these species to lose or gain subsidiary cusps or cusplets, whose presence/absence is not necessary related to phylogenetic relationships. As we noted, the subsidiary cusps and cusplets are also variable within the genus *Papagomys*.

Since there is no fossil record of *Spelaeomys florensis* predating the Liang Bua deposits, its arrival (or of its ancestors) on the island is unknown. The first occurrence at Liang Bua can be recorded at spit 46 of Sector IV, first part of Late Pleistocene. In sector IV it is scarce; on the contrary its abundance is far higher in sector VII (Late Glacial). The relatively high number of fossils found in Liang Toge suggests that the species was also more common in that area. Overall, this rare species is still enigmatic. A deeper analysis of skeletal and dentary features may provide more clues on the origin of this species.

Not many changes occurred in the 800ka preceding the first documentation at Liang Bua: the vertebrate faunas of Flores show a strong phylogenetic continuity (Meijer et al., 2010). Even hominins were already present, as proven by the presence of artefacts at Liang Bua (Morwood et al., 2009).

Unfortunately, the fossil record for Rodentia of the Middle Pleistocene is too scarce to be of much use. However, the assemblages from Liang Bua are in line with a long history of isolation. All the resident forms, with the exception of *S. Florensis*, are strictly related among them and the giant forms dwelling the island are one of the main expressions insularism.

The phylogenesis of *Papagomys armandvillei* has been studied by means of Microcomplement Fixation of Albumin (Watts and Baverstock, 1994). Before that, there were two different hypotheses: Misonne (1969) considered it related to other Malaysian murids, like *Mallomys* and *Lenothrix* and separated from the *Rattus* clade; Musser and Newcomb (1983), on the basis of cranial morphology. The Microcomplement Fixation of Albumin confirmed the latter hypothesis and placed *Papagomys* in the *Rattus*-like clade, as well as the other Flores fossil species, *Komodomys rintjanus*. Unfortunately, the other two endemics, *Paulamys* and *Rattus hainaldi* were not included in the study.

A recent paper by Meiri et al. (2008) is titled: "The island rule: made to be broken?"; it deals with the analysis of size variation among different clades and concludes that the island rule cannot be size related, but it is clade related. The "island rule" is the prediction that small bodied animals should evolve larger sizes on islands, while large bodied animals should evolve to be smaller; in this sense it is "size-related", since the variation in size depends on the size category to which animals belong. Because of this, most of the interpretations of the size variation dealt with the advantages in being larger or smaller on islands (i. e. resource availability, low predation, and intraspecific competition; Case 1978, Heaney 1978; Lomolino, 2005). According to Meiri et al. (2008), it is not the initial size to be determinant, since many species of the same size do not display the same size variation. In their opinion, some clades display an internal tendency to increase in size, other to reduce their size; i.e., among small mammals, not all of them undergo size increase on islands (usually rodents do that) while other orders, like Insectivorae, tend to keep their size. Lomolino (2005) already stated that the optimal size on islands could have been related to particular species group, and thus to phylogeny.

Rodents are one of the first groups for which island rule was used; giant rodents (above all murids, cricetids and dormice) and dwarf elephants and deer have by palaeontologists always been the main expression and manifestation of the presence of insular environment (Van der Geer et al., 2010). Furthermore, as reported in the introduction, Foster referred firstly to rodents, not to small mammals in general. But that does not mean necessary that the rule is strictly related to clade and size is not important. In my opinion, the reduced small size in rodent can still be the main trigger in the size increase on islands.

The island rule cannot be broken as a general pattern. Many categories does not seem to undergo size modification, but the fossil documentation of extinct mammals from island provides evidence of particular group of animals that repeatedly experience directional size variation, resulting in size categories not recorded or rare in the continental record (i. e., giant rats and dwarf elephants).

I agree with Lomolino (2005), which recognize important differences within the general rule, does not deny the general applicability:

*"The island rule remains a very general pattern – in one sense a relatively complex combination of patterns across a range of spatial and temporal scales, but in another sense relatively simple in that the emergent patten results from predictable differences in selective pressures among species of*

*different size, and from a tendency for convergence toward phenotypes that seem optimal for particular bau plans and ecological strategies “*

*Lomolino, 2005*

Rodents and other groups have different evolutionary rates. Rodents are tachytelic species, in which the evolutionary rate is very high, the highest among mammals; on the other hand, insectivores (the other main group of small mammals) have low evolutionary rate and species are highly persistent. Furthermore, rodents are usually more abundant than insectivores in the mainland, as well. Since the islands were reached by a sweepstake route, mainly by chance, the most abundant animal is on the mainland, the more chances it will have to reach an island and to give rise to endemic species. On islands, biodiversity is usually low and there usually are many free niches. When rodents get there, it could be easier for them to occupy earlier free niches and undergo adaptative radiation. It is also necessary to keep in mind that, together with giant rodents, “normal size” rodents dwell the islands as well and in some cases, like at Liang Bua cave, when the environmental conditions are stable and there is not disturbance for a long time, an evolutionary radiation takes place.

Nevertheless, it is true that gigantism episodes on islands in insectivores are not as frequent as in rodents. For instance, in Flores no giant insectivore is known and the two species recorded at Liang Bua do not display any size increase.

Since the presence of giant small mammals and dwarf large mammals is commonly found on islands, whilst it is rare in continental areas, and since the main factors that would trigger the size increase are related to size, I would not say that gigantism and dwarfism are not size-related. I agree that some clades undergo more easily gigantism/dwarfism episodes, but that is not enough. The categories for which the island rule does not work are also the least represented categories on islands, since carnivores and insectivores do not cross easily water barriers.

In cases of long lasting islands, giant insectivores did exist (like *Deinogalerix* in the Gargano fauna) or some of them display a slight increase in body size (i.e. *Crocidura esuae* in Sicily, *Nesiotites hidalgo*); if this is associated to lower capability in dispersal through water barriers compared to rodent, in my opinion the fact that display more often gigantism episodes cannot discard completely the strict relation between the size and gigantism episodes.

In conclusion, I do not deny the evidence that the effects of the island rule are more striking on some taxa than others, but I still think that the island rule is still widely applicable in some circumstances, and giant rats, like the ones recovered at Flores, are one of the most amazing manifestations of that.

## **Conclusion**

Large size murids recovered at Liang Bua Cave (Flores, Indonesia) could be assigned to at least three different species, all endemic to Flores: *Papagomys armandvillei*, *P. verhoeveni* and *Spelaeomys florensis*. Only the former is still living, while the other ones got extinct in recent

times. While *Papagomys* species are similar to the Middle Pleistocene rat that lived on Flores (*Hooijeromys nusatenggara*) and to ones of middle size murids (*Komodomys rintjanus* and *Paulamys naso*), *Spelaeomys naso* denotes a different origin.

