Acta zool. cracov., **39**(1): 357-372, Kraków, 15 Aug., 1996

Evolution of the first lower molar in the endemic vole *Microtus* (*Tyrrhenicola*) *henseli* (Arvicolidae, Rodentia, Mammalia) from Pleistocene and Holocene localities of Sardinia and Corsica

Cristiana MEZZABOTTA, Federico MASINI and Danilo TORRE

Accepted for publication: 10 April, 1995

MEZZABOTTA C., MASINI F., TORRE D. 1996. Evolution of the first lower molar in the endemic vole *Microtus (Tyrrhenicola) henseli* (Arvicolidae, Rodentia, Mammalia) from Pleistocene and Holocene localities of Sardinia and Corsica. Acta zool. cracov., **39**(1): 357-372.

Abstract. The first lower molars of the endemic vole *Microtus (Tyrrhenicola) henseli* from caves, karst fissures, and bone breccias of eight Sardinian localities of Middle Pleistocene and Holocene age, and from one Holocene cave deposit of northern Corsica have been studied. The material, consisting of a total of 198 m1's, has been examined by means of morphometric methods, including multivariate techniques. A further preliminary analysis of the microstructural pattern of the enamel has been also carried out, on the basis of a small number of molars. The results of these analyses are fairly congruent. The morphological analysis has demonstrated the presence of correlations between some parameters (e. g., the length of the anteroconid complex and the anterior loop, or the elongation of T6 and the pinching of the neck) that strengthen the evolutionary significance of the observed trends, even though in the evaluation of the overall evolutionary level of each population it is necessary to realize that a certain degree of independence between the characters is present (mosaic distribution). The study of enamel microstructure has demonstrated the occurrence of great intraspecific variability that should be investigated in larger subsamples, but has also identified a general trend towards reduction of the tangential layer in the trailing edges, coupled with a reduction in thickness of the whole distal enamel walls of the dental triangles. On the basis of these results, the forms from the sites studied can be arranged in two main groups: a less derived group of Pleistocene forms from six localities, characterized by small size, a simpler and somewhat shorter anteroconid complex, and a broad neck, and a more derived group, composed of latest Pleistocene to early Middle Holocene samples, that includes forms with a more complex anteroconid, a more pronounced pinching of the neck, and a tendency towards larger size. The samples from the localities of Capo Figari and Grotta Dragonara show the least derived morphologies within the group of Pleistocene localities, with molars moderately differentiated in a microtine direction as concerns the pattern of enamel microstructure, while in this group the samples from Monte San Giovanni and Bonaria display intermediate characters. In the group including the Holocene forms, with more derived morphology and a reduced layer of tangential enamel and thinner trailing edges, the sample from the Corsican site of Fontaneddu is distinct in having highly derived features coupled with a slightly less elongated anteroconid complex. The evolutionary data resulting from our study may be useful for a more detailed biochronological subdivision of the Corsica-Sardinia faunal complexes, and suggest that a marked increase in evolutionary rates should have occurred at the end of the Pleistocene, possibly due to environmental changes related to climatic factors and to the impact of human civilization on the endemic mammal community.

Key words: m1, Arvicolidae, Rodentia, biochronology, Pleistocene, Holocene.

Cristiana MEZZABOTTA, Danilo TORRE, Department of Earth Sciences, University of Firenze, Via G. La Pira 4, I-50121, Florence, Italy; Federico MASINI, Department of Geology and Geodesy, University of Palermo, C.so Tukory 131, I-90134, Palermo, Italy.

I. INTRODUCTION

Microtus (*Tyrrhenicola*) *henseli* is a common, though not dominant, fossil vole in the Pleistocene and Holocene faunas of Sardinia. The reconstruction of the succession of biochronological events in this Tyrrhenian island is highly problematic and, at present, two major biochronological units have been distinguished in the Pleistocene: an older faunal complex, characterized by the occurrence of *Nesogoral melonii*, *Prolagus figaro*, *Rhagamys minor*, *Tyrrhenoglis figariensis*, *Nesiotites corsicanus*, *Sus nanus*, and *Macaca majori*, and a more recent one, including *Microtus* (*Tyrrhenicola*) *henseli*, *Prolagus sardus*, *Rhagamys orthodon*, *Nesiotites similis*, *Megaceroides cazioti*, *Cynotherium sardous*, *Talpa tyrrhenica*, and possibly *Macaca majori* (KOTSAKIS 1980a; GLIOZZI et al. 1984; SONDAAR et al. 1984; KLEIN HOFMEIJER et al. 1987; VAN DER MADE 1988; AZZAROLI 1990). The correlations of all these faunal complexes with the geochronological scale are still not well established. The beginning of the faunal complex including *Microtus* (*Tyrrhenicola*) *henseli* has been interpreted as ranging from Early to early Middle Pleistocene (GLIOZZI & MALATESTA 1980; SONDAAR et al. 1984; VAN DER MADE 1988).

At the moment, the succession of appearance-disappearance events of the endemic and continental taxa during Holocene time is well known for Corsica only (VIGNE 1983, 1992), and it is not possible to arrange the assemblages of the Pleistocene faunal complexes in a more detailed biochronological scale.

In the present work, a detailed analysis of the evolutionary trends shown by the insular arvicolid is carried out, with the aim of contributing to the reconstruction of its evolutionary history and to supply a tool for a better definition of the biochronology of Sardinia.

Acknowledgments. The fossil material studied herein is stored in several scientific institutions and this work would not have been possible without the kind help of many people. We wish to thank Dr. M. SANGES (Archaeological Sovrintendence of Sassari and Nuoro Provinces), Prof. A. J. VAN DER MEULEN and Prof. P. Y. SONDAAR (University of Utrecht, Netherlands), Prof. B. ENGESSER (Naturhistorisches Museum, Basel), and Prof. T. KOTSAKIS (University of Rome), for permission to study museum material. We also thank Prof. O. FEJFAR (Charles University, Prague) who critically read the manuscript.

II. MATERIAL AND LOCALITIES

The examined material consists of a total of 198 first lower molars of *Microtus* (*Tyrrhenicola*) *henseli*, collected in eight Pleistocene and Holocene localities of Sardinia, and in one Holocene locality of northern Corsica (Fig. 1). The first lower molar represents a widely used tool in phylogenetic and morpho-functional studies of arvicolids. It shows significant evolutionary changes and often is the most commonly recovered dental element in fossiliferous localities.

