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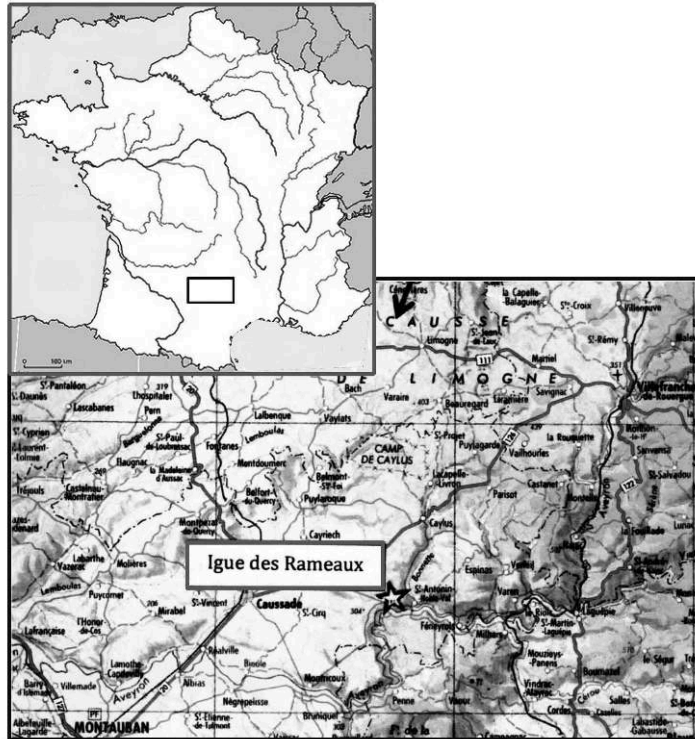
*We wish to thank the Museums of Bonn and Basel for lending us the *Apodemus agrarius* molars which enabled us to confirm our determinations and to multiply our observations and comparisons.*

## Introduction

- 1 The partial filling of a karst fissure on the southern fringes of the Causse de Quercy has yielded a rather scant but very diversified microfauna. A previous study (Jeannet 2005) brought to light the predominance of rodents, showing the progressive installation of a continental steppe environment from the base to the top, followed by an abrupt reforesting under a temperate humid climate.
- 2 Field mice (genus *Apodemus*) are represented by four species (*Apodemus flavicollis*, *A. sylvaticus*, *A. agrarius* and *A. microps* or *uralensis*), which we will describe here. The morphological and biometric study enables us to discern the evolutionary stage and to position them biochronologically in a recent phase of the Middle Pleistocene, probably at the Holsteinian/Saalian limit. This is, in any case, what the biometric study of *Arvicola cantiana* showed (Jeannet 2005), using the SDQ method (Schmelzband-Differenzierung Quotient: Heinrich 1990), which corroborates the conclusions of Rouzaud et al 1990.
- 3 Igue des Rameaux is a karst fissure opening in the southern fringes of the Causse du Quercy, about 400 m above the Aveyron River (fig. 1). A narrow shaft leads to the upper part of a network of partially filled sinuous galleries of varying widths. The joint effects of the slope and the underlying void played a primordial role in the formation of the

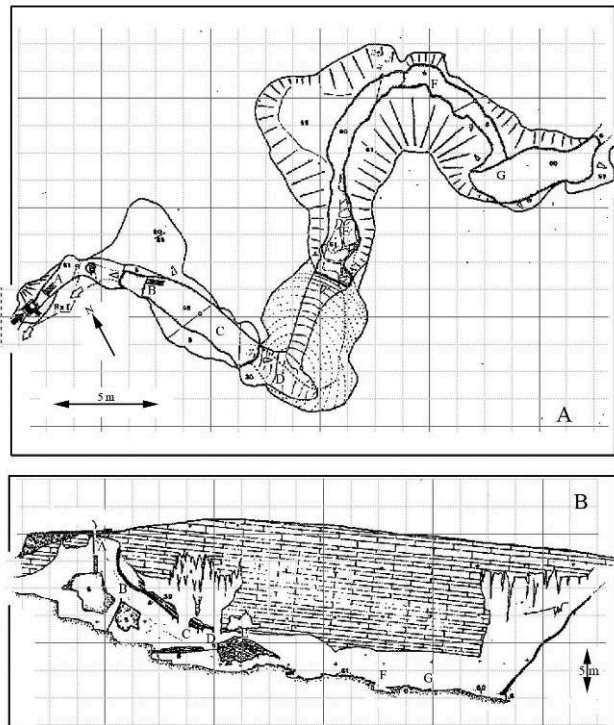
infilling and the distribution of the microfauna. The complex is divided into an upper part (B, C, D), and a lower part (E, F, G) (fig.2).

**Figure 1** – Location of l'Igue des Rameaux at Saint-Antonin-Noble-Val (Tarn-et-Garonne, France) in Quercy (south-western France).



IGN map 2012 and Géoportail

Figure 2 – l'Igue des Rameaux. Topographic map of the site (2a) and longitudinal profile (2b) showing the excavated areas.



From ROUZAUD and *al.*, 1990.

- 4 The first part contains a mass of sediments retained by collapsed blocks and capped by a flowstone. As suffosion removed part of the infilling, the lower part of the flowstone has been dismantled and the sediments have partially crept downwards. This part of the network is still active, judging by the accumulation of lagomorph remains on the surface, and the subsidence marks engraved on the clay against the wall. In an earlier note (Jeannet 2005), the distribution and the biometric study of *Arvicola* showed that these sediments are nested under deposits containing older remains. In this way, layer 30 remained suspended above more recent deposits but is older than the deposits in the lower sector. Beyond sector G, the gallery forms a right angle filled with scree that may come from a possible second, now obstructed entrance, through which carnivores could have entered the cavity. Three large predators used this sector of the cavity as their den: the lion, the wolf and the hyena. They left abundant bones, sometimes in loose connection, and left wide incisions on several large herbivore remains (equids in particular), indicating a certain degree of consumption (scavenging?). Carnivores of all ages are represented. The hyena in particular left a layer of coprolites of mixed sizes (Rouzaud *et al.* 1990). Humans also visited the cavern but only left rare choppers and quartz artefacts in the upper sector. No large herbivore remains in this sector bear butchery marks.

## Sampling and preparation of the material

- 5 The search for microfauna took place over the last three excavation campaigns (1988-1990) and samples were taken during the course of the excavation from the

whole cavity and from all the main layers. As time was limited, we could not sieve all the sediments removed from the cavity, and it was up to the excavators, first of all, to carry out sampling. Subsequently, the initial results guided complementary sampling, corresponding in volume to the capacity of a bucket (about 8 to 10 kg). The central axis yielded the most material and gave a significant overall view (tab. 1 and 2).

**Table 1** – l'Igüe des Rameaux. Summarized plan of the site showing sampling zones. Each square indicates the layer and the number of samples. Areas B, C and D constitute the upper zone; E, F and G, the lower zone.

Zone	Y Carré	US/nb	X Carré		
			L	M	
G	4	US	c60		
		nb	6		
	3	US		c60	
		nb		14	
	2	US		c60	c60
		nb		24	16
	1	US		c60	c60
		nb		18	2
F	5	US		c62	
		nb		9	
	4	US	c60	c60	
		nb	6	13	
	3	US		c62	
		nb		10	
	2	US	c62	c62	
		nb	9	21	
	1	US		c62	
		nb		16	
E	15	US		c62	
		nb		22	
	14	US		c60	
		nb		15	
	9	US		c61	
		nb		2	
D	2	US		c54	
		nb		17	
	1	US	c30		
		nb	33		
Csup	5	US		?	
	nb			12	
B	6	US		c50	
		nb		1	
	4	US	c503		
		nb	5		
	3	US		c503	
		nb		5	
	2	US		c502	
		nb		8	



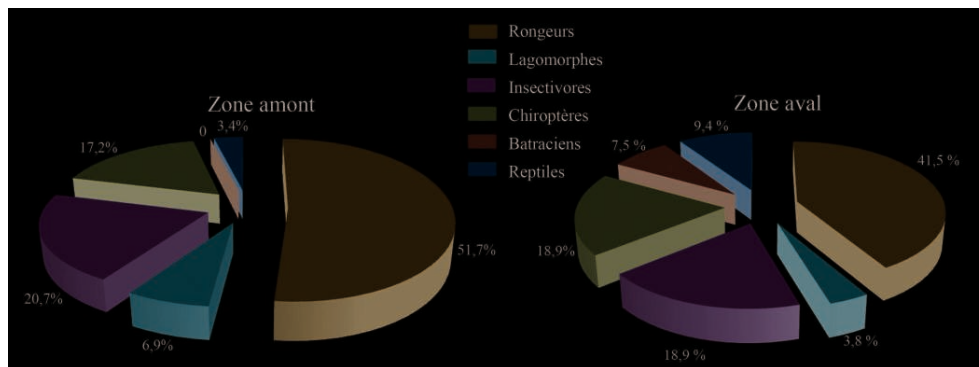
## Taphonomic diversity

- 9 The overall aspect of the remains is very diversified as bone mineralization is very variable among the samples. Some bones are translucent, others are brownish-red or even sometimes bright red; others are totally black or marbled. Most of them are white and opaque. Other very white bones are totally covered in calcite. Only the bones from sector B are consolidated by mineralization. Most of the remains are from young individuals and did not undergo corrosion. The alteration of the remains is predominantly mechanical, causing clean breaks and rounded angles which could be imputable to transport or possibly to soil compaction.
- 10 The taxa are relatively abundantly represented in all layers, apart from four taxa. Yet, we observe that some well-represented taxa in one sample are very rare, or even absent in another sample, even it is copious and of the same origin. The remains from the same species (maybe even from the same individual) seem to have been deposited in bulk in a given place or as if the animal died in this narrow space. This is the case, in particular, for the vertebrae from reptiles and several rodents. It is also the case for the David's hedgehog (*Erinaceus davidii* Jammot, 1973), which was found in four contiguous squares, in the same layer. This pattern points to death during hibernation. But how can we interpret the presence of a small snake lying on a lateral rocky bench, in perfect anatomic connection and covered with a film of calcite? Its stretched-out position is not generally the position adopted during hibernation. Chiroptera bones were petrified, probably in identical conditions. This group appears to have been the first occupant of the cavern.
- 11 The lagomorphs are a case apart. They are overabundant in sector D, with an enormous quantity of juvenile bones and teeth (non-worn milk teeth), clearly showing that this taxon nested in this sector, where it must have considerably disturbed the levels.
- 12 The distance between this accumulation from the entrance and the relatively good conservation of fragile non-mineralized bones appears to preclude the transport of these remains. In the other sectors, their presence is less marked and may correspond to their dispersal into deeper levels, and thus to the transport of bones rather than to a habitat.
- 13 Taphonomic conditions play an important role in understanding the stratigraphy, the chronology and the environment, through faunal associations, but they are still difficult to elucidate. Generally, microvertebrate remains come from bird of prey pellets, who could easily have nested on the cliff or in a fissure. In this case, the remains accumulate on the ground in a narrow space and are constant throughout the infilling, although there are variations in density, due to run-off or modifications as a result of the wall effect. At Igue des Rameaux, the fairly uniform distribution of the remains in the axis of the gallery and throughout the levels, in spite of the fact that they are not very well represented, implies that overall, apart from the case of hibernating animals and lagomorphs, the animals fell into a natural lapiaz trap and their skeletal remains could have undergone creep action with the solifluction silts. The upper deposits (C and D) are scree, with a gradual lateral rarefaction of the remains. The absence of small predator bones (birds of prey and small mustelids) in the series, in keeping with the difficult access of the site, clearly accounts for the good surface condition of the micromammal bones, the absence of digestion marks, as well as the absence of the clustering of the remains around a possible nesting area (tabl.1).