## Appendix Chapter X



ID	sector	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
LBM 1508	VII	70	<i>Papagomys amandvillei</i>	5.804	4.012										
LBM 1536	VII	69	<i>Papagomys amandvillei</i>					4.665	4.322						
LBM 1537	VII	69	<i>Papagomys amandvillei</i>			4.561	4.479								
LBM 1538	VII	69	<i>Papagomys amandvillei</i>	5.92	3.973										
LBM 1539	VII	69	<i>Papagomys amandvillei</i>			4.593	4.402								
LBM 1540	VII	69	<i>Papagomys amandvillei</i>					4.701	4.342						
LBM 1562	VII	63	<i>Papagomys amandvillei</i>	6.07	3.835	4.162	4.1	4.088	3.661						
LBM 633	III	36	<i>Papagomys amandvillei</i>									4.69	4.34	4.78	3.52
LBM 1569	VII	61	<i>Papagomys amandvillei</i>			5.554	4.64								
LBM 705	III	40	<i>Papagomys amandvillei</i>							7.65	4.99	5.38	4.47		
LBM 558	III	31	<i>Papagomys amandvillei</i>									5.22	4.5		
LBM 785	III	45	<i>Papagomys amandvillei</i>							6.66	4.95	4.5	4.57	4.79	3.75
LBM 560	III	31	<i>Papagomys amandvillei</i>							8.3	4.98	5.38	4.64	4.2	3.83
LBM 1045	IV	15	<i>Papagomys amandvillei</i>							7.03	4.6	4.9	4.59	4.44	3.96
LBM 679	III	38	<i>Papagomys amandvillei</i>									4.8	4.65	4.99	4.34
LBM 804	III	46	<i>Papagomys amandvillei</i>									4.71	4.65		
LBM 802	III	46	<i>Papagomys amandvillei</i>									4.98	4.66		
LBM 1288	IV	10	<i>Papagomys amandvillei</i>							7.12	4.83	4.55	4.51		
LBM 997	IV	18	<i>Papagomys amandvillei</i>							7.27	4.94				
LBM 1318	IV	8	<i>Papagomys amandvillei</i>							7.32	4.83				
LBM 750	III	42	<i>Papagomys amandvillei</i>							6.8	5.17	4.61	4.73	4.6	3.78
LBM 559	III	31	<i>Papagomys amandvillei</i>							7.65	5.23	5.01	4.76		
LBM 939	IV	24	<i>Papagomys amandvillei</i>							7.35	4.39	5.12	4.58	4.17	4.06
LBM 1577	VII	59	<i>Papagomys amandvillei</i>							8.637	5.387	6.271	5.034		
LBM 1186	IV	12	<i>Papagomys amandvillei</i>							7.37	4.94	4.82	4.86	4.91	4.02
LBM 979	IV	22	<i>Papagomys amandvillei</i>							7.37	4.67				
LBM 16	IV	26	<i>Papagomys amandvillei</i>							7.41	5.18	5.4	4.62	4.86	3.94
LBM 1580	VII	58	<i>Papagomys amandvillei</i>			4.516	4.568								
LBM 85	IV	32	<i>Papagomys amandvillei</i>							7.42	4.8				
LBM 35	IV	29	<i>Papagomys amandvillei</i>							7.52	4.97				
LBM 1277	IV	11	<i>Papagomys amandvillei</i>							7.63	5.33				
LBM 1581	VII	58	<i>Papagomys amandvillei</i>					3.737	4.14						
LBM 1073	IV	14	<i>Papagomys amandvillei</i>							7.67	4.87	5.11	4.48	4.09	3.83
LBM 361	IV	47	<i>Papagomys amandvillei</i>							7.68	4.77				
LBM 287	IV	42	<i>Papagomys amandvillei</i>							7.8	5				
LBM 1583	VII	58	<i>Papagomys amandvillei</i>	5.518	3.746										
LBM 187	IV	37	<i>Papagomys amandvillei</i>							7.85	4.84				
LBM 84	IV	32	<i>Papagomys amandvillei</i>							7.9	5.13				
LBM 1022	IV	15	<i>Papagomys amandvillei</i>							7.95	4.75	5.14	4.55	4.55	3.74
LBM 330	IV	46	<i>Papagomys amandvillei</i>							8.49	5.79	5.39	5.13		
LBM 362	IV	47	<i>Papagomys amandvillei</i>							8.59	5.03				
LBM 451	IV	51	<i>Papagomys amandvillei</i>							8.85	5.59	5.57	5.6		
LBM 329	IV	46	<i>Papagomys amandvillei</i>							8.9	5.37				
LBM 1597	VII	58	<i>Papagomys amandvillei</i>	5.81	3.88										
LBM 1599	VII	58	<i>Papagomys amandvillei</i>			4.147	3.938								
LBM 1602	VII	57	<i>Papagomys amandvillei</i>							7.25	5.162				
LBM 800	III	46	<i>Papagomys amandvillei</i>							6.98	4.51				
LBM 732	III	41	<i>Papagomys amandvillei</i>							7.59	4.53				
LBM 639	III	37	<i>Papagomys amandvillei</i>							7.5	4.64			4.63	3.84
LBM 751	III	42	<i>Papagomys amandvillei</i>							6.97	4.77			4.67	3.68
LBM 813	III	47	<i>Papagomys amandvillei</i>							7.74	4.8				
LBM 809	III	47	<i>Papagomys amandvillei</i>							7.94	5				
LBM 812	III	47	<i>Papagomys amandvillei</i>							6.88	5.05				
LBM 1605	VII	57	<i>Papagomys amandvillei</i>	6.259	4.14	4.044	4.259	3.729	3.597						
LBM 605	III	35	<i>Papagomys amandvillei</i>							8.41	5.17				
LBM 706	III	40	<i>Papagomys amandvillei</i>							7.26	5.18				
LBM 1606	VII	57	<i>Papagomys amandvillei</i>	5.795	4.003	4.102	4.238	3.942	3.78						
LBM 562	III	31	<i>Papagomys amandvillei</i>							7.82	5.2				
LBM 774	III	44	<i>Papagomys amandvillei</i>							8.09	5.31				
LBM 634	III	36	<i>Papagomys amandvillei</i>									5.32			
LBM 761	III	43	<i>Papagomys amandvillei</i>							8.74	5.37				
LBM 561	III	31	<i>Papagomys amandvillei</i>							9.06	5.42				
LBM 520	III	10	<i>Papagomys amandvillei</i>	6.07	3.85	4.56	4.35	4.75	4.23						
LBM 531	III	29	<i>Papagomys amandvillei</i>	6.08	4.02	4.81	4.23	4.83	4.03						
LBM 538	III	29	<i>Papagomys amandvillei</i>	5.74	4.04	4.16	4.33	4.31	3.81						
LBM 572	III	33	<i>Papagomys amandvillei</i>	6.25	4.25	4.57	4.41	4.58	4.1						
LBM 597	III	35	<i>Papagomys amandvillei</i>	6.34	4.2	4.49	4.28	4.85	4.02						
LBM 527	III	27	<i>Papagomys amandvillei</i>												
LBM 528	III	27	<i>Papagomys amandvillei</i>	6.11	3.93										
LBM 529	III	27	<i>Papagomys amandvillei</i>												
LBM 599	III	35	<i>Papagomys amandvillei</i>	5.91	4.02	4.66	4.11	4.71	3.8						
LBM 623	III	36	<i>Papagomys amandvillei</i>	6.65	4.49	4.9	4.73	5.37	4.37						
LBM 534	III	29	<i>Papagomys amandvillei</i>												
LBM 688	III	40	<i>Papagomys amandvillei</i>	5.93	4.25	4.09	4.07	4.34	3.6						
LBM 760	III	43	<i>Papagomys amandvillei</i>	6.28	4.27	4.57	4.54	4.96	4.24						
LBM 771	III	44	<i>Papagomys amandvillei</i>	6.42	4.63	5.03	5.09	5.5	4.39						
LBM 549	III	31	<i>Papagomys amandvillei</i>	5.69	3.87										
LBM 571	III	33	<i>Papagomys amandvillei</i>												
LBM 573	III	33	<i>Papagomys amandvillei</i>												



