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Distribution and evolution of *Arvicola* LACÉPÈDE, 1799 (Mammalia, Rodentia) in France and Liguria (Italy) during the Middle and the Upper Pleistocene

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Abstract. A study of *Arvicola* (*Mammalia*, *Rodentia*) populations of France (Gaudry, Vaufrey, Suard, l'Eglise, Artenac, Moula-Guercy, Lazaret and Gigny) and Liguria (Arma delle Manie and Ripario Mochi) has permitted the systematic and evolution specifications of this genus at the end of the Middle Pleistocene and the Upper Pleistocene. The enamel thickness shows temporal and geographic variations which allow precise statement of the biochronological framework. The migration of *Arvicola* from Northern Europe, during a cold stage dating back to the end of the Middle Pleistocene, and the persistence of the primitive *Arvicola* population, isolated in Liguria during the Upper Pleistocene, should explain the wide variation observed in the relative thickness of the enamel band.

Key words – Systematic, *Arvicola*, biochronology, Middle Pleistocene, Upper Pleistocene.

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I. INTRODUCTION

The evolutionary trend in the *Arvicola* lineage has been established after years of research.

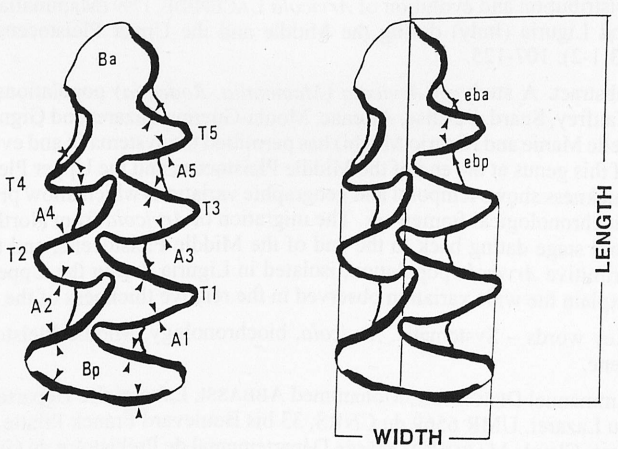
HINTON (1926) described late *Mimomys* (*M. intermedius* and *M. bactonensis* = *M. savini*) and early *Arvicola* (*Arvicola cantianus*). This author proposed that *Arvicola* evolved from *Mimomys*. He was also the first to note that the check teeth of *Arvicola* species displayed a peculiar enamel differenciation during the Quaternary. In 1955, HEIM DE BALZAC and GUISLAIN showed the existence of three species in Western Europe: *Arvicola sapidus* both in the North and the South, sympatric with *Arvicola sherman* the small Central European species and *Arvicola terrestris* the Eastern and Northern watervole.

Primitive representatives of *Arvicola* (*A. bactonensis*, *A. greenii*, *A. praeceptor,* and *A. mosbachensis*) were defined in different Middle Pleistocene sites in Central and Western Europe by KRETZOI (1956), FEJFAR (1961, 1965), JANOSSY (1965), and CHALINE (1972). SUTCLIFFE & KOWALSKI (1976) demonstrated that those species could in fact be included, in *Arvicola cantianus* described by HINTON (*op. cit.*).

KOENIGSWALD (1973, 1980) distinguished three microstructural types in the enamel of *Arvicola* and proposed the following stratigraphical division:

- Middle Pleistocene: *Arvicola cantianus*
- Middle and Upper Pleistocene transition: *Arvicola cantianus/terrestris*
- Upper Pleistocene: *Arvicola terrestris*

HEINRICH (1978) proposed calculation of the "enamel quotient" (SDQ = Schmezband-Differenzierungs-Quotient) in order to quantify the differences observed in the enamel thickness and to trace the evolutionary trend in the *Arvicola* lineage (Fig. 1). This author demonstrated that enamel quotients, calculated for individuals and populations, can be used for biostratigraphical framework based on *Arvicola* (HEINRICH 1982, 1987 and 1990). A continuous decrease in SDQ values during the Middle and Upper Pleistocene could be noted in central Europe and in the Pannonian basin.



$$\text{SDQ prism : } SDQ_p = \frac{ebp}{eba} \times 100$$

$$\text{SDQ M/1 : } SDQ_{M/1} = \frac{\Sigma\, SDQ_p}{7}$$

$$\text{SDQ population : } SDQ_{pop} = \frac{\Sigma\, SDQ_{M/1}}{n}$$

Fig. 1. – *Arvicola* M_1 nomenclature with position of various measurements points and enamel thickness. With T : salient angles, A :re-entrant angles, Ba :anterior loop, Bp : posterior loop, eba : measuring point of anterior wall, ebp : measuring point of posterior wall.

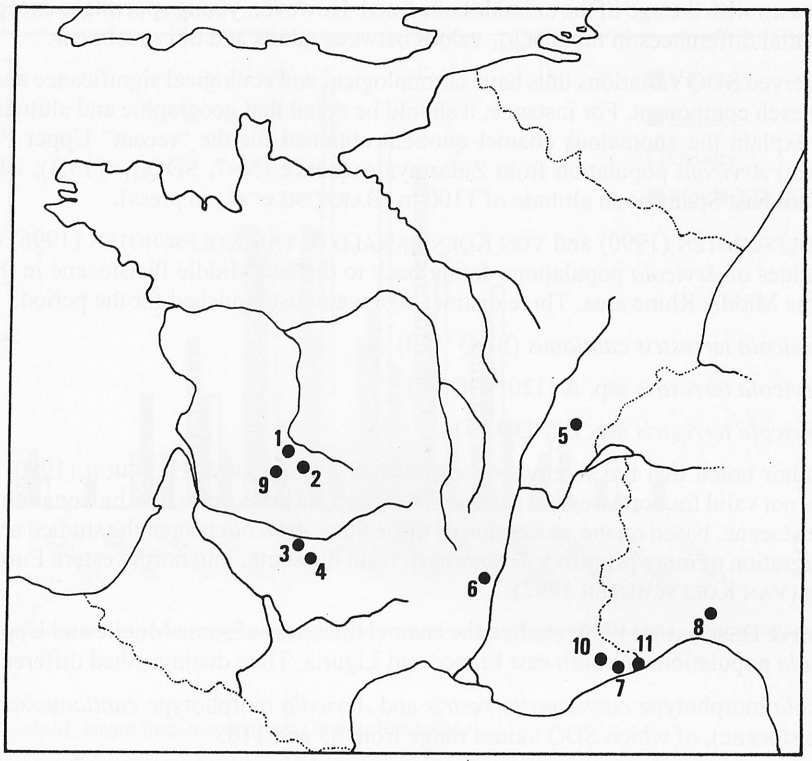


Fig. 2. – Location of Studied sites. With : Suard, 2 : Gaudry, 3 : Vaufrey, 4 : Eglise, 5 : Gigny, 6 : Moula-Guercy, 7 : Lazaret, 8 : Arma delle Manie, 9 : Artenac, 10 : Pié Lombard and 11 : Ripario Mochi.