The rarity of breaks, in spite of fragility due to corrosion, is probably due to movement in muddy masses, which is characteristic of this type of transport. In addition, for different reasons, bioturbation is always possible on micro-remains. However, in sectors E, F and G, the successive habitats of large predators tend to show the stability of the stratigraphy, which could also be the case for the underlying small bones. The transverse layout of zone H brings to light the absence of a link between the levels of zones E, F, G and the scree sediments. In this case, there cannot be any mixing of the microvertebrates.

- 14 In accordance with the behaviour and the topographic distribution of the taxa, we compared the associations from the upper and lower areas to assess the similarities or the differences between them (fig. 3). The circular diagrams underline the low representation of the reptiles and batrachians from the upper zone. This implies that the herpetological group entered the lower zone, probably to hibernate, through the entrance currently obstructed by scree and concretions. The other taxa are distributed relatively evenly in both parts of the cavern.

**Figure 3** –l'Igüe des Rameaux. Pie charts showing microfaunal distribution between upper and lower zones (in % per species).



- 15 In spite of the abundance of lagomorph remains, it is difficult to assess differences within the group and in relation to other groups, due to the restricted number of taxa (four species).
- 16 Therefore, it seems that, in spite of stratigraphic disturbances, the remains in the lower area appear to mostly come from the upper area. This is also clear in the columns in table 2, where the same taxa coexist in both sectors.

## Taxonomic diversity (tabl. 2)

- 17 A first sorting operation brought to light the predominance of rodents from the five main European families (Arvicolids, Murids, Glirids, Cricetids and Sciuridae). Early forms such as *Pliomys lenki*, *Arvicola cantiana* and *Allocrietus bursae* point to a Middle Pleistocene chronology and more specifically to the Holsteinian / Saalian interface, or even to an early phase, due to the climatic conditions recorded in the diverse layers, where the oldest phase records a dry steppe-like period evolving towards a humid warming period favouring the development of forest cover. The second argument refers to the SDQ Heinrich values obtained regularly on all the *Arvicola* molars (Jeannet 2005), confirming its chronological position. Lastly, the taxonomy of certain taxa (lion, hyena, wolf, equids) confirms this age, according to the conclusions of Rouzaud *et al.*



(1990). Among the other groups, lagomorphs are the most abundant and belong, at least in sector D, to the European rabbit (*Oryctolagus cuniculus*), which also lives in dry caverns where it shelters its abundant young. This behaviour contrasts with that of the brown hare (*Lepus europaeus*), who prefers to live outside in vast open spaces. Its remains are only found in cave contexts when it falls in accidentally (Jeannet 2000), or more frequently due to the intervention of a predator. Then come the batrachians, with a limited number of taxa (4: *Rana dalmatina*, *Bufo bufo*, *Bufo calamita*, *Urodela* cf. *Triturus* sp.), but plentiful bones. Again, hibernation may account for this abundance. The numerous bat species (11: *Myotis myotis*, *M. blythii*, *M. bechsteinii*, *M. nattereri*, *Plecotus auritus*, *P. austriacus*, *Rhinolophus mehelyi*, *Rh. euryale*, *Rh. ferrumequinum*, *Miniopterus schreibersi*, *Barbastella batbastellus*) are also a result of hibernation, but there are few remains per taxon. They tend to be clustered in the same sector (15 M) and in the same level 60. Although several bat species often hibernate in the same cave, it is at times impossible to find a common link between them attracting them to the same site, as their behaviour is very different. We can deduce that the atmosphere of the place varied throughout time, rather than the adaptive capacities of the bats, which can flee if they are disturbed. No guano accumulation has been identified, and thus it is plausible that their visits to the site were short rather than for nursery purposes. We can conclude that the site was only used occasionally during local, often individual movements, as is traditional for bats. David's hedgehog (*Erinaceus davidii*) comes from the deep layers 60 and 62 (lower sector) and may also have hibernated,. But if the habits of this hedgehog are the same as those of the present-day hedgehog, this is not its preferred place: it prefers heaps of rotting leaves that give off heat. The hedgehog was also discovered at La Fage (Jammot 1973), in layers dated to the Middle Pleistocene and at Baume Moula at Soyons (Desclaux and Defleur 1997). Its presence in zone B of the upper sector, far from sectors E, F, and G, indicates that most of this infilling is from the Middle Pleistocene, as this species is not known at other periods, and is associated here with *Arvicola cantiana*. The other insectivores include the European mole (*Talpa europaea*), represented by a high number of remains that may belong to a small number of individuals. The small mole, *Talpa minor* is only represented by a single individual. The group of shrews is well represented with seven species indicating a very diversified ecosystem, including the rather rare dwarf shrew. The latter lives in continental climates and its rarity is due to its tiny size and fragility. The other species of the shrew family are *Crocidura russula* (the great white-toothed shrew), *Crocidura suaveolens* (the lesser white-toothed shrew), *Suncus etruscus* (the Etruscan shrew), *Neomys fodiens* (the Eurasian water shrew), *Sorex araneus* (the common shrew), *Sorex minutus* (the pygmy shrew). They are only represented by several remains but live in very diverse environments. There are also abundant reptile remains, such as the green whip snake (*Coluber viridiflavus*), the grass snake (*Natrix natrix*), the ladder snake (*Rhinechis scalaris*), the European aspic (*Vipera aspis*), Ursini's viper (*Vipera ursinii*) and the common European adder (*Vipera berus*). These remains are mostly clustered together in two contiguous squares, and appear to come from hibernating animals, although they do not generally hibernate so deep down.

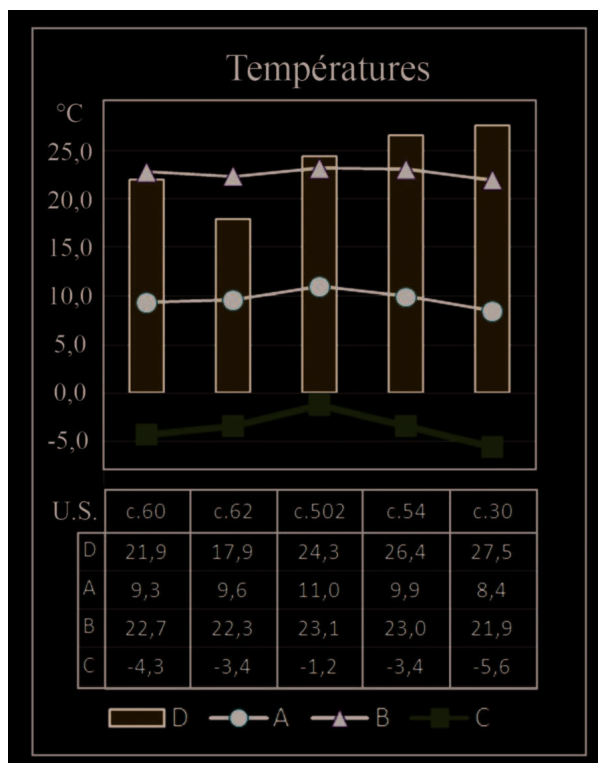
## Environment

- 18 In order to confirm this homogeneous distribution and biodiversity, we drew up histograms of the main environmental parameters (fig. 4 to fig. 8), where possible

internal variations underline significant differences. In this aim, we used the “quantified ecology” method (Jeannet 2010; Jeannet *et al.* 2013; Jaubert *et al.* 2005; with the chronoclimatic base; Martinson *et al.* 1987).

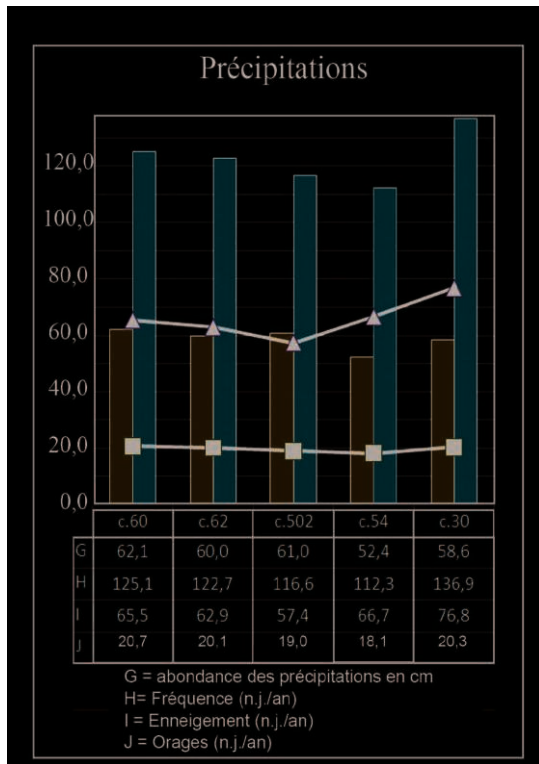
- 19 In spite of the uncertain stratigraphic sequence due to the considerable drop separating the upper and lower sectors and the presence of older layers (c30) suspended on flowstones (Rouzaud *et al.* 1990) affected by underlying suffosion (Jeannet 2005), we respected the previously established order.
- 20 As regards the temperature (fig. 4), the seemingly low variations between the levels are interesting to observe given their stratigraphic position. The lowest value (8.4°C) is from what is considered to be the oldest layer. It is equivalent to the annual average values for Bourg-Saint-Maurice (Savoy), Bamberg (Bavaria), Cluj (Romania) or Rostov (C.E.I./Azov). The highest (11.4°) is the current value from the centre of France (Lyon, Bourges). It is slightly higher than the value recorded in 5e at Coudoulous II (10.7°C) (Jeannet 2010). The winter/summer difference is limited to 27.5°C and conveys a semi-continental aspect on the deeper levels. The climate warms progressively in the recent levels to become cool and temperate.

Figure 4 - l'Igue des Rameaux. Temperature diagram.



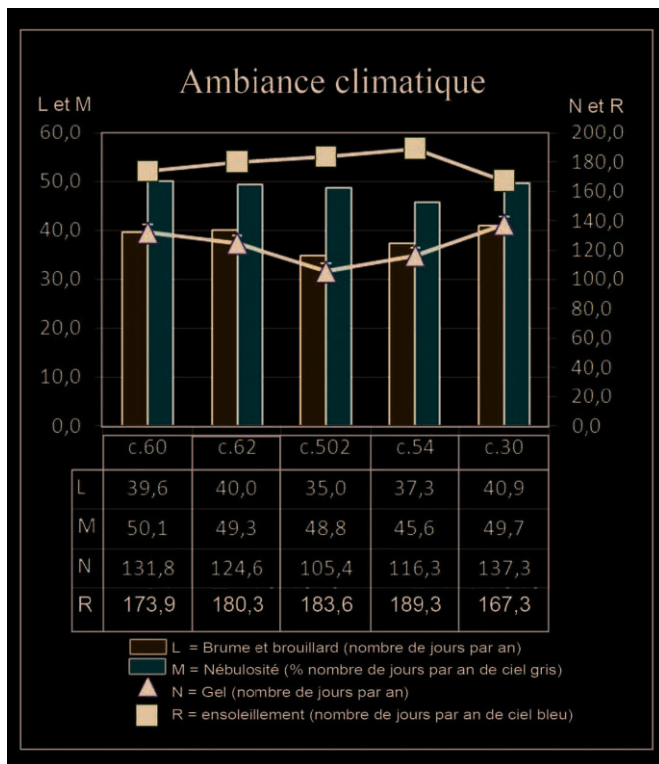
- 21 Precipitation (fig. 5) confirms the climatic conditions inferred from temperatures. Precipitation is low: 60 cm (currently 90 cm in France) and spread out over a rather long period (5 months under a rigorous climate in c.30). In spite of climatic warming, precipitation remains low and increases very gradually. The parallel between the frost (N) and snow curves (I) are naturally oriented in the opposite direction to the TMA (annual average temperature).

