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Parameterization of the distribution of arvicolid tooth enamel

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Abstract. Morphological Units and Enamel Units can be defined on the basis of the morphology of the tooth enamel in arvicolids. These units can then be used in an analytical method known as Enamel Units Methodology by which we can: 1) identify genera, species and populations; 2) provide data relevant to phylogeny and evolutionary processes; 3) infer genetic characteristics and ecological conditions.

Key words: Arvicolidae, tooth morphology, enamel, evolution, palaeoecology, systematics.

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I. INTRODUCTION

The data obtained in the study of the tooth morphology of arvicolid fossils using different methods (HINTON 1926; CHALINE 1972; VAN DER MEULEN 1973; KOENIGSWALD 1980; RABEDER 1981; HEINRICH 1982) permits the definition of morphotypes that can be used in systematics. The aim of this paper is to propose a method to describe and quantify enamel morphology. This is a continuation of previous papers published by RUIZ BUSTOS (1987, 1988, 1992, 1993a), in which the Morphologic Unit (MU) and the Enamel Unit (EU) are defined (Fig. 1). Both units represent morphotypes: one based on initial and definitive folds in the anteroconid complex and the other based on the length of the enamel in the folds.

In this paper, I use this methodology to examine a Late Pleistocene (upper half of the Mediterranean Würm according to RUIZ BUSTOS 1993c) fossil population of *Microtus arvalis*. This population was collected from a sediment layer formed during infill of the karstic cavity known as Cueva de la Pastora. The cave is located at 30SWG228349, at 1350 m above sea level in the Betic Cordillera (south Spain). The data obtained from the fossil population in Cueva de la Pastora are compared with those obtained from two living populations of *Microtus arvalis* from Segovia and Teruel, which represent two extremes of the morphological variation found in this species in Spain. The Segovian population belongs to the subspecies *Microtus arvalis asturianus* (MILLER, 1908) and the Teruel population to *Microtus arvalis meridianus* MILLER, 1908.

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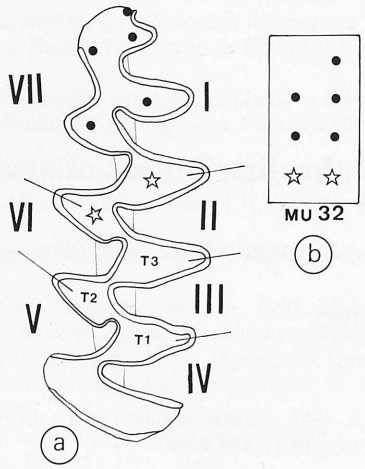

Fig. 1. a) Scheme of the Enamel Units as defined in *Microtus arvalis*; b) Representation of Morphologic Unit MU32. (.) initial fold; (*) definitive fold.

II. DEFINITION OF MORPHOLOGIC UNIT (MU) AND ENAMEL UNIT (EU)

The biological nature of Enamel and Morphological Units is based on the fact of enamel fold formation from points in the dental papilla, whose cells undergo intensive mitosis during embryonic development. These points are known as mitosis areas (m). The location of each fold on the crown, its form and size are characteristic and hereditary. This implies that there are coded instructions in the genotype corresponding to each fold and, therefore, to the Morphologic Units (MU) and Enamel Units (EU). These instructions are responsible for the entire process of development from the mitosis area to enamel fold formation in the tooth of the adult animal.

The Morphologic Unit (MU) is a specific kind of morphotype made up of both definitive and initial folds that are constant in number and location on the crown. Initial folds are those new folds that frequently appear in such tooth zones as the anteroconid complex. Definitive folds, on the other hand, are stable folds appearing in other areas, such as the first three triangles of M/1. These folds are always present and cannot increase in size.

In some groups of arvicolids, the successive appearance of initial folds is common in the anteroconid complex, whereas in other groups it is rare. I propose a theoretical model with all possible Morphologic Units (MU) (Fig. 2) and explain the transformations amongst them within the anteroconid complex. The different morphologies of the anteroconid complex occurring in nature can be obtained from a sequence made up of successive anteroconid complexes through time, in which the more recent complexes have a higher number of initial folds. The transformation of initial folds to definitive folds can be reproduced by two sequences. In the first, this transformation takes place one by one, starting with T4, followed by T5, T6 and so on. In the other sequence, the transformation occurs two by two, starting with the T4-T5 pair, then T6-T7 and so on. The MU that could be formed, up to six definitive folds in the anteroconid complex, were numbered by RUIZ BUSTOS (1988). Thereafter, naturally occurring MU with more than six folds are given the next number after the last published MU number.