This evolution of enamel quotient permitted the following morphological division to be proposed:

- *Arvicola cantianus* (SDQ 100)
- *Arvicola terrestris* (SDQ 100)

According to this author, the transition between *A. cantianus* and *A. terrestris* coincides approximately with the Eemian/Weichselian boundary.

However, studies of the modern species *Arvicola terrestris* and *Arvicola sapidus* have shown that, in fact, SDQ value interpretations are more complex and related to a chronomorphocline and to a geographical and climatological cline :

RÖTTGER (1986, 1987) established that there is a great variation in the enamel quotient related to the area of *Arvicola* species in Europe and the Middle East area. Western European populations show *Arvicola* enamel differenciation (72.5 SDQ_{M1} 120.8). Turkish (SDQ_{M1}= 124.6) and Iranian (SDQ_{M1}=134.4) populations have a *Mimomys* enamel quotient.

KRATOCHVIL (1980, 1981) demonstrated that the enamel quotient of living water vole populations generally increases with geographical altitude. That is the reason why *Arvicola* populations from Switzerland (Vaud Canton, for example, 1160 m above sea level) show an *Arvicola cantianus* SDQ value. According to HEINRICH (1990), the reasons for "altitude-polymorphism" are far from

clear and need further investigations. KRATOCHVIL (1980) also noted that the enamel quotient generally decreases with the age of the animals concerned. However, young specimens excepted, there are no essential differences in the SDQ_{M1} values between adults and old specimens.

The observed SDQ variations thus have chronological and ecological significance and we must to estimate each component. For instance, it should be noted that geographic and altitudinal variations may explain the anomalous enamel quotient obtained for the "recent" Upper Pleistocene (Weichselian) *Arvicola* population from Zafarraya sequence (N=7, SDQ_{M1}=113.3), which is located in south-east Spain, at an altitude of 1100 m (BARROSO et al., in press).

VAN KOLFSCHOTEN (1990) and VON KOENIGSWALD & VAN KOLFSCHOTEN (1996) calculated the SDQ values of *Arvicola* populations dating back to the late Middle Pleistocene in the Netherlands and the Middle Rhine area. Three distinct taxa were distinguished for the period:

- *Arvicola terrestris cantianus* (SDQ 120)
- *Arvicola terrestris* ssp. A (120 SDQ 95)
- *Arvicola terrestris* ssp. B (SDQ 95)

This author noted that the subdivision established by FEJFAR & HEINRICH (1990) in central Europe was not valid for northwestern Europe. Therefore, he proposed a new biozonation of the late Middle Pleistocene, based on the succession of those three *Arvicola* taxa in the studied area. He observed a migration of more primitive *A. terrestris*, from the south, into northwestern Europe during the Eemian (VAN KOLFSCHOTEN 1992).

ABBASSI & DESCLAUX (1996) studied the enamel thickness of some Middle and Upper Pleistocene *Arvicola* populations in south east France and Liguria. They distinguished different taxa :

– *Arvicola* morphotype *cantianus/terrestris* and *Arvicola* morphotype *cantianus/sapidus* (late Middle Pleistocene), of which SDQ values range from 85 and 110.

– *Arvicola sapidus*, which appears at the beginning of the Upper Pleistocene and shows SDQ below 100.

In the present work, *Arvicola* populations from 11 Middle and Upper Pleistocene sites from the South of France and Liguria (Italy) will be studied for a better understanding of systematic, stratigraphical succession and evolution of watervoles in this area (Fig. 2).

Because of the geographical and chronological origin of diachronic variations of *Arvicola* enamel quotient, chronological and palaeontological data (excepted *Arvicola*) have been taken into account in order to establish the biochronological framework of studied localities.

II. SYSTEMATICS

The great diversity of fossil species described in the past decade prompted the present authors to take into account enamel thickness, morphology, and dimensions (length) of *Arvicola* M_1 in order to make a specific determination (Figs 3 & 4).

The two species of *Arvicola* (*A. sapidus* and *A. terrestris*), which occur today in western Europe, were recognized by MARQUET (1989) and ABBASSI & DESCLAUX (1996) in Middle and Upper Pleistocene faunas from the South of France. M_1 of specimens assigned to *A. sapidus* are characterized by great dimensions and T4-T5 alternate prisms. M_1 of *A. terrestris* have smaller dimensions and T4-T5 confluent prisms. Generally, the morphology of the anterior loop of fossil *Arvicola* populations shows great variation. Thus, some M_1 show a triangular and symmetrical anterior loop, with an important constriction (morphotype *greenii* defined by HINTON 1926). Other specimens have a rather wide and dissymetrical anterior loop with variable constriction (morphotype *praeceptor* according to HINTON 1926). In fact, most of the M_1 have an intermediate morphology.

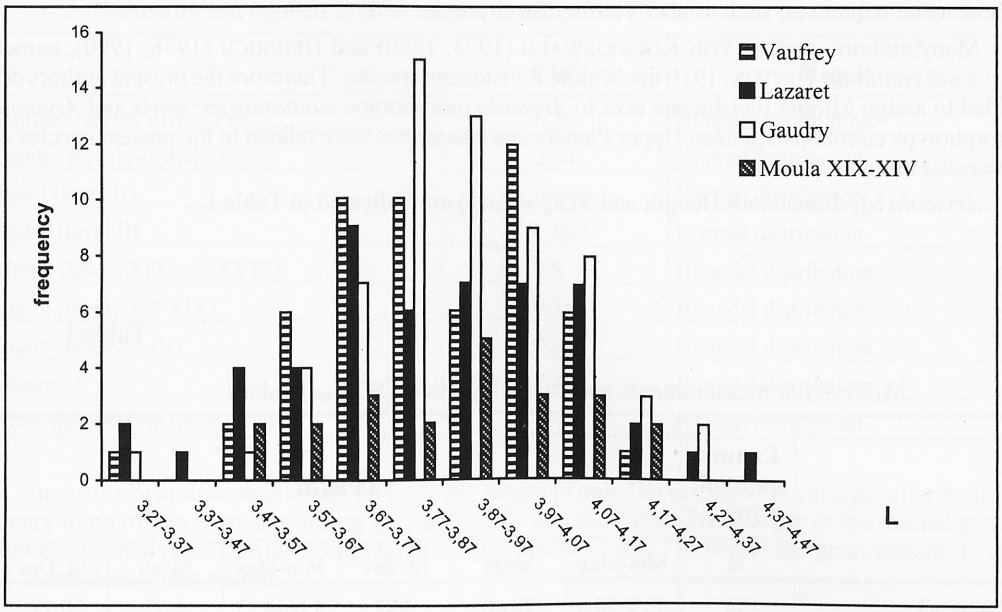


Fig. 3. – *Arvicola* M_1 length frequency diagram (Middle Pleistocene).

