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# Occurrence of the Stripe Field Mouse lineage (*Apodemus agrarius* Pallas 1771; Rodentia; Mammalia) in the Late Pleistocene of southwestern France

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## Abstract

The Stripe Field Mouse lineage (*Apodemus agrarius*) was present in the Late Pleistocene in southwestern France (locality of Bouziès-Q, Quercy), according to the age of ca. 17,417–17,044 BC of the collected sample (AMS  $^{14}\text{C}$  dating of collagen extracted from small mammal bones). This occurrence demonstrates that a much western expansion of the Stripe Field Mouse lineage than believed occurred at the end of the last cold phase of the Pleistocene, the few fossil populations up to now known being both younger and located inside the present-day distribution area of the lineage. The AMS  $^{14}\text{C}$  date supports the hypothesis of the late migration of this species into Europe. If tooth morphology indicates clear differences with respect to *Apodemus sylvaticus* or *A. flavicollis*, there are appreciable ones between the Bouziès-Q population and the present-day *Apodemus agrarius* of western Europe, likely indicating evolution at the sub-specific level despite the short time period involved. *To cite this article: J.-P. Aguilar et al., C. R. Palevol 7 (2008).*

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## Résumé

**Extension dans le Sud de la France, au Pléistocène terminal, du mulot rayé (*Apodemus agrarius* Pallas, 1771 ; Rodentia ; Mammalia).** Le gisement de Bouziès-Q (Quercy, Sud-Ouest de la France) a livré quelques dents d'un rongeur se rattachant à la lignée du mulot rayé, *Apodemus agrarius*. Une datation AMS  $^{14}\text{C}$  du collagène d'un échantillon d'os du site a fourni un âge calibré entre 17 417 et 17 044 av. J.-C., ce qui correspond à la fin du dernier âge glaciaire. L'âge de la population de Bouziès-Q appuie l'hypothèse d'une arrivée récente de cette lignée en Europe, et démontre une extension vers l'ouest plus forte que celle déduite des quelques fossiles de cette espèce récemment collectés en Europe. Si la morphologie dentaire sépare aisément cette population

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des *Apodemus sylvaticus*, elle révèle aussi des différences sensibles avec l'actuel *A. agrarius* occidental, ce qui soulignerait une évolution des populations survenue dans un court laps de temps. *Pour citer cet article : J.-P. Aguilar et al., C. R. Palevol 7 (2008).* © 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

**Keywords:** Rodentia; *Apodemus agrarius*; Late Pleistocene; France; Germany

**Mots clés :** Rodentia ; *Apodemus agrarius* ; Pléistocène tardif ; France ; Allemagne

## Version française abrégée

L'aire du mulot rayé *Apodemus agrarius* s'étend aujourd'hui du centre de l'Europe en direction de la Russie et plus à l'est encore, en Asie. L'espèce, qui a son origine en Asie, aurait atteint l'Europe occidentale au début de l'Holocène [8,12]. Le signalement de cette espèce par Toskan et Krystufek [16] en Europe centrale, dans des faunes vieilles de quelques milliers d'années, est en accord avec l'interprétation de Kowalski. La détermination dans le gisement quercinois de Bouziès-Q (Lot) [3] d'un *Apodemus cf. agrarius* établit que la lignée aurait eu auparavant, à l'occasion même de son expansion, une aire de répartition momentanément plus étendue vers l'ouest. Une datation AMS  $^{14}\text{C}$  (spectrométrie de masse avec accélérateur) à partir du collagène d'os de petits mammifères du site, effectuée par le Centrum voor Isotopen Onderzoek de l'université de Groningue (Pays-Bas), a donné un âge de  $15\,990 \pm 70$  BP (échantillon Bouziès n°1, GrA n° 34 357) ou, en âge calibré, 17 417–17 044 av. J.-C. Cet âge indique le Pléistocène terminal. La présence d'un *A. agrarius* en situation géographique tout aussi occidentale avait été signalée antérieurement, mais dans un niveau pléistocène nettement plus ancien, à l'Igue-des-Rameaux [6]. L'âge proposé dans ce cas pour le niveau comportant le mulot rayé est d'environ 300 ka BP. Il s'agit d'un âge estimé à partir d'un indice morphologique dentaire [7], relatif au campagnol *Arvicola*. L'intérêt du site de Bouziès-Q est d'apporter une documentation concrète notable sur une lignée dont l'expansion vers l'ouest serait récente, et qu'il est possible de comparer aux populations actuelles, situation favorable à la mise en évidence de phénomènes microévolutifs.