Figure 5 - L'Igue des Rameaux. Precipitation diagram.



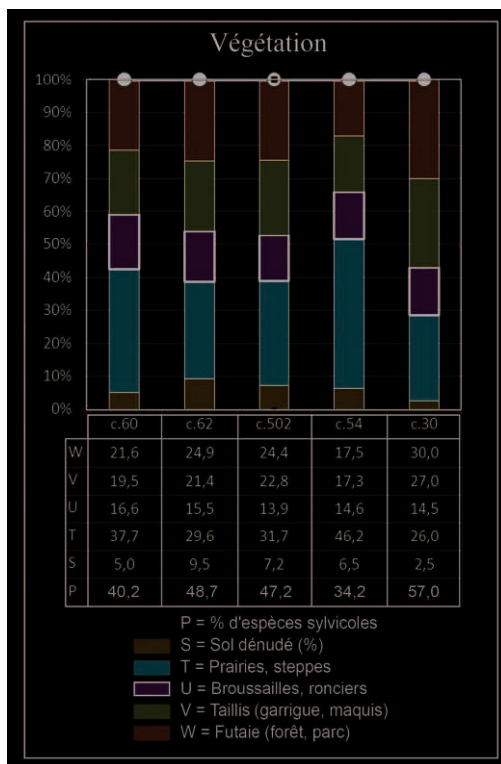
22 The climatic atmosphere (fig. 6) gathers secondary but palpable data regarding daily life (frost, sunshine, nebulosity).

Figure 6 - L'Igue des Rameaux. Atmosphere diagram.



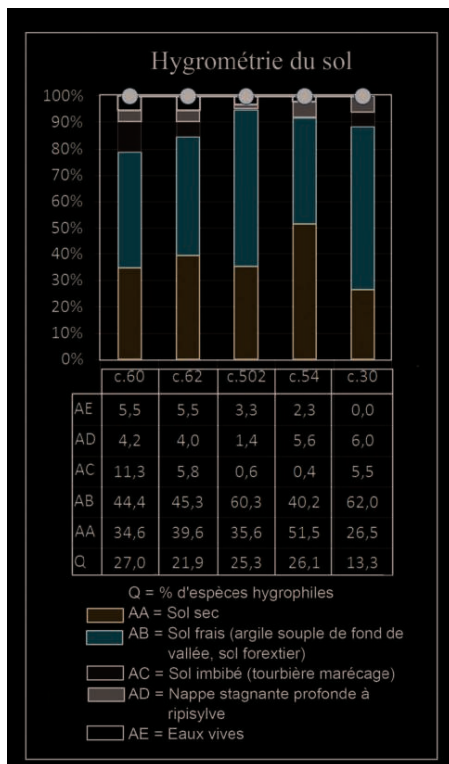
- 23 At Rameaux, frost (N) lasts for 4 months under cloud cover (M) every other day, masking the sun (R).
- 24 The vegetation (fig. 7) under cool temperate thermal conditions consists of 20 to 30% of high forest (W). Coppice and scrub (U, V) occupy the outskirts of the forest judging by their fluctuation at the same time as trees. The meadow (T) is dominant on 37 to 46 % of the territory. The marked difference in level reveals relatively constant exposed soils (S). Paradoxically, their extreme reduction in the least favourable climatic phase (c. 30), which is compensated for by the high forest, could be explained by the development of the pine grove on dry and cool soil, announcing a sharp warming in a contrasted landscape where forest species (P) then decline sharply (c. 54), with the expansion of meadowland.

Figure 7 - L'Igüe des Rameaux. Vegetation diagram.



- 25 Soil humidity (fig. 8) is particularly marked by drought over 50 % of the area. It is associated with cool soils and affects between 80 to 95 % of the territory. These two parameters coincide closely with the steppe-type cover.

Figure 8 - L'Igüe des Rameaux. Ground hygrometry.



- 26 Hygrophilous species (Q) are poorly represented but also tend to be more frequent in open landscapes. Their reduced rate in c. 30 confirms the presence of pine forests.
- 27 Table 2 contains two interesting points. The agile frog (*Rana dalmatina*) is more terrestrial. The other anurans are toads (*Bufo bufo* and *Bufo calamita*) with semi-aquatic lifestyles. Their presence is thus linked to hibernation. As mentioned above, their presence in the lower zone shows that they came into the cave by the now obstructed opening.
- 28 The diverse environmental parameters show the complexity of the biostratigraphy. The temperatures denote a semi-continental climate evolving from a rigorous stage to a warm temperate interglacial-type phase before becoming cool and humid with frequent but not very abundant precipitation. These thermal and hygrometric conditions are experienced differently depending on the type of vegetation and ground humidity, and vary greatly in the different faunal associations. Woody vegetation is always dominant.
- 29 Coppice and shrubs, on the forest edge, conserve constant values and evolve with high forest fluctuations. The high percentage of hygrophilous species (Q) underlines this. The cool soil favours forested and open environments.

## European field mice (Corbet 1978)

- 30 Before addressing the systematics, we wished to situate the field mice from Rameaux in a European context (Miller 1912), based on the biometry of the first molars from several sites from the literature (tabl. 3, tabl. 4 and tabl. 5), excluding the small forms (*A microps* or *uralensis* type) due to their limited number. Table 3 presents the data from

the dispersion diagrams from figures 9 and 10. The species names are presented as initials (AA= *Apodemus agrarius*; AF= *Apodemus flavicollis*; AM= *A. microps*; AS= *Apodemus sylvaticus*). The determinations are those of authors cited in the bibliographic references (Bartolomei 1964; Brugal 1981; Dietrich and Maul 1984; Jeannet 1977; Koenigswald 1972; Kowalski 1956; Kretzoi 1956; Malez and Rabeder 1984; Mauk 1990; Meulen 1973; Kratochvil and Rosicky 1952; Popov 1988; Schaub 1938; Steiner 1978; Storch and Lutt 1989). The term “northern” is applied to populations in latitudes above 45° N. The term “southern” concerns the sites below this latitude. Measurements are given in mm/100.

- 31 The diagram of the first upper molars ( $M^1$ ) (fig. 9) shows the clustering and the lateral position of the present-day or fossil *A. agrarius*  $M^1$ . We also observe the “advanced” position of the *A. flavicollis* molars, with lengths often exceeding 193, for fossil and present-day, “southern” and “northern” specimens. The biometry does not distinguish them from *A. sylvaticus* on the sole basis of this criterion as the fossil forms of this species cover the whole cloud for the yellow-necked mouse *A. flavicollis*. With one exception, we observe that the present-day or “northern” wood mouse (*A. sylvaticus*), does not exceed a length of 190. It is thus possible to differentiate *A. sylvaticus* and *A. flavicollis* populations on the basis of length.
- 32 Like for the  $M^1$ , it is possible to distinguish the two present-day species on the sole basis of the length of the lower first molars ( $M_1$ ) (fig. 10), as those of *A. sylvaticus* are limited to 176. The fossil or present-day *A. flavicollis*  $M_1$  constantly exceeds 174. The fossil forms may be the smallest for the species.

## Systematics of murid rodents

- 33 We will only retain the systematic study of the Murid rodents from the study of *Arvicola* published in an earlier note (Jeannet 2005). They are not very abundant but seem interesting for the systematics, paleogeography and biochronology.
- 34 Biometry and morphoscopy are invaluable tools for the description of the different odontological forms characterizing species and sub-species. Note that morphometric geometry methods, in particular, have developed a lot over the past years; they have proved useful for accurately differentiating species, subspecies or populations, allowing for the quantification of variations in conformation and size. Many authors have focused on this method of determination and comparison, particularly for Murids, but most of the research concentrates on whole skulls. The teeth studied are upper first molars (the largest and the most complex). Comparative studies of *Apodemus agrarius* are thus still very limited, especially as those from Rameaux were the first discovered in France. Although the present study is not based on geometric morphometry, it cannot ignore these techniques which allow for the description of a new subspecies, attributing the smallest species to *Apodemus maastrichtiensis* and differentiating *Apodemus sylvaticus* and *Apodemus flavicollis* at a European scale (e.g. Janzekovic and Krystufek 2004, Renaud 2005, Barciova and Macholan 2006, Jangjoo 2010).

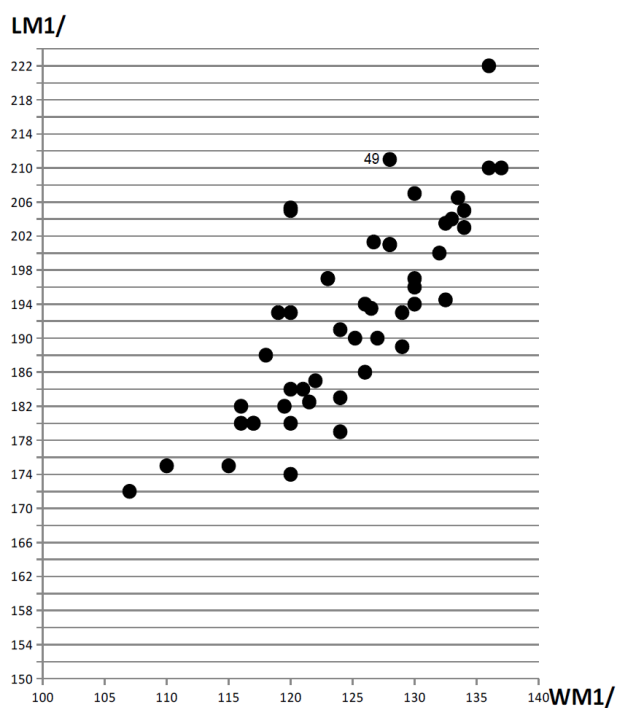




**Tableau 5 - L'Igüe des Rameaux. Measurements, type and localization of lower molars of *Apodemus*. The sketched elements are indicated in the last column.**

