

The house mouse from a prehistoric site in Fuerteventura (Canary Islands, Spain)

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Abstract. Remains of a rich mouse population from a prehispanic site of human occupation in Villaverde (Fuerteventura, Canary Islands) of an age around 1000—1700 years B. P. is studied. Eleven characters in teeth, skull and postcranial skeleton are compared with European and African forms of house mouse and wild mice. Four characters are shared with *Mus musculus*, two with *Mus spretus* and five are peculiar features. Most of the eleven characters are shared by the recent house mouse of the Canary Islands. This suggests that both the subfossil and the recent Canarian mouse belong to a different subspecies of *M. musculus*. Some of its peculiarities (relatively large teeth and hind limbs) appear to be related to a semi-commensal and wild habitat. The origin of the house mouse of the Canary Islands may be the Western European or Northern African populations of *M. m. domesticus*.

Key words. Mammalia, Muridae, *Mus musculus*, Canary Islands.

Introduction

The settlement of islands by wild life and prehistoric men is a puzzling problem, particularly in the case of oceanic islands (Axelrod 1972; Carlquist 1974). The Canary Islands have a rich endemic flora and fauna suggesting a long isolation period, and it has a primitive culture of prehistoric men, indicating an old settlement. But the absolute ages of both, substratum and culture seem to be relatively young (Martin de Guzmán 1978; Araña et al. 1978; Cuscoy 1983; Onrubia 1987).

In this paper a rich subfossil population of house mice is described. It is associated with a prehispanic human habitat from Villaverde (Fuerteventura, Canary Islands) and it is dated between 1000 and 1700 years B. P. Domestic and commensal animals are an important link among human cultures, because they are closely related to the immigration history of the people. At the same time, they allow to know the recent evolutionary process leading to the speciation phenomena. The study of the commensal island animals leads to obtain both kinds of information.

The problem of the house mouse

The house mouse and the wild mouse in Europe and North Africa were recognized by Miller (1912) and Cabrera (1914) as two sympatric species, but many different names were used for local demes (Miller 1912; Cabrera 1911; 1923). Schwarz et al. (1943) and Ellerman et al. (1951) assemble both species and all names applied to the demes as junior synonyms of only one single species, *Mus musculus* Linnaeus. Many subspecific names were then employed for sympatric, differentiated demes. This irregular situation (subspecies are not sympatric because they hybridize in the absence of a genetic isolation system) was studied by Britton et al. (1976), Orsini (1982),

Orsini et al. (1982), Bonhomme et al. (1983) and Bonhomme (1986) among others. They propose a new scheme, where two mice species may coexist in a region.

According to these authors, two geographical races of the house mouse, *M. m. musculus* in North Central Europe and *M. m. domesticus* in South Western Europe and Africa, may have either wild or commensal demes. On the other hand, the wild mouse belongs to two or three different species: *M. spicilegus* (Northern and Southern form) in the East Mediterranean and Danube region, and *M. spretus* in the West Mediterranean area; the latter species is occasionally semi-commensal and it is displaced by *M. musculus* in the richer and wetter places (Carrascosa, in press). According to Orsini (1982) the North-Eastern subspecies of the house mouse, *M. m. musculus*, followed probably the immigrations of the Indoeuropean peoples from Asia. The Western subspecies *M. m. domesticus* is probably related to Middle-East and Punic paths of settlement. *Mus spretus* is claimed to have a North African origin (Schwarz et al. 1943; Orsini 1982; Palomo et al. 1983). A chart of the mice species distribution is shown in fig. 1.

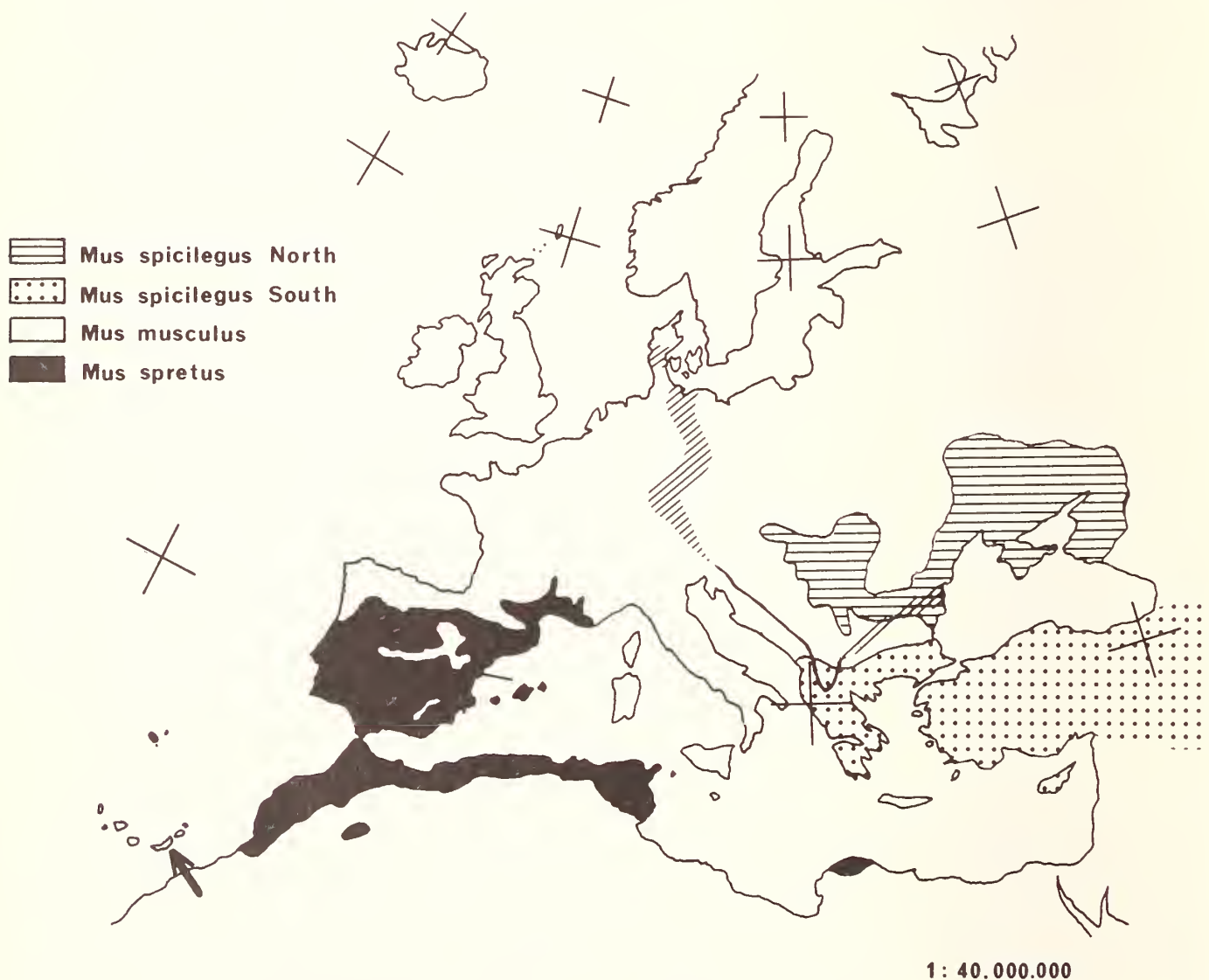


Fig. 1: Geographical distribution of *Mus* species. *Mus musculus* is present in the whole area; slanting bars indicate the hybridization zone between its western and eastern subspecies: *M. m. domesticus* and *M. m. musculus* respectively. The arrow shows the Fuerteventura Island situation.