LBM 1607	VII	57	<i>Papagomys armandvillei</i>	5.907	3.939	4.064	3.998	3.679	3.844										
LBM 1616	VII	57	<i>Papagomys armandvillei</i>	5.919	4.091	4.53	4.41	4.921	4.271										
LBM 1620	VII	57	<i>Papagomys armandvillei</i>					7.694	5.31	6.087	5.003								
LBM 1636	VII	55	<i>Papagomys armandvillei</i>	5.887	4.113	4.514	4.387	4.89	4.057										
LBM 1637	VII	55	<i>Papagomys armandvillei</i>	6.224	4.511	4.545	4.816	4.3	4.215										
LBM 1639	VII	55	<i>Papagomys armandvillei</i>							6.961	5.11	4.705	4.776	4.685	3.974				
LBM 44	IV	31	<i>Papagomys armandvillei</i>	6.3	4.09														
LBM 160	IV	35	<i>Papagomys armandvillei</i>	6.36	3.94	4.64	4.12												
LBM 162	IV	35	<i>Papagomys armandvillei</i>	6.39	4.42	4.86	4.48												
LBM 57	IV	31	<i>Papagomys armandvillei</i>	6.41	4.67	4.69	4.99												
LBM 1207	IV	12	<i>Papagomys armandvillei</i>	6.47	4.1	4.71	4.44												
LBM 134	IV	33	<i>Papagomys armandvillei</i>	6.47	4.2	4.61	4.7	5.37	4.47										
LBM 145	IV	34	<i>Papagomys armandvillei</i>	6.48	4.34														
LBM 992	IV	18	<i>Papagomys armandvillei</i>	6.56	4.48	4.67	4.81												
LBM 102	IV	32	<i>Papagomys armandvillei</i>	6.58	4.14														
LBM 106	IV	32	<i>Papagomys armandvillei</i>	6.71	4.35	4.82	4.63	5.4	3.96										
LBM 315	IV	44	<i>Papagomys armandvillei</i>	6.88	5.03														
LBM 94	IV	32	<i>Papagomys armandvillei</i>									4.18	4.66	4.47	3.83				
LBM 146	IV	34	<i>Papagomys armandvillei</i>									4.43	4.58						
LBM 881	IV	39	<i>Papagomys armandvillei</i>									4.86	4.78						
LBM 89	IV	32	<i>Papagomys armandvillei</i>									4.88	4.28						
LBM 93	IV	32	<i>Papagomys armandvillei</i>									4.96	4.78						
LBM 414	IV	49	<i>Papagomys armandvillei</i>									4.97	4.7						
LBM 88	IV	32	<i>Papagomys armandvillei</i>									5.17	4.69						
LBM 1023	IV	15	<i>Papagomys armandvillei</i>									5.36	4.27						
LBM 87	IV	32	<i>Papagomys armandvillei</i>									5.38	4.51						
LBM 212	IV	38	<i>Papagomys armandvillei</i>									5.62	4.76						
LBM 43	IV	31	<i>Papagomys armandvillei</i>									5.66	4.64						
LBM 1644	VII	54	<i>Papagomys armandvillei</i>							7.35	5.213	5.102	4.393						
LBM 1661	VII	54	<i>Papagomys armandvillei</i>														4.689	3.955	
LBM 1663	VII	54	<i>Papagomys armandvillei</i>			4.363	4.325												
LBM 1664	VII	54	<i>Papagomys armandvillei</i>	5.64	3.988	4.299	4.282	3.644	3.852										
LBM 1665	VII	54	<i>Papagomys armandvillei</i>	5.641	4.027														
LBM 1666	VII	54	<i>Papagomys armandvillei</i>							8.215	5.194	5.518	4.772	4.675	3.839				
LBM 1671	VII	53	<i>Papagomys armandvillei</i>									7.267	4.444						
LBM 1672	VII	53	<i>Papagomys armandvillei</i>	6.425	4.127														
LBM 1236	IV	12	<i>Papagomys armandvillei</i>														4.77	4.17	
LBM 1025	IV	15	<i>Papagomys armandvillei</i>			4.3	4.14	4.2	3.59										
LBM 1012	IV	17	<i>Papagomys armandvillei</i>														4.21	3.91	
LBM 935	IV	24	<i>Papagomys armandvillei</i>			4.81	4.35	4.95	3.88										
LBM 45	IV	31	<i>Papagomys armandvillei</i>			4.9	4.72												
LBM 46	IV	31	<i>Papagomys armandvillei</i>					4.61	4.42										
LBM 117	IV	32	<i>Papagomys armandvillei</i>																
LBM 77	IV	32	<i>Papagomys armandvillei</i>			4.28	4.34												
LBM 81	IV	32	<i>Papagomys armandvillei</i>			4.29	4.89												
LBM 79	IV	32	<i>Papagomys armandvillei</i>			4.56	4.41												
LBM 80	IV	32	<i>Papagomys armandvillei</i>			4.6	4.57												
LBM 86	IV	32	<i>Papagomys armandvillei</i>																
LBM 83	IV	32	<i>Papagomys armandvillei</i>					5.2	4.13										
LBM 97	IV	32	<i>Papagomys armandvillei</i>					4.75	4.05										
LBM 95	IV	32	<i>Papagomys armandvillei</i>																
LBM 124	IV	33	<i>Papagomys armandvillei</i>			4.83	4.36												
LBM 135	IV	33	<i>Papagomys armandvillei</i>																
LBM 148	IV	34	<i>Papagomys armandvillei</i>																
LBM 166	IV	35	<i>Papagomys armandvillei</i>					4.77	3.82										
LBM 167	IV	35	<i>Papagomys armandvillei</i>					5.48	4.21										
LBM 153	IV	35	<i>Papagomys armandvillei</i>					5.17	4.28										
LBM 207	IV	38	<i>Papagomys armandvillei</i>			4.19	4.36												
LBM 208	IV	38	<i>Papagomys armandvillei</i>																
LBM 210	IV	38	<i>Papagomys armandvillei</i>																
LBM 1694	VII	53	<i>Papagomys armandvillei</i>			4.258	3.991												
LBM 1702	VII	52	<i>Papagomys armandvillei</i>	6.688	4.401	4.863	4.607	4.724	4.482										
LBM 514	IV	60	<i>Papagomys armandvillei</i>			4.51	4.46												
LBM 1704	VII	52	<i>Papagomys armandvillei</i>					4.058	3.786										
LBM 1709	VII	52	<i>Papagomys armandvillei</i>			4.111	4.216												
LBM 1718	VII	52	<i>Papagomys armandvillei</i>					3.891	4.081										
LBM 1741	VII	49	<i>Papagomys armandvillei</i>			3.925	4.052												
LBM 1751	VII	48	<i>Papagomys armandvillei</i>							7.175	5.329		4.812						
LBM 1755	VII	48	<i>Papagomys armandvillei</i>			4.322	4.564	4.443	4.089										
LBM 1773	VII	48	<i>Papagomys armandvillei</i>	5.516	3.843														
LBM 1775	VII	48	<i>Papagomys armandvillei</i>			4.827	5.007												
LBM 1792	VII	47	<i>Papagomys armandvillei</i>	6.301	4.41														
LBM 1802	VII	45	<i>Papagomys armandvillei</i>	5.497	4.071	3.947	4.06												
LBM 1844	VII	43	<i>Papagomys armandvillei</i>	6.123	4.431														
LBM 1845	VII	43	<i>Papagomys armandvillei</i>	6.034	4.225														
LBM 1853	VII	34	<i>Papagomys armandvillei</i>	5.566	3.708														
LBM 1860	VII	30	<i>Papagomys armandvillei</i>			4.236	4.417												

Table VIII-9: specimens and measurements (mm) of *Papagomys armandvillei*

ID	sector	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
LBM 879	IV	39	<i>Papagomys theodorverhoeveni</i>							5.53	3.98				
LBM 246	IV	39	<i>Papagomys theodorverhoeveni</i>							5.71	3.5				
LBM 776	III	44	<i>Papagomys theodorverhoeveni</i>							5.44	3.43	3.36	3.2		
LBM 727	III	41	<i>Papagomys theodorverhoeveni</i>							5.18	3.55	3.55	3.29	2.85	2.84
LBM 143	IV	33	<i>Papagomys theodorverhoeveni</i>							5.75	3.95				
LBM 213	IV	38	<i>Papagomys theodorverhoeveni</i>							5.75	3.57				
LBM 1460	IV	1	<i>Papagomys theodorverhoeveni</i>							5.78	3.37	3.93	3.18	2.73	2.71
LBM 8	IV	25	<i>Papagomys theodorverhoeveni</i>							5.91	3.76				
LBM 828	III	51	<i>Papagomys theodorverhoeveni</i>									4.11	3.52		
LBM 988	IV	19	<i>Papagomys theodorverhoeveni</i>							5.92	3.6	3.75	3.41	3.04	2.93
LBM 211	IV	38	<i>Papagomys theodorverhoeveni</i>							5.93	3.79				
LBM 91	IV	32	<i>Papagomys theodorverhoeveni</i>							5.94	3.6	3.69	3.59	3.36	3.04
LBM 989	IV	18	<i>Papagomys theodorverhoeveni</i>							5.94	3.6	3.96	3.41	3.37	3.02
LBM 154	IV	35	<i>Papagomys theodorverhoeveni</i>							5.96	3.78				
LBM 940	IV	24	<i>Papagomys theodorverhoeveni</i>							5.97	4.03	3.95	3.74	3.39	3.16
LBM 880	IV	39	<i>Papagomys theodorverhoeveni</i>							5.97	3.7				
LBM 533	III	29	<i>Papagomys theodorverhoeveni</i>							5.41	3.61	4	3.74	3.52	3.2
LBM 171	IV	36	<i>Papagomys theodorverhoeveni</i>							6.02	3.59				
LBM 172	IV	36	<i>Papagomys theodorverhoeveni</i>							6.07	3.74	3.93	3.43	2.82	2.85
LBM 532	III	29	<i>Papagomys theodorverhoeveni</i>							6.35	4.37	4.25	3.98	4.26	3.32
LBM 996	IV	18	<i>Papagomys theodorverhoeveni</i>							6.12	4.12	4.56	3.84	3.57	3.28
LBM 959	IV	23	<i>Papagomys theodorverhoeveni</i>							6.14	3.83	4.09	3.55	2.97	2.92
LBM 1566	VII	62	<i>Papagomys theodorverhoeveni</i>							6.497	4.373				
LBM 961	IV	23	<i>Papagomys theodorverhoeveni</i>							6.17	3.82	4.04	3.59	3.18	3.03
LBM 911	IV	24	<i>Papagomys theodorverhoeveni</i>							6.17	3.67	4.26	3.61		
LBM 125	IV	33	<i>Papagomys theodorverhoeveni</i>							6.26	3.31				
LBM 890	IV	25	<i>Papagomys theodorverhoeveni</i>							6.27	3.59	3.8	3.31	3.02	3.07
LBM 20	IV	27	<i>Papagomys theodorverhoeveni</i>							6.32	3.7				
LBM 912	IV	24	<i>Papagomys theodorverhoeveni</i>							6.55	3.94				
LBM 1308	IV	9	<i>Papagomys theodorverhoeveni</i>							6.57	4.5				
LBM 21	IV	27	<i>Papagomys theodorverhoeveni</i>							6.66	3.87				
LBM 817	III	47	<i>Papagomys theodorverhoeveni</i>							6.02	3.53				
LBM 753	III	43	<i>Papagomys theodorverhoeveni</i>							5.54	3.68				
LBM 1590	VII	58	<i>Papagomys theodorverhoeveni</i>							6.07	4.177				
LBM 635	III	36	<i>Papagomys theodorverhoeveni</i>							6.5	3.71				
LBM 1591	VII	58	<i>Papagomys theodorverhoeveni</i>							5.025	3.402				
LBM 595	III	35	<i>Papagomys theodorverhoeveni</i>							5.89	4				
LBM 1596	VII	58	<i>Papagomys theodorverhoeveni</i>							6.365	5.186				
LBM 1598	VII	58	<i>Papagomys theodorverhoeveni</i>										4.09		
LBM 1600	VII	58	<i>Papagomys theodorverhoeveni</i>									3.513	3.252		
LBM 815	III	47	<i>Papagomys theodorverhoeveni</i>							6.59	4.27				
LBM 704	III	40	<i>Papagomys theodorverhoeveni</i>							6.53	4.29				
LBM 825	III	48	<i>Papagomys theodorverhoeveni</i>							5.87	4.34				
LBM 1601	VII	58	<i>Papagomys theodorverhoeveni</i>											3.229	3.362
LBM 1618	VII	57	<i>Papagomys theodorverhoeveni</i>							6.06	4.051				
LBM 1638	VII	55	<i>Papagomys theodorverhoeveni</i>							6.447	4.539				
LBM 363	IV	47	<i>Papagomys theodorverhoeveni</i>									3.64	3.05		
LBM 962	IV	23	<i>Papagomys theodorverhoeveni</i>									3.68	3.7	3.9	3.73
LBM 977	IV	22	<i>Papagomys theodorverhoeveni</i>									3.69	3.53	3.68	3.02
LBM 864	IV	39	<i>Papagomys theodorverhoeveni</i>									3.78	3.63	3.84	3.1