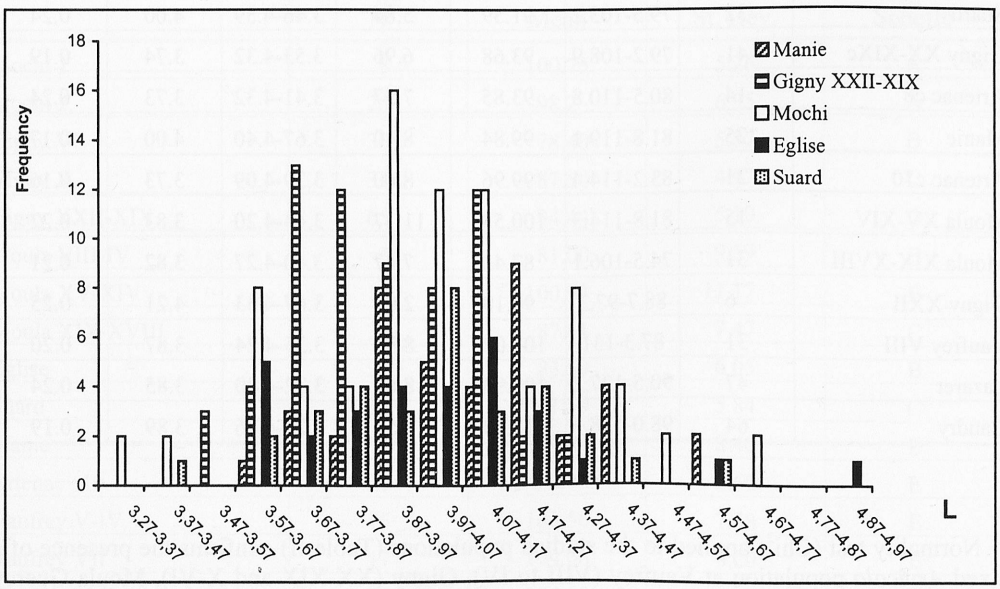


Fig. 4. – *Arvicola* M_1 length frequency diagram (Upper Pleistocene).

It should be remembered that MARQUET (1989), in his study of south-west Pleistocene *Arvicola* populations, already distinguished two species (a large one and a small one) in different late Middle Pleistocene sequences, such as abri Vaufrey for example.

Many authors, such as VON KOENIGSWALD (1973, 1980) and HEINRICH (1978, 1990), named *Arvicola cantianus* HINTON, 1910 the Middle Pleistocene species. Therefore the present authors decided to assign Middle Pleistocene taxa to *Arvicola* morphotype *cantianus/terrestris* and *Arvicola* morphotype *cantianus/sapidus*. Upper Pleistocene specimens were related to the present species *A. terrestris* and *A. sapidus*.

Arvicola M_1 dimensions (length and SDQ values) are indicated in Table I.

Table I

M_1 *Arvicola* measurements and enamel quotient (SDQ_{M1}) values

	Enamel quotient (SDQ_{M1})	**Length**					
	N	Min-Max	Mean	St. dev	Min-Max	Mean	St. Dev
Gigny VI	30	62.5-90.6	78.40	5.87	3.66-4.27	4.07	0.17
Gigny X	34	78.5-99.3	87.50	4.97	3.51-4.12	3.89	0.15
Moula VIII-IV	5	74.0-97.3	81.00	9.59	3.65-4.16	3.90	0.18
Eglise	31	68.1-96.0	83.59	6.05	3.62-4.97	4.02	0.30
Gigny XIXa	18	85.6-106.0	96.40	6.51	3.59-4.12	3.76	0.17
Suard	32	79.5-103.2	91.59	5.84	3.46-4.59	4.00	0.24
Gigny XX-XIXc	41	79.2-108.9	93.68	6.96	3.53-4.32	3.74	0.19
Artenac c8	14	80.5-110.8	93.85	7.57	3.41-4.32	3.73	0.24
Manie	25	81.8-119.1	99.84	8.40	3.67-4.40	4.00	0.17
Artenac c10	21	83.2-114.4	99.96	8.60	3.39-4.09	3.73	0.16
Moula XV-XIV	15	81.8-114.3	100.53	11.17	3.43-4.20	3.83	0.22
Moula XIX-XVIII	31	74.5-106.1	87.41	7.47	3.40-4.27	3.82	0.21
Gigny XXII	6	88.7-97.3	94.19	2.91	3.67-4.33	4.21	0.25
Vaufrey VIII	31	87.3-131	104.00	8.90	3.35-4.24	3.87	0.20
Lazaret	47	90.5-127.2	107.90	8.67	3.32-4.40	3.85	0.24
Gaudry	64	98.0-138.7	113.90	8.50	3.27-4.36	3.89	0.19

Normality test (Chi^2) applied to the studied populations (Table II) confirms the presence of a mixed *Arvicola* population at Vaufrey (VIII to IV), Gigny (XX-XIX and X-VI), Moula-Guercy (XIX and XVIII), and Lazaret.

Table II

Normality test applied to *Arvicola* M_1 length.

	Chi²	**Result**
Vaufrey (levels VIII to IV)	6,29	Bimodal distribution
Gaudry (levels 4a and 4)	2,04	Normal distribution
Suard (level II)	0,016	Normal distribution
Eglise (level II)	1,047	Normal distribution
Moula (levels XIX and XVIII)	7,8	Bimodal distribution
Gigny (levels XX-XIX)	9,169	Bimodal distribution
Gigny (levels X-IV)	9,8	Bimodal distribution
Lazaret	7,45	Bimodal distribution
Arma delle Manie (levels 7 to 3)	7,4	Normal distribution

Analysis of variance applied to *Arvicola* M_1 length (Table III) does not reveal a peculiar evolutionary trend of this character during the late Middle and the Upper Pleistocene in the studied area. Conversely, analysis of variance applied to SDQ_{M1} means (Table IV) shows the great variability of the factor during this period.

Table III

Arvicola M_1 length: analysis of variance. Means with the same letter do not significantly differb ($p>0.05$).

	N	Mean	St. Dev.	Scheffé
Mochi 1	8	100.75	5.26	A
Mochi 2	25	98.2	6.95	A
Gigny VI	30	78.40	5.87	B
Gigny X	34	87.50	4.97	C
Gigny XXII-XIX	65	94.44	5.10	D
Moula VIII-IV	5	81.00	9.59	B
Moula XV-XIV	15	100.53	11.17	E
Moula XIX-XVIII	31	87.41	7.47	C
Eglise	31	83.59	6.05	B
Suard	32	91.59	5.84	C
Manie	25	99.84	8.40	E
Artenac c10	21	99.96	8.60	E
Vaufrey V-IV	16	103.56	7.58	E
Vaufrey VII	17	104.06	9.20	E
Vaufrey VIII	31	104.00	8.90	E
Lazaret	47	107.90	8.67	EA
Gaudry	64	113.90	8.50	F

Table IV

Arvicola SDQ_{M1} : analysis of variance. Means with the same letter do not significantly differ ($p>0.05$).