The mouse now living in the Canary Islands is considered to be *Mus musculus* (Cabrera 1914; Rey 1975; Santos Guerra 1977), but neither caryological nor electrophoretic analysis have been made, and its origins are unknown. The tail/body length ratio, allowing to distinguish the house mouse (*M. musculus*) from the other wild *Mus* species, supports the specific status of the recent Canarian mouse (pers. obs.). The archaeological site of Cueva Villaverde (Fuerteventura) demonstrates that the house mouse occupied the island together with the aboriginal men before the hispanic colonization. We study this population with modern systematic criteria, in order to elucidate its identity for a better knowledge of the settlement of the Canary Island.

The archaeological site

Cueva Villaverde is a cave in a 200 m long volcanic tube, inhabited by men. Archaeological and zoological remains lie both inside and outside the cave entry. The site is located at the Villaverde town, near La Oliva (22° 38' 10" N and 10° 12' 30" W G. M.) in Northern Fuerteventura, Canary Islands, Spain (fig. 2). The details of the excavation and the human finds (ceramics, tool implements, human skeletons) are described in Garralda et al. (1981), Meco et al. (1982) and Hernández & Sánchez (1986).

The cave is about 5 m deep, 16 m long and the height between the recent floor and the roof is around 1.5 m. Some big semicircular and transverse stone walls were built near the sides of the tube, closing the archaeological site to the East. The West end seems to be the original entry, and was filled by debris, rocks and even a mill stone, after the burial of an adult man and a child.

Four squares (A₁–A₄) of 4 m² each at the northern side of the cave, and three sections (C₁–C₃) at the outside around the entry of the cave, have been excavated since 1979. Sixty samples containing microfauna were collected: of these, 40 are from the cave and 20 from outside. Most of the samples come from the first centimetres of sediments containing ceramics. The thickness of the archaeological layer varies from about 180 cm outside, to 60 cm near the entry of the cave, and to 30 cm at the rear. Different levels have been distinguished using some ash planes as markers and discontinuities. Stratigraphic correlation between levels of the different sections is not yet possible.

Absolute dating has been obtained by C¹⁴ analysis of coal. Age calculations vary from 1070 ± 50 BP at the surface, to 1730 ± 50 BP at level 3 in the cave. Samples from outside were dated from 1080 ± 80 BP to 1390 ± 80 BP at level 3 (Hernández & Sánchez 1986).

The finds from Villaverde, other than archaeological and human remains, are mainly molluscs and vertebrate bones. Ash and coal rests are also frequent. Some vertebrate bones were partially burned.

Eighteen species of marine and six species of terrestrial molluscs have been identified respectively by Meco et al. (1982) and Hutterer (pers. comm.). Fishes are frequent; large specimens of *Sparisoma cretensis* L. are common; but the majority of the fish fauna has not been studied yet. Three species of reptiles have been recognized by Sanchiz & López-Jurado (pers. comm.); Gekkonidae (*Tarentola mauritanica*) appear to be the most abundant. Birds are under study by Mourer-Chauvire (in litt.); a preliminary report indicates the presence of fifteen species, where the quail (*Coturnix coturnix*) is the best represented one. The large mammals have been published by Meco et al. (1982), indicating the abundance of goat (more than 8000 bone fragments of about one hundred individuals), the presence of pig (five individuals) and a seal.

Small mammals are very frequent in the Villaverde cave and in the deposits outside the cave. The most abundant species is a large murid of the size of a young rat, which is now being studied in co-operation with R. Hutterer (Bonn) and J. Michaux (Montpellier). An unexpected and peculiar shrew is also present in all the microfaunal samples. No living representatives were known hitherto in the Canary Islands but it has recently been found still living in the Eastern Canaries (Martín et al. 1984) and since then has been described as a new species of *Crocidura* (Hutterer et al. 1987).

The remains of the house mouse become progressively more abundant in the upper sediments; it is almost absent (less than 0.1 %) in the samples number 586 and 588 (A₄ level 3). These samples yielding extremely rich microfaunal remains were collected some 15 cm below the lowest archaeological level. The increasing abundance of mice in the sediments of Villaverde appears to be related to that of the human settlement.

In order to give an idea of the preservation of mice remains, table 1 shows the amount of skeletal elements of the house mouse recovered in eight representative samples. Sample C₂ 1041 was taken with sediment, and sorted in the laboratory; it contains the best preserved elements (skulls).

Table 1: Number of skeletal elements in various representative samples from outside and inside the Villaverde cave. NMI: Minimum number of individuals, NR: Total number of elements recovered.

	Outside			Cave				
	Level 2 no. C ₁ 406	C ₂ 1041	Level 3 C ₃ 2066	Surface no. A ₁ 188	A ₁ 194	A ₂ 389	Level 2 A ₃ 436	Level 4 A ₁ 384
Skull	—	6	—	—	—	—	—	—
Upper Maxilla	19	23	1	3	19	16	1	—
Lower Jaw	90	6	6	23	51	127	6	—
Scapula	1	4	—	—	5	4	—	—
Humerus	—	5	3	4	50	61	4	—
Radius	—	?	—	—	5	20	—	—
Ulna	—	?	—	1	24	35	6	—
Pelvis	9	8	4	14	56	133	11	—
Femur	7	7	10	9	117	184	27	—
Tibia	11	8	8	14	155	233	57	1
NMI (Min. Ind.)	56	18	6	14	78	161	30	1
NR (No. total)	137	67	32	68	482	813	112	1

The Villaverde house mouse

Fifteen samples have been chosen from Villaverde, according to their richness and stratigraphical position, in order to study *Mus musculus*. Morphological and biomechanical variability have been controlled for taxonomic identification.

A first comparison among the various samples showed their homogeneity. We will refer to it as the Villaverde population of the subfossil house mouse, though the assemblage has been accumulated during more than 500 years.

A second direct comparison was made between the Villaverde population and several subfossil and recent *Mus* samples from the Canary Islands, Morocco and Western Europe. Finally, we have used the data from the abundant literature about wild and commensal house mice for an indirect comparative study. This last source of data must be carefully selected, because many of the authors between 1940 and 1980 do not distinguish between the different species of mice, and their results are therefore unreliable.

The main features allowing the distinction between mouse taxa are the size, the colour, and the relative length and thickness of the tail (Thomas 1896; Miller 1912; Cabrera 1914). The different development of a notch in the upper incisor was mentioned by Miller (1912) to distinguish the two sympatric species of *Mus* in the Mediterranean area. This last character used to be the only criterion to identify mice species

from owl pellets, scats and osteological collections; but the systematics of mice was misunderstood by Schwarz et al. (1943) and later authors and this feature was wrongly applied.

After the biochemical confirmation of the existence of two sympatric species in the Mediterranean area, Darviche (1978) found some new differential characters in the mouse skeleton and teeth, inspired by the work of Marshall (1977) on Asiatic mice. Later, Darviche & Orsini (1982), Orsini (1982) and Orsini et al. (1983) improved the system for the morphological differentiation of the *Mus* species, allowing the correct identification of osteological remains.