ID	sector	spit	Species	LM <sub>1</sub>	WM <sub>1</sub>	LM <sub>2</sub>	WM <sub>2</sub>	LM <sub>3</sub>	WM <sub>3</sub>	LM <sup>1</sup>	WM <sup>1</sup>	LM <sup>2</sup>	WM <sup>2</sup>	LM <sup>3</sup>	WM <sup>3</sup>
LBM 248	IV	39	<i>Spelaeomys florensis</i>							6	4.19				
LBM 92	IV	32	<i>Spelaeomys florensis</i>							6.1	4.27				
LBM 331	IV	46	<i>Spelaeomys florensis</i>							6.3	4.24				
LBM 1545	VII	68	<i>Spelaeomys florensis</i>			4.257	4.014	3.985	3.303						
LBM 1579	VII	58	<i>Spelaeomys florensis</i>									4.122	4.09		
LBM 1603	VII	57	<i>Spelaeomys florensis</i>							6.595	4.376				
LBM 1623	VII	56	<i>Spelaeomys florensis</i>							6.344	4.158		4.061		
LBM 1624	VII	56	<i>Spelaeomys florensis</i>												
LBM 1634	VII	55	<i>Spelaeomys florensis</i>												
LBM 1667	VII	54	<i>Spelaeomys florensis</i>												
LBM 1681	VII	53	<i>Spelaeomys florensis</i>												
LBM 1717	VII	52	<i>Spelaeomys florensis</i>			4.365	3.897								
LBM 749	III	42	<i>Spelaeomys florensis</i>												
LBM 248	IV	39	<i>Spelaeomys florensis</i>							6	4.19				
LBM 92	IV	32	<i>Spelaeomys florensis</i>							6.1	4.27				
LBM 331	IV	46	<i>Spelaeomys florensis</i>							6.3	4.24				
LBM 1545	VII	68	<i>Spelaeomys florensis</i>			4.257	4.014	3.985	3.303						
LBM 1579	VII	58	<i>Spelaeomys florensis</i>									4.122	4.09		
LBM 1603	VII	57	<i>Spelaeomys florensis</i>							6.595	4.376				
LBM 1623	VII	56	<i>Spelaeomys florensis</i>							6.344	4.158		4.061		
LBM 1624	VII	56	<i>Spelaeomys florensis</i>												
LBM 1634	VII	55	<i>Spelaeomys florensis</i>												
LBM 1667	VII	54	<i>Spelaeomys florensis</i>												
LBM 1681	VII	53	<i>Spelaeomys florensis</i>												
LBM 1717	VII	52	<i>Spelaeomys florensis</i>			4.365	3.897								
LBM 749	III	42	<i>Spelaeomys florensis</i>												

Table VIII-11: specimens and measurements (mm) of *Spelaeomys florensis*

# IX. Liang Bua rodent succession

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*“It is not the facts but the relation of things that results in the universal harmony that is the sole objective reality.”*

*Robert M. Pirsig*

## **Introduction**

After the considerations made on single groups in chapters 6, 7 and 8, in the next paragraph I will discuss the rodent succession at Liang Bua as a whole. Since the remains of shrew rates are very few and have not been identified, they will not be taken into account. Usually the analyses of the small faunal successions in archaeological/paleontological deposits are used for:

- paleo-environmental reconstructions by the study of the variation in relative abundances;
- correlations with already known environmental events.

These aspects are quite difficult to test at Liang Bua, for many reasons.

First, almost all the rodent species can be referred to a single group, Muridae. Usually great ecological differences are recognized among families (Gliridae are usually more adapted to forest environment, Arvicolidae to dry environments) and smaller ecological differences among difference species. The only small mammals recovered that do not belong to Muridae are very few, both in absolute and in relative abundance, so that their presence is not indicative from an ecological point of view. Furthermore, the great part of species involved are highly endemic, and their ecology is not very clear; even the species that did not go extinct are very rare now, with an areal which is reduced by the introduction of cosmopolitan species by man. Thus, the actual distribution cannot be necessary related to ecological preferences. The biodiversity is also quite low.

Luckily, many dating have been carried out at Liang Bua cave, and it is possible to correlate some modifications with already known environmental changes.

However, the Liang Bua succession allows studying the relationship of small mammals with man. Usually small mammals are accumulated in fossil sites by natural processes and they are used more effectively than large mammals for paleo-environmental reconstructions in archaeological sites because their accumulation is not affected by man. At Liang Bua the situation is different in many aspects. Large mammals are very few, which raises questions on the diet of *Homo floresiensis*. The last occurrence of *Stegodon florensis insularis*, the only large mammal found on the island before Holocene is in spits just underneath the volcanic deposits dating to Late Glacial. Before the Neolithic, only *Sus celebensis* reached the island. But as the small mammals are not

really small at all - giant rats can reach a body length of 60 cm - the rodents may have been used as an important food resource. Actually, the use of Muridae as food item is known in Polynesia (Matisoo-Smith et al., 1999); even the smallest rat in the world, *Rattus exulans*, was eaten by New Zealand populations. Therefore, an increase in Giant rats' relative abundance, considering that such a big prey would not be hunted by owls, could be related to a variation in human behavior.

In the next paragraph, I will consider the relative abundances of rodents at Liang Bua, and try to relate them to the main climate modifications of Holocene and Pleistocene. Finally, possible human influence on the composition of the Liang Bua fossil rodent assemblages will be discussed.

## ***Materials and Methods***

In this analysis the relative abundance of all rodents remains recovered in Sector IV, Sector III and Sector VII will be considered. As already explained in Chapter V, only part of the material from Sector III and VII was available. For every sector the number of remains of every single species will be considered, rather than calculating the Minimum Number of Individuals (MNI), in order to have sufficiently large sample sizes. MNI can be useful in assemblages with species with different dental formula and dental features, leading to significant differences in the method of counting. For instance, arviculids are usually identified by one single molar,  $M_1$ , while other species like dormice can be identified by all the teeth and the occurrence of entire mandibles/upper maxillaries is rare. As we noted, only one rodent family was present in Liang Bua. Considering that the great part of the material is represented by mandibles and maxillary remains, with very few isolated teeth, all the species can be considered equivalent in identification and recovery potential.

The number of remains will be plotted against spits.

## ***Results***

### **Sector IV**

Sector IV is the most complete sector considered, with the material coming from all the excavations carried out in this area, from the uppermost levels to the deepest ones. In the stratigraphy, a huge sedimentary gap has been found at around 4 m depth, where erosive processes took out significant portions of the sediments still present in the sectors excavated close to the walls of the cave. Central portions of the cave were strongly affected by the water action. Thus, upper spits yield many traces of Neolithic culture, whilst underlying layers can be referred to more ancient units (3 and 4), over 61ka BP.