The Enamel Unit (EU) is a segment of enamel long enough to identify a fold. RUIZ BUSTOS (1988) established seven EU, whose numerical values set in a constant order are a direct

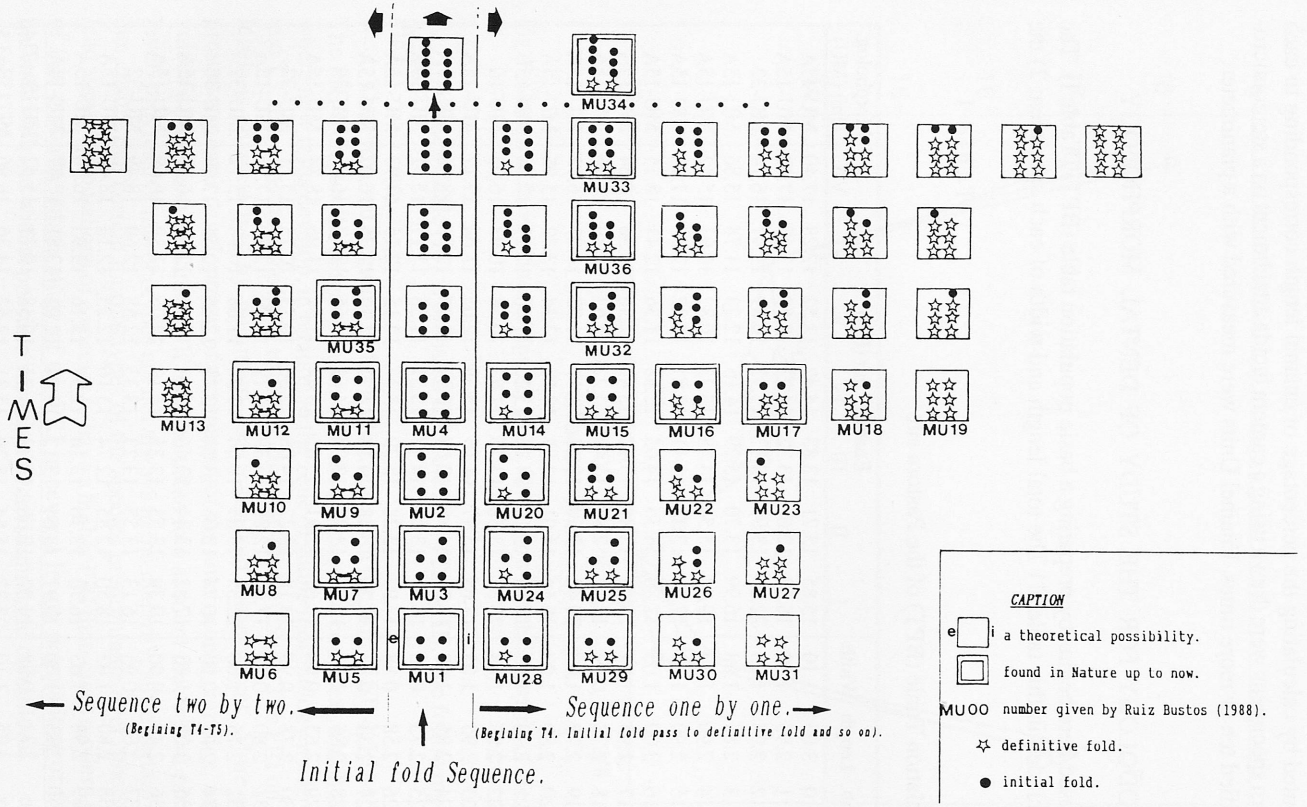

Fig. 2. Theoretical model to explain the morphological transformations of the anteroconid complex in M/1 of arvicolids. Each anteroconid complex is represented by a square. The right side of the square represents the labial side of the tooth and the left is the tooth's lingual side. The initial folds (.) and definitive folds (*) are shown inside each square. The squares thus far observed in natural populations of arvicolids are drawn with double lines, while squares with sigle lines represent theoretical possibilities. The initial fold sequence is set in the middle of the picture. It is made up of successive anteroconid complexes over a period of time, in which the more recent complexes have a higher number of initial folds. Transformations of initial folds to definitive folds can be reproduced by two sequences. On the right side, this transformation toccurs one by one, starting with T4, followed by T5, T6 and so on. On the other side, the sequence of transformation takes place two by two, starting with the T4-T5 pair, then T6-T7 and so on. Arvicolids with roots can have different morphologies depending on the height of the tooth, and therefore different Mophological Units from the bottom to the top. The Morphological Units at the top of rooted teeth have many initial folds. Each Morphologic Unit is defined by the sign MU plus a number, but if the tooth has a root it is advisable to use MUr. Each new Morphologic Unit found in nature is given the next number after the last published MU number.

representation of the size and position of the enamel folds. EU-I and EU-VII measure the length of the enamel in the anteroconid complex. EU-I measures the lingual side and EU-VII the labial side. The remaining five EU measure the length of the enamel on the three basic or initial triangles found in all Arvicolidae. In order to eliminate differences due to individual size, measurements are proportionally distributed by calculating the percentage of enamel length corresponding to each EU. Fossils and modern specimens were drawn using a camera lucida attachment on a stereomicroscope and then magnified ten or more times. Enamel Units were measured with a planimeter.