According to their results, the Western European and African mouse species, *Mus spretus* and *M. musculus domesticus* may be distinguished by 1) the zygomatic coefficient, 2) the anterior profile of the zygomatic plate, 3) the zygomatic foramen, 4) the squamosal-parietal suture, 5) the notch of the upper incisor, 6) the cusps of the M_1 and 7) the size of bones and teeth. All these characters have been studied in the Villaverde population, and some other peculiar features of its own.

The zygomatic coefficient

This feature observed by Orsini (1982) is the best diagnostic character differentiating *M. musculus* from *M. spretus*. It may be measured dividing the minimal width of the frontal branch of the maxilla by the maximal width of the descending branch joining the zygoma (Orsini et al. 1982, 1983). This index has small values in *Mus musculus* (CZ = 0.34–0.66; \bar{x} = 0.50) and larger ones in *Mus spretus* (CZ = 0.60–1.08; \bar{x} = 0.80) and the wild Eastern *Mus* species. Palomo et al. (1983) quoted a decrease of this index in *M. spretus* southward from Spain: CZ = 0.58–1.52, \bar{x} = 0.86 in the North and CZ = 0.32–1.20, \bar{x} = 0.76 in the South. These authors describe the way to take the measurements, that should be standardized.

Table 2 shows the values of this index for the various samples of the Villaverde mouse, for the outside and the cave associated samples, and finally for the whole population. The values are intermediate between those of both mice species.

In table 3 we compare the values and parameters of the distribution of this index for several samples of *Mus spretus*, *Mus musculus* and for a mixed association of both species from Valencia (Spain). The hypothesis of a blend of species in Fuerteventura mouse samples may be excluded after comparison with the high variability index (CV) of such a mixed association. The values from Villaverde show a normal variability as a homogeneous population.

After comparison between tables 2 and 3, it is clear that the mean zygomatic coefficient of the Villaverde mouse is significantly larger than those of *Mus musculus domesticus* and *M. m. musculus*, and smaller than that of *M. spretus*. Table 4 shows the results of the Student's test, which gives a rough idea of the signification of the differences. The two specimens of the recent *Mus musculus* from Gran Canaria used for comparison show also a CZ close to that of Villaverde house mouse (\bar{x} = 0.61).

Anterior profile of the zygomatic plate

This character was studied by Marshall (1977) and applied to European *Mus* by Darviche (1978), but this feature does not enable a correct discrimination between the

Table 2: Zygomatic coefficient values in the Villaverde house mouse population. SE: Standard error, SD: Standard deviation, CV: Coefficient of variation.

	Outside				Cave					
	No. sample	N	$\bar{x} \pm SE$	SD	CV	No. sample	N	$\bar{x} \pm SE$	SD	CV
Surface						A1—188 + 194 A2—389	14 9	0.64±0.06 0.48±0.08	0.11 0.11	17.17 23.64
Level 1						T2—394	24	0.68±0.03	0.09	12.61
Level 2	C1—406 C2—1041	10 29	0.57±0.05 0.64±0.03	0.07 0.09	12.56 13.97	A2—204 + 430 A3—436 + 509	5 9	0.57±0.07 0.66±0.05	0.07 0.07	11.84 9.90
Level 3 & 4 All outside	C1/2.1444	2 41	0.60 0.63±0.03	0.09	14.33	A1—436 All cave	1 62	0.64 0.64±0.03	0.11	17.50
Altogether		103	0.63±0.02	0.10		Range 0.375—0.883				16.02

Table 3: Zygomatic coefficient values in several populations of Spanish *Mus spretus*, European *Mus musculus* and a mixed association of *M. spretus*—*M. musculus* from Valencia (Spain). Data of Spanish populations are obtained from owl pellets. Data of other European mice are from Orsini (1982).

	N	\bar{x}	SD	CV	Range
<i>Mus spretus</i>					
PANCORBO	12	0.83	0.13	15.47	0.56—0.97
CARTUJA	12	0.88	0.13	15.01	0.67—1.16
VILLARIEZO	10	0.83	0.18	21.18	0.57—1.11
ARCOS	75	0.75	0.17	23.17	0.41—1.45
PINAR 1	37	0.78	0.20	25.43	0.49—1.34
PINAR 2	23	0.76	0.15	19.72	0.49—1.04
NO LOCALITY	81	0.84	0.18	21.77	0.48—1.35
ADAJA	57	0.83	0.15	18.57	0.51—1.18
<i>M. spretus</i> + <i>M. musculus</i>					
VALENCIA	77	0.70	0.30	43.23	0.22—1.37
<i>Mus musculus</i>					
HUNGARY	11	0.44	0.05	11.36	
AUSTRIA	33	0.45	0.05	11.11	
BULGARIA	30	0.48	0.12	25.00	
GREECE	22	0.47	0.05	10.64	
FRANCE	34	0.50	0.08	16.00	

species. *Mus spretus* sometimes has a rounded profile, and *Mus musculus* a straight profile in the anterior border of the zygomatic plate. Darviche (1978) found an ambiguous distribution of this character in *M. spretus* from Spain and Algeria. In our Canarian mouse, the profile is straight in most cases (pl. 1, figs. 1 b, 2).

Zygomatic foramen

A small foramen in the ventral part of the zygomatic plate is variably present in *Mus musculus* and absent in *Mus spretus*. The population from Villaverde presents a zygomatic foramen in some 40 % of the observed cases.

Squamosal-Parietal suture

According to Orsini (1982), *Mus musculus* has a deep, complex, irregular suture between the parietal and the squamosal, while *M. spretus* has a simple, regular, gently curved one. This character has rarely been observed in the Villaverde population, because the skulls were usually broken at the braincase. Some isolated squamosals show a rather simple suture, but its completeness cannot be warranted.

Upper incisor notch

This peculiar feature is extremely frequent in the Villaverde sample. The notch is almost always present and it is deep and in an advanced position in the middle of the shaft (pl. 1, figs. 1 b, 2). *Mus spretus* has no notch or only a very shallow one

Table 4: Comparison of the mean zygomatic coefficient between several samples of the Villaverde house mouse and several *M. spretus* and *M. musculus* populations. The lower half of the table shows the Student's test values and the degrees of freedom. The upper half shows the significance of each test (* = 95 % significance level, ** = 99 % significance level).

		VILLAVERDE (Fuerteventura)							<i>Mus spretus</i>		<i>Mus musculus</i>	
		1041	188 + 194	394	OUT- SIDE	CAVE	ALL	ARCOS	PINAR 2	AUST	FRAN	GRE
VILLAVERDE (Fuerteventura)	1041		—	—	—	—	—	**	**	**	**	**
	188 + 194	0.09 41	—	—	—	—	—	*	**	**	**	**
	394	1.69 51	—	—	*	*	—	*	**	**	**	**
	OUT- SIDE	0.41 68	—	2.20 63	—	—	**	**	**	**	**	**
	CAVE	0.04 89	0.06 74	1.58 84	0.47 101	—	—	**	**	**	**	**
<i>Mus spretus</i> SPAIN	ALL	1.17 130	1.19 115	2.34 125	0.21 142	1.06 163	—	**	**	**	**	**
	ARCOS	3.37 102	2.31 87	1.99 97	4.25 114	4.44 135	7.28 176	—	**	**	**	**
	PINAR 2	3.65 50	2.57 35	2.29 45	4.38 62	4.05 83	8.82 124	0.17 96	**	**	**	**
<i>Mus musculus</i>	AUST	10.35 60	8.20 45	12.65 55	10.16 72	9.17 93	29.79 134	9.75 106	11.04 54	**	**	—
	FRAN	6.43 61	4.92 46	8.11 56	6.44 73	6.35 94	14.86 135	8.03 107	8.47 55	3.05 65	—	—
	GRE	7.89 49	6.33 34	9.95 44	7.60 61	6.79 82	7.77 123	7.47 95	8.60 43	1.45 53	1.56 54	—