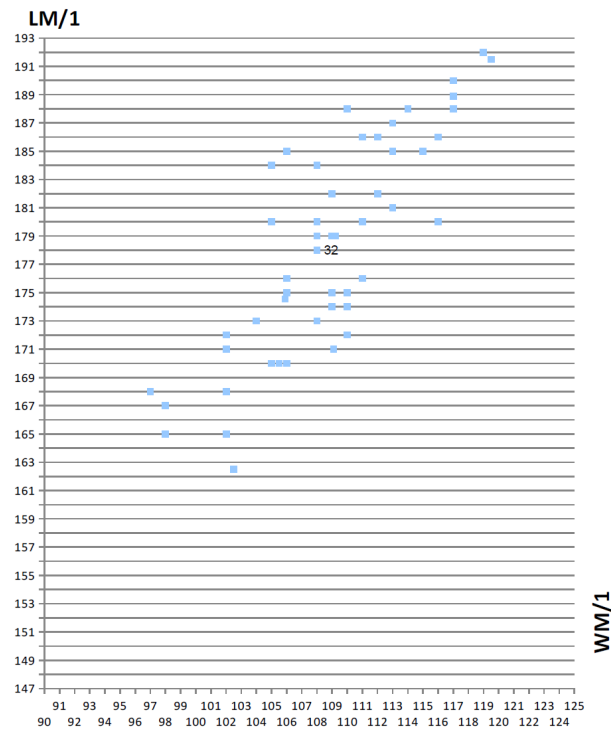
ZONE	NIV.	N°	ESPECÈ	TYPE	L	W	N° Fig.
					mm/100		fig. et n°
C sup	30	Rx 18-1	<i>A. flavicollis</i>	M1/D	181	107	
E14	60	Rx 59-4	<i>A. flavicollis</i>	M1/D	181	105	
E15M	62	Rx 71-2	<i>A. flavicollis</i>	M1/G	177	101	
E15M	62	Rx 71-4	<i>A. flavicollis</i>	M1/D	183	110	
F1M	62	Rx 86-1	<i>A. flavicollis</i>	M1/D	188	106	
F2M	62	Rx 101-4	<i>A. flavicollis</i>	M1/D	179	105	
F2M	62	Rx 101-5	<i>A. flavicollis</i>	M1/D	178	100	
F2M	62	Rx 101-6	<i>A. flavicollis</i>	M1/G	178	103	fig. 13 n° 14
F2M	62	Rx 101-9	<i>A. flavicollis</i>	M1/G	180	102	
G2M	60	Rx 158-8	<i>A. flavicollis</i>	M1/D	192	114	
D1L	30	Rx 20-2	<i>A. sylvaticus</i>	M1/D	175	111	fig. 13 n° 21
E15M	62	Rx 71-1	<i>A. sylvaticus</i>	M1/G	175	104	
F2L	62	Rx 89-3	<i>A. sylvaticus</i>	M1/D	173	106	
F2M	62	Rx 101-8	<i>A. sylvaticus</i>	M1/G	174	107	fig. 13 n° 15
F2M	62	Rx 101-10	<i>A. sylvaticus</i>	M1/G	175	107	
G1M	60	Rx 154-1	<i>A. sylvaticus</i>	M1/G	181	114	
G2M	60	Rx 158-10	<i>A. sylvaticus</i>	M1/G	179	114	
G2M	60	Rx 158-11	<i>A. sylvaticus</i>	M1/G	176	105	fig. 13 n° 16
G2M	60	Rx 158-7	<i>A. sylvaticus</i>	M1/G	177	111	
D1L	30	Rx 26-3	<i>A. agrarius</i>	M1/D	168	104	
E15M	62	Rx 71-3	<i>A. agrarius</i>	M1/G	167	109	
G2M	60	Rx 158-6	<i>A. agrarius</i>	M1/G	168	105	
G2M	60	Rx 158-9	<i>A. agrarius</i>	M1/G	175	113	fig. 12 n° 7
G2M	60	Rx 158-12	<i>A. agrarius</i>	M1/D	172	110	fig. 12 n° 8
G2N	60	Rx 169-1	<i>A. agrarius</i>	M1/D	172	110	
G3M	60	Rx 176-2	<i>A. agrarius</i>	M1/G	175	113	fig. 12 n° 6
D	54	Rx 44-1a	<i>A. microps</i>	M1/G	145	96	fig. 13 n° 17
E15M	62	Rx 71-5	<i>A. microps</i>	M1/D	164	97	
E15M	62	Rx 71-10	<i>A. microps</i>	M1/G	159	100	fig. 13 n° 20
F2M	62	Rx 101-3	<i>A. microps</i>	M1/G	165	100	fig. 13 n° 19
F2M	62	Rx 101-7	<i>A. microps</i>	M1/D	165	97	
E15M	62	Rx 71-11	<i>A. flavicollis</i>	M2/D	126	111	fig. 12 n° 16
E15M	62	Rx 71-12	<i>A. flavicollis</i>	M2/D	118	105	
F1M	62	Rx 86-3	<i>A. flavicollis</i>	M2/D	118	102	
F2M	62	Rx 101-14	<i>A. flavicollis</i>	M2/G	119	102	
G1M	60	Rx 154-4	<i>A. flavicollis</i>	M2/G	126	116	
G2M	60	Rx 158-20	<i>A. flavicollis</i>	M2/D	123	104	
G2M	60	Rx 158-17	<i>A. sylvaticus</i>	M2/G	111	98	fig. 12 n° 10
G2M	60	Rx 158-18	<i>A. sylvaticus</i>	M2/D	117	99	
D1L	30	Rx 26-4	<i>A. sylvaticus</i>	M2/G	120	104	
G2M	60	Rx 158-16	<i>A. agrarius</i>	M2/G	120	88	fig. 12 n° 11
G2M	60	Rx 158-19	<i>A. agrarius</i>	M2/D	120	108	fig. 12 n° 12
D	54	Rx 44-1b	<i>A. uraleensis</i>	M2/G	100	88	fig. 13 n° 17
F2M	62	Rx 101-15	<i>A. agrarius</i>	M3/G	108	94	fig. 13 n° 18

**Figure 9 - European *Apodemus*. Dispersal diagram of M1 from some European populations, including all types, periods and locations (see tabl. 3)**





**Figure 10** - Dispersal diagram of  $M_1$  from some European *Apodemus* populations, including all types, periods and locations (see tabl.3):  $LM_1$  = length of the first lower molar;  $W/1$  = width of the first lower molar. Except the small types, the diagram points out the difficulties, or even the impossibility, of discriminating species using only biometric data.



35 Below, we recall the classification of the Murid family:

36 Family: Muridae Gray, 1821

Sub-Family: Murinae Baird, 1857

Genus: *Apodemus* Kaup, 1829

Sub-Genus: *Sylvaemus* Ognev and Worobiew, 1923

Species: *Apodemus flavicollis* Melchior, 1834; *Apodemus sylvaticus* Linné, 1758 ; *Apodemus uralensis* Pallas, 1778

Syn. *Apodemus microps* Kratochvil and Rosicki, 1952; † *Apodemus maastrichtiensis* Kolschoten, 1985

Sub-species: *Apodemus* Kaup, 1829

Species: *Apodemus agrarius* Pallas, 1771

Sub-species: *Apodemus agrarius iguensis* n.ssp

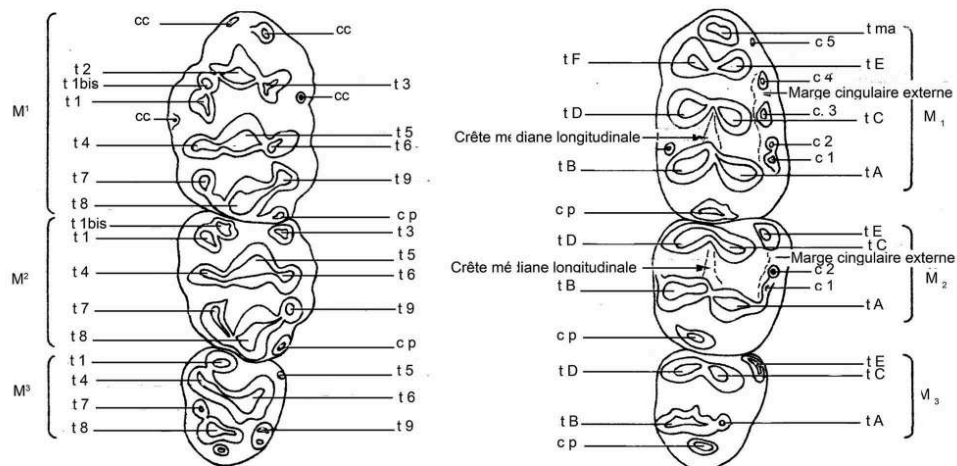
## The muridids from igue des rameaux

37 When we began the study of the murid rodents from Igue des Rameaux, we thought that, like for most Pleistocene sites, we would only encounter one or two species at the most. A more in-depth examination revealed characteristic forms of *Apodemus flavicollis*, *A. sylvaticus*, *A. agrarius* and the measurements brought to light *A. uralensis* (cf *Apodemus microps*). We thus tried to define the species for each molar. Biometry and statistic tests enabled us to isolate four forms of  $M^1$  and  $M_1$  but they were not sufficient to separate the  $M^2$  from  $M_2$ . For the latter, it was necessary to combine two techniques:

morphology and biometry. For the  $M_2$ , in particular, uncertainty prevails concerning *A. flavicollis* and *A. sylvaticus*, as the latter is rare. The nomenclature of the dental structures is from Michaux (1971) (fig. 11), slightly modified by the addition of cingulate margins and the longitudinal median crest. Tables 4 and 5 present the measurements of the molars and their position at the site and figures 12 and 13 illustrate the drawings. The reference molars of present-day *A. agrarius* are presented in figure 14. The dispersion diagram is established with lengths and widths (fig. 15), separating the diverse species. The regression lines follow the main axis of the ellipses and are not illustrated here.

- 38 The measurements used are the classical length (L) and width (W). However, the technique used may differ from that adopted by certain researchers, without necessarily being more effective. It aims to reduce the parasitic influence of size variations imputable to certain subsidiary cusps. These external protuberances are often used as a reference for the initial position of the reticule of the micrometer, but we prefer to align the reticule on the tangents at t8 and t5 for the upper molars, and on the posterior angles of the chevrons (tC-tB and tE-tF) for the lower molars.

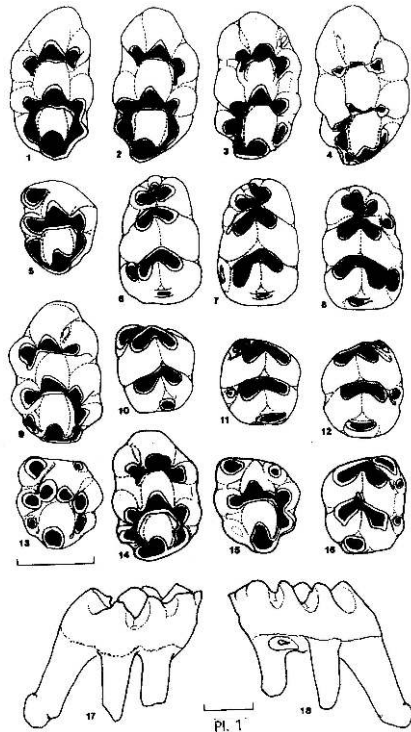
**Figure 11** – Descriptive schema of the various structures of the *Apodemus* mastication table (after Michaux 1971)



### *Apodemus flavicollis* Melchior and *Apodemus sylvaticus* Linné (fig. 12 and 13).

- 39 Although present-day *Apodemus flavicollis* is, on average, larger in size than *A. sylvaticus*, these two species are morphologically and biometrically very similar and the description of one requires a comparison with the other. For this reason, we will consider them simultaneously and compare them here. The specimens and measurements are indicated in tables 4 and 5.