	N	Mean	St. Dev.	Scheffé
Mochi 1	11	4.06	0.21	A
Mochi 2	29	3.96	0.31	A
Gigny VI	30	4.07	0.17	A
Gigny X	34	3.89	0.15	B
Gigny XXII-XIX	65	3.89	0.20	B
Moula VIII-IV	5	3.90	0.18	A
Moula XV-XIV	15	3.83	0.22	AB
Moula XIX-XVIII	31	3.82	0.21	AB
Eglise	31	4.02	0.30	A
Suard	32	4.00	0.24	A
Manie	25	4.00	0.17	A
Artenac c10	14	3.73	0.24	AB
Vaufrey V-IV	16	3.93	0.23	B
Vaufrey VII	17	3.95	0.20	B
Vaufrey VIII	31	3.87	0.20	B
Lazaret	47	3.85	0.24	B
Gaudry	64	3.89	0.19	B

We must note too that ABBASSI & DESCLAUX (1996) also demonstrated that the SDQ values obtained for each species were similar for Middle and Upper Pleistocene populations. For instance, *Arvicola* morphotype *cantianus/terrestris* (N=20, SDQ_{M1}=87.85) and *Arvicola* morphotype *cantianus/sapidus* (N=11, SDQ_{M1}=86.60) show a similar enamel quotient. Therefore, it is possible to calculate a global SDQ value for mixed populations.

A list of localities with *Arvicola* is presented in Table V.

III. SOUTH-WEST FRANCE

III. a. Abri Vaufrey or Grotte XV at Cénac-et-Saint-Julien (Dordogne)

Excavations at the Vaufrey rock shelter, during the 1970s, produced abundant palaeontological and archaeological remains. This site has been the focus of much research into stratigraphy, chronology, palaeoecology, archaeozoology, and archaeology (RIGAUD et al. 1988). According to MARQUET (1989), the rodent fauna permit the elaboration of a biostratigraphical hypothesis. The lower levels (XIa and XIb) date back to the ancient Middle Pleistocene (Oxygen Isotop Stage (OIS) 10, Mindel-Riss) while the upper level (I) can be assigned to the start of the Upper Pleistocene (OIS 5). Concerning levels VIII to IV, which have been taken into account in this study, the succession of rodent faunas shows a rather homogeneous cold climate and open environment, contemporary with OIS 6 ("Riss", Saalian). They are characterized by an abundance of *Microtus gregalis* and the punc-

Table V

Identified taxa in studied localities

	Arvicola morphotype *cantianus/terrestris*	*Arvicola* morphotype *cantianus/sapidus*	*Arvicola terrestris*	*Arvicola sapidus*
Mochi 1				+
Mochi 2				+
Gigny VI			+	+
Gigny X			+	+
Moula VIII-IV				+
Eglise			+	
Gigny XIXa			+	+
Gigny XX-XIXc			+	+
Suard			+	
Artenac c8			+	
Artenac c10			+	
Pié lombard				?
Manie				+
Moula XV-XIV				+
Gigny XXII	+			
Moula XIX-XVIII	+	+		
Vaufrey V-IV	+	+		
Vaufrey VII	+	+		
Vaufrey VIII	+	+		
Lazaret	+	+		
Gaudry	+			

tual presence of Arctic or Boreal species (such as *Lemmus lemmus*, *Dicrostonyx torquatus*, *Sicista betulina*, and *Microtus malei/oeconomus*).

Arvicola morphotype *cantianus/terrestris* and *Arvicola* morphotype *cantianus/sapidus* have been identified in the sequence (Fig. 5). The SDQ_{M1} value, which does not show any great variation from level VIII to IV (Tabl. I), is similar to the enamel quotient observed by HEINRICH (1990) for *Arvicola* faunas of the late Saalian and Eemian in central Europe.

III. b. Grotte de l'Église or Grotte XIII at Cénac-et-Saint-Julien (Dordogne)

Arvicola from the upper unit (level II), which consists in sandy insertions within a stalagmitic flowstone dating back to the Upper Pleistocene (LAVILLE et al. 1972; LAVILLE 1973), have been studied. According to MARQUET (1989), rodent associations indicate a temperate climate and show various environmental conditions, with the presence of forest zones, humid open spaces of grassland type.

Arvicola terrestris has been identified (Fig. 6). The SDQ_{M1} value (N=21, SDQ_{M1}=83.59) is similar to the enamel thickness obtained by HEINRICH (1990) for *Arvicola terrestris* from central

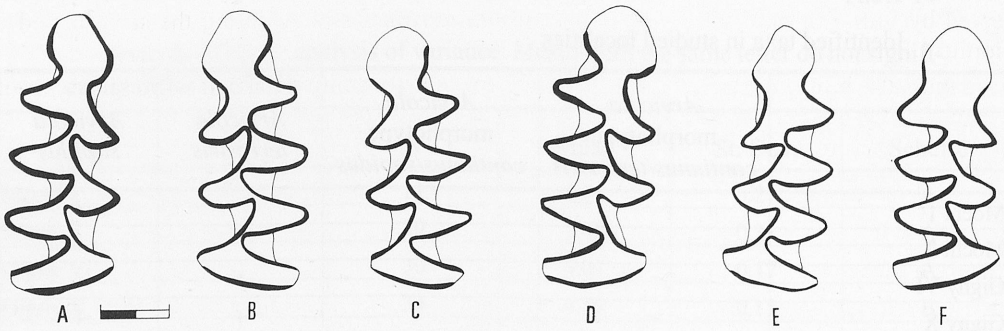


Fig. 5. – Grotte Vaufrey *Arvicola* M_1 morphology (scale = 1 mm). With A : *Arvicola* morphotype *cantianus/sapidus* right M_1 cVIII E 521, B : *Arvicola* sp. left M_1 cVIII E522, C : *Arvicola* morphotype *cantianus/terrestris* left M_1 cIV E 916, D : *Arvicola* morphotype *cantianus/sapidus* right M_1 cIV E 539, E : *Arvicola* morphotype *cantianus/terrestris* left M_1 cV E872 and F : *Arvicola* morphotype *cantianus/terrestris* right M_1 cV E 542.