A list of the material, with the chronological position of the studied localities is presented in Table 1. The reader is referred to specific papers for more detailed information.

III. MORPHOMETRIC ANALYSIS: RESULTS AND DISCUSSION

A set of morphological analyses has been performed on the material at our disposal by utilizing the parameters proposed by VAN DER MEULEN (1973), with the addition of other measurements and indices that have been selected in order to provide a more complete picture of the specific evolutionary tendencies of *Microtus* (*Tyrrhenicola*) *henseli* (Fig. 2).

The morphometric analysis has been carried out using the univariate, bivariate, and multivariate statistical methodologies (analysis of variance, bivariate scatter diagrams and correlations, cluster analysis, factor analysis) available in the SPSS/PC+ statistical package.

The studied populations have first been compared by one-way analysis of variance, with the provenances as the classification criterion, utilizing all the descriptive parameters (variables plus

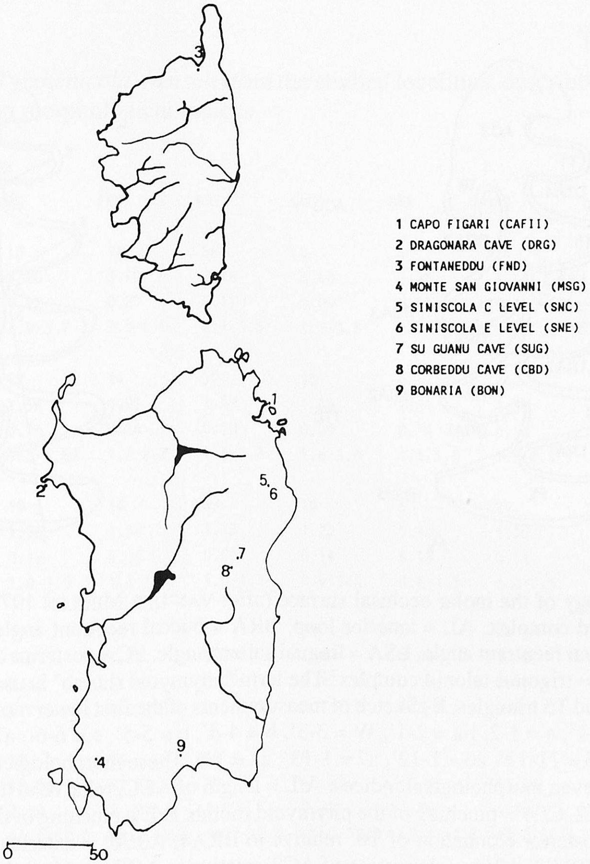


Fig. 1. Studied fossiliferous localities of Sardinia and Corsica.

Table I

The samples studied and their ages

Locality	left m1's	right m1's	Age	Human culture	Ref.
Capo Figari II	5	4	Middle Pleistocene		1, 2
Dragonara Cave	5	4	Middle to Late Pleistocene		3, 4
Fontaneddu	7	7	Holocene	Neolithic	5, 6
Monte San Giovanni	27	32	Middle to Late Pleistocene		7, 8
Siniscola C level	7	5	Middle to Late Pleistocene		12
Siniscola E level	4	2	Middle to Late Pleistocene		12
Su Guanu Cave	12	13	<4900-4830±50 yr. B. P.	Neolithic	9
Corbeddu Cave	11	17	14.000±8.000 yr. B. P.	pre Neolith. & E. Neolith.	10, 11
Bonaria	22	17	Middle to Late Pleistocene		7

References: 1. GLIOZZI et al. 1980; 2. VAN DER MADE 1988; 3. KOTSAKIS 1980a,b; 4. MALATESTA 1970; 5. VIGNE 1983; 6. VIGNE 1988; 7. FORSYTH MAJOR 1882; 8. FORSYTH MAJOR 1905; 9. SANGES & ALCOVER 1980; 10. KLEIN HOFMEJER et al. 1987; 11. SONDAAR et al. 1984; 12. MEZZABOTTA et al. 1995.

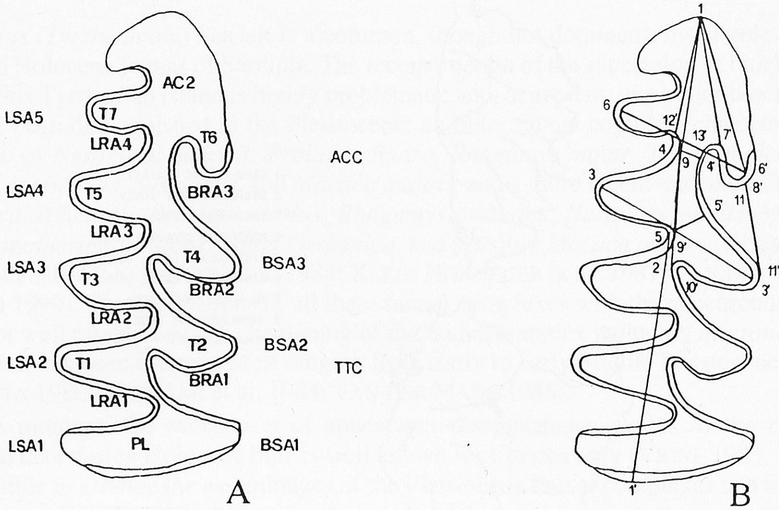


Fig. 2. A) Terminology of the molar occlusal surface (after VAN DER MEULEN 1973). AC2 = anterior cap, ACC = anteroconid complex, AL = anterior loop, BRA = buccal reentrant angle, BSA = buccal salient angle, LRA = lingual reentrant angle, LSA = lingual salient angle, PC = posterior cap, PL = posterior loop, T = triangle, TTC = trigonid-talonid complex. The term "pitymyoid rhomb" is used in the text to indicate the confluent T4 and T5 triangles; B) Sketch of measurements of the first lower molar (m1). Morphological parameters: L = 1-1', a = 1-2, l-a = 2-1', W = 3-3', b = 4-4', c = 5-5', e = 6-6', a1 = 1-7', a2 = 1-8', a3 = 9-9', a4 = 9-10', a5 = 11-11', a6 = 1-12', a7 = 1-13', a8 = 1-6. These morphological parameters have been used to calculate seven morphological indices: A/L = length of ACC, relative to the total length L, B/W = pinching of the AC2, C/W = pinching of the pitymyoid rhomb, B/E = pinching of the neck, relative to AC2 width, A1/A2 = posterior elongation of T6, relative to BRA4, A3/A4 = anterior position of the apex of LRA3, relative to BRA2, A7/A = elongation of AC2, relative to ACC total length. Two semi-quantitative morphological indices (IT8 and IT9), expressing the degree of development of BRA4 and LRA5, respectively, have been also added.

indices). The significance of the differences between the provenances has been tested with the Scheffé and Student-Newman-Keuls procedures. The differences in the number of specimens between the samples, and the very small samples from Capo Figari, Dragonara Cave and Siniscola are undesirable features of the data set that indicate that we must interpret the results with some caution.