The distribution of small mammals in the stratigraphy is reported in Figure IX-1.



From the diagram, it is possible to notice a rough division in three main parts, the small mammal distribution of which is synthesized in Figure IX-4. In the deepest spits (54-82) the amount of small mammals' remains is very low and there are entire spits from which no remains have been recovered; for this reason these spits have not been considered indicative.

Deeper spits (53-36): the assemblage is dominated by *Rattus hainaldi* (61.5%); middle size murids, *Paulamys naso* and *Komodomys rintjanus*, are equally represented (7.6 % each one). Giant rats represent around 24%: *Papagomys armandvillei* is the most abundant, *Spelaeomys florensis* is scarcely represented. At a depth of 4 m from the surface there is a layer of with tuffaceous silts, accumulated during a volcanic eruption that occurred between 12-11 ka (Westaway et al., 2009a). Under these layers, the deposits can be ascribed to Unit 4 (Westaway et al., 2009b), that is considered Late Pleistocene (74-61ka). This unit also yielded *Stegodon* and *Homo floresiensis* remains.

Middle spits (spits 35-15): the small mammal association in completely changed in this part. Giant rats are dominant in this portion (76%); *Spelaeomys florensis* is still very scarce, while *Papagomys armandvillei* and *P. verhoeveni* are abundant and equally distributed (38% each one). Only *Paulamys naso* does not show any significant variation in the relative abundance, while all the others underwent a strong reduction. According to Morwood et al. (2009), at a depth of 170 cm there are the first evidence for the Neolithic and dating from spit 15 gave an age of 3.62ka (Roberts et al., 2009). In these levels, the arrival of modern human is attested and *Stegodon florensis insularis* is not present anymore. There is evidence for a change in human behaviors, among which a more extensive exploitation of marine food resources (Van den Bergh et al., 2009).

Upper spits (spits 14-1): in these spits there is again a complete renewal of small mammal association. New arrivals/introductions (*Rattus exulans* and *Rattus rattus*) represent a high part of the remains (around 37%), and their abundance increases even more in the uppermost spits. This phase corresponds to the Neolithic (since 3.63ka, Roberts et al., 2009) and apart from rodents many introductions are evident in large mammal record, as well (*Sus scrofa*, *Macaca fascicularis*, *Paradoxurus hermaphrodites* and *Hystrix javanica*; Bergh et al., 2009). These species were probably introduced as food resources, pest control or as pet (Groves, 1976; van den Bergh et al., 2009).

The discontinuities/changes in the rodent association correspond well to the chronological discontinuities in the sequence and to the main cultural changes documented in the other records (anthropological, geological and vertebrate). The number of remains recovered in every spit is not enough to make a significant correlation with climatic change.



## Sector III

This sector is strongly affected by erosion. Furthermore, since layers are not horizontal, it is also difficult to assign safely the material to different Units, causing a great deal of stratigraphic uncertainty. In general, the distribution of rodents is similar to the one of the middle portion of Sector IV, with giant rats dominating the association (Figure IX-2). In Sector III *Spelaeomys florensis* seems more abundant than in other ones, but sample sizes in the various spits are low. According to Westaway et al. (2009a), the profile of Unit 9 (Younger occupation, Neolithic) reaches a depth of more than 3 m in some points of the sector. Two remains of *Rattus exulans* that were recovered from deep spits thus have been interpreted as younger remains.

In general, *Papagomys armandvillei* is the more abundant (52.58%), followed by the co-generic *Papagomys theodorverhoeveni* (26.80%) (Figure IX-4). These two species, together with the other giant rat *Spelaeomys florensis* represent more than 80% of all murid remains. *Komodomys rintjanus* is particularly scarce and has been recovered from a few spits only. In spits 21-29 *Rattus hainaldi* is quite abundant, but the total number of remains is quite low.

These remains can be assigned to Unit 8-9 (Late Glacial, 16-11ka and Holocene, Roberts et al., 2009). In fact, one dating from spit 37 gave an age of only 1.37 ka BP, whilst from spit 45 16.4 ka. Two teeth of *Homo floresiensis* have been recovered from spits 48 and 51 (Morwood and Jungers, 2009b).

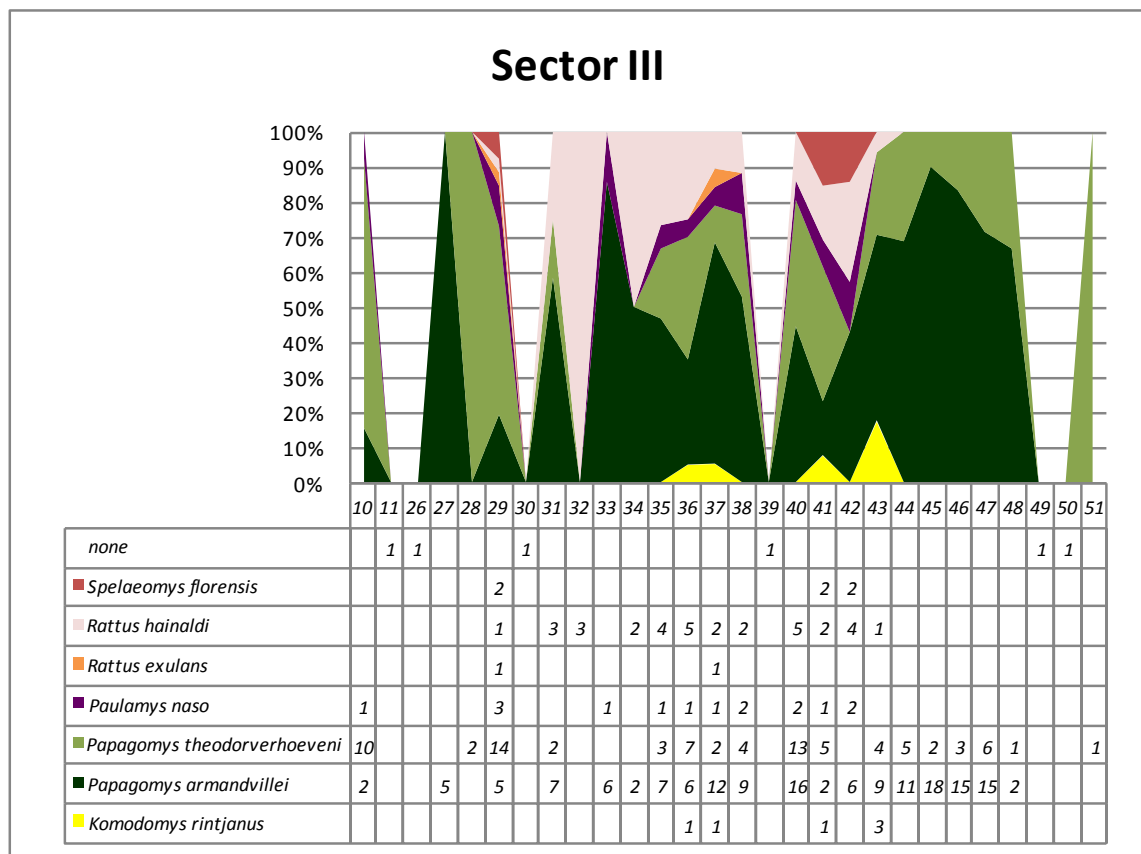


Figure IX-2: Stratigraphic distribution of rodents in Sector III

## Sector VII

The spits investigated in this sector are also dominated by giant rats (Figure IX-3); nevertheless it is possible to detect a change in the sequence: whilst the relative abundance of *Papagomys* species is quite constant, the other species' relative abundance varies. *Komodomys rintjanus* decreases going upwards, and is replaced first by *Spelaeomys florensis* and then by *Rattus hainaldi*. Only one specimen of *Paulamys naso* has been recovered.

The remains from Sector III can be assigned to the Late Glacial, since C<sup>14</sup> dating from spits 45-67 range ages between 12.9 and 19 ka BP (Roberts et al. 2009). *Homo floresiensis* has been recovered from spits 50-69 (Morwood and Jungers, 2009).

