

THE ROLE OF THE WATER VOLES (ARVICOLA, RODENTIA) IN THE QUATERNARY

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ABSTRACT

Arvicolids are rodents which have molars with a morphology formed by a sequence of enamel folds similar to the curve $y = \sin f(x)$. The morphology of the crown of the first lower molar (m1) of living species of *Arvicola* (large voles) is identified with six criteria, irrespective of tooth size. When rootless arvicolid fossil communities are analysed, it can be seen that the m1 morphology of *Arvicola* is present in those communities represented by specimens of small size at the beginning of the Quaternary. Before this data was known, the presence of *Arvicola* communities could only be detected in the second half of the Quaternary, when the specimens were comparable to the large size characterizing living species. The existence of communities of small-sized *Arvicola* at the beginning of the Quaternary implies that the m1 of *Arvicola* undergoes a continuous and accelerated growth throughout the entire Quaternary, which allows representatives the genus to be used as a chronological tool. These data mean that it is necessary to change the concept of the genus *Allophaiomys* and to formulate a new classification to reflect evolutionary relationships of quaternary arvicolids.

Key words: *Arvicolids, mammals, enamel, sistematic, ecology, Quaternary.*

RESUMEN

Los arvicolidos son roedores que tienen la morfología de la corona de los dientes formada por una secuencia de pliegues de esmalte que se asemeja a la curva $y = \sin f(x)$. Las especies actuales del género *Arvicola* cumplen en la morfología del molar m1, seis criterios que son independientes de la talla. El examen de las poblaciones de arvicolidos sin raíz, procedentes del Pleistoceno inferior, indica la existencia de molares con una morfología idéntica a la de los ejemplares vivos de *Arvicola*, pero con menor talla. La existencia de esta identidad permite proponer la hipótesis de poblaciones primitivas del género *Arvicola* con pequeña talla durante el Pleistoceno inferior. Estas han pasado desapercibidas entre las poblaciones de *Allophaiomys*, a causa de su identidad morfológica entre ambos. La hipótesis de la existencia de *Arvicola* en el Pleistoceno inferior supone un profundo cambio en el concepto de *Allophaiomys* como género y convierte la talla de *Arvicola*, por su continuo crecimiento durante todo el Pleistoceno, en un útil instrumento cronológico.

Palabras clave: *Arvicolidos, mamíferos, esmalte, sistemática, ecología, Cuaternario.*

Introduction

Arvicolids are frequently present in fossil sites, in high numbers. The morphology of the enamel line on the crown and the size of molars change throughout time. These conditions mean that arvicolids become a reliable tool for biostratigraphical correlations in the Northern Hemisphere during the Quaternary.

The aim of this paper is to discuss the problems which arise from the fact that the teeth of genera

Arvicola and *Allophaiomys* have the same morphological pattern, for the m1, which consists of a posterior loop, three closed triangles (T1, T2, T3) and an anteroconid complex made up of a single dentine field with four large folds. The two genera are distinguished by size, with *Arvicola* being larger than *Allophaiomys*. This can be observed in most regions by comparing Middle and Upper Pleistocene specimens of *Arvicola* with Lower Pleistocene specimens of *Allophaiomys*. However, it can be difficult

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to distinguish between them towards the end of the Lower Pleistocene, since the larger specimens of *Allophaiomys* tend to be similar in size to the smaller *Arvicola*. Size no longer appears to be an adequate criterion for differentiation.

The *Allophaiomys* paradigm

The systematics and biostratigraphy of arvicolids since the beginning of the century is governed by the so-called *Allophaiomys* paradigm (Hinton, 1926; Kormos, 1932; Chaline, 1972; Koenigswald, 1973; Meulen, 1973; Heinrich, 1982; Repenning, 1992; Rekovets and Nadachowski, 1995). This is based on the assumption that the genus *Allophaiomys* represents those rootless arvicolids with three definitive triangles, a simple anteroconid complex and the presence of cement, and which lived during the Lower Pleistocene throughout the Northern Hemisphere. Another assumption is that the genus *Arvicola* originated out of *Mimomys savini* at the beginning of the Middle Pleistocene. Morphometric criteria to distinguish these species have been simple, since they measure only the minimum distances between various landmarks, rather the sinuous line forming the enamel between the landmarks is not measured.