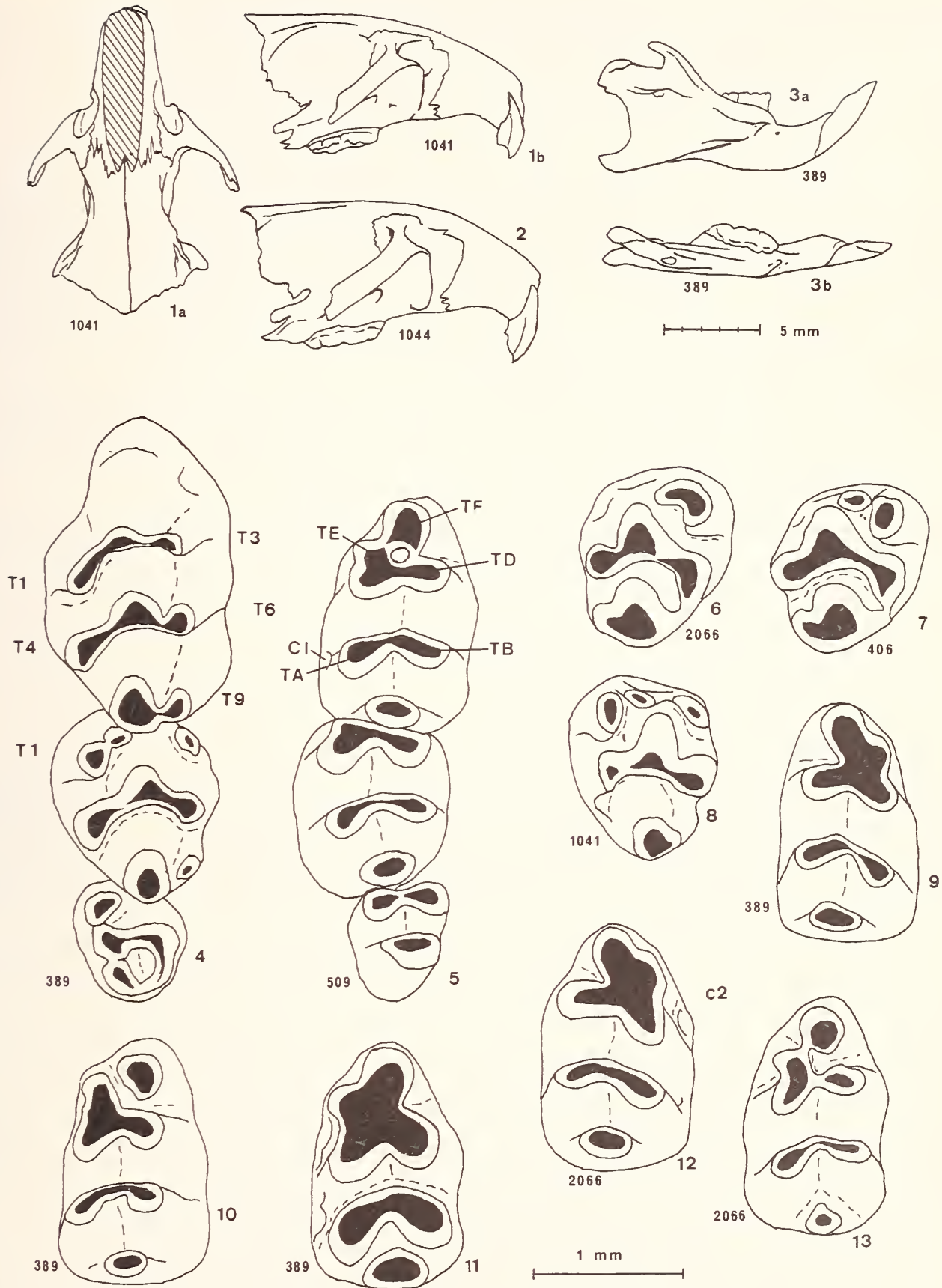


Plate 1: *Mus musculus* from Villaverde (Fuerteventura, Canary Islands). Skull and mandible: 1a, b — Dorsal and lateral view, EX V-1041; 2 — Lateral view of a larger specimen, EX V-1444; 3a, b — Lateral and occlusal view of the mandible, CV-389. Note the strong tubercle of the incisor root. Dentition: 4 — Upper tooth row, CV-389; 5 — Lower tooth row, CV-509. Isolated molars: M², 6 — EX V-2066; 7 — CV-406; 8 — EX V-1041. Note the double T1 in figs. 4, 7 and 8. M₁, 9, 10 and 11 — CV-389; 12 and 13 — EX V-2066. Note the small TE, the isolation of TF in the figs. 5, 10 and 13, and the accessory cusps c1 and c2 in the figs. 5, 11 and 12.

(91.8 %, Palomo et al. 1983). According to Orsini (1982), the notch is more frequent in *M. musculus domesticus* (96 %) than in *M. m. musculus* (75 %). The Villaverde population exceeds the high frequencies observed in *M. m. domesticus*.

Cusp of the lower M_1

The trilobed anterior part of the lower first molar differentiates *M. musculus* from the four-lobed morphology of *M. spretus* (and Eastern wild mouse species). The first anteroexternal cusp of M_1 (labial anteroconid, or TE) is reduced and poorly individualized in *M. musculus*; on the contrary, it is well developed and distinct from its surrounding cusps in *M. spretus*. Darviche (1978) noted that in *M. spretus* from North Africa this feature is pronounced.

In the 180 specimens from Villaverde the M_1 is trilobed and it has an extremely reduced TE (pl. 1, figs. 9–13). This character approaches undoubtedly our Canarian mouse to *Mus musculus*, and most probably to *M. m. domesticus*, that show this feature strongly marked (Orsini et al. 1983).

Besides this feature, the Villaverde population frequently (28 %) shows some small accessory cusps in the external valleys of the M_1 (c1 and c2, see pl. 1, figs. 5, 11, 12). These accessory cusps have been noted with some frequency in *M. spretus* (especially c1, see Darviche 1978; Orsini 1982; Darviche et al. 1982); its absence is considered the rule for *M. musculus*.

Size of bones and teeth

In spite of its variability, the size of the skeleton and teeth is a very interesting feature related to ecological and evolutionary factors. The species of mice differ clearly in this character, but ecological and geographical variation may overlap the taxonomic differences. This character is also the best documented in the literature (see above the warning observations).

We compared tooth size to the size of the limb bones. Using the skull size as a variable is not possible as skulls are scarce and/or broken in Villaverde. The size of the mandibula is not used either in this case, as this element hardly shows any variability. Table 5 shows the parameters of the distribution of several biometric variables: maximal length and width of the M^1 and M_1 , maximal length of the upper and lower tooth row, humerus, radius, femur and tibia. For the sake of comparison, we have measured the length of some femurs from the head, without taking into account the first trochanter (Cabrera 1980). We have also measured the tibia without proximal epiphysis, as the majority of such bones were not ossified.