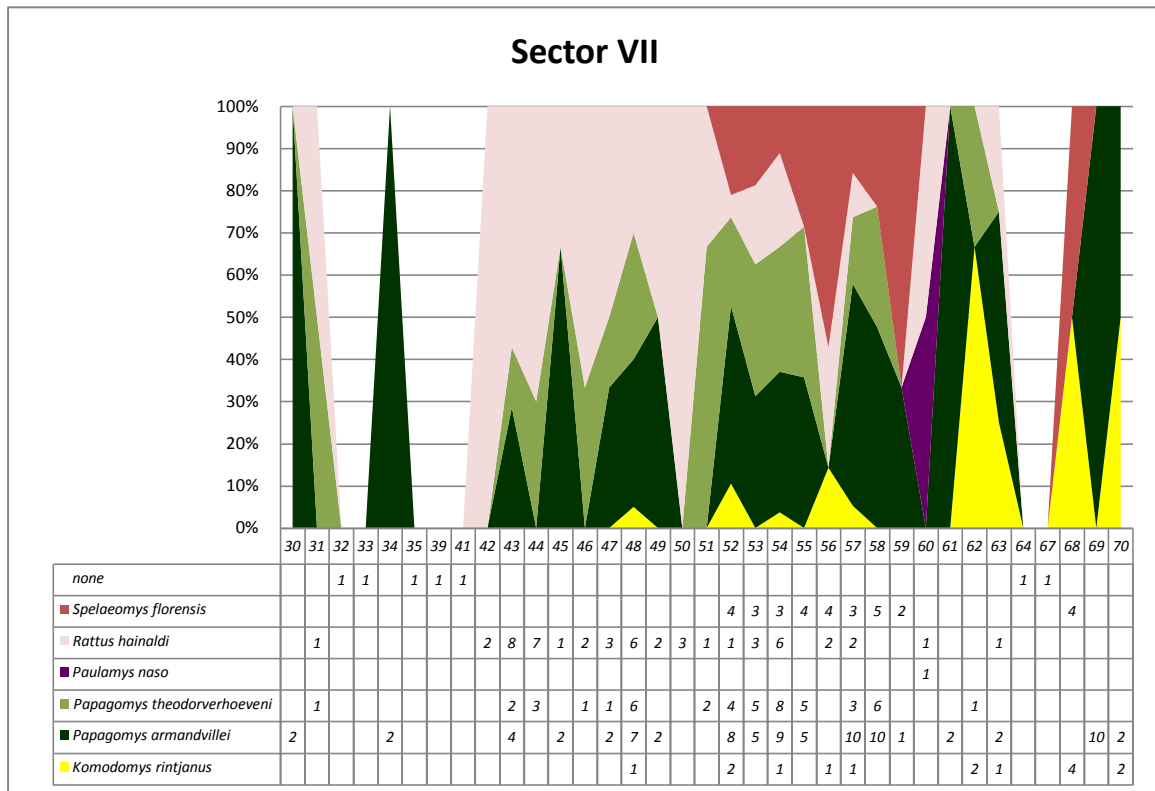
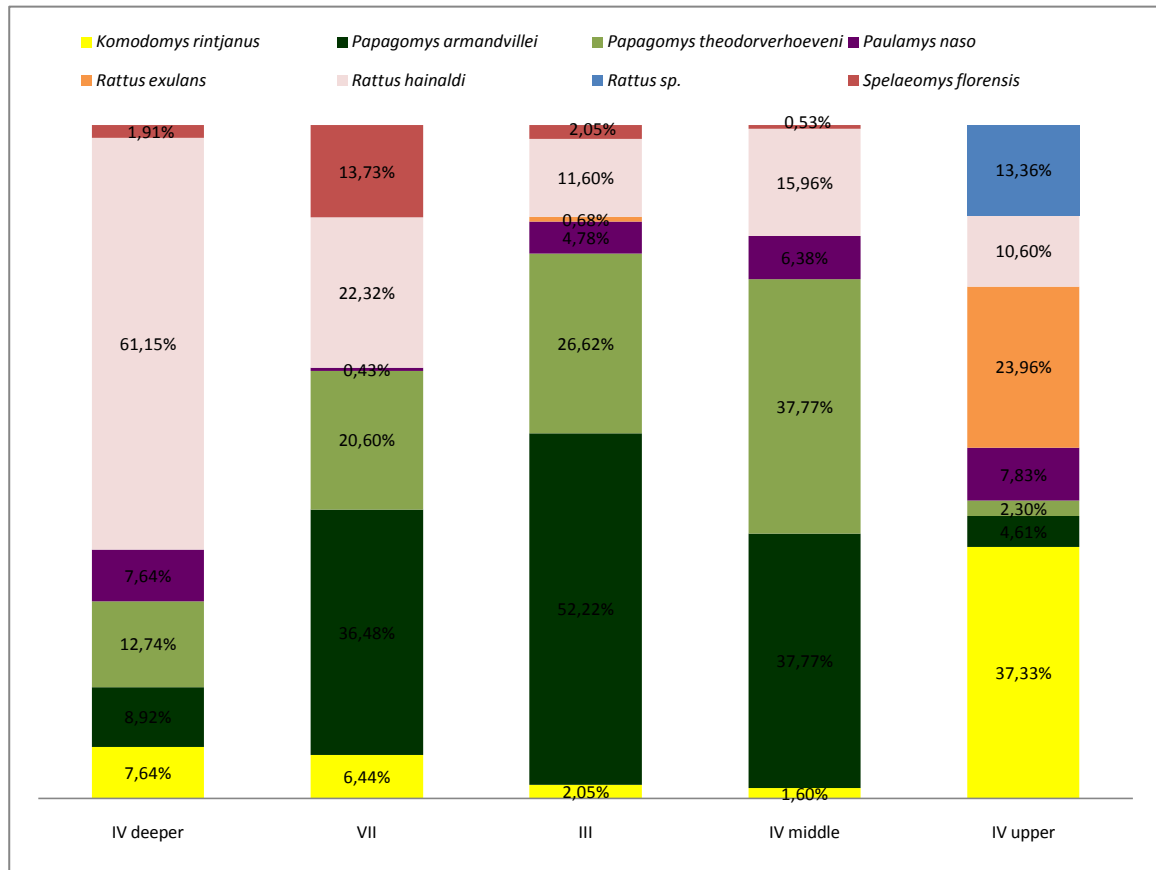


Figure IX-3: Stratigraphic distribution of rodents in Sector VII

## Discussion and conclusions

Comparing the rodent association from different sectors (Figure IX-4), it is clear that there are strong similarities among the middle portion of Sector IV and Sectors III and VII. The deepest and the uppermost spits yielded a completely different faunal association. During the Early Pleistocene, *Rattus hainaldi* dominated the association; most of the other species are equal, with about 10% of relative abundance, with the exception of *Spelaeomys florensis*, which is particularly rare. Late Glacial and Early Holocene deposits (Units 8 and deepest 9) are characterized by the predominance of giant rats; in particular *Papagomys armandvillei* and *P. verhoeveni* (*Spelaeomys florensis* is abundant only in sector VII – 13.73%). In Late Holocene (after around 4ka BP) there is a complete renewal in the association, with the drop in the relative

abundance of endemics and the occurrence of cosmopolitan species. The last occurrence of *Spelaeomys florensis* is recorded in Early Holocene deposits from sector IV.



**Figure IX-4: Relative abundance of rodents in sectors. Since Sector IV spans a longer time (last 100ka) and changes in the distribution of rodents have been detected, it has been divided in three different parts, explained in the text.**

No other extinction is recorded among rodents, but *Papagomys theodorverhoeveni* has not been found living in Flores at the moment and most endemics are now very rare. The passage between Late Glacial and Early Holocene, that is particularly harsh in continental record, does not have great repercussions on Liang Bua rodent association. The arrival of modern human after the volcanic events at 16-11 ka does not seem to affect the association deeply, except for a further increase in the abundance of *Papagomys* species remains and a further decrease in *Spelaeomys florensis*. The arrival of Neolithic agriculturalists had much stronger effects. Cosmopolitan species (*Rattus exulans* and *Rattus sp.*) were introduced and their abundance increases quite suddenly, so that in the uppermost spits they represent almost the whole of the remains recovered. The more stable species is *Paulamys naso*, which keeps its relative abundance always around 6%; it undergoes a reduction in Late Glacial, indicating weak tolerance towards dryer environments.

The stratigraphy spans all Late Pleistocene and Holocene. Great climatic change occurred in this period (Westaway et al., 2009b). However, we do not have a continuous record for the rodents. In the material examined there is a large temporal gap, since no material from Units 5-6 was available at the moment of the study. Thus, the material considered comes from:

- Units 2, 3 and 4 (Sector IV, from around spit 35 downwards); Late Pleistocene, 61-130 ka BP (Westaway et al., 2009a);

- Unit 7 (Sector VII, from around spit 55 to spit 70); Late Glacial, 18-16 ka;
- Unit 8 (Sector III; VII, spit 55-30); Late Glacial, 16-11 ka;
- Unit 9 (Sector III; Sector IV spits 30-1); Holocene. Since spit 17 first evidence of Neolithic.