However, I have observed some contradictions in the paradigm. In the Betic Cordillera (Spain), for instance, in the Cullar de Baza I site a primitive *Arvicola* population has an average m1 length of 3.40 mm and the hypsodonty index is 161.7. The mean length of the *Mimomys savini* from layer under Cullar de Baza I is 3.61 mm and its hypsodonty index 174.5. In general, from the Betic Cordillera to the Ukraine, *Mimomys savini* shows very hypsodont crowns, roots are very rare and *Mimomys*-ridge is not abundant (up to 5 %). In contrast to this, teeth of the first populations attributed to *Arvicola* in this territory are less hypsodont while the *Mimomys*-ridge is frequent (20 %). It is not possible for this southern *Mimomys savini* to be the ancestor of a smaller and less hypsodont *Arvicola*, since the increase in size (length and hypsodonty) over time is the rule for the arvicolids. According to the *Allophaiomys* paradigm, this can be explained by the possibility of the origin of *Arvicola* having occurred in other Eurasian areas of greater latitude, probably in the temperature area of Europe and/or Western Siberia from forms which show a higher frequency of specimens with *Mimomys*-ridge (up to 40 %). This would suggest that the *Arvicola* communities migrated to Southeastern Europe from northern areas (Rekovets and Nadachowski, 1995).

There is a gradual decrease in the relative thickness of the enamel band over time for genus *Arvicola* (Koenigswald, 1973; Heinrich, 1982, 1987; Röttger, 1986; Kolfshoten, 1990). The formula of the enamel thickness quotient index (SDQ) is equal to the thickness of the trailing edge multiplied by 100 and divided by the thickness of the leading edge. The SDQ of one molar is the mean of the SDQ-values of all salient angles.

The SDQ values of the *Arvicola* molars of the Dutch faunas (Kolfshoten, 1990) and of the populations from Central Europe (Heinrich, 1987), both successions show the same trend. The older populations are characterized by high SDQ values whereas the younger populations have lower values. The mean SDQ values of the *Arvicola* molars from the older sites of Dutch and Central Europe (Neede 146.58, Miesenheim-I 152.03 and Hundsheim 135.15) are higher than the older Central Europe sites, which only molars of *Mimomys savini* are present (Prezletice site 132.98, Voigtstedt site 139.09 and Koneprusy site 141.69).

The problem is that, if the last *Mimomys savini* is the origin of *Arvicola*, it is not possible for the last *Mimomys savini* to have smaller SDQ than in the first *Arvicola* populations. This argument is ruled out when defenders of the paradigm (Chaline *et al.*, 1993; Neraudeau *et al.*, 1995) observe that the thickness index displays a clinal variation from northern to southern Europe, and southern populations have a more primitive appearance with a higher index. Consequently they explain the cause of the reversal anomalies in the thickness index (SDQ) as being due to the dispersal of primitive *Arvicola* populations from southern areas to the northern region. In this case, it would be possible to find populations of *Arvicola* in more recent layers than the layers where the populations of *Mimomys savini* are enclosed, but with larger SDQ in *Arvicola* than in *Mimomys savini*.

Dispersal explanations which the paradigm offers for the anomalies in the thickness of the enamel and the hypsodonty are contradictory. *Arvicola* must have migrated from north to south for its size to be compatible with those of *Mimomys savini*, and *Arvicola* must also have migrated simultaneously from south to north in order for the thickness of the enamel to be compatible.

It is also difficult for *Mimomys savini* predecessors and *Arvicola mosbachensis* descendants to have survived together in Middle Pleistocene sites until the end of the Upper Pleistocene (Sen *et al.*, 1991), sharing the same aquatic margins, without the descendants more adapted expelling the predecessors. Even within the same genus *Allophaiomys*, there are contradictions, since it is unlikely, that the

species *Allophaiomys deucalion* to have a greater average size than the *Allophaiomys pliocaenicus* when the first is older than the second.