The size of *Mus musculus* is significantly larger than that of *M. spretus* and the other Eastern wild species of mice. This difference is apparent in the skull and body length, weight and limb bone length (Miller 1912; Cabrera 1914; Darviche 1978). However, the teeth and the femur are exceptions to that rule; they are significantly larger in *M. spretus* than in most of the populations of *M. musculus*. The different size of the teeth is revealed both in the length of the tooth rows, and in the length and width of the isolated molars.

The same geographical race may have significant differences in size, as e. g. *M. m. domesticus* in Northern and Southern France (Darviche et al. 1982). That has been

Table 5: Dental and postcranial measurements (in mm) of the Villaverde house mouse population.

VARIABLE	N	$\bar{x} \pm SE$	SD	CV	Range	Observations
Length M ¹	51	1.97±0.01	0.06	3.35	1.84— 2.12	
Width M ¹	51	1.22±0.00	0.03	2.67	1.16— 1.3	
Length M ₁	168	1.56±0.00	0.04	2.88	1.44— 1.72	
Width M ₁	168	0.9 ±0.00	0.03	3.67	0.92— 1.08	
L. Upper tooth row	41	3.54±0.04	0.14	4.15	3.2 — 3.8	
L. Lower tooth row	77	3.2 ±0.02	0.09	3.01	2.96— 3.48	
L. Humerus	25	11.18±0.35	0.87	7.83	9.5 —12.3	
L. Radius	17	10.38±0.25	0.51	4.97	9.3 —11.5	
L. Femur	4	15.37±1.65	1.43	9.34	14.2 —17.5	Length to head
	56	14.54±0.32	1.21	8.35	12 —18.2	L. Max.
L. Tibia	11	18.00±0.51	0.80	4.47	17 —19	Ossified
	114	15.99±0.17	0.94	5.88	13.1 —18.1	No prox. epiphysis

explained as an ecotypic change related to a stronger commensalism in the Northern populations (Orsini 1982; Darviche et al. 1982). Recent island populations of mice show sometimes a shift in size. It is the case of e. g. *M. m. domesticus* from Faeroe Island (Miller 1912), from Corsica and, in a lesser degree, also from Sardinia (Orsini 1982). But in the majority of recent *Mus* populations of islands the size does not differ notably from continental ones (see Reichstein 1978; Sans Coma et al. 1979; Alcover 1979, 1980; Engels 1980), and it may have even a smaller size (*Mus spretus parvus* from Ibiza, see Alcover et al. 1985).

We have divided the study of the size into two parts: the tooth size, and the limb bone size.

Size of the molars

According to Gingerich (1980), the size of the molars in mammals is highly correlated with the body size, and this function has been largely used in evolutionary studies. Island mammals show some cases of inverse correlation: the body size may decrease in large mammals without any variation in tooth size (Sondaar 1986) and, on the contrary, the tooth size may apparently increase in small mammals with no changes in body size. This last process seems also related with a wild habitat in the case of the house mouse (Orsini 1982).

As we noted above, the molars of *Mus spretus* are relatively larger than those of *M. musculus* and, in many cases, even larger in absolute value. We have compared the length and width of the first molars in both species and in the Canarian mouse. Figs. 2 and 3 show the scatter diagram of these variables. The absolute value of molar size of the Villaverde house mouse is larger than that of both Western Mediterranean species, notably in the first upper molar. The first lower molar is wider, but not significantly longer. Some few specimens from the recent house mouse of Gran

Table 6: Dental measurements of various *Mus* populations taken from the literature.

	Upper tooth row				Lower tooth row			
	N	\bar{x}	SD	Range	N	\bar{x}	SD	Range
<i>Mus spretus</i>								
HUESCA	93	3.35	0.10	3.1–3.7	93	3.12	0.10	2.9–3.3
JAEN	24	3.40	0.10	3.2–3.6	24	3.16	0.12	3.0–3.3
MALAGA ¹⁾	67	3.37	0.13	3.1–3.7	64	3.12	0.13	2.7–3.5
BADAJOS	13	3.38	0.20	2.9–3.7	13	3.21	0.09	3.1–3.4
S. FRANCE ²⁾	53	3.49	0.11	3.3–3.9	49	3.20	0.08	3.0–3.4
N. AFRICA ³⁾	25	3.39	0.13					
<i>M. m. domesticus</i>								
I. MEDAS	73	3.18	0.10	3.0–3.4	72	2.99	0.09	2.8–3.8
BARCELONA ⁴⁾	25	3.17	0.10	3.0–3.3	24	2.98	0.09	2.8–3.2
ITALY ²⁾	15	3.35	0.15	3.1–3.7	14	2.97	0.10	2.8–3.1
S. FRANCE	81	3.40	0.13	3.2–3.7	77	3.02	0.08	2.8–3.2
N. AFRICA	10	3.51	0.13	3.3–3.7	9	3.01	0.09	2.9–3.2
CORSICA	17	3.64	0.13	3.4–3.9	27	3.14	0.08	3.0–3.3
N. FRANCE	38	3.60	0.16	3.3–3.9	16	3.19	0.07	3.1–3.3
W. GERMANY ³⁾	7	3.28	0.08					

1) Palomo et al. 1983, 2) Darviche 1978, 3) Engels 1980, 4) Sans Coma et al. 1979

Table 7: Comparison of the upper (UTR) and lower (LTR) toothrow size between the Villaverde house mouse and several other *Mus* populations. Each square shows the Student's test values and the degrees of freedom. NS = test is not significant.

UTR	LTR	VILL.	<i>M. spretus</i>		<i>M. m. domesticus</i>				
			HUE	S. FR.	I. MED.	S. FR.	N. AFR	CORS.	N. FR.
	VILL.		8.54 168	2.90 124	15.85 147	15.77 152	6.94 84	5.24 102	(2.28) 91
<i>M. spretus</i>	HUE.	8.48 132		4.92 140	8.38 163	7.19 168	3.29 100	N.S.	2.76 107
	S. FR.	N.S.	7.71 144		12.17 119	12.21 124	6.37 56	3.18 74	N.S.
<i>M. m. domesticus</i>	I. MED.	15.40 112	10.54 164	16.42 124		(2.01) 147	N.S.	7.06 97	7.60 86
	S. FR.	5.22 120	2.75 172	4.07 132	11.32 152		N.S.	6.72 102	7.91 91
	N. AFRIC.	N.S.	4.51 101	N.S.	9.29 81	(2.42) 89		4.19 34	5.53 23
	CORS.	(2.43) 56	10.20 108	4.76 68	15.94 88	6.67 96	(2.48) 25		2.16 41
	N. FRAN.	N.S.	10.38 129	3.82 89	16.47 109	6.99 117	N.S.	N.S.	

Table 8: Postcranial measurements of various *Mus* populations taken from the literature.