The Late Glacial and Early Holocene association is different from the previous one and is characterized by the abundance of giant rats. The main question is: is this change in relative abundance related to the environmental change or is it related to human behaviour? The latter seems to be the most likely explanation. First, giant rats are difficult to hunt by most birds because of their size. At Liang Bua the presence of giant birds has been demonstrated (van den Bergh et al, 2009; Meijer et al., 2010), but the accumulation in cave of rodents' bones can be usually ascribed to few species; animals of the size of *Papagomys* species and *Spelaeomys florensis* are not usually prey. Therefore, accumulation cannot be explained with owl or raptor pellets.

Many mandibles were burnt (but of course we cannot know if it was accidental or intentional). The increase in giant rats' relative abundance coincides with the disappearance of the only large mammal present in the island before the Holocene introductions, *Stegodon florensis insularis*. Its last occurrence is in Unit 8, before the volcanic episodes that took place in Late Glacial. Its disappearance could have affected notably the diet of *Homo floresiensis* and later of *Homo sapiens*. On the other hand, the strong increase in giant rats is already recorded in the deepest spits of Sector VII (at the beginning of Late Glacial), when many remains of the elephantoid have been recovered. Furthermore, the climatic condition during Late Glacial were likely very different than the ones attested before.

Westaway et al. (2009a) attests dry conditions until 17ka and wet conditions since 11ka, with a transitional phase in the middle. If small mammals were so susceptible to these climate changes, we should notice a striking difference between Early Holocene layers in Sector IV and the initial phase in Sector VII; the only significant difference is the variation of middle size murids: *Komodomys rintjanus* is more abundant in dry conditions and *Paulamys naso* in wet ones. *Spelaeomys florensis* seems to be less abundant in wet environment. *Papagomys armandvillei* and *P. theodorverhoeveni* do not seem to be particularly sensitive to climatic/environmental change and this could support the hypothesis of a relationship with human diet.

Stronger evidence could be found with the study of eventual cutmarks on post-cranial bones, but these have not been studied yet. Comparing the recent distribution of these species, living specimens show a different ecological adaptation: *Komodomys rintjanus* seems to be adapted to dry, thorny scrub habitats (Aplin et al., 2008), *Paulamys naso* seems to be more adapted to montane forest (Musser and Carlton, 2005), which are wetter environments than the former. Thus, *Komodomys* can be considered as an indicator of dryer climate, whereas *Paulamys* preferred moister conditions (related to the general climate present on Flores). Thus, the relative abundance of Late Glacial-Early Holocene rodents remains reflects well the present knowledge about the ecology of these endemics and there is not contrast with the climatic information collected by Westaway et al. (2009a) on the basis of the analysis of Oxygen isotopes in stalagmites of Liang Bua cave. Recent renewal in rodent association cannot be attributed to climatic change, but is ascribable to the introduction of new species by Neolithic agriculturalists and maybe to the disturbance effect of the spreading of agricultural activities.

# PART 3

## X. Conclusions

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*"We shall not cease from exploration/And the end of all our  
exploring/Will be to arrive where we started/And know the place for  
the first time."*

*T. S. Eliot*

Since the first purpose of this thesis was to detect and compare the traces of isolation and in particular the effects of insularism on Quaternary fossil assemblages of some small mammals, in the next paragraphs I will consider the main aspects related to insularism and I will see which were the responses in Sicily and in Flores. The different results on them will be related to the different features of these islands: the first is a large island, very close to the mainland; the latter is part of a large archipelago and surrounded exclusively by islands.

I will take into account the mammal communities; since Chiroptera are flying mammals, and the conditions for their dispersals are different from other mammals, they have not been considered in the present study.

### ***Arrivals***

Two different aspects are related to this topic: how many dispersals events took place and which were the modalities of colonization. In Sicily, it is possible to notice that many dispersal events took place in Quaternary. Five different faunal complexes followed one another, and each one is characterized by new arrivals, and at least two dramatic faunal renewals with an almost complete substitution of the faunal elements took place at the transition between M. Pellegrino Faunal Complex (FC) -*E. falconeri* FC and *E. falconeri* FC– *E. mnaidriensis* FC (Figure X-1). The first transition regards the substitution between two highly endemic and unbalanced faunas, while the second one marks the breakdown of a period of strong geographic isolation and records the arrival on the island of several large mammalian taxa from the continent.

The ancient faunal complexes are characterized by the “elephant-deer” fauna sensu Sondaar (1977); since more vagile species characterize these faunal complexes, the colonization probably took place in consequence of stochastic events, by a sweepstake route. *E. mnaidriensis* faunal complex records the occurrence of a less impoverished fauna, and in Pianetti-San Teodoro FC the fauna is balanced, with species from all the orders, even perissodactyls. The presence of a balanced fauna, even if impoverished compared to the contemporaneous peninsular one, can be a consequence of brief connections with the mainland, likely in correspondence of the sea low-standing phases of the Last Glacial cycle.

Quaternary mammal list of Sicily				
Monte Pellegrino	Elephas falconeri	Elephas mnaidriensis	Pianetti-San Teodoro	Castello
<i>Pannonicus arzilla</i>	<i>Vulpes</i> sp.	<i>Panthera leo</i>	<i>Crocota crocata</i> cf. <i>spelaea</i>	<i>Canis lupus</i>
<i>Asoriculus burgtol</i>	<i>Lutra trinae</i>	<i>Crocota crocata</i> cf. <i>spelaea</i>	<i>Canis</i> cf. <i>lupus</i>	<i>Vulpes vulpes</i>
<i>Apodemus maximus</i>	<i>Elephas falconeri</i>	<i>Canis lupus</i>	<i>Vulpes vulpes</i>	<i>Equus caballus</i>
<i>Leithia</i> sp.	<i>Crocidura esuae</i>	<i>Lutra trinae</i>	<i>Ursus</i> cf. <i>arctos</i>	<i>Equus hydruntinus</i>
<i>Mahlams</i> cf. <i>gollcheri</i>	<i>Leithia carrei</i>	<i>Ursus</i> cf. <i>arctos</i>	<i>Elephas mnaidriensis</i>	<i>Sus scrofa</i>
<i>Pellegrinia panormensis</i>	<i>Leithia melitensis</i>	<i>Elephas mnaidriensis</i>	<i>Sus scrofa</i>	<i>Cervus elaphus</i>
<i>Hypolagus</i> sp.	<i>Mahlams</i> <i>gollcheri</i>	<i>Sus scrofa</i>	<i>Equus hydruntinus</i>	<i>Bos primigenius</i>
		<i>Hippopotamus pentlandi</i>	<i>Cervus elaphus siciliae</i>	<i>Erinaceus europaeus</i>
		<i>Cervus elaphus siciliae</i>	<i>Dama carburangelensis</i>	<i>Crocidura</i> cf. <i>sicula</i>
		<i>Dama carburangelensis</i>	<i>Bos primigenius siciliae</i>	<i>Apodemus</i> cf. <i>sivaticus</i>
		<i>Bos primigenius siciliae</i>	<i>Erinaceus europaeus</i>	<i>Microtus (Terricola)</i> ex gr. <i>savii</i>
		<i>Bison prisacus siciliae</i>	<i>Crocidura aff. esuae</i>	
		<i>Erinaceus europaeus</i>	<i>Leithia</i> cf. <i>melitensis</i>	
		<i>Crocidura aff. esuae</i>	<i>Mahlams</i> cf. <i>wiendictensis</i>	
		<i>Leithia</i> cf. <i>melitensis</i>		
		<i>Mahlams</i> cf. <i>wiendictensis</i>		

Figure X-1: list of species Quaternary mammal successions from Sicily



In Flores the situation is different. Three faunal successions took place (plus the recent one), but among them there is always been a high degree of continuity (Figure X-2). When the faunal renewal took place, there was usually phyletic continuity between the old species and the more recent one. This could also be affected by the scant knowledge of oldest faunal associations and the big gap in fossil documentation during Middle Pleistocene; nevertheless it is undeniable that the few species known from the oldest faunal complexes are strictly phylogenetic related to the more recent ones (i.e. elephants and rodents). Thus, the island has been highly isolated for long, and species evolved on the island.