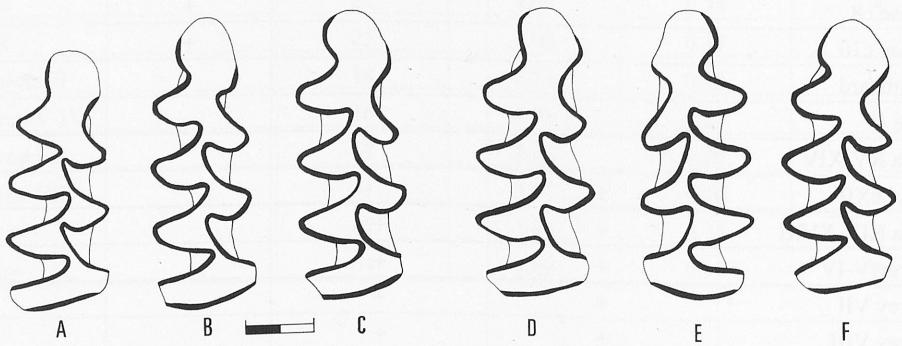


Fig. 6 – Grotte de l'Eglise *Arvicola terrestris* M_1 morphology (scale = 1 mm). With A : right M_1 c2 E 1399, B : right M_1 c2a/2b E 1398, C : right M_1 c2a/2b E 1398 (1197), D : right M_1 c2 E 1411, E : left M_1 c2 E 1411 and F : right M_1 c2 E 1405 (1152).

European Upper Pleistocene sequences. It can also be compared to the SDQ observed by VAN KOLFSCHOTEN (1990) for *Arvicola terrestris* ssp. B from northern European Weichselian (Upper Pleistocene) and Saalian (Middle Pleistocene).

III. c. Abri Gaudry (Montgaudier sequences) at Monbron (Charente)

During the 1970s, excavations at the Gaudry rock shelter provided palaeontological and archaeological remains assigned to the Middle Pleistocene (DEBENATH 1974).

Arvicola from levels 4 and 4b were studied.

According to MARQUET (1989), the presence of rodent species such as *Lemmus lemmus*, *Dicrostonyx torquatus* of *Allocricetus bursae,* and the abundance of *Micotus arvalis* and *Microtus gregalis* are characteristic of a rather cold and arid climate and an open environment. The morphology and dimensions of *Allocricetus bursae*, *Arvicola cantianus*, and *Microtus gregalis* indicate a Middle Pleistocene age (OIS 6, Saalian).

Arvicola morphotype *cantianus/terrestris* was identified (Fig. 7). The SDQ value (N=64, SDQ_{M1}=113.9) is similar to the enamel thickness obtained by HEINRICH (1990) for *Arvicola cantia-*

nus from central European Middle Pleistocene sequences. It can also be compared to the SDQ observed by VAN KOLFSCHOTEN (1990) for *Arvicola terrestris* ssp. A during the same period in Northern Europe.

It must also be noted that a few *Arvicola* specimens show primitive characters (presence of roots and enamel islets).

III. d. Grotte-abri Suard at Vouthon (Charente)

According to DEBENATH (1974), excavations at grotte-abri Suard produced palaeontological and archaeological remains dating back to the late Middle Pleistocene (levels IV and III) and the Upper Pleistocene (levels II and I).

Rodent associations (MARQUET 1989) indicate a cold climate and an open environment (presence of *Dicrostonyx torquatus*, *Lagurus lagurus*, *Microtus gregalis*, *Allocricetus bursae* and *Microtus arvalis*). More humid environments are also attested by the abundance of *Arvicola terrestris* and *Microtus agrestis*.

Arvicola terrestris, with a SDQ value (N=32, SDQ_{M1}=91.59) similar to the enamel thickness observed by VAN KOLFSCHOTEN for late Middle Pleistocene populations from northern Europe and by HEINRICH during the early Upper Pleistocene from central Europe, was identified (Fig. 8).

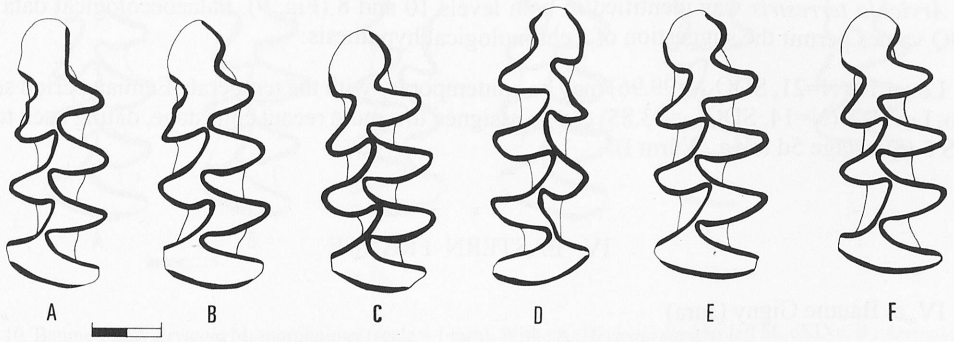


Fig. 7. – Abri Gaudry *Arvicola* morphotype *cantianus/terrestris* M_1 morphology (scale = 1 mm). With A : left M_1 N1667, B : left M_1 N1667, C : left M_1 N1667, D: right M_1 N1667, E : left M_1 N1667 et F : left M_1 N 1667.

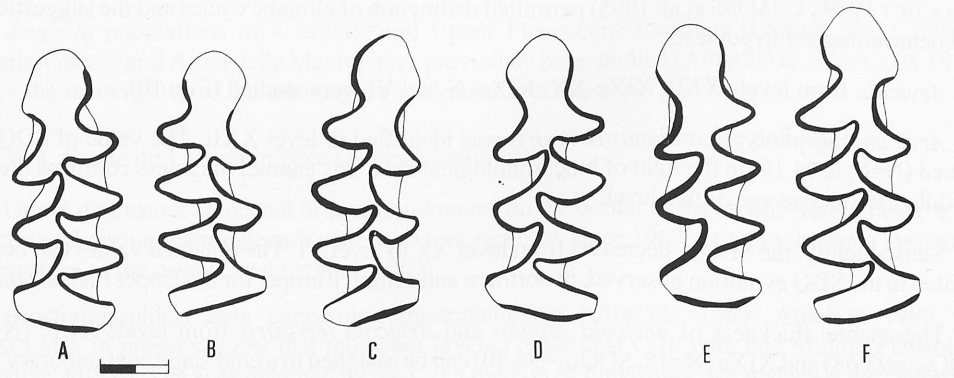


Fig. 8. – Abri Suard *Arvicola terrestris* M_1 morphology (scale = 1 mm). with A : left M_1 cII, B : right M_1 cII, C : right M_1 cII, D: left M_1 cII, E : left M_1 cII and F : right M_1 cII.

III. e. Grotte d'Artenac (Charente)

Since 1995, excavations at Artenac cave have been providing abundant palaeontological and archaeological remains. Most of the data concerning chronology, environment, and human occupation of the levels 10 and 8, which have been taken into account in this study, have not yet been published.

However, it may be mentioned that preliminary palaeontological results permit the assignation of those deposits to the Upper Pleistocene.

Thus, according to TOURNEPICHE & ARMAND (1997), large mammals indicate a temperate climate assigned to the early Upper Pleistocene (OIS 5).