<i>M. spretus</i>						<i>M. musculus</i>					
	LOC. AUT.	N	\bar{x}	SD	Range	LOC. AUT.	N	\bar{x}	SD	Range	
HUMERUS	S. FRANCE ¹⁾	27	10.3	0.45	9.3–11.2	S. FRANCE ¹⁾	24	11.00	0.50	10 –11.5	
	SPAIN	41	10.35	0.59	9.1–11.5	SPAIN ²⁾	9	10.59	0.45	9.75–11.95	
	MALAGA ¹⁾	439	9.92	0.41		CHIOS ³⁾	14	10.5			
						G. CANARIA	3	11.1		10.56–11.4	
RADIUS	SPAIN	58	10.28	0.70	8.4–11.7	SPAIN ²⁾	9	10.09	0.67	8.80–11.25	
						CHIOS ³⁾	12	10.8			
						G. CANARIA	2	10.51		10.3 –10.8	
FEMUR	S. FRANCE ¹⁾	27	13.5	0.72	12.8–15.2	S. FRANCE ¹⁾	24	13.1	0.70	11.2 –14.6	
	SPAIN*	51	13.05	0.65	12.0–14.4	SPAIN ²⁾ *	11	13.42	1.04	12.05–15.35	
	MALAGA ⁴⁾	401	12.65	0.65		CHIOS ³⁾	14	13.3			
						G. CANARIA	3	14.75		14.10–15.20	
TIBIA	S. FRANCE ¹⁾	18	15.6	0.47	14.5–16.5	S. FRANCE ¹⁾	27	16.3	0.60	15 –16.9	
	SPAIN	32	15.88	0.73	14.4–17.1	SPAIN ²⁾	11	15.96	0.96	14.5 –17.75	
	SPAIN*	29	15.34	0.95	13.8–17	CHIOS ³⁾	11	15.9			
						G. CANARIA	1	18.2			

1) Darviche 1978, 2) Cabrera 1980, 3) Kock 1974, 4) España 1983, * incomplete bones (lack trochanter or epiphysis)

Canaria have also a larger molar size, intermediate between the largest *M. m. domesticus* — *M. spretus* molars and the Villaverde sample, which exceeds the size of all compared populations.

The length of the tooth row is much more frequently used for size studies. The comparison with the data from literature (tables 6 and 7) shows that the upper tooth row length in the Villaverde house mouse is significantly larger than that of most of the samples (only two cases exceed it in size) and it has the longest lower toothrow of all of them. The reason of the largest size of the lower toothrow in the Villaverde house mouse must be necessarily the larger size of the M_2 and M_3 , since the M_1 , as we have seen above, is not significantly longer in the Villaverde mouse than in the other *Mus* populations.

The relation between tooth and body size is shown in fig. 4. According to this distribution, both variables are not highly correlated. *M. spretus* shows relatively larger teeth and shorter bodies than *M. musculus* from North Mediterranean populations. However, recent populations of *M. musculus* from Libya (Engels 1980), Corsica (Orsini 1982), and Gran Canaria (pers. obs.) show the *M. spretus* size pattern. The wild habitat reached by these house mouse populations has been related with this change in the size pattern (Orsini 1982).

The body size of the Villaverde house mouse cannot be obtained and must be inferred from the study of limb bones.

Size of the limb bones

We measured the maximal length of the humerus, radius, femur, and tibia in the Villaverde house mouse (table 5) and compared it with some other populations of

M. musculus and *M. spretus* (table 8). The estimation of the size may be obtained not only from the mean values, but also from the range, because the distributions are somewhat asymmetric. In general, the size of the limb bones, as that of the head and body, is larger in *M. musculus* than in *M. spretus*. The *M. musculus* population from Gran Canaria has a larger body size than that of the same species in Southern France, Spain, and Chios Island, but the size of the Villaverde house mouse limbs (table 5) is even larger than that of the recent Gran Canaria mouse. That is in agreement with the results of the tooth size comparison.

Special characters

Some peculiar features are observed in the Villaverde house mouse.

In the molar crown pattern, the T1 of the second upper molar is strongly developed, and it may be frequently double (pl. 1, figs 4, 7, 8); a small cusp near the T1 is then isolated in the anterior border of the crown.

In some cases the first lower molar presents an isolated anterior cusp (TF); a deep valley separates it from the next posterior cusp TD. The small anteroexternal TE may also be isolated or it may have a weak connection with TF. These features may persist in rather old individuals, but usually they disappear with wear.

The postcranial skeleton presents also a peculiar feature. Hind limbs are relatively longer than fore limbs, even with no data about metapods; the femur and tibia present an extreme elongation in relation to humerus and radius.

According to Cabrera (1980), the limb length ratio has an important functional value (LLR = length of the humerus plus radius divided by the length of the femur plus tibia, $(LH + LR) / (LF + LT)$). It allows the distinction between cursorial and fossorial rodents, with larger values of LLR ($\bar{x} = 0.77$, SE = 0.03, Range: 0.723–0.850) on the one hand, and scansorial and jumping rodents with smaller values of LLR ($\bar{x} = 0.678$, SE = 0.03, Range: 0.640–0.735) on the other. After studying the skeletons of 228 specimens belonging to 17 European rodent species, Cabrera (1980, p. 93) found highly significant differences in the LLR value of both groups, with almost no overlap among them. The arviculids fit mostly in the first group (fossorial–cursorial); sciurids, glirids and murids belong to the second group (scansorial–jumping). *Arvicola sapidus* was excluded from both groups: its intermediate value ($\bar{x} = 0.722$, SE = 0.01, Range: 0.699–0.747) may be related to its aquatic way of life.

Mus musculus domesticus has a LLR value of 0.714 according to Cabrera (1980) (N = 9, SE = 0.04). We measured the LLR value of 25 specimens of *M. spretus* from Spain, with a result of $\bar{x} = 0.719$ (SE = 0.012). There are no differences in the LLR value between both species.

In the case of mixed skeletons, with no individual measurements of LLR available, only the mean value of this variable may be estimated from the mean length values of the isolated bones. In the populations quoted above, *M. m. domesticus* presents a mean LLR value of 0.698, and *M. spretus* 0.713. These estimations are then included in the confidence interval of the mean population values.

The Villaverde house mouse, as well as the recent Gran Canaria house mouse, have an index value lower than that of both species; in the fossil population, LLR is 0.652,