III. A METHODOLOGY FOR THE STUDY OF DENTAL MORPHOLOGY

The method proposed here begins by preparing a basic population table (BPT) (Table I). The following data are included in this table: 1) The total length and width of each specimen; 2) the

Table I

Basic Population Table (BPT) of the Pastora site

Date	Site	Spec.	Symb.	Length	Width	Enamel Unit (EU) I	II	III	IV	V	VI	VII	Morpholog. Unit (MU)
UPPER PLEISTOCENE Upper Half Mediterranean Würm	Pastora site	*Microtus arvalis*	P-110	3.05	1.10	15.85	13.71	13.83	14.42	12.52	12.28	17.40	MU-15A
			P-111	2.93	1.03	16.39	12.68	13.32	14.21	12.58	13.57	17.29	MU-15A
			P-112	2.93	1.03	22.25	13.99	12.73	11.93	10.89	11.47	16.74	MU-32
			P-113	2.85	1.08	16.99	13.70	15.29	14.16	12.23	11.78	15.86	MU-15A
			P-114	2.90	1.00	19.33	15.54	14.73	13.23	10.82	10.93	15.42	MU-15A
			P-115	2.90	1.00	17.66	12.88	13.41	13.81	12.22	12.88	17.13	MU-15A
			P-116	3.00	1.05	17.80	13.35	14.05	12.88	11.36	12.41	18.15	MU-15A
			P-117	2.95	1.03	15.15	13.85	13.97	13.46	12.56	14.36	15.64	MU-15A
			P-118	2.78	0.99	14.02	12.82	13.49	13.22	13.62	13.89	18.96	MU-15A
			P-119	2.75	1.00	20.46	13.90	13.13	13.39	11.33	11.07	16.73	MU-15A
			P-120	2.80	1.00	16.64	14.01	13.87	13.87	13.34	13.32	15.95	MU-15A
			P-121	2.80	1.00	18.63	13.13	14.25	13.25	11.50	12.25	17.00	MU-15B
			P-222	2.85	1.08	23.37	13.58	13.76	11.73	10.58	10.93	16.05	MU-16
			P-223	2.95	1.03	17.65	13.97	14.16	13.39	12.03	11.64	17.17	MU-15A
			P-224	2.85	1.00	16.55	14.10	12.87	13.59	12.26	12.56	18.08	MU-15A
			P-225	2.75	0.90	18.30	13.65	14.48	15.31	11.58	11.17	15.51	MU-15A
			P-226	2.58	0.88	17.93	13.28	13.39	13.17	12.15	12.15	17.93	MU-15A
			P-227	2.33	0.93	17.73	13.38	14.18	13.71	12.17	12.76	16.07	MU-15A
			P-228	2.85	1.00	16.46	13.79	13.27	14.61	12.65	13.17	16.05	MU-33
			P-229	2.63	0.90	18.62	12.91	13.02	13.44	11.22	11.96	18.84	MU-15A
			P-230	2.78	0.95	23.18	13.22	14.08	12.36	10.73	10.73	15.71	MU-32
			P-231	2.80	0.95	17.66	12.80	13.39	14.19	12.00	12.70	17.26	MU-15A
			P-232	2.75	1.00	22.35	13.83	13.54	12.50	11.08	10.98	15.72	MU-32
			P-234	2.65	0.90	16.74	13.08	13.18	13.81	12.66	12.55	17.99	MU-36
			P-235	3.00	1.03	17.82	13.84	13.46	13.84	12.23	12.51	16.30	MU-15A
			P-236	2.40	0.90	19.39	13.53	13.75	13.19	12.06	11.39	16.69	MU-15A
			P-237	2.60	0.95	16.13	13.55	13.23	13.33	12.58	12.69	18.49	MU-32
			P-238	2.80	1.03	18.50	12.85	12.74	13.16	12.23	12.13	18.40	MU-15A
			P-239	2.98	1.03	16.70	13.16	13.16	12.97	13.16	13.95	16.90	MU-15A
			P-240	2.83	1.00	15.91	13.64	13.12	13.74	12.91	12.81	17.87	MU-15A
			Min.	2.33	0.88	14.02	12.68	12.73	11.73	10.58	10.73	15.42	MU 15A=73.4
			Max.	3.05	1.10	23.37	15.54	15.29	15.31	13.62	14.36	18.96	MU 15B=3.3
			Mean	2.80	0.99	18.07	13.52	13.63	13.46	12.04	12.30	16.98	MU 16=3.3
													MU 32=13.4
													MU 33=3.3
													MU 36=3.3

seven EU (I, II, III, IV, V, VI, VII) expressed as percentages of each specimen; the maximum, minimum and mean values of the EU in the population of the BPT. These data can be represented by a diagram of the mean values of EU in each population (Fig. 3); 3) the morphological unit to which each specimen belongs.