Level 10 micromammal associations (DESCLAUX 1997) are characteristic of a temperate climate. The landscape consists in an alternation of a forested environment (presence of *Clethrionomys glareolus*, *Eliomys quercinus*, *Apodemus sylvaticus*, *Myotis* cf. *emarginatus*, *Myotis nattereri*, *Myotis bechsteini,* and *Vespertilio murinus*) and a rather humid and open one (*Microtus* morphotype *arvalis/agrestis*, *Sorex* morphotype *araneus/coronatus*, and *Arvicola terrestris*). Level 8, characterized by the abundance of *Microtus arvalis* and *Microtus gregalis*, indicates an open environment and a cold climate.

Arvicola terrestris was identified in both levels 10 and 8 (Fig. 9). Palaeoecological data and SDQ values permit the suggestion of a chronological hypothesis:

Level 10 (N=21, SDQ_{M1}=99.96) may be contemporary with the temperate Eemian period sensu lato. Levels 8 (N=14, SDQ_{M1}=93.85) can be assigned to a more recent cold stage, dating back to the OIS 5 (Substage 5d to 5a, Würm I).

IV. EASTERN FRANCE

IV. a. Baume Gigny (Jura)

The Gigny site is located on the Western side of the Jura range. A multidisciplinary approach (CAMPY et al. 1989) produced an exceptional chronological log of climatic patterns for this Pleistocene sequence covering the late Middle Pleistocene (pre-Eemian) and the Upper Pleistocene (Eemian, Weichselian), as well as a part of the Holocene. Rodent associations (CHALINE & BROCHET 1989 ; CHALINE et al. 1995) permitted distinction of climatic cycles and the suggestion of a biochronological hypothesis.

Arvicola from levels XXII, XIXc-XX, XIXa, X and VI were studied (Fig. 10).

Arvicola morphotype *cantianus/terrestris* was identified in level XXII. The value of SDQ obtained (N=6) is 94.19. In the light of biochronological data, this enamel thickness confirms the late Middle Pleistocene age of this level.

Subsequently, the SDQ_{M1} decreases from level XX to level VI. The obtained values can be correlated to the SDQ evolution observed, in northern and central Europe, for the Upper Pleistocene:

The enamel thickness of *Arvicola sapidus* and *Arvicola terrestris* from levels XIXc (N=41, SDQ_{M1}=93.68) and XIXa (N=18, SDQ_{M1}=96.40) can be assigned to a cold stage contemporary with the early Upper Pleistocene (OIS 5 or 4).

SDQ of *Arvicola terrestris* of levels X (N=34, SDQ_{M1}=87.50) and VI (N=30, SDQ_{M1}=78.20) indicate a more recent age, which can be contemporary with OISs 3 or 2.

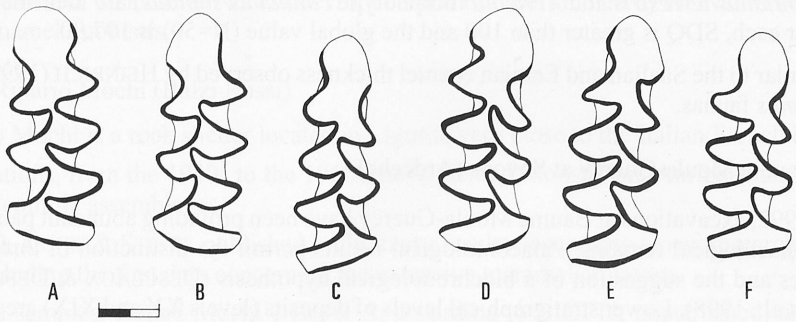


Fig. 9. Grotte d'Artenac *Arvicola terrestris* M_1 morphology (scale = 1 mm). With A : left M_1 d25 c10 déc.1, B : left M_1 d25 c10 déc.1, C : right M_1 d25 c10 déc.1, D : right M_1 e19 c8 déc.2, E : right M_1 e18a c8 déc.4 and F : right M_1 e18a c8 déc.4.

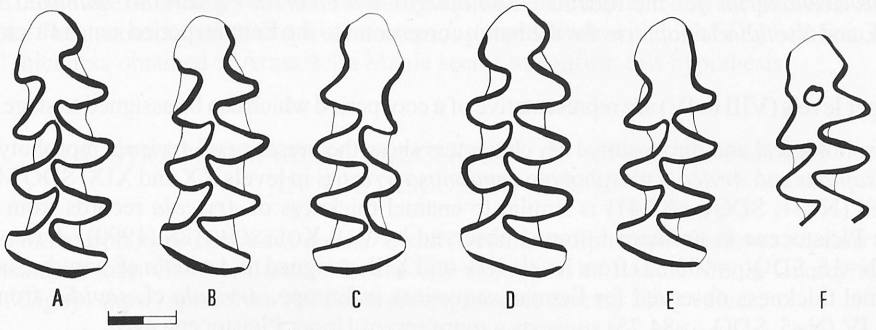


Fig. 10. Baume Gigny *Arvicola* M_1 morphology (scale = 1 mm). With : A : *Arvicola sapidus* left M_1 cXIXc, B : *Arvicola sapidus* left M_1 cXIXc, C : *Arvicola* cf. *terrestris* right M_1 cXX, D: *Arvicola sapidus* left M_1 cX, E : *Arvicola terrestris* left M_1 cX and F : *Arvicola* sp. left M_1 cXX.

V. SOUTH-EAST FRANCE

Arvicola populations of 4 Middle and Upper Pleistocene localities (Lazaret, Pié Lombard, Moula-Guercy and Arma delle Manie) have previously been studied (ABBASSI & DESCLAUX 1996). Only the main results of the analysis are integrated into this paper.

V. a. Grotte du Lazaret in Nice (Alpes-Maritimes)

Grotte du Lazaret is located in southern France, on the border of the city of Nice. The cave was discovered during the nineteenth century. More recently, since 1967, LUMLEY began a systematic excavation of the cave (LUMLEY et al. 1969).

Biostratigraphical data concerning micromammals (CHALINE 1969; ABBASSI 1999, and DESCLAUX in press) suggest that the upper layers ("ensemble CIII") are late Middle Pleistocene (Saalian, OIS 6). The ages obtained by the U-Th method of flowstones, located upon the "ensemble CIII", fall between 70 000 and 130 000 yr. B.P. (FALGUERES et al. 1992). Other radiometric results (MICHEL 1995) likewise show that the studied part of the sequence coincides with the late Middle Pleistocene.

Morphological and dimensional characters of *Arvicola* have shown that two taxa (*Arvicola* morphotype *cantianus/terrestris* and *Arvicola* morphotype *cantianus/sapidus*) are identified in the sequence. For each, SDQ is greater than 100 and the global value (N=50) is 107.90.

It is similar to the Saalian and Eemian enamel thickness observed by HEINRICH (1990) for *Arvicola cantianus* faunas.