Characteristics of the genus *Arvicola*

In a *Dicrostonyx* embryonic molar, Hinton (1926) has shown empirical evidence of the relation between each enamel fold and at least one tubercle. Data provided by Kollar and Baird (1969), Osborn (1978), Ten Cate (1985) and Ruiz Bustos (1988, 1995, 1996) show that each mammal molar tubercle originates from a point of the dental papilla where cells are suffering intense mitosis and the number is constantly increasing and at a greater rate than in the nearby surrounding area. This precise increase in the volume of the papilla induces the genesis of an enamel fold. These points are interpreted as concentrations of cells in mitosis and are therefore known as mitosis areas. Each enamel fold in the adult tooth corresponds to a particular area of mitosis in the embryo. The development of the enamel folds in the arvicolid teeth can be observed during the embryonic development in points of the dental papilla where enamel deposition begins. The location and mitosis rate of each mitosis area are determined by its genes and are independent of the other areas in the tooth. This is explained by the fact that mitosis areas are subject to inheritance. Therefore, the length of the fold of enamel covering these areas must also be subject to the laws of inheritance.

The Enamel Units Methodology (Ruiz Bustos, 1995, 1996) describes and quantifies the enamel line on the crown of the tooth. The present and fossil morphologies of arvicolid can be defined through Morphological Units (MU) made up of a constant number of folds in the anteroconid complex, and Enamel Units (EU). An enamel unit is a segment of enamel large enough for at least one fold to be identified. The m1 of the arvicolids has seven enamel units and their numerical values, set in a constant order, are a direct representation of the size and position of the enamel folds. To eliminate those differences resulting from individual size, measurements are proportionally distributed on the basis of 100, by calculating the percentage of enamel length corresponding to each enamel unit.

The Biological Nature of a fold may be defined as the largest or smallest inheritance capacity of each fold (Morphological Units), and when two folds appear with the same frequency in descendants, then the fold possessing the greatest functional role will prevail. This role is greater than the relative size of the fold in the tooth crown (Enamel Units). The enamel and morphological units can be

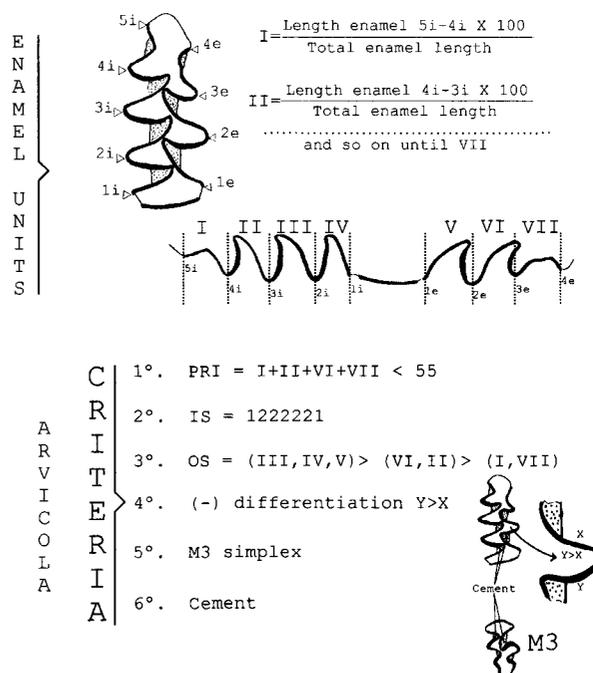


Fig. 1.—The Enamel Units Methodology identifies arvicolid morphologies using Morphological Units (MU) and Enamel Units (EU). The six criteria which define the genus *Arvicola* are: 1. Proximal regional index (PRI). 2. Identity sequence (IS). 3. Ordering sequence (OS). 4. Enamel differentiation. 5. Morphology of the upper molar (M3). 6. Cement.

considered as the phenotypic expression of the genes codifying the point of intense mitosis (mitosis areas) in the dental papilla where the fold of the tooth crown develops.

The living and fossil populations of the genus *Arvicola* are identified by at least six criteria for tooth morphology using Enamel Units, irrespective of individual size (fig. 1).