Le mulot rayé de Bouziès-Q est représenté par trois fragments de mandibule avec m1–m2 et 14 dents isolées (mensurations reportées dans le Tableau 1). La difficulté bien connue que présente la détermination spécifique de dents isolées chez les mulots de taille moyenne (*A. agrarius*, *A. sylvaticus*, *A. flavicollis*) a justifié une analyse morphologique attentive. Une vingtaine de spécimens, avec crânes et mandibules, prêtés par le musée Alexander-Koenig (Bonn, Allemagne), fournit le matériel de comparaison. Si, dans la faune de Bouziès-Q,

les dents référables aux *Apodemus sylvaticus* et *A. flavicollis* sont beaucoup plus abondantes, la présence du mulot rayé a d'abord été reconnue par des M2 (seconde molaire supérieure) caractéristiques. Toutefois, il est possible de reconnaître également les M1, m1, m2 et m3 qui appartiennent à cette espèce (Tableau 2). La population allemande d'*A. agrarius* a ensuite permis de mettre en évidence quelques différences avec la population de Bouziès-Q (Tableau 3). Toutefois, le mulot rayé de Bouziès-Q n'a pas été déterminé de manière définitive comme *A. agrarius*, en raison de ses quelques singularités. Les différences portent, pour l'essentiel, aussi bien sur le volume relatif des tubercules principaux que sur celui des tubercules accessoires, comme aussi sur l'allure des chevrons. La reconsideration de ces caractères se justifiera lors d'une étude plus vaste de la variation de la forme et de la taille des molaires au sein de cette espèce, qui a fait récemment l'objet d'études phylogéographiques [10,11,14].

En conclusion, une troisième lignée de mulots était présente en France aux côtés de *A. sylvaticus* et *A. flavicollis*, à la fin du dernier épisode glaciaire, entre 17 417 et 17 044 av. J.-C. Les dents du mulot rayé de Bouziès-Q ont des dimensions comparables à celles du mulot rayé actuel et présentent avec celles-ci des différences non négligeables, de l'ordre de celles qui peuvent entrer dans la reconnaissance de sous-espèces ou proches espèces de Murinae. Cet *Apodemus cf. agrarius* de Bouziès-Q pourrait donner l'image des premières populations arrivées de l'est, avant que l'aire de répartition de l'espèce ne se rétracte, et que ces populations ne soient remplacées par celles que nous connaissons en Europe centrale. La découverte et la datation de la population de Bouziès-Q relancent l'intérêt du site de l'Igue-des-Rameaux, justifiant une nouvelle datation de la couche 30, en même temps qu'une étude des quelques autres populations d'âge Pléistocène moyen ou supérieur signalées en Europe centrale ou orientale. La population de Bouziès-Q montre que les processus évolutifs responsables de différences morphologiques sensibles peuvent être rapides, et qu'en conséquence une analyse dentaire plus approfondie (morphologique et morphométrique), étendue aux différentes populations actuelles d'*Apodemus agrarius*, mériterait d'être reprise.

## 1. Introduction

The Stripe Field Mouse (*Apodemus agrarius* Pallas, 1771) has today a wide area of distribution, from the centre of Europe (Denmark, Germany, Italy, North of Greece) to Russia and, farther to the east, to Asia, China, Korea, and Japan. This species has its origin in Asia and reached Western Europe likely at the beginning of Holocene [2,8]. In agreement with Kowalski's views are the finds of Toskan and Krystufek [16], who recently recorded this species in Slovenia in several-thousand-year-old faunas (9600–7800 BP for the oldest one). However, a Field Mouse called *Apodemus cf. agrarius* is also quoted in several older Pleistocene deposits in Europe [8]. As it will be shown with the present study, a definitive determination of this material needs detailed qualitative and biometrical analyses. The Stripe Field Mouse has also been cited in a rather old Pleistocene level in France in the fossil mammal-bearing locality known as Igues-Rameaux [6]. This author suggests that the level (C 30) with the Stripe Field Mouse is Middle Pleistocene, according to the high enamel thickness index (SDQ) of the water vole determined as *Arvicola cantiana* (reference in [7]). An age ca 300 ka old is suggested for this level.