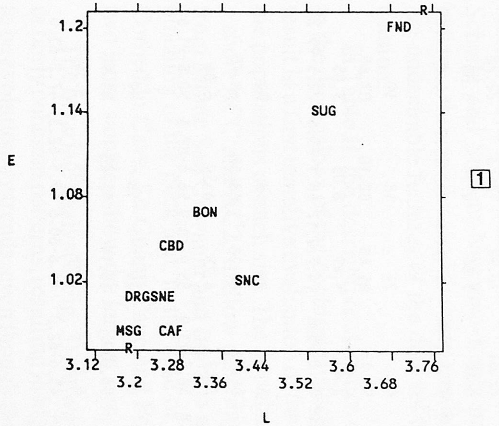
In Table II, the descriptive statistics of the morphological indices and rough variables relating to the dimensions of the occlusal surface and the ACC length for each population are listed. They result in a first tentative evaluation of the most significant morphological features that characterize the populations of each site. The populations of Capo Figari, Dragonara Cave and Siniscola share a short ACC and AC2, shallow pinching of the neck, and poorly developed T6. The specimens from Monte San Giovanni and Bonaria are characterized by slightly more elongated ACC, deeper pinching of the neck and, in the case of Bonaria also a more elongated T6. In the populations of Corbeddu Cave, Su Guanu Cave and Fontaneddu all these characters are highly developed. The two latter samples show the largest size.

The bivariate analysis (Fig. 3) shows that the differences between the populations are arranged in fairly coherent patterns, resulting in high correlations. These patterns can be confidently assumed to be evolutionary trends, even though the differences between the population means do not always reach statistical significance in the univariate analysis of variance.

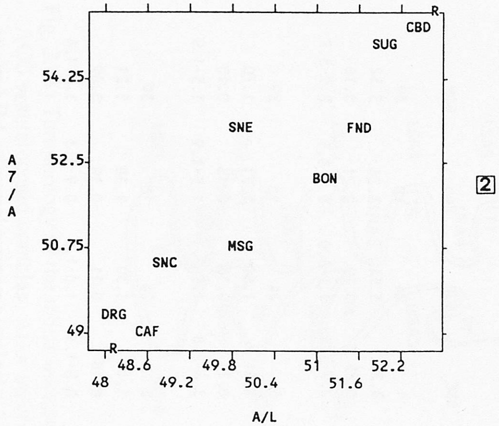
Table II

Microtus (*Tyrrhenicola*) *henseli* from the studied localities: descriptive statistics of variables and morphological indices

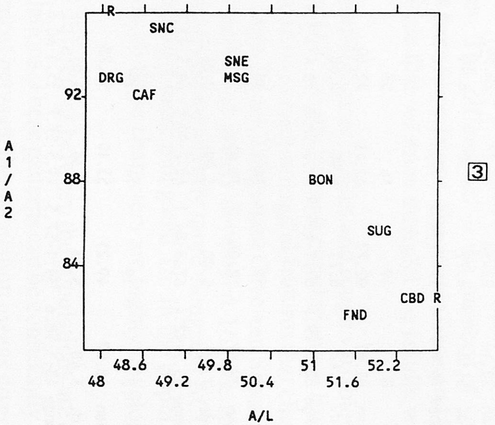
		CAF	DRG	FND	MSG	SNC	SNE	SUG	CBD	BON
	n	6	18	14	54	8	4	24	18	39
L	mean	3.27	3.20	3.70	3.18	3.40	3.25	3.54	3.26	3.32
	s.d.	0.28	0.22	0.21	0.17	0.09	0.25	0.29	0.21	0.16
	range	2.9-3.6	2.9-3.7	3.3-4.0	2.7-3.5	3.3-3.5	2.9-3.5	3.1-4.0	2.9-3.5	2.9-3.7
	n	9	19	14	59	10	6	24	18	39
A	mean	1.63	1.54	1.91	1.59	1.66	1.61	1.84	1.71	1.70
	s.d.	0.16	0.14	0.14	0.10	0.09	0.14	0.18	0.13	0.10
	range	1.4-1.9	1.3-1.87	1.7-2.2	1.3-1.8	1.6-1.8	1.4-1.8	1.5-2.1	1.5-1.9	1.5-1.9
	n	8	19	14	59	10	6	24	18	39
W	mean	1.20	1.23	1.34	1.18	1.22	1.19	1.30	1.18	1.21
	s.d.	0.08	0.12	0.10	0.08	0.14	0.18	0.11	0.10	0.09
	range	1.1-1.3	1.0-1.5	1.1-1.5	1.0-1.3	0.9-1.4	0.8-1.3	1.0-1.5	0.9-1.3	1.0-1.4
	n	9	19	14	59	10	6	24	18	39
E	mean	0.99	1.01	1.20	0.99	1.02	1.00	1.13	1.05	1.07
	s.d.	0.07	0.12	0.10	0.09	0.12	0.11	0.10	0.10	0.11
	range	0.9-1.1	0.7-1.2	1.0-1.3	0.8-1.1	0.9-1.2	0.8-1.1	0.9-1.3	0.8-1.2	0.9-1.3
	n	6	18	14	54	8	4	24	18	39
A/L	mean	48.55	48.08	51.56	49.93	48.85	49.89	51.96	52.39	51.07
	s.d.	1.24	2.30	2.09	1.89	2.28	1.88	1.49	1.73	2.03
	range	47.4-50.6	44.0-52.0	48.2-54.3	46.9-55.6	45.9-52.6	48.1-51.7	49.2-54.6	49.0-55.3	46.1-54.5
	n	8	19	14	58	10	6	24	18	39
B/W	mean	21.48	19.02	11.81	17.13	18.85	19.30	16.54	15.77	19.69
	s.d.	3.84	4.75	2.44	5.52	2.77	6.28	4.98	4.27	5.25
	range	14.4-25.4	12.1-28.9	6.9-16.0	9.4-34.0	14.0-22.4	11.0-26.8	8.8-26.5	7.7-22.9	11.0-29.8
	n	9	19	14	58	10	6	24	18	39
B/E	mean	25.10	22.98	13.27	20.59	22.74	22.61	18.92	17.73	22.28
	s.d.	5.16	4.77	3.02	6.44	4.55	6.44	5.84	4.39	5.80
	range	16.9-31.6	15.5-32.3	7.8- 18.8	10.2-37.8	16.1-31.0	13.1-29.5	9.7-30.5	8.7-23.9	11.8-31.8
	n	8	19	14	57	10	6	24	18	39
A1/A2	mean	91.61	92.71	81.43	92.60	95.34	93.12	85.40	82.10	87.65
	s.d.	5.42	6.71	5.98	6.68	9.88	5.63	5.99	8.03	5.85
	range	82.5-99.5	81.1-105.9	72.0-92.7	76.4-116.4	79.4-112.9	84.2-98.6	74.7-95.7	68.1-93.6	72.5-99.2
	n	9	19	14	59	10	6	24	18	39
A3/A4	mean	76.57	78.04	75.81	72.02	66.59	64.39	68.28	68.68	68.75
	s.d.	7.63	5.00	6.29	7.86	8.44	6.47	4.75	6.59	6.84
	range	65.7-92.4	67.8-84.1	68.7-90.5	49.5-91.3	56.4-79.8	58.5-73.9	55.9-78.9	56.4-87.3	50.8-91.6
	n	8	19	14	59	10	6	24	18	39
A7/A	mean	48.97	49.21	53.10	50.78	50.50	53.09	55.10	55.23	51.98
	s.d.	5.40	5.13	2.36	4.61	6.12	6.11	3.94	3.59	3.34
	range	43.1-58.6	39.1-57.5	49.5-57.7	35.1-60.6	39.4-61.4	45.6-62.0	46.6-60.6	49.5-62.3	47.2-63.0