1. The proximal regional index (PRI) indicates the length of the enamel line in the anteroconid complex, and it consists of the sum of EU: I, II and VII. The PRI is equal to or less than 52. Occasionally, subadult or adult specimens belonging to the Morphological Units MU-2 and MU-3 may have a PRI close to 55.

2. The identity sequence (IS) is defined as the indices obtained by dividing the values of each enamel unit of m1 by the value of EU-VII. The IS indicates the relation of the size of all EU to EU-VII. For ease of comparison between indexes, these are expressed by the following approximation: values from 0 to 0.99 are considered as (0), from 1 to 1.49 as (1), from 1.50 to 2.49 as (2), and so on. The most frequent IS in *Arvicola* is: 1,2,2,2,2,1. Other IS are possible, but they always show high values in EU-III, EU-IV and EU-V in relation to EU-I and EU-VII.

3. The ordering sequence (OS) to which more than 90 % of specimens belong, fulfil the condition: (III, IV, V) > (VI, II) > (I, VII). In adult specimens EU-I and EU-VII are never equal to or greater than the remaining five Enamel Units. The EU-II and EU-VI are never in first or second position.

4. The enamel shows negative differentiation (the distal side of the enamel fold Y is broader than the proximal side X, see fig. 1), except in some communities from the Upper Pleistocene with a phylogeny close to the species *Arvicola terrestris*.

5. The upper molar M3 always belongs to the simplex type, this is characterized by having two closed folds and a distal lobe without folds, similar to a circle (fig. 1).

6. Cement is present.

Small-sized species of the *Arvicola* genus

Arvicola and *Allophaiomys* have the same m1 tooth shape. *Arvicola* lives on the margins of continental waters and *Allophaiomys* appears to have lived in meadows in continental lands. The ecological competition between both genera is less than that accepted by the *Allophaiomys* paradigm between the descendant (*Arvicola*) and its predecessor (*Mimomys savini*). However, it is not impossible for individuals of both genera to live in an owl's hunting territory, and to have their bones preserved in the same owl pellets.

By examining *Allophaiomys* populations living during the Lower Pleistocene using the Enamel Units Methodology, two groups of specimens with different enamel distribution can be seen within these populations. One group fulfils all of the six *Arvicola* criteria, whereas in the other group some of these criteria are not fulfilled. The first group of specimens must be considered true *Arvicola*, since their morphological pattern and enamel distribution are the same as *Arvicola*. This suggests the existence of small-sized *Arvicola* communities contemporary to *Allophaiomys* and which have previously gone unnoticed in the samples.

The majority of specimens of the *Allophaiomys deucalion* communities, including the holotype, comply with the six criteria which define *Arvicola*. The seven enamel units (EU) of the holotype of *Allophaiomys deucalion* coincide with the average values of the seven enamel units measured in the *Arvicola mosbachensis* community from the beginning of the Middle Pleistocene in the Cullar de Baza I site (Ruiz Bustos, 1988). The SDQ value of *Allophaiomys deucalion* from Plines site is bigger than SDQ value of the most primitive *Arvicola mosbachensis* community in the Cullar Baza I site,

and both species have negative enamel differentiation. The smallest specimens of the *Arvicola mosbachensis* communities are identical to the largest specimens of *Allophaiomys deucalion*. In accordance with these data, *Allophaiomys deucalion* must be identified as an *Arvicola*.

The *Arvicola* paradigm

The existence of species of the genus *Arvicola* in the Lower Pleistocene supposes the appearance of a new paradigm which I have named the *Arvicola* Paradigm. This assumes that the *Arvicola* communities have been present since the beginning of the Quaternary.

Within the *Allophaiomys* paradigm, the species *Mimomys tornensis* is considered to be the predecessor of *Allophaiomys deucalion*, although there is little agreement about the area where the transformation occurred (Rabeder, 1981; Garapich and Nadachowski, 1996). The phylogenetic relation between *Mimomys tornensis* and *Allophaiomys deucalion* in hypsodonty and in the thickness of the enamel does not present the difficulties which I have observed in the phylogenetic union between *Mimomys savini* and *Arvicola*. If I consider *Allophaiomys deucalion* to be an *Arvicola*, there will consequently be a continuous phylogenetic line from *Mimomys tornensis* to *Arvicola mosbachensis* through *Arvicola deucalion*.