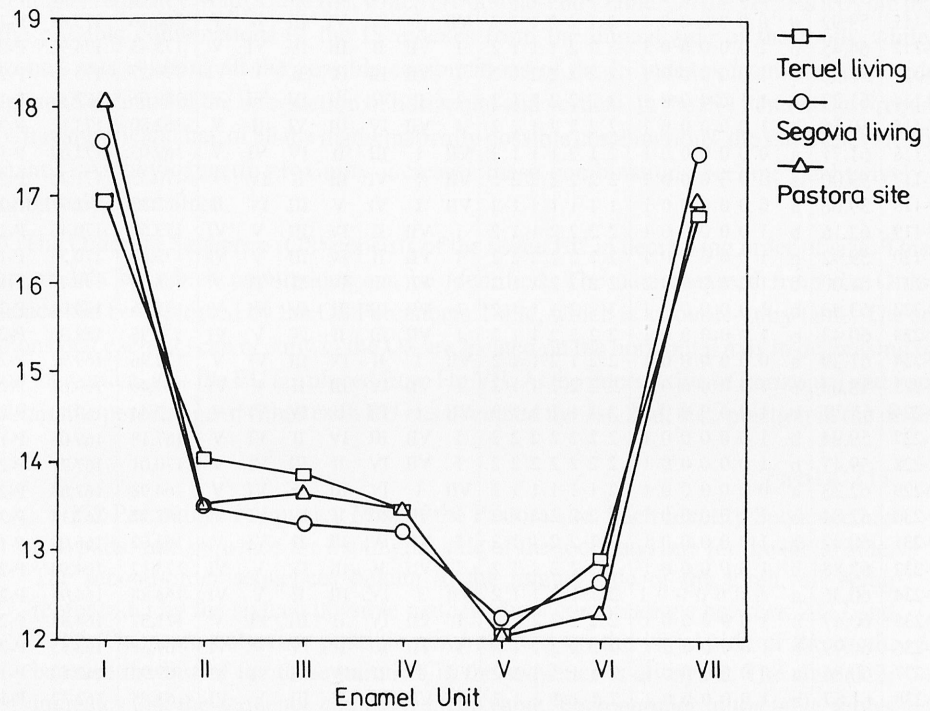

Fig. 3. Graphs of mean values of Enamel Units. They show the characteristic of the species level.

The Index Table (IT) is prepared from the BPT (Table II). The following indexes are shown in the IT:

1. The Proximal Regional Index (PRI) consists of the sum of EU-I, EU-VII, EU-II, and EU-VI. The PRI indicates the length of enamel in the anteroconid complex, which is the zone of the tooth where new folds develop, in relation to the zone of stable morphology made up of triangles T1, T2 and T3, that constitute the basic triplet common to all arvicolids. The PRI on the genus and species levels is characterised by minimum, maximum and mean values. More evolved species often present a greater development of the enamel of the anteroconid complex, which gives higher PRI values a progressive character. It must be taken into account that within each species (population level) progressive morphotypes are not always in the majority, since certain ecological conditions can ensure that certain morphotypes of the species predominate over others and this, in turn, can lead ancient populations of a species to have a higher PRI than more modern populations. Analysis of this problem entails study of the PRI in several living populations of the same species from habitats with the widest possible variation in environmental conditions.

2. The Identity Sequence (IS) is defined as the indexes obtained by dividing the values of the seven EU of M/1 by the value of EU-VII and expressing them in order from I to VII. I have chosen EU-VII as the denominator, as both it and EU-I are representative of the anteroconid complex, which is of greater phylogenetic interest than the basic triplet, whose morphology is more stable.