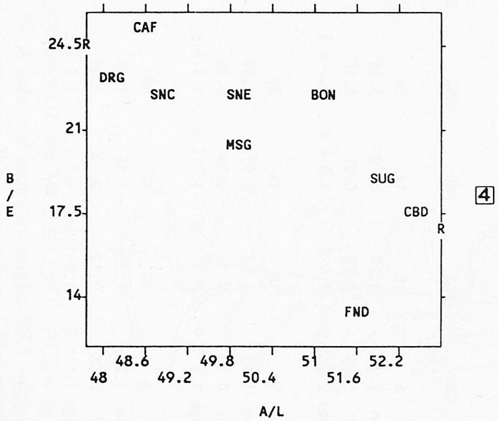
Regression statistics of E on L:
Correlation .91855; R Squared .84374; S.E. of Est .03066; Sig. .0005



Regression statistics of A7/A on A/L:
Correlation .92544; R Squared .85645; S.E. of Est .94003; Sig. .0003

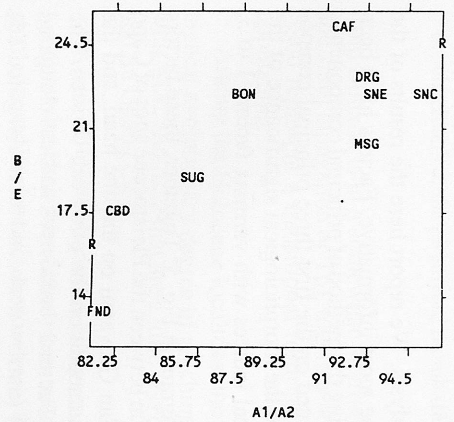


Regression statistics of A1/A2 on A/L:
Correlation -.87008; R Squared .75704; S.E. of Est 2.70216; Sig. .0023



Regression statistics of B/E on A/L:
Correlation -.75381; R Squared .56823; S.E. of Est 2.50968; Sig. .0190

Fig. 3. Bidimensional plots using the mean values of the morphological parameters. For legend, see Fig. 1.



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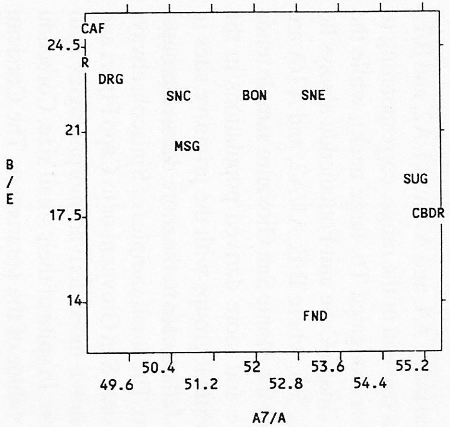
Regression statistics of B/E on A1/A2:
Correlation .82811; R Squared .68577; S.E. of Est 2.14099; Sig. .0058



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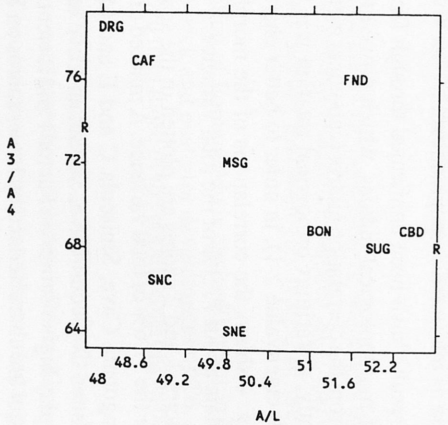
Regression statistics of B/E on A7/A:
Correlation -.66159; R Squared .43770; S.E. of Est 2.86403; Sig. .0523



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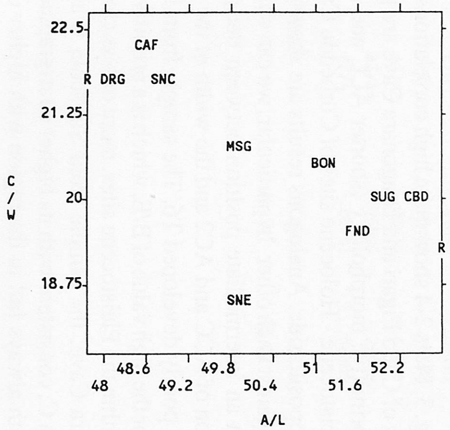
Regression statistics of A3/A4 on A/L:
Correlation -.35744; R Squared .12777; S.E. of Est 4.81200; Sig. .3450



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Regression statistics of C/W on A/L:
Correlation -.64604; R Squared .41736; S.E. of Est .97646; Sig. .0601

Fig. 3. Ctd.