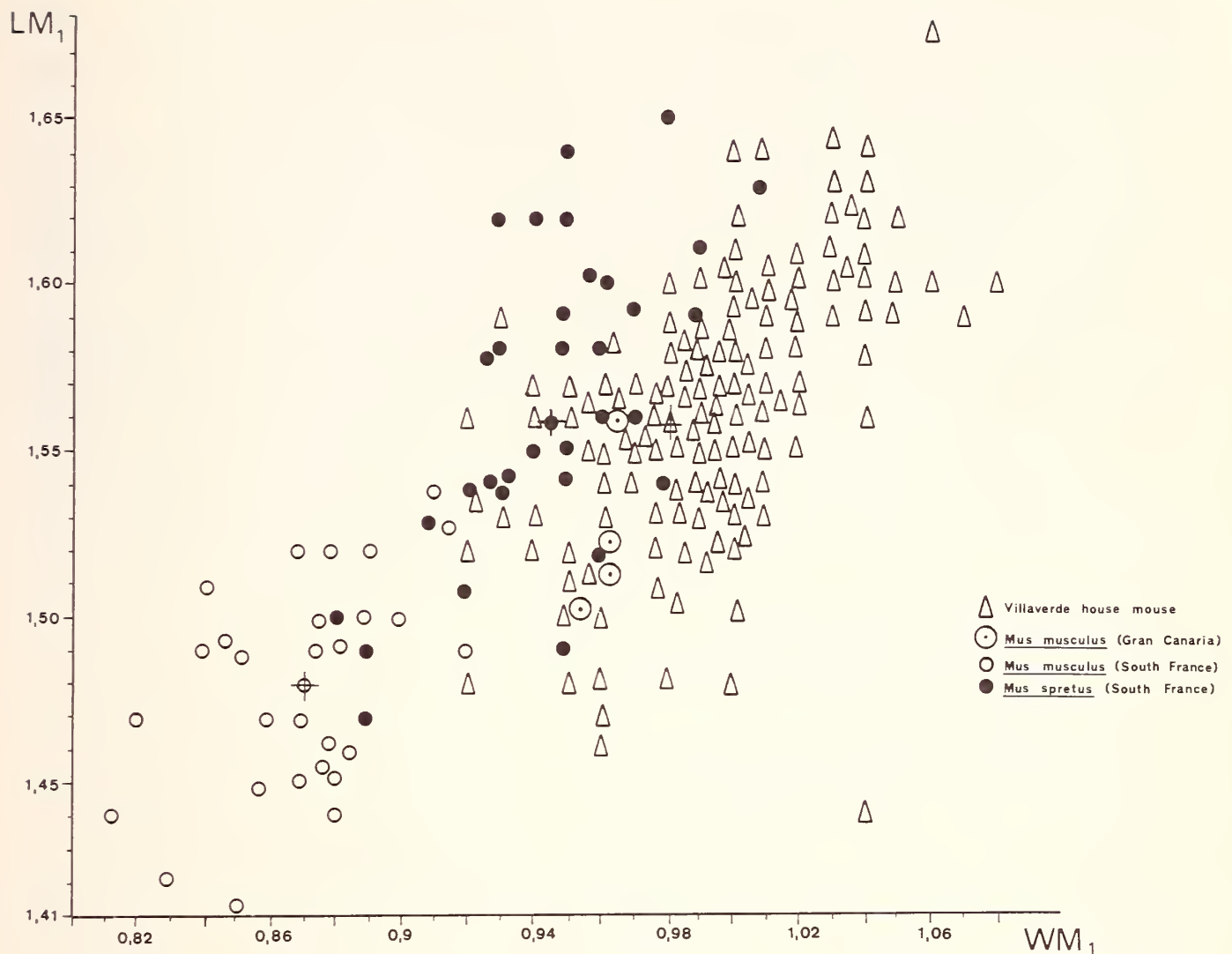


Fig. 2: Diagram showing the relation between the length and the width of the M_1 in different *Mus* populations. Measurements are in mm. Data of Southern France populations are from Darviche et al. (1982). Each cross indicates the mean of the population.

and in Gran Canaria it is 0.655. This difference is highly significant as it has been corroborated by statistical tests. This extremely high scansorial adaptation of the house mouse in the Canary Islands may be related to its wild life in the volcanic landscape. The '*malpais*' offers a very rough surface for small mammals, formed by blocks of lava with a large number of vertical planes, holes, and cliffs. Their movements may be frequent in vertical directions, and they may be favoured by lengthened hind limbs.

Results and conclusions

The characters studied in the Villaverde subfossil mouse population allow us to attribute it to the *M. musculus* species. There are no significant differences between the various levels of the site, and the whole population may be considered as homogeneous, even if there are more than 500 years between the oldest and the youngest sample.

The clearest features shared by continental and Villaverde *Mus musculus* are 1) the notch of the upper incisor, 2) the trilobed pattern of the M_1 , 3) the straight profile of the zygomatic plate, and 4) the zygomatic foramen. Features 1 and 2 are par-

ticularly present in *M. m. domesticus*, (the Mediterranean house mouse), which frequently shows a notch and a strongly reduced TE in M_1 ; these two features approach the Villaverde house mouse to the subspecies *M. m. domesticus*.

However, two other features of the Villaverde *Mus* are shared by *M. spretus* and differ from *M. musculus*: The accessory cusps of the M_1 , c_1 and c_2 , and the teeth/body length ratio. The first character could be considered as a homoplasy. The second may be related to the wild habitat of these mice, just like the Corsica house mouse shown by Orsini (1982) and considered as an ecotypic variation.

Most of the characters of the Villaverde house mouse appear to be peculiar features of their own. The zygomatic coefficient differs significantly from the recent species of *Mus*. The M^2 shows a large even doubled T_1 ; M_1 frequently has an

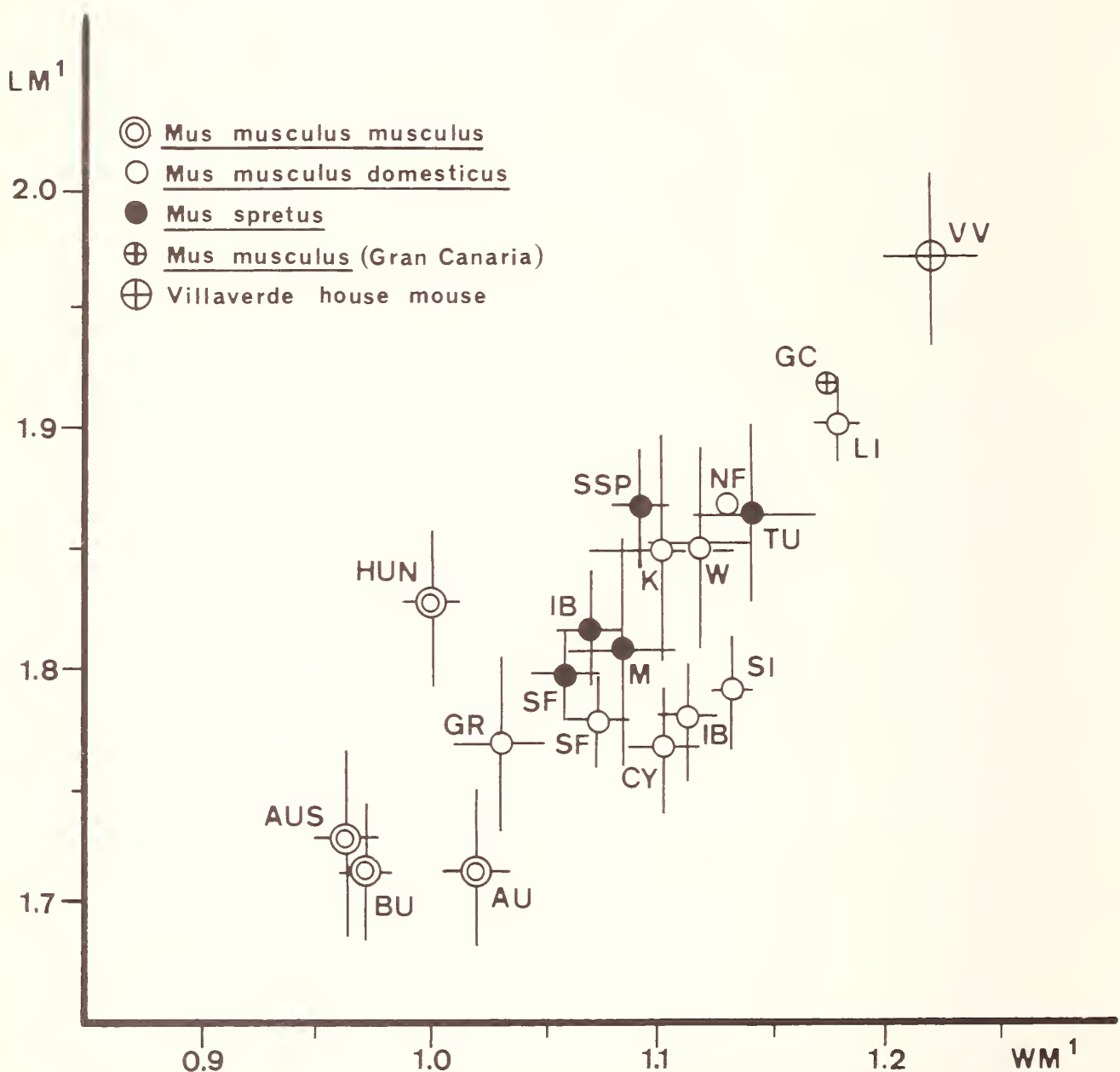


Fig. 3: Diagram showing the relation between the length and the width of the M^1 in different *Mus* populations. Measurements are in mm. AU: Austria, CY: Cyprus, IB: Iberian Peninsula, K: Kreta, LI: Libya, M: Morocco, SI: Sicily, SSP: South Spain, TU: Tunisia, W: West Germany (Engels, 1980); AUS: Austria, BU: Bulgaria, GR: Greece, HUN: Hungary, NF: North France, SF: South France (Orsini, 1982). Lines represent the confidence interval of the mean over each axis (mean ± 2 standard error).

isolated TD. Finally, the hind limbs present an extreme elongation in relation with fore limbs. These characters differentiate the Villaverde house mouse from the other forms of mice used for comparison.