Table II

Index Table (IT) of the Pastora site

Symb.	PRI	Identity Sequence IS1	IS2	Ordering Sequence OS	MSI	Simil. Sequen. SS
P-110	59.24	a 0 0 0 0 0 0 1	2 2 2 2 1 1 2	VII I IV III II V VI	170.46	189.06 P-114
P-111	59.92	a 0 0 0 0 0 0 1	2 1 2 2 1 2 2	VII I IV VI III II V	160.26	175.43 P-112
P-112	64.45	b 1 0 0 0 0 0 1	3 2 2 1 1 1 2	I VII II III IV VI V	175.43	174.96 P-224
P-113	58.32	b 1 0 0 0 0 0 1	2 2 2 2 2 1 2	I VII III IV II V VI	170.27	173.95 P-223
P-114	61.22	f 1 1 0 0 0 0 1	3 2 2 2 1 1 2	I II VII III IV VI V	189.06	173.58 P-119
P-115	60.56	b 1 0 0 0 0 0 1	2 2 2 2 1 2 2	I VII IV III VI II V	162.80	173.12 P-232
P-116	61.71	a 0 0 0 0 0 0 1	2 1 2 1 1 1 2	VII I III II IV VI V	169.03	172.62 P-120
P-117	59.00	a 0 0 0 0 0 0 1	2 2 2 2 2 2 2	VII I VI III II IV V	170.33	171.75 P-222
P-118	59.68	a 0 0 0 0 0 0 1	1 1 1 1 1 1 2	VII I VI V III IV II	162.32	171.57 P-235
P-119	62.16	b 1 0 0 0 0 0 1	2 2 2 2 1 1 2	I VII II IV III V VI	173.58	170.46 P-110
P-120	59.92	b 1 0 0 0 0 0 1	2 2 2 2 2 2 2	I VII II IV III V VI	172.62	170.33 P-117
P-121	61.00	b 1 0 0 0 0 0 1	2 2 2 2 1 1 2	I VII III IV II VI V	166.09	170.27 P-113
P-222	63.93	b 1 0 0 0 0 0 1	3 2 2 1 1 1 2	I VII III II IV VI V	171.75	170.01 P-228
P-223	60.43	b 1 0 0 0 0 0 1	2 2 2 2 1 1 2	I VII III II IV V VI	173.95	169.96 P-240
P-224	61.29	a 0 0 0 0 0 0 1	2 2 1 2 1 1 2	VII I II IV III VI V	174.96	169.92 P-237
P-225	58.63	b 1 0 0 0 0 0 1	2 2 2 2 1 1 2	I VII IV III II V VI	169.40	169.67 P-236
P-226	61.29	b 1 0 0 0 0 0 1	2 1 1 1 1 1 2	VII I III II IV VI V	167.64	169.40 P-225
P-227	59.94	b 1 0 0 0 0 0 1	2 2 2 2 2 2 2	I VII III IV II VI V	167.18	169.03 P-116
P-228	59.47	b 1 0 0 0 0 0 1	2 2 2 2 2 2 2	I VII IV II III VI V	170.01	167.77 P-230
P-229	62.33	a 0 0 0 0 0 0 1	2 1 1 1 1 1 2	VII I IV III II VI V	164.98	167.64 P-226
P-230	62.84	b 1 0 0 0 0 0 1	3 2 2 2 1 1 2	I VII III II IV VI V	167.77	167.18 P-227
P-231	60.42	b 1 0 0 0 0 0 1	2 1 2 2 1 1 2	I VII IV III II VI V	162.02	166.09 P-121
P-232	62.88	b 1 0 0 0 0 0 1	3 2 2 2 1 1 2	I VII II III IV V VI	173.12	164.98 P-229
P-234	60.36	a 0 0 0 0 0 0 1	2 1 1 2 1 1 2	VII I IV III II V VI	164.88	164.95 P-239
P-235	60.47	b 1 0 0 0 0 0 1	2 2 2 2 2 2 2	I VII IV II III VI V	171.57	164.88 P-234
P-236	60.99	b 1 0 0 0 0 0 1	2 2 2 2 1 1 2	I VII III II IV V VI	169.67	163.65 P-238
P-237	60.86	a 0 0 0 0 0 0 1	2 1 1 1 1 1 2	VII I II IV III VI V	169.92	162.80 P-115
P-238	61.87	b 1 0 0 0 0 0 1	2 1 1 1 1 1 2	I VII IV II III V VI	163.65	162.32 P-118
P-239	60.71	a 0 0 0 0 0 0 1	2 2 2 2 2 2 2	VII I VI V II III IV	164.95	162.02 P-231
P-240	60.23	a 0 0 0 0 0 0 1	2 1 1 2 1 1 2	VII I IV II III V VI	169.96	160.26 P-111
		% frequency	% frequency	% frequency		Similit. Succ.
Min.	58.32	a=36.66			160.26	(SS/95)
Max.	64.45	b=60.00	(See IS2 Map	(See OS Table of Percent.	189.06	
Mean	60.87	f=3.34	Table III)	Table IV)	169.32	(See Table V)

The EU-VII is chosen, rather than EU-I, as it is smaller and its indexes are almost invariably greater than unity. The IS indicates the relationship of the size of each EU to EU-VII.

The purpose of these indexes is to quantify the morphotypes formed by the enamel folds on the crown. These morphotypes cannot be differentiated using traditional parameters such as total length and width of the tooth. Quantification of the size of the folds is necessary to establish objective differences between them. By expressing the EU in percentages all the stems are made equivalent to 100, and therefore the environmental influence on the stem is reduced. The relationship between the genes coding for the size of the cusps can be inferred from the values contained in the IS. The different IS in a population indirectly reveal the different genetic combinations present in that population.

The formula of the General Identity Sequence (IS1) is:

IS1 = I/VII; II/VII; III/VII; IV/VII; V/VII; VI/VII; VII/VII,

while the formula of the Reduced Identity Sequence (second order) is:

IS2 = I/(VII/2); II/(VII/2); III/(VII/2); IV/(VII/2); V/(VII/2); VI/VII/2); VII/(VII/2).