V. b. Baume Moula-Guercy at Soyons (Ardèche)

Since 1992, excavations at Baume Moula-Guercy have been providing abundant palaeontological and archaeological remains. Palaeontological results permit the distinction of three main climatic cycles and the suggestion of a biochronological hypothesis (DESCLAUX & DEFLEUR 1997; DEFLEUR et al., 1998). Lower stratigraphical levels of deposits (levels XX and XIX) are representative of a cold period, characterized by the abundance of *Microtus gregalis* and *Allocricetus bursae*, and by the presence of *Dicrostonyx torquatus*, *Sicista* cf. *betulina*, *Citellus superciliosus* and *Microtus malei/oeconomus*, which may be related to the end of the Middle Pleistocene (Saalian, OIS 6).

Intermediate stratigraphical levels (levels XIV and XIII), which contain an abundant temperate and forested fauna (*Clethrionomys glareolus*, *Apodemus sylvaticus*, *Eliomys quercinus* and *Muscardinus avellanarius* for the rodents ; *Miniopterus schreibersii*, *Pipistrellus nathusii*, *Nyctalus noctula,* and *Nyctalus lasiopterus* for the bats), correspond to the Eemian period sensu stricto (OIS 5 e).

Upper levels (VIII to IV) are representative of a cool period which can be assigned to stage 5 or 4.

Morphological and dimensional M_1 characters show the presence of *Arvicola* morphotype *cantianus/sapidus* and *Arvicola* morphotype *cantianus/terrestris* in levels XX and XIX. SDQ M1 value obtained (N=31, SDQ_{M1}=87.41) is similar to enamel thickness of *Arvicola* records from the late Middle Pleistocene in northern Europe., observed by VAN KOLFSCHOTEN (1990). *Arvicola* SDQ value (N=15, SDQ_{M1}=100.53) from levels XIV and XIII, assigned to *Arvicola* cf. *sapidus*, is similar to enamel thickness observed for Eemian sequences in Europe. *Arvicola* cf. *sapidus* from levels VIII to IV (N=5, SDQ_{M1}=84.25) suggests a more recent Upper Pleistocene age.

V. c. Pié Lombard at Tourettes-sur-Loup (Alpes-Maritimes)

The latest excavations of the Pié Lombard rock shelter, during the sixties and the seventies, provided abundant mousterian artefacts and mammal remains. Biostratigraphical and palaeoecological data concerning large mammals (GERBER 1973; BRUGAL, unpublished), birds (MOURER-CHAUVIRE 1975), and micromammals (CHALINE, unpublished and DESCLAUX, unpublished) indicate a rather cool climate, contemporary with the early Upper Pleistocene (OIS 5, Würm I).

Only four *Arvicola* M_1 were collected. Hence, this material is assigned to *Arvicola* sp. It should be noted that those molars show alternate T4 and T5 prisms and constricted anterior loops with deep re-entrant angles A6 and A7. The enamel quotient value is 101.02 (N=4). It is similar to SDQ observed in central Europe for Eemian sequences.

VI. LIGURIA (ITALY)

VI. a. Arma delle Manie (Finale Ligure)

Excavations at Arma delle Manie, since the 1980s, have provided typical mousterian artefacts with abundant faunal remains.

Studied M_1 of *Arvicola* (N=25) come from levels VIII to III, assigned to the Weichselian period (OIS 4, Würm II) by LUMLEY (1969), ARRODA et al. (1976), and FORNASIERO (1989).

The M_1 morphology is characteristic of *Arvicola sapidus*. The SDQ value is 99.84. *Arvicola* faunas of Eemian and Weichselian localities from central Europe, studied by HEINRICH (1990), show identical enamel quotients.

VI. b. Ripario Mochi (Balzi Rossi)

Ripario Mochi is a rock shelter located in Liguria, very close to the Italian/French border.

Excavations, from the 1940s to the 1960s, have yielded Mousterian, Aurignacian, Gravettian, and Epipaleolithic assemblages.

In 1992, KUHN & STINER published preliminary results concerning a new research on Ripario Mochi, including the first data concerning the extensive mammalian fauna.

Studied samples, named Mochi 1 (level A, according to BIETTI, unpublished) and Mochi 2 (level EF), come from the upper stratigraphical unit which is characterized by the presence of Upper Paleolithic artefacts and can be assigned to OIS 3. Rodent associations indicate a rather cold climate and an open environment (ABBASSI 1999).

Arvicola sapidus was identified in both samples. The values of SDQ obtained, which are close to 100 (N=25, SDQ_{M1}=98.20 for Mochi 1 and N=8, SDQ_{M1}=100.75 for Mochi 2), are in contradiction with the recent age of those levels. Such a configuration can be explained by the persistence, during the Upper Pleistocene, of primitive *Arvicola sapidus* populations with high SDQ values in Liguria. Enamel thickness obtained at Arma della Manie seems to confirm this hypothesis.

VII. STRATIGRAPHICAL SUCCESSION OF *ARVICOLA* FAUNAS IN THE DISCUSSED AREA

Arvicola morphotype *cantianus/terrestris* and *Arvicola* morphotype *cantianus/sapidus* of Middle Pleistocene (abri Gaudry, Lazaret, levels XIX and XVIII of Baume Moula-Guercy and level XXII of Gigny) show, apart from the defined morphotype, diverse SDQ values.

The enamel thickness quotient of *Arvicola* of abri Gaudry at Montgaudier is greater than 110. According to the values observed in Middle Pleistocene European localities (von KOENIGSWALD and VAN KOLFSCHOTEN 1996), an early Saalian or a late Holsteinian age may be suggested. This hypothesis may be confirmed by the presence of a few rooted M_1 with enamel islets.

Arvicola populations of Vaufrey (levels VIII to IV) and Lazaret, which show an enamel thickness quotient between 110 and 100, are more recent and represent a more evolved stage of first *Arvicola* in western Europe. The comparison with SDQ values obtained in central Europe by HEINRICH (1990) and in Northern Europe by VAN KOLFSCHOTEN (1990) suggests a late Middle Pleistocene age for those levels (Saalian, OIS 6).

Both morphotypes of *Arvicola* from levels XIX and XVIII of Baume Moula-Guercy and level XXII of Gigny show SDQ values lower than 100. They are similar to the enamel thickness quotient of late Saalian localities in northern Europe observed by VAN KOLFSCHOTEN (1990).

Thus, the hypothesis may be suggested that the later Middle Pleistocene (late Saalian, iostopic stage 6) morphotype defined by VAN KOLFSCHOTEN (*Arvicola terrestris* ssp. B) had a punctual expansion in the western area. Baume Moula-Guercy and Gigny, which are located near the Rhône valley area, were affected by this migration. The Mediterranean coastline (Grotte du Lazaret), which is located beyond the ecological barrier constituted by the Alps, and the south-west France (Vaufrey) were not affected (Fig.11).

Overall, *Arvicola* populations, assigned to *Arvicola terrestris* or *Arvicola sapidus*, of Upper Pleistocene localities are not characterized by a continuous decrease in the SDQ values. Therefore climatic and biostratigraphical data must be taken into account in order to elaborate a coherent chronology.