In the plots of Fig. 3, the mean values for each population are shown: in particular, Plot 1 illustrates the correlation between total length (L) and width of the anterior cap (E). The graphs show a marked trend towards increasing size, which is mainly due to the very large size of the Holocene populations of Su Guanu Cave and Fontaneddu, while the Pleistocene samples and the sample from Corbeddu Cave tend to group very close to each other towards the low end of the range. These results are roughly consistent with the ages of the samples.

In Fig. 3, Plots 2-4 show quite high correlations between index A/L and A7/A, A1/A2, and B/E. The sites of Capo Figari and Dragonara Cave are placed at one end of the range, corresponding to a more primitive morphology (shorter ACC and AC2, less elongated T6, large neck), while the latest Pleistocene - Holocene sites of Corbeddu Cave, Su Guanu Cave and Fontaneddu always lie on the opposite side. Analogous results are shown in Plots 5-6, where B/E, A1/A2, and A7/A are plotted against each other. In particular, we can observe that the Monte San Giovanni sample tends to fall in an intermediate position between the primitive and more derived populations in the elongation of ACC and AC2 and the width of the neck, while it groups with the primitive sites in having a poorly developed T6. The sample from Bonaria falls closer to the more derived groups, except for the high value of B/E, which is a primitive feature. The small samples of Siniscola always group within the Pleistocene sites, more or less close to Monte San Giovanni or to Capo Figari and Dragonara Cave; the sample from Siniscola E always shows more derived morphologies than Siniscola C, consistent with its higher stratigraphic position. In spite of their small size, Corbeddu Cave teeth always fall in the region with higher derived values of the parameters. The Corsican sample of Fontaneddu is relatively distinct from the latest Pleistocene-Holocene sites of Sardinia in having the largest size and the narrowest neck, coupled with a somewhat less elongated ACC.

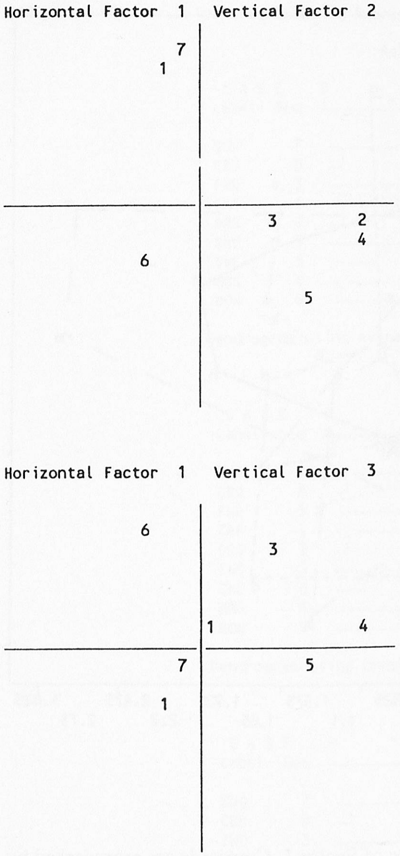
Plots 7 and 8, which concern the morphology of the pitymyoid rhomb, show less significant results, but suggest a weak trend towards a narrowing of this feature from the sites of Capo Figari, Dragonara Cave, and Siniscola C to the Holocene sites. Again, Monte San Giovanni and Bonaria are intermediate, the former falling closer to the less derived populations, the latter closer to the most derived ones.

The differences between the less derived and the most derived populations are significant in the analysis of variance.

The results of the bivariate analysis have indicated some morphological trends that are largely congruent with the chronological position of the samples. These trends tend to display a pattern of mosaic distribution among the populations, especially as far as the features of the neck and of the pitymyoid rhomb are concerned, but have, however, allowed us to recognize Monte San Giovanni and Bonaria as intermediate populations.

These results have been confirmed through factor analysis. We report here the results of the analysis of morphological indices, which proved to be the most informative. Factors have been extracted from the correlation matrix (canonical metric) using the method of principal components. Subsequently, a Varimax orthogonal rotation was performed on the first three principal components (with eigenvalue ≥ 1), in order to better characterize the morphological significance of the factors. Fig. 4 shows the correlations of the morphological indices with varimax factors 1 to 3, which explain about 77.3% of the total variance.

The Factor 1 and 2 scores are plotted in the scatter diagram in Fig. 5. Together, these factors account for the 57.6% of total variance. A marked distinction between the Pleistocene sites of Capo Figari, Dragonara Cave, Siniscola C and E and Monte San Giovanni on the one hand, and the Holocene sites Corbeddu Cave, Su Guanu Cave and Fontaneddu on the other can be seen. The former display higher scores on Factor 1 and lower ones on Factor 2 (broad neck and less elongated T6), the latter are characterized by lower scores on Factor 1 (narrow neck, and more elongated T6) and higher scores on Factor 2 (relatively high degree of ACC and AC2 elongation). The sample


Horizontal Factor 1 Vertical Factor 2

Horizontal Factor 1 Vertical Factor 3

Symbol	Variable	FACTOR 1	FACTOR 2	FACTOR 3
1	A/L	-.18179	.76024	-.22427
2	B/W	.95186	-.04730	.05661
3	C/W	.41635	-.02493	.77851
4	B/E	.95499	-.15310	.05761
5	A1/A2	.63635	-.44435	-.01974
6	A3/A4	-.23095	-.22968	.84419
7	A7/A	-.08181	.82885	-.04584
	Variance	2.49941	1.54146	1.37805
	%	35.56	22.02	19.68

Fig. 4. Factor analysis: correlation of the morphological indices with Varimax factors (Factor 1 to 3). Factor 1 is related to indices expressing the elongation of T6 (index A1/A2), the degree of pinching of the neck relative to the width of the pitymyoid rhomb (index B/W), and the width of AC (index B/E). Negative factor scores correspond to more derived morphotypes, characterized by low values of B/E and B/W (deep pinching), and A1/A2 (quite elongated T6). Factor 2 is related to ACC and AC elongation (indices A/L and A7/A) relative to the total length of the crown and the anteroconid complex, respectively. The derived morphotypes are characterized by high scores on this factor. Factor 3 is related to the indices dealing with the characters of the pitymyoid rhomb (indices C/W and A3/A4). For legend, see Fig. 2.

from Bonaria is in a somewhat intermediate position in having primitive characters (broad neck and short elongation of T6), together with more derived features (elongated ACC and AC2), and could represent a transitional form to the more derived morphologies typical of the Holocene populations.