For ease of comparison between indexes, these are expressed by the following approximation: values from 0 to 0.90 are considered as "0", from 1 to 1.49 as "1", from 1.50 to 2.49 as "2", from 2.50 to 3.49 as "3" and so on.

The data obtained from the second order Identity Sequence (IS2) can be expressed by the IS2 Percentage Frequency Map (Table III), which is a double-entry table. On the vertical axis are placed all the possible combinations of the IS indexes from the lingual side of the tooth, while the horizontal axis contains all the possible combinations of the IS indexes from the labial side. A complete IS is found at the intersection of horizontal and vertical. In the IS2 Percentage Frequency Maps it is significant that, of all the mathematically possible combinations, the same ones are found constantly. As phylogenetic proximity increases these combinations become qualitatively and quantitatively more alike.

3. The Ordering Sequence (OS) consists of the seven EU in decreasing order of size. This is a group of data by which populations can be identified. The data obtained from the Ordering Sequence can be expressed by the OS Percentage Table, which is a double-entry table. The seven positions that each EU can occupy in the OS are located on the horizontal axis in decreasing order and on the vertical axis the EU are placed from I to VII. At the intersection of horizontal and vertical we obtain the percentage of times each EU has occupied the 1st, 2nd, etc., position in the different

Table III

IS2 Percentage Frequency Map of the Pastora site. Each Identity Sequence has two parts: one sequence for the lingual side of the tooth and one for the labial side. The second-order sequences belong to the lingual side of the tooth, all being represented by the sixteen possible mathematical combinations between 2222 and 1111. There are only four possible combinations on the labial side of the tooth, because the last of the three numbers in the sequence is always 2. The sign (3:2) indicates that the sequence can have either value. Each number in the table shows the percentage of teeth in the population that belongs to each Identity Sequence. The total represents the sum of the percentages in each lingual horizontal line and each labial vertical line

Lingual side \ Labial side	222	212	122	112	Total
(3:2)222	20%	3.3%	3.3%	30.0%	56.6%
(3:2)221				6.6%	6.6%
2212				6.6%	6.6%
2122			3.3%	3.3%	6.6%
1222					0%
2211					0%
2112				3.3%	3.3%
1122					0%
2121				3.3%	3.3%
1221					0%
1212					0%
1112					0%
1121					0%
1211					0%
2111				13.3%	13.3%
1111				3.3%	3.3%
Total	20%	3.3%	6.6%	69.7%	

OS of a population. These data can be used to obtain the Ordering Sequence of Maximum Percentages and each of the values represented by those percentages (Table IV).

Table IV

Ordering Sequence Percentage Table of the Pastora site. The first column shows the Enamel Units that appear in the first position in the Ordering Sequence. Of the teeth in the population, 60% have EU-I in the first position and the remainder have EU-VII in the first position. The second column shows that EU-VII appears in the second position in 56.6% of the population, EU-I in 40% and EU-II in 3.3%, and so on to the seventh position. The Enamel Units with the highest percentage in each column, make up the Ordering Sequence of Maximum Percentage

UE	in decreasing order						
	1º	2º	3º	4º	5º	6º	7º
I	60	40	0	0	0	0	0
II	0	3.3	20	33.3	33.3	6.6	3.3
III	0	0	30	33.3	33.3	3.3	0
IV	0	0	36.6	23.3	30	6.6	3.3
V	0	0	0	6.6	0	36.6	56.6
VI	0	0	10	3.3	3.3	46.6	36.6
VII	40	56.6	3.3			0	0
Ordering Sequence of Maximum Percentages							
I-60							
VII-56.6							
IV-36.6							
II-33.3 III-33.3							
II-33.3 III-33.3							
VI-46.6							
V-56.6							

When comparing the OS in different populations using the percentage table of the OS it must be borne in mind that the sum of the individual percentages corresponding to each EU at each of the seven horizontal positions is 100.

4. Morphological Similarity Index (MSI). This index must be specific in order to characterise each specimen. The MSI attempts to avoid accidental representation of teeth with different morphologies in a population by the same numerical value. The MSI will be more or less similar depending on the relative similarity of the teeth represented.

The formula to obtain the MSI of the teeth in the populations of Arradiculatinae is:

MSI= (1/2*I) + (10*II) + (3/5*III) – (1/10*IV) + VII + (1/5*VI) – (1/10*V).

The Morphological Similarity Index (MSI) in arvicolids with rooted molars has the formula:

MSI= (1/5*I) + (4*II) + (3*III)+ V +(1/3*VI) – ((1/5* VII) + (1/2*IV).

The MSI formulas are the results of empirical tests.