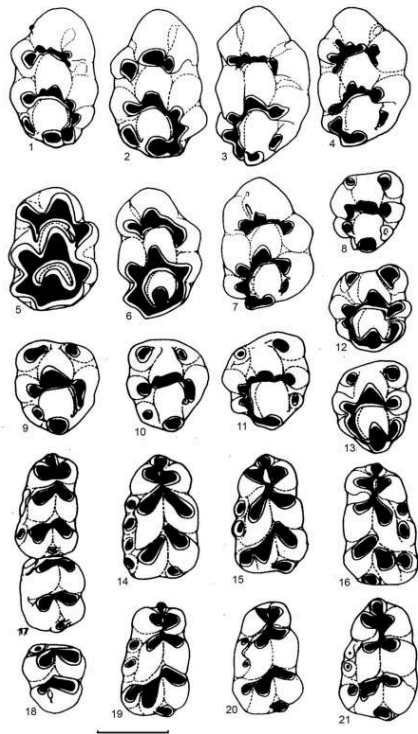
Figure 12 - *Apodemus agrarius* (n° 1, 2, 3, 4, 5, 6, 7, 8, 11, 12) ; *Apodemus flavicollis* n° 9, 13, 16) ; *Apodemus sylvaticus* (n° 10, 15, 17, 18) ; *Apodemus uralensis* (n° 14)



1 = M<sub>1</sub>G ; 2 = M<sup>1</sup>D ; 3 = M<sup>1</sup>D ; 4 = M<sup>1</sup>D ; 5 = M<sup>2</sup>G ; 6 = M<sub>1</sub>G ; 7 = M<sub>1</sub>G ; 8 = M<sub>1</sub>D ; 9 = M<sup>2</sup>G ; 10 = M<sub>2</sub>G ; 11 = M<sub>2</sub>G ; 12 = M<sub>2</sub>D ; 13 = M<sup>2</sup>G ; 14 = M<sup>1</sup>D ; 15 = M<sup>2</sup>G ; 16 = M<sub>2</sub>D ; 17-18 = M<sup>1</sup>D

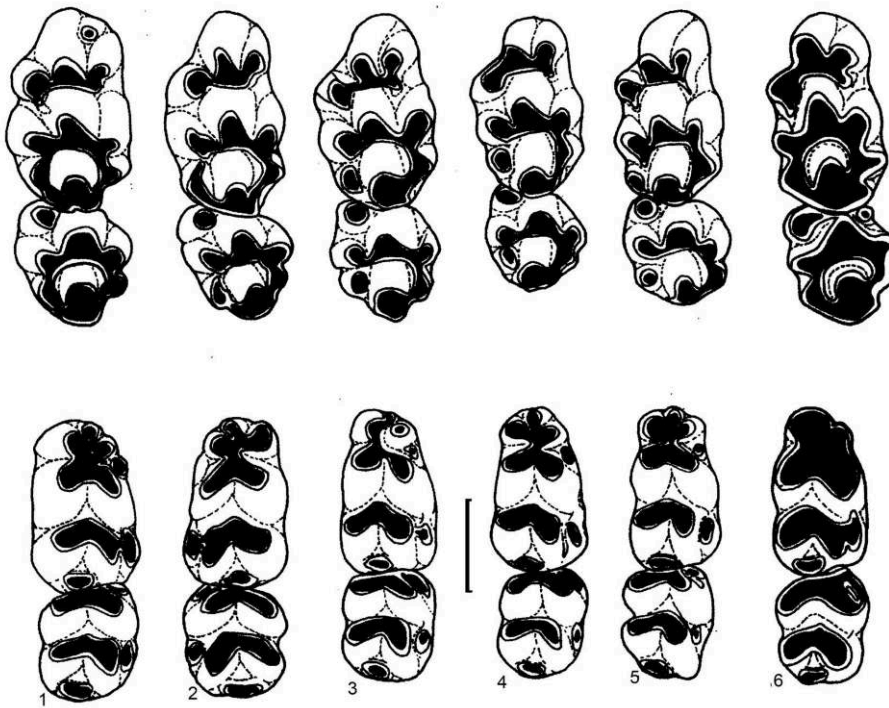
- 40 **M<sup>1</sup>** – As we know from the exhaustive studies of L. PASQUIER (1974), the morphological characteristics of the M<sup>1</sup> are too unstable to distinguish *A. flavicollis* and *A. sylvaticus* on the basis of the molars. In the present case, after separating them with biometry, we observe the following differences:
- the silhouette is slightly thicker for *A. sylvaticus* than for *A. flavicollis* (L/W is respectively 1.52 and 1.59);
  - t1 in relation to t2/t3: clearly receding in *A. sylvaticus*; very slightly receding in *A. flavicollis*. This situation results in a very open angle of the syncline separating t1 from t2 in *A. sylvaticus*;
  - t4 in relation to t6: receding in *A. sylvaticus*, advanced in *A. flavicollis*;
  - t7: isolated in *A. flavicollis*, linked to t8 or adjoining t4 in *A. sylvaticus*. These characteristics are not yet visible on n° 7 (fig. 13) due to its young age.

Figure 13 - *Apodemus flavicollis* (n° 1, 2, 3, 4, 9, 10, 11, 13, 14, 16, 18) ; *Apodemus sylvaticus* (n° 5, 6, 7, 8, 12, 15, 21) ; *Apodemus uralensis* (n° 17, 19, 20).



1 = M<sup>1</sup>G ; 2 = M<sup>1</sup>G ; 3 = M<sup>1</sup>D ; 4 = M<sup>1</sup>D ; 5 = M<sup>1</sup>D ; 6 = M<sup>1</sup>D ; 7 = M<sup>1</sup>D ; 8 = M<sup>2</sup>D ; 9 = M<sup>2</sup>G ; 10 = M<sup>2</sup>G ; 11 = M<sup>2</sup>D ; 12 = M<sup>2</sup>D ; 13 = M<sup>2</sup>D ; 14 = M<sub>1</sub>G ; 15 = M<sub>1</sub>G ; 16 = M<sub>1</sub>D ; 17 = M<sub>1,2</sub>G ; 18 = M<sub>3</sub>G ; 19 = M<sub>1</sub>G ; 20 = M<sub>1</sub>G ; 21 = M<sub>1</sub>G.

- 41 **M<sup>2</sup>** – This molar is the easiest to determine on account of the morphology of t9. But there are two intermediary types between the two typical forms of *A. flavicollis* (fig 12 n°13) and *A. sylvaticus* (fig.13 n° 8). The “reduced t9” form characteristic of *A. flavicollis* reaches a climax on specimens 9 and 10 (fig. 13), where t9 is absorbed by t6. The other extreme case concerning *A. sylvaticus* (fig. 13 n° 8) presents a t9 directly linked to a t8 by a brief isthmus of enamel.
- The posterior cingulum (cp) is reduced to a narrow rod placed on the side of t8 and dipping towards the front;
  - t7 is low, not worn, isolated from t4 and t8 (type *A. flavicollis*).

Figure 14 - M1-M2/ and M/1-M/2 of *Apodemus agrarius* Pallas, 1771.

N° 1 to 5: Bonn Museum collections.

N° 6: Basel Museum collections.

Origin: n°1: (n° 55/03 ♀) –Niedersachsen-Hörden a Harz (Germany).

N°2: (N° 56/7 ♂) – Niedersachsen Willershauser a Harz (Germany).

N°3: (N° 55/18 ♂) – Niedersachsen Willershauser a Harz (Germany).

N°4: (N° 54/15 ♀) - Niedersachsen Willershauser a Harz (Germany).

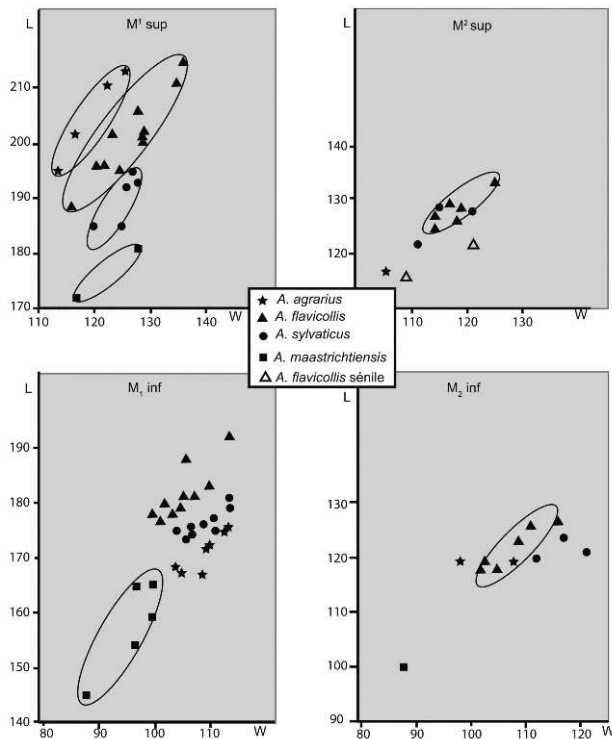
N°5: (N° 56/3 ♂) - Niedersachsen Willershauser a Harz (Germany).

N° 6: (N° 97/70 ♀) – Siaolin-Kirin; Manchou du Kuo (Manchuria).

Note: on the M1/ cusp lengthening; on the M2/ the absence of t3 (except n° 6); on M/1 and M/2 the absence of the external cingulate margin

- 42 The dispersion diagram (fig. 15) shows that biometry cannot be used to separate the two species based on the  $M^2$ .

**Figure 15** – l'Igüe des Rameaux – Molar dispersal diagrams of the various *Apodemus* species collected. The  $M^2$  cannot be specifically separated by their dimensions but by their structures.  $LM^1/$  = length of the first upper molar;  $WM^1/$  = width of the first upper molar, etc.



- 43 The morphological comparison of  $M^1$  and  $M^2$  shows that the form of the posterior part is rather different for these molars. This is due to the variability of the shapes, as for a same individual, the “rosette” pattern is very similar.
- the posterior cingulum, always present and often enormous on the  $M^1$ , is absent or simply laminar on the  $M^2$ ;
  - strong to very strong t9 on the  $M^1$ , it is still quite strong for *A. sylvaticus* and can reduce and disappear on the *A. flavicollis*  $M^2$ .
- 44 These disparities identified between the two main molars of these two species are not universal but are nonetheless very interesting on a local basis for their distinction.
- 45  $M_1$  – No morphological criteria for the  $M_1$  enabled us to clearly differentiate these two field mice species. This was only possible through biometry and dispersion diagrams (fig. 15). Like for the  $M^1$ , we observe that the *A. sylvaticus* molars are stocky, shorter and proportionally wider, with a Length/width ratio of 1.72 for *A. flavicollis* and 1.61 for *A. sylvaticus*, but this difference is not statistically significant (tabl. 6). For comparative purposes, we illustrate (fig. 9 and 10) the dispersion diagrams of the first molars of all types of European field mice, from all periods. This showed that the  $M_1$  from southern populations of *A. sylvaticus* are proportionally wider than in northern and eastern populations, for present-day and fossil specimens. As for the length, it is slightly shorter than for *A. flavicollis* during the Middle Pleistocene, but is still very marked in present-day southern populations; in particular for the Iberian forms that reach the size of present-day western *A. flavicollis* (Jeannet 2000b). The dimensions of the fossil and present-day molars of *A. flavicollis* seem to be stable (superior in length to *A. sylvaticus* and proportionally narrower). We also note that the populations from Eastern

Europe (Austria and Berlin) are larger than western populations. This diagram classification is largely based on and confirms the observations of Pasquier (1974).