The small *Mimomys* close to *Mimomys tornensis* have all the characteristics to be the predecessor of *Arvicola*, since they have a strong retardation in the formation of their phenotypic root. The roots close long after the tooth has started to be functional, even after more than half the tooth height has been worn away by use. There is a reduction in the number of roots. The hypsodonty is very great. The anteroconid complex has symmetrical lingual and labial edge. They have small dimensions, the mean length and width of the m1 crown is 2.73 x 1.20 mm, and the crown has equal length from the top to the bottom of the tooth. The cement is present. This kind of *Mimomys* lived between 2.5 and 1.6 myr, and they made up a group called *Mimomys reidi* group in the meaning by Ruiz Bustos (1987).

At the end of the Pliocene in some specimens of the *Mimomys reidi* group underwent a mutation and its genetic root is eliminated. The *Arvicola* paradigm implies a split between the *Mimomys reidi* group and the first individuals of *Arvicola deucalion* and a model of Phyletic gradualism between *Arvicola deucalion* and *Arvicola mosbachensis*. In this case, the association imposed by the *Allophaiomys* paradigm to transform *Mimomys savini*

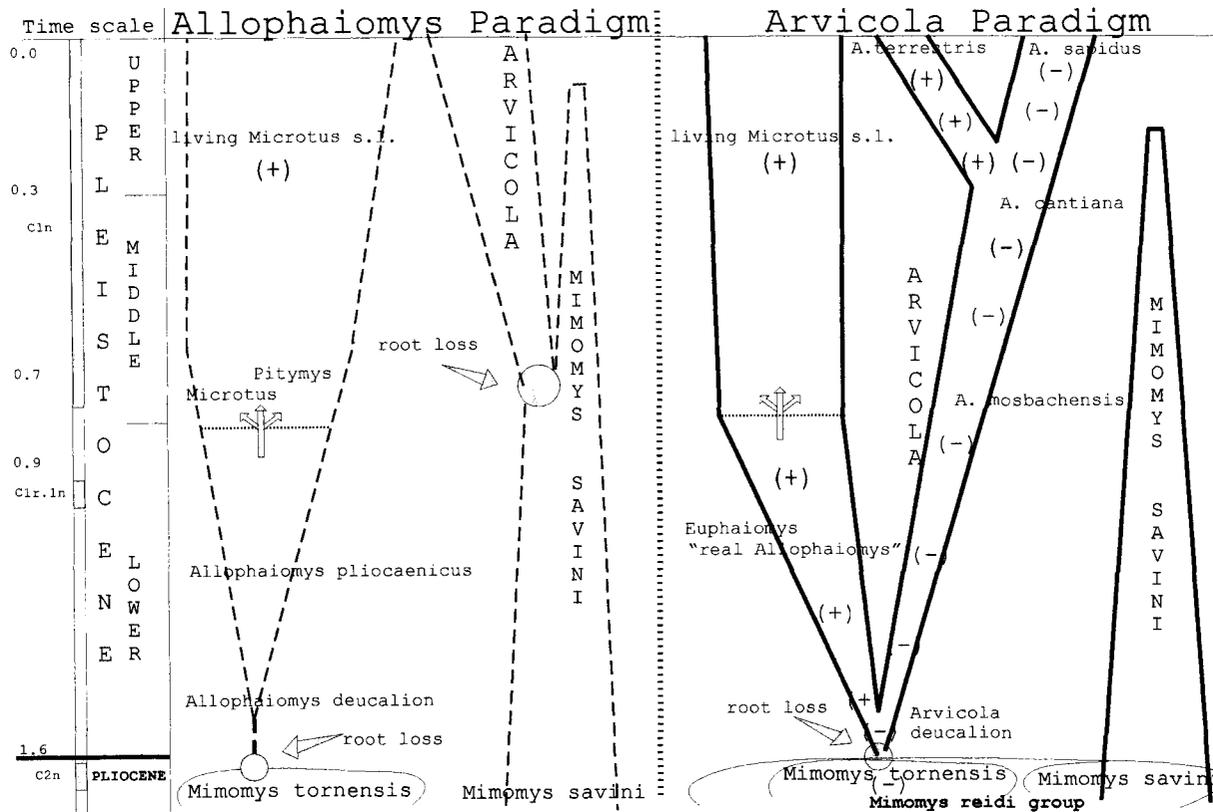


Fig. 2.—The paradigms on *Arvicola* and *Allophaiomys*. The main difference between both paradigms is the concept of root loss. Genetic root loss is a mutation. This should not be confused with the quantitative alterations which retard phenotypic formation in animals which have genetic root. *Mimomys savini* never loses its genetic root. The signs (-) and (+) in the diagram correspond to negative and positive differentiation respectively.

into *Arvicola mosbachensis* is no longer the only one possible but rather is unnecessary.

For the *Arvicola* paradigm, the genus *Allophaiomys* consists of the rootless specimens with cement from the Lower Pleistocene, and which do not have at least some of the six criteria defining *Arvicola*. In this case the name *Allophaiomys* becomes a taxonomic problem, since the holotype of the type-species of *Allophaiomys* defined by Kormos (1932) is a young specimen of *Arvicola* and the holotype of *Allophaiomys deucalion* belongs to the *Arvicola* genus. Therefore this group of specimens which lack at least some of the six criteria defining *Arvicola* was given the new generic *Euphaimys* by Ruiz Bustos (1988). A diagrammatic representation of the *Arvicola* paradigm is shown in figure 2.