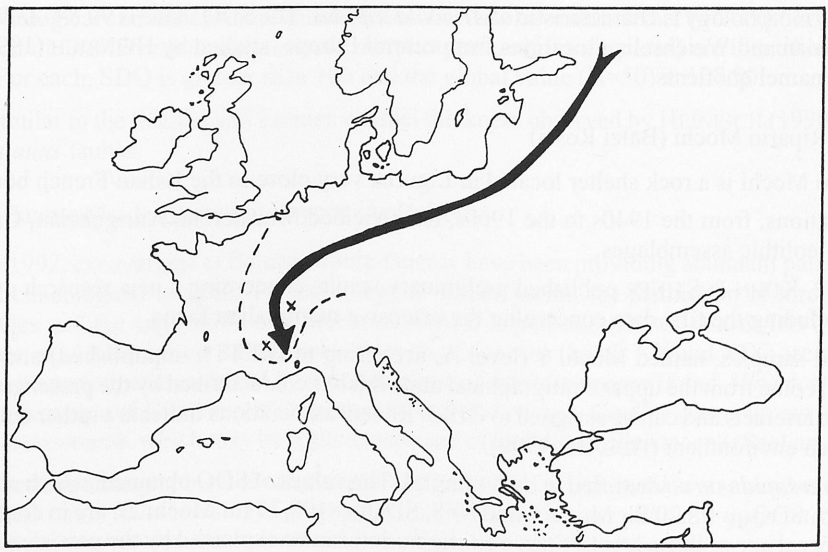


Fig. 11. – *Arvicola* population immigrations during the late Middle Pleistocene. With : x = affected localities (Gigny and Moula-Guercy) and 0 = non affected localities (Lazaret and Vaufrey).

High SDQ_{MI} values observed at Ripario Mocchi, and to a lesser extent Arma delle Manie, can be explained by the persistence of isolated primitive *Arvicola* populations in Liguria during the Upper Pleistocene.

Thus, despite the large enamel thickness variations observed, it is possible to state precisely the biochronological framework of studied localities (Fig. 12).

VIII. DISCUSSION

Morphological and dimensional data allow the definition of 4 taxa of *Arvicola* from the Middle and Upper Pleistocene of France and Liguria (Italy).

The Middle Pleistocene representatives of the genus *Arvicola* are now assigned to *Arvicola* morphotype *cantianus/terrestris* (characterized by small dimensions and T4-T5 confluent prisms) and *Arvicola* morphotype *cantianus/sapidus* (great dimensions and T4-T5 alternate prisms). Upper Pleistocene representatives are assigned to *Arvicola sapidus* and *Arvicola terrestris*.

The comparison of *Arvicola* SDQ values of grotte Vaufrey (levels VIII to IV) and Lazaret with those obtained in central Europe by HEINRICH (1990) and in northern Europe by VAN KOLFSCHOTEN (1990) suggests a late Middle Pleistocene age for those levels (Saalian, OIS 6).

Arvicola from levels XIX and XVIII of Baume Moula-Guercy and level XXII of Gigny are similar to the enamel thickness quotient of late Saalian localities in northern Europe observed by VAN KOLFSCHOTEN (1990). Thus, the late Middle Pleistocene morphotype defined by VAN KOLFSCHOTEN (*Arvicola terrestris* ssp. B) had a punctual expansion in the western area, which affected the Rhône valley area. The Mediterranean coastline (Lazaret) and the south-west France (Vaufrey) were not affected.

High SDQ values obtained for Ripario Mochi (OIS 3) and Arma delle Manie (Stage isotopic 4) populations can be related to the persistence of isolated primitive *Arvicola* in this area during the Upper Pleistocene.

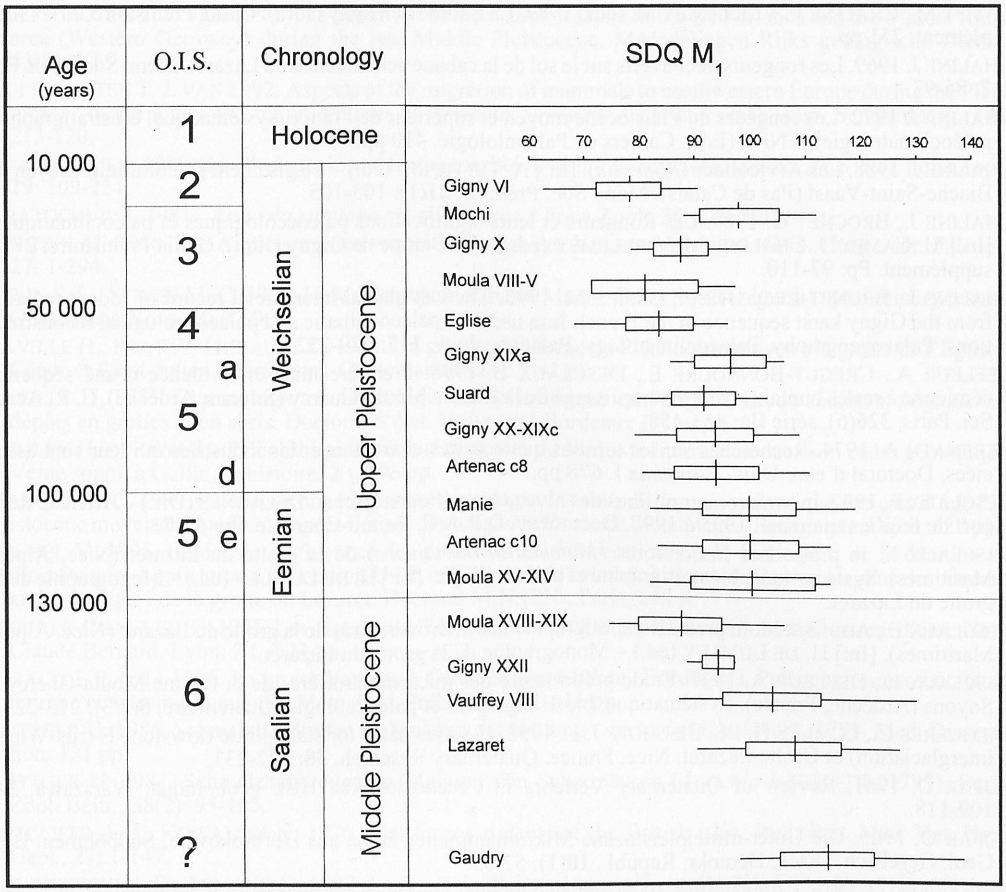


Fig. 12. – *Arvicola* M_1 enamel quotient variation (mean, standard deviation and range) in rance and Liguria during Middle and Upper Pleistocene.

The disappearance of *Arvicola terrestris* from the south-east of France and Liguria, during the early Upper Pleistocene (OIS 5) may also confirm the hypothesis of a migration of this species into north-west Europe, coinciding with the Eemian climatic change, as suggested by VAN KOLFSCHOTEN (1992).

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