Among the Holocene localities, the population of Fontaneddu is again different in having the highest evolutionary degree of pinching of the neck and posterior development of T6, associated with ACC and AC2 that are a little less developed than those of the populations of Corbeddu Cave and Su Guanu Cave.

A set of Q-mode cluster analyses, computed from the mean values of all the descriptive variables for each population, has been used to evaluate the similarity relationships among the studied samples. Euclidean, cos-ϕ and Pearson's correlation metrics have been used together with U.P.G.M.A., W.P.G.M.A. and Complete Linkage clustering methods. The negligible differences

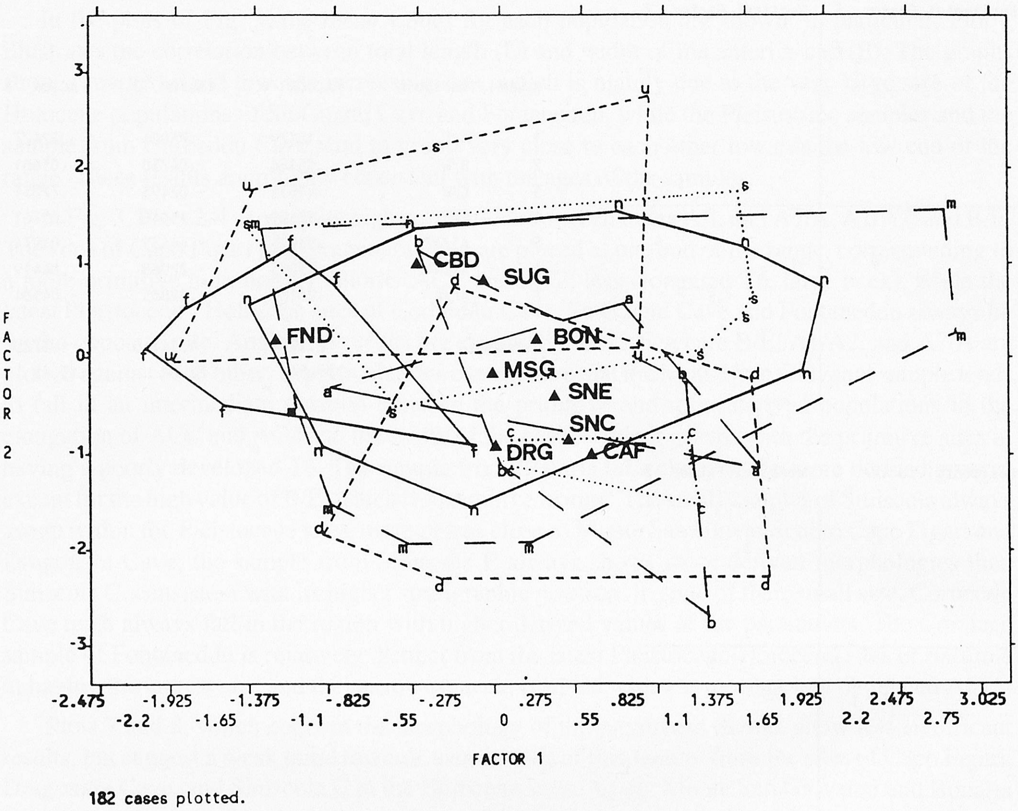


Fig. 5 Scatter diagram with scores of Factor 2 plotted against scores of Factor 1. Centroids are represented by filled triangles (▲). Legend: Capo Figari = c; Dragonara Cave = d; Siniscola C level = b; Siniscola E level = a; Monte San Giovanni = m; Corbeddu Cave = u; Su Guanu Cave = s; Fontaneddu = f; Bonaria = n.

observed between the nine solutions thus obtained confirm the high stability of the classification. Fig. 6 shows the results of the application of the cos-ϕ metric. The separation into two groups suggests two important issues:

1) evidence of a morphological distance between the Pleistocene and the latest Pleistocene to Holocene localities; 2) the possibility of arranging the Pleistocene sites in an evolutionary sequence, beginning from the primitive cluster of Capo Figari and Dragonara Cave to the more derived cluster of Monte San Giovanni and Bonaria.

IV. ANALYSIS OF MORPHOTYPES

The morphometrically investigated characters (i. e. ACC length, degree of pinching of the neck, posterior development of T6) have been used to group the specimens at our disposal into morphotypes coupled with numerical and statistical control. Other qualitative characters of the anterior cap have been also used for this purpose: the extent of the mesial enamel-free area, the occurrence of the seventh and ninth triangles (T7 and T9) and the shape and symmetry of the