Relationship between genetic and phenotypic root

One of the main differences between the two paradigms is the concept of root loss. In the *Allophaiomys*

paradigm, root loss is produced because the animal's life span is not long enough for roots to appear, and the ontogeny of tooth development is not completed. The *Arvicola* paradigm consider the relationship between genetic root and phenotypic root. The genetic root loss is a mutation and implies a qualitative change in the information which codifies the individual. The lack of genetic root, this should not be confused with the quantitative alterations which retard phenotypic formation in animals which have genetic roots. If there is genetic information (genetic root) which may or not be seen in the phenotype (phenotypic root), the animal have root. Only in this case does the phenotypic root formation depend on the longest or shortest life span of the individuals. The species *Mimomys savini* never loses its genetic root, and even in the last communities at the end of the Upper Pleistocene, when the majority of the specimens lack a phenotypic root, there are always some teeth with roots or they have signs at the bottom of their enamel folds of root existence. The moment when the mutation which eliminates the genetic root in some speci-

Table 1.—Data of the m1 of *Arvicola* genus in the Betic Cordillera during the Quaternary

	Approximate age in myr	Betic Cordillera sites	N. ^o	m1 length in mm		
				Max.	Min.	Mean
Upper Pleist.	0.00	Living	16	5.08	4.03	4.27
	0.03	Zafarraya	5	4.23	3.56	4.05
	0.07 ± 0.010	Carihuela	3	4.22	3.78	3.96
Middle Pleist.	0.25	Cueva del Agua	4	4.12	3.60	3.88
	0.30	Solana	3	4.04	3.57	3.83
	0.50 ± 0.025	Cuarterones	1			3.61
Lower Pleist.	0.70	Cullar de Baza I	20	3.95	3.04	3.40
	0.90	Cueva Victoria	17	3.35	2.72	3.13
	1.00	Atalaya	1			2.95
	1.30 ± 0.050	Venta Micena	13	2.96	2.60	2.80
	1.60	Cerro Parejo	1			2.58
		Plines	1			2.70

mens of the genus *Mimomys* is produced is unique and exceptional and it occurs at the beginning of the Quaternary.