5. The Similarity Sequence (S) is the decreasing ordering of the MSI. The relative positions of the teeth in the Similarity Sequence (S) indicate their morphological relationships. The morphological similarity between two specimens (A and B) is expressed as a percentage. The formula is:

S = 100-(((MSI specimen A – MSI spec.B)*100)/(max. MSI – min. MSI of the sample)).

It is possible that the maximum or minimum MSI or both will be from specimens of teratological morphology. The solution to this problem is to make two groups: one with the specimens that have an MSI greater than the mean MSI of the sample, and the other with the specimens that have an MIS lower than the mean MSI of the sample. I replace the maximum MSI of the sample in the S formula by the mean of the group which has the bigger MSI, and the minimum number of MSI is replaced by the mean of the group which has the lower MSI. In natural populations the value of S is similar in the two cases.

We can determine which groups of teeth have a relative similarity of 95% or higher, which I refer to as Series 95 (S95), each of which is characterised by an individual specimen with the highest MSI (Maximum 95 - M95) (Table V).

Series 95 (S95) allows us to detect the position of the morphologies of each specimen in relation to the population as a whole as well as the number of specimens in each S95 group. Analysis of S95 reveals the most frequent morphologies, the minority morphologies, the size of the gaps between S95 and the relative position of each tooth in the population (Table V). This can be used to identify fossil populations of the same species.

The data obtained for S95 in living populations can be useful for confirming mixing in populations from cave fillings. Ecological conditions can be deduced from the distribution of the morphotypes in the population.

The Results Table (RT) (Table VI) presents the data identifying each population and allows comparisons between populations.

IV. CONCLUSIONS

The mean values of Enamel Units in the three populations are the same because they show the characteristics of the species level.

The index values obtained from the Cueva de la Pastora, Segovia and Teruel populations show the characteristics of the population level. Greater similarity is observed between the Cueva de la Pastora and Segovia populations than between either and the Teruel population.

The S95 in Pastora and Segovia shows a predominance of the morphology in the Maximum 95 corresponding to 170, and also coincide in the values of 166-165 and 163. The distribution of morphology in the Teruel population is quantitatively uniform and rather variable. This indicates that all the morphotypes have similar survival expectancy as regards natural selection by the habitat and, therefore, the population is ready to widen its area and colonise. When ecological conditions are adverse, on the other hand, the morphological characteristics become discontinous prior to leaving the habitat, but the S95 does not show as much continuity and regularity in the Maximum 95. In my opinion, a study of the Teruel population using the Enamel Units method over a period of years would be necessary in order to solve this question satisfactorily.

The similarity between the Pastora and Segovia populations is much greater than could reasonably be expected considering that Cueva de la Pastora is a karstic infill in southern Spain and the Segovia population is currently living over 500 km north of Pastora. As the biocenograms (RUIZ BUSTOS 1993b) show, there are at present climatic differences between these two geographical regions. The conservation of the morphology between Pastora and Segovia, with similar quantities and qualities of morphotypes, suggests that the ecological conditions of the fossil habitat were similar to the current conditions in the habitat of the Segovia population.

The data obtained show that the Enamel Units method can distinguish between populations by reestablishing the morphological distance between the Teruel and Segovia populations observed by MILLER (1908) and CABRERA (1914). These authors used a different method, using the body of

Table V

Series 95 of the Pastora site. The column of symbols between the two vertical lines on the left side of the table includes all specimens in the population. Each row is a Series 95. For example, the row of specimen P110 begins with 170.46, representing the MSI value of that specimen. The morphologic similarity between P110 and the next specimen (P117) is 99.6%, the similarity between P110 and specimen P113 is 99.3%, the similarity between P110 and specimen P228 is 98.4%, and so on, to specimen P116, which is 95% similar to P110. Specimen P230 cannot be included in the P110 Series because its similarity is lower than 95%. The N symbol indicates the number of teeth in each Series 95. I calculate the importance of each Maximum within the population in relation to the number of teeth belonging to that Maximum.

95 Series or Maximum	Similitude Successions (SS/95)																N	Importance of Maximum
	P114																1	
	P112	P224	98.4														2	
	P224	P223	96.5	P119	95.2												3	
173.95	P223	P119	98.7	P232	97.1	P120	95.4										4	17.39
	P119	P232	98.4	P120	96.7												3	
	P232	P120	98.3	P222	95.2												3	
	P120	P222	97.0	P235	96.4												3	
	P222	P235	99.4	P110	95.5	P117	95.1										4	
	P235	P110	96.2	P117	95.7	P113	95.5										4	
170.46	P110	P117	99.6	P113	99.3	P228	98.4	P240	98.3	P237	98.1	P236	97.3	P225	96.3	P116	95.0	9	39.13
	P117	P113	99.8	P228	98.9	P240	98.7	P237	98.6	P236	97.7	P225	96.8	P116	95.5			8	
	P113	P228	99.1	P240	98.9	P237	98.8	P236	97.9	P225	97.0	P116	95.7					7	
	P228	P240	99.8	P237	99.7	P236	98.8	P225	97.9	P116	96.6							6	
	P240	P237	99.9	P236	99.0	P225	98.1	P116	96.8									5	
	P237	P236	99.1	P225	98.2	P116	96.9											4	
	P236	P225	99.1	P116	97.8													3	
	P225	P116	98.7															2	
169.03	P116	P230	95.6	P226	95.2													3	13.04
	P230	P226	99.6	P227	98.0													3	
	P226	P227	98.4															2	
	P227	P121	96.2															2	
166.09	P121	P229	96.1	P239	96.0	P234	95.8											4	17.39
	P229	P239	99.9	P234	99.7	P238	95.4											4	
	P239	P234	99.8	P238	95.5													3	
	P234	P238	95.7															2	
163.65	P238	P115	97.0	P118	95.4													3	13.04
	P115	P118	98.3	P231	97.3													3	
	P118	P231	99.0															2	
	P231																	1	
	P111																	1	