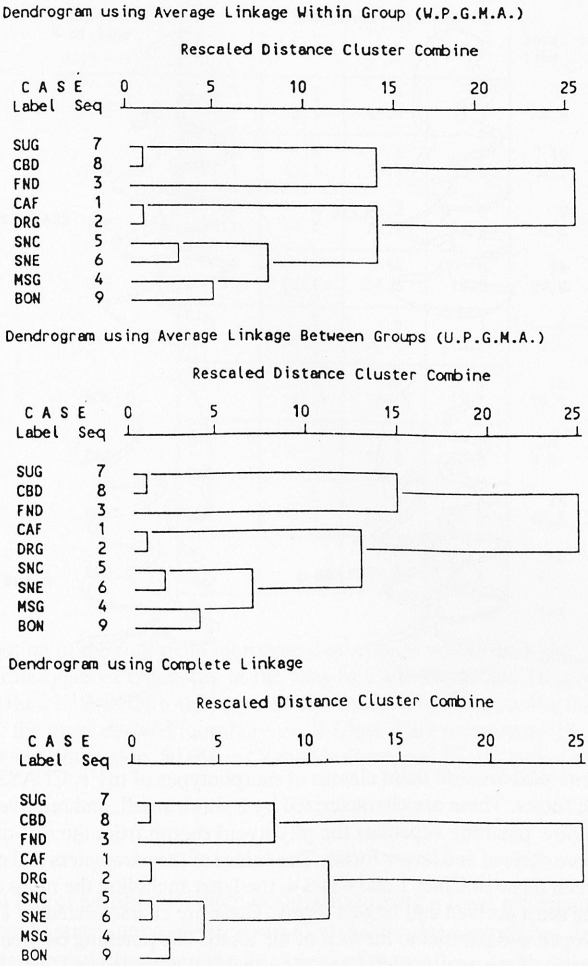


Fig. 6. Dendrograms resulting from cos-ϕ similarity matrix. A strict similarity between pairs of Pleistocene sites (Capo Figari and Dragonara Cave, Siniscola C and E, Monte San Giovanni and Bonaria, Corbeddu Cave and Su Guanu Cave) is seen. At a lower level of similarity, two groups with different degrees of evolution can be distinguished: the Pleistocene localities and the Upper Pleistocene-Holocene Sardinian and Corsican localities of Su Guanu Cave, Corbeddu Cave and Fontaneddu. For legend, see Fig. 1.

anterior cap. The classification has been done through a stepwise procedure. We started from a very detailed distinction that resulted in 20 morphotypes. Since this classification was too fragmentary and not effective in describing the variability among the samples, we merged the initial morphotypes into a smaller number of morphological classes, using quantitative methods (one-way analysis of variance and cluster analysis). The procedure was recursively repeated, until we obtained four main morphological classes, described in Fig. 7.

In the table of Fig. 8, the absolute and relative frequencies of the classes of morphotypes at each site are reported. The results of the analysis of morphotype frequencies again support the distinction between the Pleistocene and Holocene sites, the former showing higher frequencies of

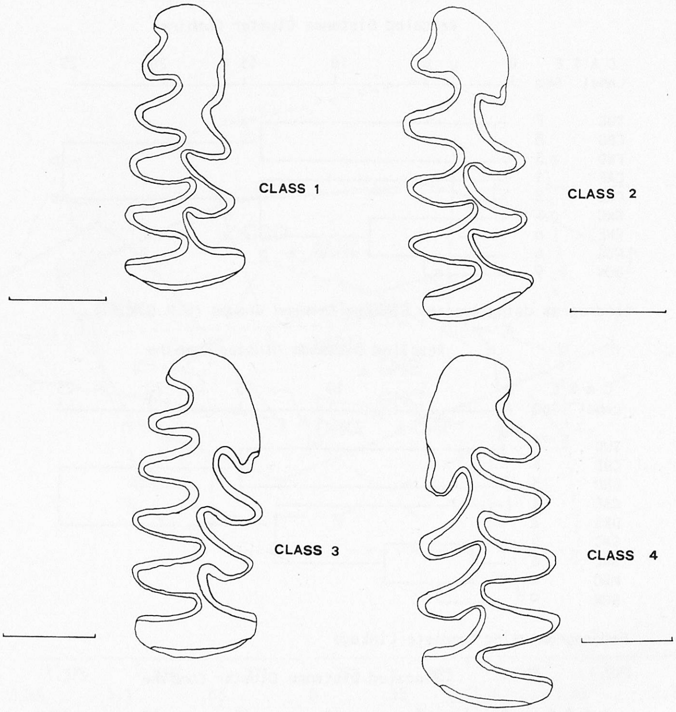


Fig. 7. *Microtus (Tyrrhenicola) henseli*: main classes of morphotypes of m1's. CLASS 1: Includes the most primitive and smallest forms. These are characterized by a short, small, and relatively simple AC2. T6 is not evident, and a shallow pinching separates the pitymyoid rhomb from the rest of the tooth. CLASS 2 and 3: Both include more derived and larger forms. The values of the parameters and morphological indices are intermediate between those of Class 1 and Class 4, the latter including the more derived morphotypes. CLASS 4: Includes the most derived and largest forms. These are characterized by a long and asymmetric AC2. T6 is well developed and parallel to the axis of the tooth. The pinching between BRA3 and LRA4 is very narrow. On the basis of the results of the one-way analysis of variance, Class 2 is close to Class 1 in characters of the ACC (indices A/L and A7/A), while other morphological characters (indices A1/A2 and B/W) place it closer to Class 3. Class 3 is connected to the more primitive Class 1 and Class 2, and to Class 4, in the tendency to have high values of L and A7/A and low values of B/E, and in the development of the ninth triangle, T9, in the anterior cap. Scale bars indicate 1 mm.

more primitive morphotypes. Among the Holocene sites the Corsican population of Fontaneddu shows the highest number of derived morphotypes, suggesting the greatest degree of evolution.

V. ANALYSIS OF ENAMEL MICROSTRUCTURE

A tentative analysis of enamel microstructure has been carried out on selected specimens from all the localities with the aim of identifying possible trends in the enamel pattern. An m1 of *Microtus (Allophaiomys)* cf. *ruffoi* (Cava Pirro, Apulia, late Early Pleistocene) was also examined, in order to compare our samples with a primitive species of the genus *Microtus*.

The observations have been mostly made on the posterior and anterior walls of the first three dental triangles. The ratio between the thickness of the posterior and anterior walls has also been

Abundance % of line	Morphological Classes				Total of line
LOCALITIES	1	2	3	4	
CAF	1 11.1	3 33.3	4 44.4	1 11.1	9 4.6
DRG	4 21.1	8 42.1	5 26.3	2 10.5	19 9.7
SNC	1 11.1	4 44.4	2 22.2	2 22.2	9 4.6
MSG	4 6.9	14 24.1	34 58.6	6 10.3	58 29.7
SNE		1 16.7	4 66.7	1 16.7	6 3.1
BON		18 47.4	15 39.5	5 13.1	38 19.5
CBD			9 50.0	9 50.0	18 9.2
SUG		2 8.3	8 33.3	14 58.3	24 12.3
FND			2 14.3	12 85.7	14 7.2
					195

Fig. 8. Table of distribution of the four main morphological classes within each site. The highest abundance of the primitive morphotypes of Class 1 is in the sites of Capo Figari and Dragonara Cave, where they represent 11.1% and the 21.1% of the total, respectively. On the other hand, in Fontaneddu, Su Guanu Cave, and Corbeddu Cave, the more derived morphotypes of Class 4 are represented by a very high percentage of specimens (85.7% in Fontaneddu, 50.0% in Corbeddu Cave, and 58.3% in Su Guanu Cave). For legend, see Fig. 1.

roughly evaluated on larger samples of each population using a light microscope. The microstructural study of the selected specimens of *Microtus* (*Tyrrhenicola*) *henseli* has demonstrated a certain degree of variability in the ratio between the thickness of the trailing and leading edges. The enamel zone in the posterior wall tends to be thinner than that in the anterior wall, their ratio roughly varying from 1.00 to 0.50. Interesting results have been obtained from the ratio between the thickness of the zone of tangential and radial enamel in the trailing edges (Table III).