In the *Allophaiomys* paradigm, the transitional populations between *Mimomys savini* and *Arvicola* are established when there is small percentage of rooted molars with a strong retardation in the formation of their phenotypic root, and this is therefore the reason why it only occurs in three of the hundreds of sites where *Mimomys* and *Arvicola* exist together, and one of these is Cueva del Agua site (López and Ruiz Bustos, 1977) in the Betic Cordillera. As opposed to the hypothesis of transitional population between *Mimomys savini* and *Arvicola* of the *Allophaiomys* paradigm, I put forward the possibility that these transitional populations are a special combination of *Arvicola* teeth on the one hand, from smaller-

sized specimens, and *Mimomys savini* on the other hand which compete with the *Arvicola* populations retarding the formation of their phenotypic roots, since *Mimomys savini* and *Arvicola* undergo a long process of morphological convergence.

The *Arvicola* genus as chronological tool

The genus *Arvicola* defined using the six criteria of the Enamel Units Methodology, show through the quaternary deposits of the Betic Cordillera a continuous growth in size (table 1). This case about growth in the size of the genus *Arvicola* without any change in its morphology during the last 1.6 myr is not an exception, and also occurs in other arvicolidids close to aquatic margins as in the case of the genus *Ondatra* and for a longer period of time.

The relationship among data of *Arvicola* in the region can be better understood using an empirical mathematical model represented by the equation (1), that it relates the length m1 (L) and the absolute age (t). The graphic representation of the model is shown in figure 3.

$$L = \frac{11 - (1 + t)\log t}{3.15 - (1 - 2.5t + t^2)t} \quad (1)$$

In a few years, if more data are available, the new quaternary sites in the region can be dated by means of the tool provided by the *Arvicola* paradigm.

Conclusions

The arvicolidids without genetic roots appeared for the first time at the beginning of the Pleistocene, and is a response to the ecological requirements. They show a high degree of morphological convergence with *Mimomys savini*, because it outlived the

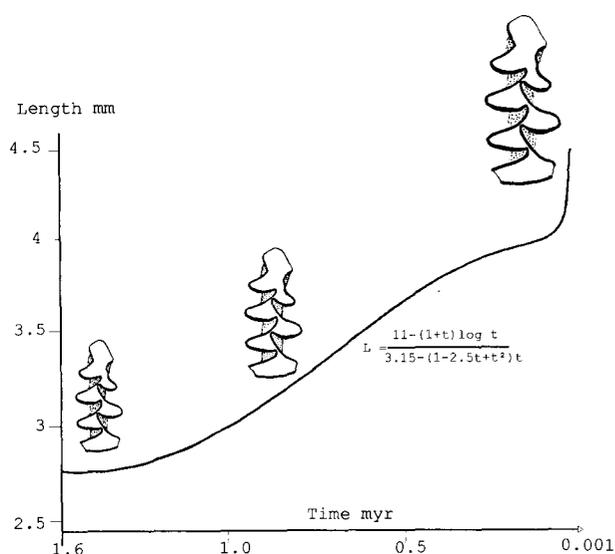


Fig. 3.—Changes occurred in the m1 length of the genus *Arvicola* communities with negative (-) enamel differentiation during the last 1.6 myr in the Betic Cordillera.

new cold climatic conditions. The arvicolid originating from the mutation and which lose the genetic root are included in the subfamily *Arradiculatinae* Ruiz Bustos, 1987.

When the new arvicolid group begins its dispersion, several animals live near the continental waters. The grass here is quite independent of the weather and it is always sufficiently abundant and soft. Because of this, the animal populations preserve their initial tooth morphology and so there is no reason for them to change the shape of the crown of the tooth. The populations of the genus *Arvicola* will live and grow in size and hypsodonty until the present. There are other groups living within the continental lands, but these have found different grass in relation to climate and soil, and have greater difficulty eating. In these circumstances, their enamel morphology suffers different adaptative responses.

The Enamel Units analysis of the Lower Pleistocene arvicolids casts doubt on the taxonomic identity of *Allophaiomys* as a genus, since within *Allophaiomys* there are communities of small-sized *Arvicola*. The idea of *Arvicola* originating from *Mimomys savini* at the beginning of the Middle Pleistocene is also a doubtful hypothesis.

The beginning of the Lower Pleistocene and therefore the end of the Villafranchian (Upper Pliocene) is marked by the appearance of rootless arvicolids, and the increase in size of the *Arvicola* genus is a biostratigraphic indicator of the creation of a timescale useful for the entire Quaternary.

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