Table VI

Table of Results for the Pastora site and Teruel and Segovia (living populations). In the left column are the indexes used in the methodology of Enamel Units and the remaining columns are the results obtained for each population. The scale of Maxima has values in relation to the highest and lowest values found in the population studied.

Parameters		fossil samples PASTORA	living samples TERUEL *M. arvalis*	SEGOVIA *M. a. astrurianus*
num. specim.		30	37	41
Morph. Unit	MU 15A	73.4	97.3	85.3
	MU 15B	3.3	0	2.4
	MU 16	3.3	0	0
	MU 32	13.4	3.7	12.2
	MU 33	3.3	0	0
	MU 36	3.3	0	0
lengh (mean)		2.80	2.93	2.99
width (mean)		0.99	0.99	1.04
EU (mean)	I	18.07	16.95	17.65
	II	13.52	14.03	13.45
	III	13.63	13.84	13.24
	IV	13.46	13.41	13.24
	V	12.04	12.07	12.16
	VI	12.03	12.90	12.64
	VII	16.98	16.80	17.62
RPI (mean)		60.87	60.68	61.36
MSI (mean)		169.32	173.88	168.85
IS1 (%)	a	36.66	45.95	46.34
	b	60.00	48.65	53.66
	c	0	2.70	0
	d	0	0	0
	e	0	0	0
	f	3.34	0	0
	g	0	2.70	0
IS2 (Total)	2222	56.6	86.4	41.5
	2221	6.6	5.4	7.3
	2212	6.6	0	2.4
	2122	6.6	0	2.4
	1222	0	0	0
	2211	0	2.7	0
	2112	3.3	0	0
	1122	0	0	0
	2121	3.3	0	0
	1221	0	0	0
	1212	0	0	0
	1112	0	0	0
	1121	0	0	0
	1211	0	0	0
	2111	13.3	5.4	43.9
	1111	3.3	0	2.4
	222	20.0	29.7	12.2
	212	3.3	2.7	2.4
	122	6.6	2.7	12.2
	112	69.7	40.5	73.1
OS	1º	I-60	I-51.4	I-56.5
	2º	VII-56.6	I-48.6	VII-56.5
	3º	IV-36.6	II-54.1	II-39.1
	4º	II&III-33.3	III-37.8	III-39.1
	5º	II&III-33.3	IV-43.2	IV-34.8
	6º	VI-46.5	VI-67.6	VI-65.2
	7º	V-56.6	V-94.6	V-78.3
Maximum SS/95	(scale)			
	180		* 7.69	* 8.6
	179			
	178		* 12.82	
	177			* 8.6
	176			* 8.6
	175		* 12.82	
	174			* 8.6
	173	* 17.39		
	172		* 12.82	* 20.0
	171		* 12.82	* 14.3
	170	* 39.13	* 10.25	
	169	* 13.04	* 10.25	
	168		* 10.25	
	167		* 10.25	
	166	* 17.39		
	165			* 14.3
	164			
	163	* 13.04		* 11.4
	162			
	161			* 5.7
	160			

the animals to obtain their parameters. CABRERA (1914) considered *Microtus arvalis asturianus* to be an animal inhabiting high-altitude regions (1200m a. s. l.). If we consider that Cueva de la Pastora is located at 1350m a. s. l., it is significant that the Enamel Units method shows a similarity between the Pastora and Segovia populations.

These results suggest that the fossil population from Cueva de la Pastora is unmixed and therefore a sample from a single population.

The method described above can also be used to examine the morphology of the teeth in different populations of the same species. We can therefore identify populations from different parts of the species' distribution and observe the relationship between tooth morphology and environmental conditions. Study of living populations over several years would show how different natural events (fire, drought, etc.) and human activity (use of pesticides, industrial installations, reforestation, etc.) affect tooth morphology.

Fossil populations, especially from the Quaternary, can be analysed in the light of the data provided by living populations.

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