The two specimens available of the recent house mouse from Gran Canaria, resemble the Villaverde population. The only difference is the larger size of the subfossil mouse. The peculiar features of the subfossil population are also shared by the recent Canarian house mouse: the zygomatic coefficient, the larger tooth size in relation to body size, the relatively lengthened hind limb, etc. The scarcity of the recent Canarian mouse material prevents to extend the conclusion to other peculiar characters of the Villaverde mouse. The four osteological features shared by the Villaverde mouse and *Mus musculus* from the continent (notch, trilobed M_1 , zygomatic plate and foramen) are also present in the recent Canarian mouse, plus the relation of the tail and head-body length. We may conclude that both Canarian mouse populations belong to the species *Mus musculus*, but differ in many features from all the subspecies described in Europe and North Africa.

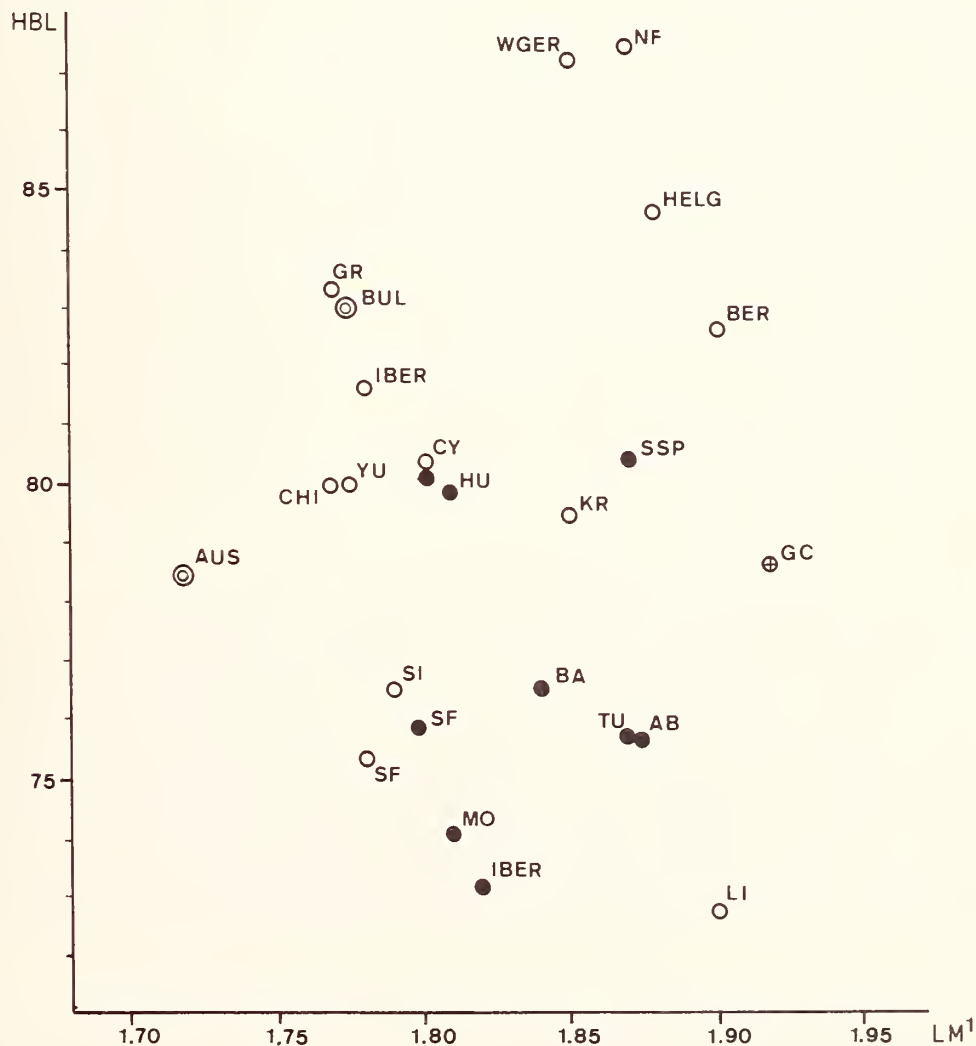


Fig. 4: Diagram showing the relation between tooth (LM^1) and body (HBL) size in several *Mus* populations. Measurements are in mm. CY: Cyprus, IBER: Iberian Peninsula, KR: Kreta, LI: Libya, MO: Morocco, SI: Sicily, SSP: South Spain, TU: Tunisia, WGER: West Germany (Engels, 1980); AB: Albacete, BER: Berlin, CHI: Cyprus, HELG: Helgoland, YU: Yugoslavia (Reichstein, 1978); AUS: Austria, BUL: Bulgaria, GR: Greece, NF: North France, SF: South France (Orsini, 1982); BA: Badajoz, HU: Huesca (Palomo et al. 1983). Symbols are equal to those in figure 3.

The differences between the Canarian semi-commensal mouse and the house mouse from the continent are more important than those between the two subspecies *musculus* and *domesticus*. It is probable that a subspecific differentiation occurred after the settlement of the Canary Islands by the commensal population of *Mus musculus*, and its spreading in the wild country. Its origin is nearer to *M. m. domesticus* than to *M. m. musculus*, and it may be related to the Iberian, to the Punic or to the North African human populations, which are hosts of that mouse subspecies.

The presence of *Mus musculus* ssp. in Villaverde before the human occupation of the cave is probable, because some specimens were present below the older archaeological level. The provenance of the mice in the sediments may be from owl pellets and other predators' activity. After human settlement in Villaverde, *Mus* becomes more and more abundant in the sediments (from 0.1 % in the pre-archaeological level, 1.6 % in level 3, to 6 % in level 2, and 24 % at the surface). Its provenance may be mainly related to bird predation, according to the following criteria:

- 1) Patchy spatial distribution of the microfaunal remains.
- 2) No spatial relations with ash and human activity places.
- 3) Broken braincases, typical for bird activity.
- 4) Association with shrews, *Tarentola*, and other small nocturnal vertebrates, frequent preys of owls. The reptile remains become gradually less frequent in the samples, whereas those of *Mus* keep increasing.

Some of the large mammals and middle size bones of birds were burned. The human predatory activity cannot be excluded to explain the provenance of the extremely rich microfaunal remains. But the murids, shrews and nocturnal reptiles, common in sediments before and after the human occupation appear to be mainly related to the activity of the predatory birds.

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