- 46 Table 6 summarizes (the detailed calculations are presented in tables 9 to 12) the results of the comparisons between the length and width on one hand, through the correlation coefficient, and between the diverse species using the t test. No calculations were made for the scantest series. We observe in particular that the t test based on the L/W ration between *A. flavicollis* and *A. sylvaticus* shows a highly significant difference for the M<sup>1</sup> and non-significant for the M<sub>1</sub>.
- 47 On the M<sub>1</sub>: - the tma is of average size and never absent or separate;  
 - the external cingulate margin only once bears four conules and most often two, four times three and one (n = 19);  
 - the median longitudinal crest is very frequently absent or hardly outlined;  
 - c1 is rarely linked to tA but most often contiguous or isolated. Cases of total independence are not rare but are not predominant.
- 48 M<sub>2</sub>- In the absence of sufficient material attributable to *A. sylvaticus*, we could not reliably differentiate the two species with statistical tests. However, the dispersion diagram (fig. 15) quite clearly shows a lateral position of three molars with a proportionally higher width than the others, like on the M<sup>1</sup>. Against all odds, the external cingulate margin is absent or slightly outlined (fig. 12 n° 10), unlike the others (fig. 12 n° 16). When these three molars are associated with each other in the calculations, the correlation coefficient is 0.53; individually, the coefficient reaches 0.95 for the forms with a significant external cingulate margin. This implies, with no formal statistic proof, that there is a clear difference between these two groups.
- 49 All these elements place *Apodemus sylvaticus* and *Apodemus flavicollis* in a relatively early Middle Pleistocene, as many Lower Pleistocene characteristics (absence of median crest, reduction of the tma, position of c1, number of conules) are still frequently marked, while those of the present-day forms are rare. We also observe the frequency of an enamel loop separating tE and tF.



**Table 6 - l'Igüe des Rameaux. Statistical comparison between the molars of *Apodemus*.**

CORRELATION														
entre	AF	AS	AA	AM	Global	AF & AS	AF & AA	AF & AM	AF & AS & AA	AS & AA	AS & AM	AA & AM	AF & AA+AM	AF & AS+AM
L & W M1/	0,93	0,79	0,98		0,50	0,79	0,53	0,68		0,01				
LxW & L/W M1/	-0,57	0,05	-0,47		0,19	0,06	-0,05	-1,40		0,47				
L & I M1	0,83	0,84	0,85		0,60	0,30	0,15	0,36	0,87	0,36	0,94	0,91	0,59	0,73
LxW & L/W M1	-0,70	-0,87	0,58	-0,62	-0,29	-0,47	-0,24	-0,12	0,09	-0,36	-0,79	-0,87	-0,17	-0,29

TEST T						
entre	AF & AS	AF & AA	AF & AM	AS & AA	AS & AM	AA & AM
sur						
L M1/	HS	NS		HS		
W M1/	NS	S		S		
L x W M1/	NS	NS		NS		
L/W M1/	HS	HS		HS		
L M1	S	HS	HS	HS	HS	HS
W M1	NS	NS	HS	NS	HS	HS
LxW M1	NS	NS	HS	NS	HS	HS
L/W M1	NS	HS	NS	S	S	HS

AA=*Apodemus agrarius*  
AF=*Apodemus flavicollis*  
AM= *A. microps (ouuralensis)*  
AS=*Apodemus sylvaticus*

L = Longueur  
W = largeur

AA = *Apodemus agrarius*; AF = *A. flavicollis*; AM = *A. microps*; AS = *A. sylvaticus*.

In normal populations, the correlation coefficient (r) is close to 0.85. A negative correlation indicates that one parameter evolves in the opposite direction to the other (*cf.* comparison between the product and the ratio of length and width of m1).

### ***Apodemus agrarius* Pallas, 1771 (fig. 12 and 13)**

- 50 The striped field mouse is currently an unknown species in Western Europe but extends from Eastern Europe to the Far East (China and Korea). It lives in wooded steppes, on the fringes of birch forests in a wet atmosphere up to an altitude of 900 m (von Böhme 1978; B. Sala 1974).

### **Description and comparison : (4M<sup>1</sup>; 1 M<sup>2</sup>; 7 M<sub>1</sub>; 22M<sub>2</sub>; 1 M<sub>3</sub>)**

- 51 **M<sup>1</sup>** – It is similar in size to that of *Apodemus flavicollis*, but with a very different morphology, not on account of the number or layout of the tubercles, but by their shape extending towards the front, giving the central cusps a recumbent attitude.
- 52 The anterior root is clearly protrusive (fig. 12 n° 17 and 18).  
- t1 is slightly remote in relation to t2-t3, but the anterior extension of t2 considerably widens the syncline angle separating t1 from t2;  
- the posterior cingulum, in most cases, forms an angular and bulging protuberance on the side of t8;  
- t7 is strong and linked to t8 by a strip of enamel. After a period of wear, it is linked to t4.
- 53 The clearest difference is in the L/W ratio (1.71), which denotes the tapered morphology of this molar.
- 54 **M<sup>2</sup>**- (fig. 12 n° 5). A single molar was found but its shape is typical: the total absence of t3 is characteristic of the form of the western species. A present-day series from Manchuria lent by the Museum of Basel (fig. 14 n° 6) presents a tiny t3. The dispersion diagram places it outside the overall cloud of points (fig. 15).



- 55  $M_1$  - (fig. 12 n° 6 to 8). Their morphological specificity is the absence of the external cingulate margin. Like for the present-day forms, the presence of c4 is inconsistent and can only be represented by a slight tuberosity contiguous to tE.
- c1 is isolated and is only linked to t4 after extensive wear;
  - tA and tB converge but their union is never prolonged by even an outline of a longitudinal median crest;
  - the tC - tD pair also converges;
  - the posterior cingulum forms a transverse crest between tA and tB. Unlike for present-day forms, there is no protrusion at the back of the molar;
  - the median anterior tubercle (tma) is constantly small in size.
- 56 Comments: The difference in the silhouette between the upper and lower molars is surprising. The upper molars are slender and the lower molars are chunky. This observation is clear in the L/W ratios: 1.71 for the upper molars; 1.56 for the lower molars.
- 57  $M_2$ - Two typical molars were identified (fig. 12 n° 11 and 12). Like the  $M_1$ , they are differentiated by the absence of the external lateral margin completed by the presence of a well-defined c1.
- tE is reduced and does not extend along the external edge of the molar;
  - like on the  $M_1$ , the posterior cingulum develops into a transverse crest between tA and tB;
  - like for the  $M_1$  again, the tubercles match up to form two chevrons with no trace of a longitudinal median crest;
- 58 The position of these molars in the dispersion diagram (fig. 15) shows that we cannot distinguish them on the basis of their dimensions.
- 59 Compared to the present-day forms (fig. 14), we observe that c1 is much more developed on the latter. It forms a slightly more reduced tubercle than the main cusps, almost as significant for the  $M_1$  c1. It remains separate from the neighbouring cA. The Manchuria type does not bear a c1; just a slight bulge.

### ***Apodemus agrarius iguensis* n.ssp.**

- 60 In spite of reduced numbers, the morphometric difference observed on the *Apodemus agrarius* molars incites us to create a subspecies with a biochronological vocation allowing us to position the population from Igue des Rameaux in an evolutionary framework to be broadened by future discoveries.
- 61 Family: *Muridae* Gray, 1821  
 Genus: *Apodemus* Kaup, 1826  
 Sub-genus: *Apodemus* Kaup, 1829  
 Species: *Apodemus agrarius* Pallas, 1778  
 Sub-species: *Apodemus agrarius iguensis* n.ssp.
- 62 HOLOTYPUS: First lower right molar n° SIR. 158-12 (fig. 12 n° 8) (Length x width = 172 x 110 mm/100).
- 63 DERIVATIO NOMINIS: derived from the local term "igue" designating the form of the karstic shaft opening in the lapiaz (synonyms: sink hole, joint, fissure etc.).
- 64 DIAGNOSIS: first *Apodemus* type lower molar presenting typical characteristics of the *Apodemus agrarius* species: absence of the external cingulate margin. Posterior cingulum

reduced to a ridge of enamel set between the two posterior tubercles, but does not exceed the back of the molar.

- 65 DIFFERENTIAL DIAGNOSIS: It differs from the type species by its well-developed width, giving the molar a chunky appearance with a length/width ratio of 1.56 (n= 4; max = 1.59; min = 1.55). For *Apodemus agrarius*, this is the lowest ratio for this type of molar. For present-day forms from Niedersachsen, the ratio is 1.70 for a size equivalent to 1.74. For *A. agrarius iguensis* n.ssp, this situation is more paradoxical as the silhouette of the upper molars is slender, with a L/W ratio of 1.71, which is similar to that of present-day forms (L/W = 1.74).
- 66 The  $M_2$  adopt the same profile, as the cp is inserted between the two tubercles tA and tB. This layout “shortens” the molar. tE tends to lengthen narrowly against tC but the main trait is the absence of lateral cingulate margin, like for the  $M_1$ .
- 67 The  $M^2$  is very characteristic due to the absence or extreme reduction of t3, in a very low position which only highlights it after long wear (cf. the specimen from Siaolin-Kirin, fig. 14 n° 6).
- 68 LOCUS TYPICUS: Site of Igue des Rameaux; commune of Saint-Antonin-Noble-Val (Tarn-et-Garonne, Quercy, France).
- 69 STRATUM TYPICUM: Zone G2M, layer 60, attributed to the Middle Pleistocene. The associated fauna is illustrated in table 2 and denotes a wooded steppe environment under a cool, humid and temperate climate, similar to the prevailing conditions in present-day Eastern Europe (Jeannet 2005).
- 70 PARATYPUS: The other molars likely to belong to this species contributed to the general description of the morphotypes and their biometric data are presented in tables 4 and 5. They can also be identified on the dispersion diagram (fig. 15).
- 71 The comparative elements entrusted to us by the Museum of Bonn probably come from the same enriched Niedersachsen population studied by J.P. Aguilar *et al.* (2008) (tabl. 7). Here, we use the results adding the dimensions from the Siaolin-Kirin series lent by the Museum of Basel (n°9070) (fig. 14).

**Table 7 - *Apodemus agrarius*.**

	<i>A. cf. agrarius</i> Bouziès-Q Pléist. Sup.							<i>A. agrarius</i> , Niedersachsen, Allemagne, récent						
	n	Lmin	L	Lmax	Wmin	W	Wmax	n	Lmin	L	Lmax	Wmin	W	Wmax
M1/	3	2	2	2,03	1,17	1,2	1,25	36	1,8	205	2,28	1,12	1,20	1,29
M2/	4	1,2	1,2	1,25	1,06	1,1	1,11	34	1,1	1,1	1,24	1,03	1,10	1,17
M3/								33	0,7	0,7	0,83	0,73	0,79	0,93
M/1	5	1,7	1,8	1,84	1,06	1,1	1,07	33	1,6	1,7	1,82	0,92	1,02	1,14
M/2	5	1,2	1,3	1,33	1,05	1,1	1,1	33	1,1	1,2	1,31	0,92	1,00	1,09
M/3	2	1		0,97	0,82		0,82	33	0,9	1	1,15	0,79	0,83	0,89

Origin: Bouziès (Lot), Tardiglacial period; Niedersachsen (Germany), sub-contemporaneous.

Data from Aguilar and *al.* (2008) for comparison.

- 72 We regret not having more abundant series in order to bring to light with more reliability a certain evolutionary cline that seems to be outlined on the basis of a biometric gradient. In fact, through the examination of the simple elongation ratio, we observe the growth of the index, passing from 1.56 at Igue des Rameaux (Middle Pleistocene) to 1.65 for Bouziès (Lot) (Final Pleistocene; towards 17ka B.C.) and 1.69 for the present-day forms from Niedersachsen. On the other hand, this same ratio is

relatively stable for the upper molars (1.71 for the population from Rameaux, 1.65 for Bouziès and 1.71 for Niedersachsen).