<b>Quaternary mammal list of Flores</b>		
<b>Fauna A Tangi Talo</b> <i>Stegodon sondaari</i>	<b>Fauna B</b> <i>Stegodon florensis</i> <i>Hooijeromys nusatenggara</i>	<b>Liang Bua</b> <i>Stegodon florensis insularis</i> <i>Papagomys armandvillei</i> <i>Papagomys verhoeveni</i> <i>Spelaeomys florensis</i> <i>Komodomys rintjanus</i> <i>Paulamys naso</i> <i>Rattus hainaldi</i> Shrewrat <i>Crocidura</i> or <i>Suncus</i> species A <i>Crocidura</i> or <i>Suncus</i> species B

Figure X-1: list of species Quaternary mammal successions from Flores

The arrivals were few and probably accidental, otherwise many species should have come and the endemics should have reduce (on the contrary, they are abundant till Holocene), so that the dispersal took place by a sweepstake route. Dispersals are few: before recent times, in small mammals *Spelaeomys florensis* and maybe *Rattus hainaldi* reached the island before Middle and Late Pleistocene. Insectivores are not known in Middle Pleistocene record of Flores, but two of them (both endemics) are recorded at Liang Bua (van den Hoek Ostende et al., 2007). Few remains of a shrewrat, not described yet, have been recovered (Bergh et al., 2009). Nevertheless, the great part of small mammals is made up of murids, all strictly related among them, belonging to the same clade and related to the early Middle Pleistocene form, *Hooijeromys nusatenggara*.

### **Species richness**

Species richness increased in Sicily within the younger intervals (Figure X-3 and X-4). Older faunal complexes were characterized by low biodiversity, with few species. In recent complexes (since *E. mnaidriensis* FC) the biodiversity increases; even if it is not as high as mainland ones, it is far higher than isolated insular systems, indicating a quite easy accessibility.

Order \ Faunal complex	Monte Pellegrino	<i>Elephas falconeri</i>	<i>Elephas mnaidriensis</i>	Pianetti-San Teodoro	Castello
Rodentia	4	3	2	2	2
Insectivora	1	1	2	2	2
Carnivora	1	2	5	4	2
Lagomorpha	1	0	0	0	1
Proboscidea	0	1	1	1	1
Perissodactyla	0	0	0	1	2
Artiodactyla	0	0	6	3	3
<b>Mammal species richness</b>	<b>7</b>	<b>7</b>	<b>16</b>	<b>13</b>	<b>13</b>

Figure X-3: mammal species richness in the faunal succession of Sicily

On Flores, biodiversity is low in Early and early Middle Pleistocene faunal groups. The biodiversity is higher in Late Pleistocene (Liang Bua), but the increase in species richness can be mainly assigned to species representative of few clades that probably speciated on the island because of the strong isolation. It is also necessary to take into account that the Early-Middle Pleistocene fossil documentation is very scarce.

Order \ Faunal unit	Fauna A Tangi Talo	Fauna B	Liang Bua
<b>Rodentia</b>	0	1	7
<b>Insectivora</b>	0	0	2
Carnivora	0	0	0
Lagomorpha	0	0	0
Proboscidea	1	1	1
Perissodactyla	0	0	0
Artiodactyla	0	0	0
<b>Mammal species richness</b>	<b>1</b>	<b>2</b>	<b>10</b>

Figure X.4: mammal species richness in the faunal succession of Flores

### ***Faunal association and Endemism degree***

As for the species richness, Sicily passes from a condition of very high endemism with many endemic species and entire orders not represented, to a Late Pleistocene faunal assemblage with few endemic subspecies or species and an almost completely balanced fauna. Oldest faunal complex (Monte Pellegrino FC) is made up of a mixed association, with endemic rodents among which the dormice (*Maltamys* and *Leithia* genus), *Pellegrinia panormensis* and *Apodemus maximus*, and a large endemic insectivore (*Asoriculus burgioi* is twice as large as the mainland counterpart); large mammals are absent. *Hypolagus* and *Pannonictis arzilla* are the larger forms and do not present traces of endemism. A similar condition characterises the following faunal complex, as well, *Elephas falconeri* FC, but two small carnivores are present (*Vulpes* sp. and *Lutra trinacriae*). There is also the first occurrence of the dwarf elephant that gives the name to the complex, which is the smallest elephant ever found and is in association with giant dormice and an endemic shrew (*Crocidura esuae*). The situation changes abruptly in the following faunal complex, that still presents traces of strong endemism (dwarf elephant, dormice and shrew), but presents an almost balanced association, with large carnivores and artiodactyls. The faunal balance increases in the following faunal complex, with the appearance of almost all the orders. With the exception of the old faunal complexes, where endemic genus persist long, in the next

faunal complexes the endemism degree is low (limited to size reduction) and endemic species are present for a short time.

In Flores the faunal association is always unbalanced, with only insectivores, rodents and endemic elephantoids, with the exception of Holocene association (in which man introductions are the main responsible). Because of the important gap within the fossil documentation of Middle Pleistocene, it is not possible to express a judgment on the durability of some species on the island. Nevertheless, Liang Bua cave spans all the Late Pleistocene and no faunal arrival is attested till the arrival of modern humans in the Holocene. All the species documented are endemic (always with the exception of human introductions) and some of them are highly modified (giant rats and dwarf elephants)

### ***Size variation***

Sondaar (1977) pointed out that on islands size variation is higher than on mainland species. I have noticed that size variation is effectively very high in rodents from Liang Bua, and usually there is not a clear border between the size limits of one species and the limits of the bigger/smaller one. The rodents look very similar, with the exception of *Rattus hainaldi*, *Spelaeomys florensis* and the shrewrat, and the identification of the species is very challenging in some occasions. On the contrary, not such a size variation has been detected in remains from Sicilian samples that, on the other hand, are also representative of a shorter time span.

### ***Human impact***

In Sicily it is very difficult to detect the impact of man on the fauna, since up to date no sure archaeological or anthropological remain could confirm the presence of humans on the island before the late part of Late Pleistocene. The arrival of man at San Teodoro cave is contemporary to the first occurrences in the fossil record of horses and mice. This could indicate an intentional transport as well as the dispersal through a corridor; the fauna at this point is balanced and animals could have reached the island for the same reason why the man came there at that time, probably a land-connection in correspondence of sea low-standing phases. At this point endemic dormice are disappeared, as well as the endemic shrew *Crocidura esuae*. The Savi vole is present, but is different from the *M. (Terricola)* of the previous phase. Nevertheless, this looks like a transitional complex, since the complete disappearance of endemics takes place only in Castello FC, when a landbridge was present (during LGM sea-level dropped of 120 m) (Antonioli et al, 2002).

On the other hand, in Flores the endemics lived together with an endemic human form, *Homo floresiensis*, and the only human impact can be detected with the arrival of modern man in the Holocene, who brought with him rats and large mammals (*Rattus exulans*, *Rattus rattus*, *Sus scrofa*, *Macaca fascicularis* and *Paradoxurus hermaphrodites*). There is no geological evidence that a form of landbridge or corridor could have been present at that time, despite the sea-level drop; furthermore, the arrivals did not take place during the Last Glacial Maximum, but in a

successive moment, when the sea-rising was already in progress. After *Homo sapiens* arrival, the small endemic mammals that did not get extinct reduced hugely their relative abundance.

### ***Extinction***

In Sicily, all the Pleistocene strongly endemic species got extinct. In recent time, only endemic sub-species are present, that evolved from mainland forms that reached the island during the Last Glacial cycle. In Flores few species went extinct; the great part of them, giant rats included, underwent a strong reduction, but are still dwelling the island or did not get extinct till very recent times (*Spelaeomys florensis*). *Stegodon florensis insularis* and *Homo floresiensis*, the only large mammals recorded, got extinct before or in correspondence of the volcanic episode around 16ka ago, while endemic small mammals persist (*Papagomys armandvillei*, *Rattus hainaldi*), or have a relict distribution (i.e. *Komodomys rintjanus*), or were considered extinct and have been recently re-discovered (i. e. *Paulamys* sp.). Arrivals from the mainland and climatic change (that triggers the reduction in sea barriers or the formation of corridors) affected strongly the extinction of endemics in Sicily, while in Flores did not cause significant extinctions.

### ***Conclusive remarks***

On Flores and Sicily faunal associations it is possible to see the complete different response of the faunal diversification to the difference insular condition. Sicily is the typical continental-like island, above all in Late Pleistocene, characterized by frequent arrivals, caused either by the short distance from the mainland and the relatively shallow water barrier that separates it from the mainland. With the exception of Early Pleistocene faunal successions, when it was not even an island like today, endemism degree was quite low; few endemic species, many arrivals, short species enduringness and high species diversity characterize the faunal successions. The insular condition is expressed only in Middle Pleistocene strongly endemic species and few scanty endemic sub-species from Late Pleistocene.

On the contrary, Flores is a typical oceanic island, characterized by a strongly endemic fauna: complete lack of carnivores, strongly endemic and long persistent species, and biodiversity increased only by evolutionary radiation on the island. Since it is surrounded exclusively by islands, each one with its own endemics, it is even difficult to trace the forerunners of the local species.

## XI. References

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