Though the presence of substantial intraspecific variability indicates a need to investigate larger subsamples, the enamel pattern data show a general trend towards a reduction of the tangential layer in the trailing edges, coupled with a reduction in thickness of the distal enamel walls of the dental triangles. Analogous trends occur in a number of derived continental *Microtus* lineages, but in this endemic vole, it seems to have proceeded at a markedly slower rate.

The enamel differentiation in *M.* (*Tyrrhenicola*) is in agreement with the average evolutionary degree of crown morphology in both the more primitive populations (Capo Figari and Dragonara Cave), which are characterized by poorly differentiated trailing edges, and the more derived ones (Su Guanu Cave and Fontaneddu), which show an enamel pattern that is strongly differentiated in a microtine direction. On the other hand, the populations from Monte San Giovanni, Siniscola C and E, Bonaria, and Corbeddu Cave all display a comparable degree of derivation in the features of the trailing edges, but different degrees of evolution in crown morphology. These data show that enamel differentiation and morphological evolution of the crown proceed at different rates, and are independent processes. This is also known in a number of other arvicolids. The parallel evolution observed in *M.* (*Tyrrhenicola*) and several continental microtines indicates that the

Table III

Data from the preliminary analysis of patterns of enamel microstructure

Locality	N	Trailing edge/ leading edge ratio	% thickness of tangential zone
Cava Pirro	1	1.00	50
Capo Figari	1	0.85-0.90	50
Dragonara Cave	1	0.90	40
Siniscola	3	0.60-0.80	25-45
Monte San Giovanni	1	0.80	30
Bonaria	1	0.75	35-38
Corbeddu Cave	2	0.60-0.80	25-38
Su Guanu Cave	2	0.50-0.60	20-40
Fontaneddu	3	0.60	20-40

pattern of modification of the enamel microstructure results from a morpho-functional canalization of the characters, perhaps due to changing ecological-environmental conditions (KOENIGSWALD 1980; KOLFSCHOTEN 1992).

VI. CONCLUDING REMARKS

Morphometric analyses of crown morphology and a preliminary study of enamel microstructural pattern both resulted in evidence for evolutionary trends in the first lower molar of *Microtus (Tyrrhenicola) henseli.*

These trends are briefly summarized as follows: 1) increase in tooth size; 2) increasing elongation of ACC relative to the tooth total length; 3) increasing elongation of AC2, coupled with further complication of its morphology; 4) increase in the posterior elongation of the sixth triangle (T6); 5) narrowing neck; 6) slight increase in the narrowing of the pinching of the pitymyoid rhomb; 7) general reduction in thickness of trailing edges relative to leading ones, coupled with reduction of the zone of tangential enamel in the trailing edges.

Most of these trends are correlated with each other, but the pattern of mosaic distribution of the characters indicates that the process of evolutionary differentiation is affected by stochastic fluctuations.

The development of these evolutionary tendencies is evident in the populations from the studied localities, whose age ranges from the Middle-Late Pleistocene to the Holocene. The most marked differences occur between the Pleistocene and the Holocene populations, even though a certain degree of differentiation can also be observed within the Pleistocene Sardinian populations. In the Holocene group, the population of Fontaneddu is distinct in having some peculiar characters. As a consequence, two suggestions can be made: the first deals with the relative chronological succession of the studied localities, the second concerns the supposed biogeographic differentation of the endemic vole in Sardinia and Corsica.

1) The sampled sites can be arranged in a biochronological succession, with the identification of two groups: a primitive group (Capo Figari, Dragonara Cave, Siniscola C and E, Monte San Giovanni and Bonaria) and a more derived one (Su Guanu Cave, Corbeddu Cave, and Fontaneddu). Within the first group of populations, of Middle to Late Pleistocene age, the teeth of Capo Figari and Dragonara Cave are the most primitive overall; their enamel pattern is poorly differentiated in a microtine direction. The populations of Monte San Giovanni and Bonaria show a higher degree

of evolution relative to the previously cited populations even though, in both of them, some derived characters are still associated with other more primitive features. The population of Bonaria appears to be closer to the more derived forms of the latest Pleistocene and Holocene, placed in the second group. The teeth from Siniscola are separated into two samples from different stratigraphic levels: Siniscola C, from the lower stratigraphic level, tends to group with the more primitive Capo Figari and Dragonara Cave samples, while Siniscola E is closer to the sample of Monte San Giovanni.

Within the latest Pleistocene to Holocene group, the population of Corbeddu Cave is distinct in having some primitive features, e. g., relatively small size and a less derived enamel pattern, comparable to those of the populations of the first group, but coupled with a highly derived morphology of the ACC.

In the Holocene population of Su Guanu Cave we can for the first time observe a marked increase in size, while the other morphological features remain relatively stable. This change could represent the response of the endemic vole to the impact of man just before its final extinction in Sardinia and Corsica. Other factors might also have influenced this morphological change, especially the climatic and environmental changes that occurred at the end of the last glacial cycle.

2) The population of the Corsican site of Fontaneddu is markedly distinct from the coeval Sardinian ones, and could possibly represent a distinct subspecies. At the moment, a lack of large samples does not allow us to make any taxonomic decision. It is quite probable, however, that repeated faunistic interchanges, alternating with periods of isolation, took place between the two major Tyrrhenian islands during the glacial-interglacial cycles. Further studies on *Microtus* (*Tyrrhenicola*) *henseli* from Sardinia and Corsica are therefore necessary for a better understanding of the details of the biogeography of this vole.

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