- 73 *Apodemus uralensis* Pallas, 1771 or *Apodemus microps* Kratochvil and Rosicki, 1952.
- 74 *Apodemus maastrichtiensis* Kolfshoten, 1985. (fig. 12 and 13; tabl. 8)
- 75 The Ural field mouse is a very small rodent living in the steppes of Central and Eastern Europe and the south of the Ural. Its double identity comes from the fact that certain authors distinguish two different species. It seeks out high grasses, shrubs and coppice. It is not abundant but is nonetheless present in many Pleistocene sites but due to the small size of its molars, it often goes through the sieve mesh or is mixed up with the slightly smaller Eurasian harvest mouse (*Micromys minutus*). It is however easy to differentiate their first molars. The  $M^1$  of the Eurasian harvest mouse has five roots whereas the Ural field mouse only has three, of which the two lateral roots are germinated and their liaison is highlighted by a rather shallow longitudinal furrow. The  $M_1$  of the Eurasian harvest mouse bears three roots, while the Ural field mouse only has two.
- 76  $M^1$  – The only two  $M^1$  at our disposal have a very stocky aspect, due to the symmetric position of t1 and t3, which are not very far from each other.
- 77 The rather sudden straightening of their posterior wall creates a wide space between the t1-t3 and t4-t6 pair. The posterior rosette is clearly serrated by very straightened and not very convergent peripheral cusps due to their constrained junction. The posterior cingulum is well defined and forms a posterior-external bulge.
- 78 Morphologically, it seems that the specimens at our disposal are similar to the present-day forms from the Czech Republic described by L. Pasquier (1974 p.111), or at least more evolved than the ancestral forms. The only lateral root with an oval section bearing early molars tends to flatten, developing a bulge at the anterior and posterior ends, announcing a hypothetical bifid morphotype. The reduced and elongated t7 on the early forms has become a cusp, although it is still distant from t8, to which it is linked by a strip of enamel. The posterior cingulum, imperceptible on archaic types, is particularly well developed here and independent of t9. The t1 is in a slightly more distant position in relation to t2-t3 than on the previously described forms. Size increases slightly but remains lower than that of *A. sylvaticus* and within the variation domain of *A. uralensis*.
- 79 The comparison with *Apodemus maastrichtiensis* is very limited as we only have eight molars, two of which belong to the same individual (fig. 13 n°17).
- 80 On the  $M^1$ , the straightening of the cusps is obvious on the anterior pair. The tma is generally small in size or absent. The isthmus joining the anterior set to the median pair forms a very tight narrowing and can be absent, or only appear after very pronounced wear. The length of the external cingulate margin is very variable and can be limited to a simple strip or be reinforced by two well-developed conules.
- 81 The longitudinal median crest tending to link the posterior part to the median pair is slightly outlined as tB advances and is clearly delimited from tA, with which it remains slightly joined by its anterior-internal wall. The c1 is relatively well developed, but smaller than tA, to which it is increasingly attached during the course of wear. The posterior cingulum (cp) is generally rounded and goes over the tA-tB tangent towards the back.

- 82 The only  $M^2$  at our disposal has no external cingulate margin and no c1. tE is just a small bulge at the base of tC with no posterior stretching. It is separated from tE by a short and narrow furrow. The form, volume, and position of the posterior cingulum are identical to those of the  $M^1$ .
- 83 All these specific characteristics are described in the detailed description by T. van Kolfschoten (1985) on the molars from Belvédère at Maastricht (Netherlands), which he used to create *Apodemus maastrichtiensis*. In spite of the small number of specimens at Igue des Rameaux, it is clear that our small field mouse belongs to this species.

**Table 8 - *Apodemus maastrichtiensis*. Data from Kolfschoten (1987). Sites of Belvedere 3 and 4 (Maastricht, The Netherlands), Saalian period.**

Belv.3		N	Moy	Max	Min	SIR	
M1	L	2	174	178	169	181	172
	W	2	110	115	106	128	117
m2	L	2	106	106	105	100	
	W	2	91	92	90	88	
Belv.4							
M1/	L	7	167	182	151		
	W	7	106	109	102		
M2/	L	10	110	119	94		
	W	10	102	108	99		
M/1	L	11	150	160	137		
	W	11	91	95	84		
M/2	L	8	103	116	94		
	W	8	94	98	88		

## Correlation and test (tabl. 6 and tabl. 9 to 12)

- 84 Table 6 summarizes the results of the calculations of the correlation coefficient ( $r$ ) and the test ( $t$ ) on the averages when there is a sufficient number of elements. There are insufficient numbers of  $M^2$  in particular, to carry out these calculations and obtain reliable results.
- 85 The correlation coefficient enables us to verify the homogeneity of a population. Experience shows that for field mice, the correlation between the length (L) and the width (W) of the (upper and lower) M1 is around 0.85 (reminder: a perfect correlation would give a coefficient of 1.00). When it is too low (below 50), it indicates the lack of homogeneity or insufficient data; when it is negative, it can translate an inverse evolution or a total contradiction. However, the association of members of two populations can present a high correlation without necessarily belonging to the same species. Therefore, it is essential to complete the examination by a "t" test, comparing the average lengths, widths and their association as a product or ratio.

- 86 Without examining these results in detail, it is interesting to comment the main trends (as an example), that is, those of morphologically similar species, such as *A. flavicollis* (AF), *A. sylvaticus* (AS), and *A. agrarius* (AA) or *A. microps/maastrichtiensis/uralensis* (AM). A parallel reading of table 6 and the dispersion diagram (fig. 9) facilitates this interpretation.
- 87 The  $M^1$  of *A. flavicollis* (AF) and *A. agrarius* (AA) populations are very homogeneous ( $r=0.93$  and  $0.98$ ), and *A. sylvaticus* (AS) a little less so ( $0.79$ ). When we associate populations (AF + AA + AS), the correlation falls to  $0.53$ . On the  $M_1$ , the differences increase and fall respectively to  $0.83$  and  $0.85$  to  $0.15$  collectively.
- 88 If doubt persists as to the independence of the link, the “t” test confirms the integrity of each group, indicating a highly significant difference between AF and AS, although it is not significant for the widths, and conversely, a significant difference between the widths of AF and AA for a non-significant difference between the lengths.
- 89 The  $M_1$  widths always present significant differences, even between *Apodemus flavicollis* and *A. sylvaticus*.
- 90 For the combined L and W values, as products or ratios, only the elongation ratio L/W of the  $M^1$  enables us to separate the three species (AF, AS and AA). The results on the  $M_1$  remain random.
- 91 Due to an insufficient quantity of material, we will simply present a list of several murid species and the data at our disposal.

**Table 9- l'Igue des Rameaux. Biometric data of *Apodemus*  $M^1$  and comparative statistical interspecific analyses.**

		Molaires figurées																			
M <sup>1</sup>	N°	G/D	L	W	LxW	L/W	W/L	ENSEMBLE	L	n	moy	Max	Min	s	r	a	b	Σxy	Σx	Σx <sup>2</sup>	
AF	SIR 14-1	G	211	135	28485	1,56	0,64		W	22	124,8	136	114	5,58	0,50	72,17	0,27	541917		857822	
	SIR 36-1	D	215	136	29240	1,58	0,63		LxW	22	246,3	292	201	21,07							
	SIR 521-a	G	206	128	26368	1,61	0,62		L/W	22	1,58	1,73	1,41	0,08							
SIR 71-6	D	196	122	23912	1,61	0,62	AF	L	11	201,3	215	189	7,09	0,93	-22,65	0,74	280984	2214	446170		
SIR 71-7	G	195	125	24375	1,56	0,64		W	11	126,7	136	116	5,66							1394	177010
SIR 59-3	D	202	129	26058	1,57	0,64	AF + AS	L	16	197,8	215	185	8,47	-0,79	31,69	0,48	399970	3164	626758		
SIR 88-1	D	189	116	21924	1,63	0,61		W	16	125,3	136	116	4,99							2020	255424
SIR 88-2	G	196	121	23716	1,62	0,62	AF+AS+AA	L	20	192,3	215	189	8,56	0,53	57,03	0,34	49=625	3985	795477		
SIR 101-1	G	201	129	25929	1,56	0,64		W	20	125,0	136	114	5,54							2500	313114
SIR 101-2	G	202	124	25048	1,63	0,61	AF+AA	L	15	202,3	215	189	7,34	0,68	8,06	0,58	379639	3035	614889		
SIR 158-4	D	201	129	25929	1,56	0,64		W	15	124,9	136	114	6,19							1874	234700
AS	SIR 26-1	D	185	120	22200	1,54	0,65	AS	L	5	190,0	195	185	4,20	0,79	-25,88	0,52	118986	950	180588	
	SIR 71-8	D	193	128	24704	1,51	0,66	W	5	125,2	128	120	2,79	626							78414
	SIR 158-2	D	185	125	23125	1,48	0,68	AS+AA	L	9	196,8	213	185	9,55							0,01
SIR 158-3	G	195	127	24765	1,54	0,65	AA	W	9	122,9	128	114	4,58	0,98	12,74	0,65	98655	480	57690		
SIR 158-5	D	192	126	24192	1,52	0,66		L	4	205,3	213	195	7,22							821	168719
AA	SIR 59-1	D	195	114	22230	1,71	0,60	AF	LxW	11	255,4	292	219	20,06	-0,57	1,80	0,0008	4463,8	2810	722100,3	
	SIR 59-2	G	202	117	23634	1,73	0,58	L/W	11	1,6	1,63	1,56	0,03	17,5							27,8
	SIR 158-1	D	211	123	25933	1,72	0,58	AS	LxW	5	237,9	248	222	9,90							0,05
SIR 176-1	D	213	126	26838	1,69	0,59	AA	L/W	5	1,5	1,54	1,48	0,02	-0,47	1,81	-0,0004	1668,9	987	244633,8		
							LxW	4	246,6	268	222	18,29	7,59							11,52	
AM	SIR 44-2	G	181	128	23168	1,41	0,71	AF+AS	LxW	16	250,0	292	219	19,31	0,06	1,53	0,0001	62698	3999	100566,1	
	SIR 71-9	D	172	117	20124	1,47	0,68	L/W	16	1,6	1,63	1,48	0,04	25,1							39,34
							AF+AS+AA	LxW	20	249,3	292	219	19,16	0,05	1,64	0,0002	7958,7	4986	1250301,9		
							L/W	20	1,6	1,73	1,48	0,07	31,9							51,07	
							AF+AA	LxW	15	253,1	292	219	19,93	0,40	1,93	-0,0012	6152,1	37,95,8	1250301,9		
							L/W	15	1,6	1,73	1,56	0,06	24,3							39,55	
							AS+AA	LxW	9	218,5	268	222	71,22	0,47	1,46	0,0006	3184,1	1966	475197,6		
							L/W	9	1,6	1,73	1,48	0,10	14,4							23,26	



Table 10 – l'Igue des Rameaux. Biometric data of Apodemus M<sup>1</sup> and comparative statistical interspecific analyses.

Table with columns for m1, n, moy, max, min, ΣL & ΣW, s, r, a, b, Σxy, Σx². Rows include various species codes like AF, AS, AA, AM, AA+AM and their respective biometric measurements.

Tableau 11 – l'Igue des Rameaux. Biometric data of Apodemus M<sup>2</sup> and comparative statistical interspecific analyses.

Table with columns for M2 /, N°, Spec., G/D, L, Want, Wpost, type, Wt9, %, LxW/100, L/W, W/L. Includes a large summary table at the bottom with statistical aggregates and regression coefficients.

Small murids of diverse origins

92 It is not rare to find isolated molars from very small murids The morphological or biometric variability of the members of the family often makes their determination uncertain. Those from other sites present similarities with Apodemus maastrichtiensis

Kolfschoten, 1985 and *A. agrarius* (Pallas, 1778) from Igue des Rameaux, inciting us to compare them. As the unicity of each morphotype rules out attribution to a given species or the creation of a new taxon, we did not compare the morphotypes from Rameaux to discoveries with insufficient numbers.

93 As we cannot add these sparse and unrepresentative elements to this study, we are adding a table (tabl. 13) for information, but we regret the fact that we cannot establish a phyletic and/or biochronological table for this group of murids.

Tableau 12– l'Igue des Rameaux. Biometric data of *Apodemus* M<sub>2</sub> and comparative statistical interspecific analyses.

M /	N°	G/D	L	Wa	Wp	WT	mcl	LxWa	LxWp	LxWT	L/Wa	L/Wp	L/WT	tE	WT-Wp	Wts	WT	W tC/tD	W tA/tB
AF	SIR 158-17	G	121	111	98	121	-	134,3	118,6	146,4	1,09	1,23	1,00	+	23	115	117	115	100
AS	SIR 158-18	D	123	117	99	117	+	134,3	121,8	143,9	1,05	1,24	1,05	-	18	101	117	101	99
AS	SIR 158-20	D	123	104	94	109	+	143,9	115,6	134,1	1,18	1,31	1,13	+	15	98	109	95	92
AS	SIR 26-4	G	120	104	87	112	-	127,9	104,4	134,4	1,15	1,38	1,07	+	25	104	109	109	92
AS	SIR 71-11	D	126	111	103	111	+	124,8	129,3	139,9	1,13	1,22	1,13	-	8	100	114	103	90
AS	SIR 71-12	D	118	105	98	105	+	123,9	115,6	123,9	1,12	1,20	1,12	-	7	96	105	98	94
AS	SIR 86-3	D	118	102	87	106	+	120,3	102,7	125,1	1,16	1,36	1,11	+	19	998	106	100	88
AS	SIR 101-14	G	119	12	87	105	+	121,4	103,5	124,9	1,17	1,37	1,13	+	18	98	105	99	90
AS	SIR 134-4	G	126	116	99	116	+	142,2	120,7	146,2	1,09	1,27	1,09	-	17	103	117	105	100
AM	SIR 44-1b	G	100	88	82	88	-	88	82	88	1,14	1,22	1,14	-	6	83			
AA	SIR 158-16	G	120	98	93	98	-	117,6	111,6	117,6	1,22	1,29	1,22	-	7				
AA	SIR 158-19	D	120	108	95	108	-	129,6	114	129,6	1,11	1,26	1,11	-	13				

AF+AS	n	L/Want		L/Wpost		L/WT		L/WtC-tD		L/tA-tB		WT/Wpost	
		9	9	9	9	9	9	7	7	7	7	9	9
	m(moy)	121,6	108	121,6	96,3	121,6	111,3	121,9	100,1	121,9	93,3	10	94
	s	1,95	5,54	2,95	7,35	2,95	5,4	3,27	3,04	3,27	4,3	32	4
	r	0,74		0,66		0,53		0,56		0,47		0,11	
	max	126	117	126	103	126	117	126	105	126	100	117	100
	mini	118	102	118	87	118	105	118	95	118	88	105	88
	a	-59,83		-103,09		-5,73		36,42		11,94		92,37	
	b	1,38		1,64		0,96		0,52		4,3		0,02	
	Σ	1094	972	1094	867	1094	1002	853	701	853	653	904	845
	Σxy	118260		105517		121874		85461		76619		85017	
	Σx²	133060		133060		133060		104019		104019		100186	
	Σy²	105252		84007		11188		70265		61045		79509	

AF	n	L/Want		L/Wpost		L/WT		L/WtC-tD	
		6	6	6	6	6	6	6	6
	m(moy)	121,7	107	121,7	94,7	121,7	108,7	121,7	109,3
	s	3,5	5,15	3,5	6,02	3,5	3,94	3,5	4,64
	r	0,84		0,72		0,91		0,95	
	max	126	116	126	103	126	116	126	116
	mini	118	102	118	87	118	105	118	105
	a	-44,86		-55,20		-16,32		-44,41	
	b	1,25		1,23		1,03		1,26	
	Σ	730	640	730	568	730	652	730	656
	Σxy	77958		69197		79402		79906	
	Σx²	88890		88890		88890		88890	
	Σy²	68426		53988		70944		71852	

Table 13 – Comparative data. Location and measurements of field mice from European sites of various periods. The numbers in the first column allow to connect each site to its own values.

N°	Espèce	Localité	Pays/Région	Epoque	Référence	LM1		WM1		LM1		WM1		LW		LW M1 /100							
						max/min	moy	max/min	moy	max/min	moy	max/min	moy	M1 /100	m1								
1	<i>Parapodemus coronens</i>	Podlesice	Pologne	Pliocène inf.	Kowalski 1956	1				170	140	154	100	75	89	1,73	136,3						
2	<i>Parapodemus coronens</i>	Schiernfeld	Allemagne	Pliocène final	Dehm 1982	2		165		103	140			90	1,62	170,0	1,56	126,0					
3	<i>Parapodemus coronens</i>	Gesprenberg	Hongrie	Pliocène inf.	Schau 1938	3		160															
4	<i>Parapodemus</i> sp.	Varbeshnitsa	Bulgarie	Pliocène Moyen	Popov 1988	4		165		115	162	157	160	105	97	101	1,45	189,8	1,58	161,1			
5	<i>Parapodemus</i> sp.	Tautavel	F. Roussillon	Pliocène Moyen	M.J. inédit	5								155		87				1,78	134,9		
6	<i>Parapodemus</i> sp.	L'Escalé	F. Bouches du Rhône	Pliocène Moyen	M.J. inédit	6		151		113				155			1,34						
7	<i>Parapodemus</i> sp.		De. Sudmer-Berg	Pliocène Moyen	Koenigswald 1972	7						150											
8	<i>Apodemus massichtrien</i>	Belvédér 4	NL. Maasticht	Pliocène Moyen	Kolfschoten 1985	8	182	151	167	109	102	106	160	137	150	95	84	91	1,55	180,4	1,85	136,5	
9	<i>Apodemus microps</i>		Tchécoslovaquie	Actuel	Pasquier 1974	9	187	151	170	122	98	109	170	137	152	113	91	99	1,56	185,3	1,54	150,5	
10	<i>Apodemus microps</i>		De. Donau-Auen	Actuel	Steiner/Niethammer 1982	10	177	153	165	115	100	109								1,53	179,2		
11	<i>Apodemus agrarius</i>		De. Frankfurt/Oder	Récent	Maul 1990	11		194				168		94						1,79	157,9		
12	<i>Apodemus</i> sp.	Loira	It. (Vioanza)	Pliocène Moyen	Bartolomei 1964	12		170		120	170	140	155						1,42	204,0			
13	<i>Apodemus</i> sp.	Spessa III	It. (Vioanza)	Pliocène Moyen	Bartolomei 1964	13		190		130									1,38	234,0			
14	<i>Apodemus agrarius</i>	Coudoulous II	F. Tour de Fauré (Lot)	Pliocène Moyen	M.J. inédit	14						158		95						1,66	150,1		
15	<i>Apodemus uralensis</i>	Coudoulous I	F. Tour de Fauré (Lot)	Pliocène Moyen	M.J. inédit	15	162	162	162	115	112	114							1,43	183,9			
16	<i>Apodemus agrarius</i> (MJ)	Niedersachsen	Allemagne	Actuel	M.J. inédit	16	210	190	203	121	112	117	180	163	174	109	97	103	1,74	236,9	1,70	178,5	
17	<i>Apodemus agrarius</i>	Siedolm-Kirn	Corse	Actuel	M.J. inédit	17		205		120		173							1,00	1,71	246,0	1,73	173,0
18	<i>Apodemus agrarius</i> (UP)	Niedersachsen	Allemagne	Actuel	Aguilar & al. 1985	18	228	184	205	129	112	120	182	161	172	114	92	102	1,71	246,0	1,69	175,4	
19	<i>Apodemus agrarius</i> (UP)	Bouzeux	F. Lot	Pliocène Final	Aguilar & al. 1985	19	203	197	201	125	117	122	184	168	175	107	106	106	1,65	245,2	1,67	185,5	
20	<i>Apodemus agrarius</i>	Les Rameaux	F. (Tam et Garonne)	Pliocène Moy.	M.J.	20	213	195	205	126	114	120	175	104	171	113	104	109	1,71	246,0	1,57	186,4	
21	<i>Apodemus massichtrien</i>	Les Rameaux	F. (Tam et Garonne)	Pliocène Moy.	M.J.	21	181	172	177	128	117	123	165	145	160	100	97	98	1,44	217,7	1,63	156,8	

Discussion and conclusion

94 Based on rather sparse but well-characterized populations, it is thus possible to determine molars dispersed in time and space.

- 95 These species evolve and are transformed over time in response to climatic and environmental demands. This influences metric and morphological parameters. Which corporal characteristics can be associated with specific thermal, hygrometric or orographic influences?
- 96 It is tempting to seek evolutionary or biological criteria in each morphological or biometric variation. It is also tempting to create a new taxon to concretize these differences on statistical or formal bases without identifying the natural reasons for these characteristics. Adaptation to the environment is generally the cause of morphological and metric modifications.
- 97 Which criteria allow for the creation of a sub-species? The number of individuals affected by a distinctive sign? The constant and repetitive morphological and biometric differences guarantee the reality of a morphotype, assimilated to a sub-species. These basic criteria are perfectly clear for the molars of *Apodemus agrarius iguensis* n. ssp, in spite of the limited number of samples.
- 98 However, it seems appropriate, or at least of interest, to outline a lineage with sporadic or isolated elements (for want of better) likely to bear proportional modern and archaic features. In this regard, murids have huge potential considering the number of landmarks observed on their molars and the available variation resources. But statistics have to be taken into account and therefore from *Parapodemus coronensis* during the Lower Pliocene to present-day *Apodemus microps*, there is only one genealogical step: *Apodemus maastrichtiensis*.
- 99 We do not wish to reform the principles of research and analysis, but it would be interesting, or even instructive, to be able to insert isolated morphotypes, deemed to be unclassifiable, into recognized populations and to point out their individuality. It is regrettable that even relative and random chronology must be backed up by other phyletic chains or other disciplines.
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## ABSTRACTS

The discovery of the karstic system of “l'Igue des Rameaux” at Saint-Antonin-Noble-Val (Tarn-et-Garonne, France) by the Speleologic Group of Caussade, allowed to bring out an interesting and important faunas both of large and small mammals (Rouzaudet *al.* 1990). Unusually four species of *Apodemus* have been recognized and this paper has for purpose to define their biometrical and morphological particularities. This opportunity incites us to gather some small size members of this genus, from different sites of Middle Pleistocene and propose a tentatively phyletic classification in the genealogical tree of the prolific murids family, despite the weakness of the data making the operation statistically random.

## INDEX

**Keywords:** Rodents, *Apodemus*, biometry, morphology, systematic, environment, Middle Pleistocene, karst fissure, southwestern France

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