Owing to the modern character of Bouziès-Q fauna [3], an Accelerator Mass Spectrometry radiocarbon dating (AMS  $^{14}\text{C}$  dating) was tempted on collagen of associated small mammal bones. The dating made by the Centrum voor Isotopen Onderzoek, Groningen University, The Netherlands, gives  $15,990 \pm 70$  BP (sample Bouziès No. 1, GrA No. 34,357). Once calibrated (reference in Bronk Ramsey [1]), this age falls into the interval 17,417 to 17,044 BC ( $p > 95\%$ ). The rather old Pleistocene occurrences of the Stripe Field Mouse in Europe being put aside, the occurrence of this lineage in France in the locality of Bouziès-Q in Quercy [3] demonstrates that at least a few thousand years ago, the lineage had a wider distribution in Europe toward the west [4,15,17] (Fig. 1).

## 2. Description

The Bouziès-Q material (Plate 1, middle column; Plate 2, Figs. 1–9) referred to the Stripe Field Mouse lineage includes three mandible fragments with m1–m2, and 14 isolated teeth. For a first comparison, a significant German sample from Niedersachsen (held in Museum Alexander Koenig, Bonn, Germany) was used. Table 1 gives the measurements (in millimetres) of both samples. If the second upper molars (M2) show the diagnostic character of the Stripe Field Mouse (the lack of the

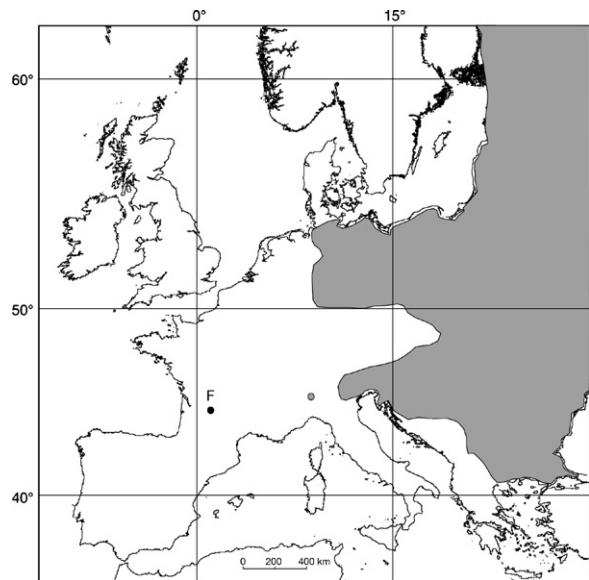


Fig. 1. Present-day distribution (grey) of *Apodemus agrarius* Pallas, 1771 in western Palearctic zone according to Mitchell-Jones, [12]), and location (F) of the Late Pleistocene Bouziès-Q site in Quercy (Lot, France).

Fig. 1. Répartition actuelle (grisé) de l'*Apodemus agrarius* Pallas, 1771 en zone paléarctique occidentale d'après Mitchell-Jones [12] et localisation (F) du site Pléistocène terminal de Bouziès-Q (Lot, Quercy, France).

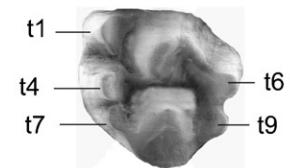
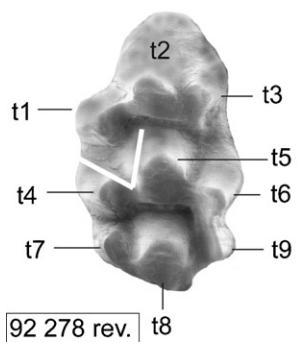
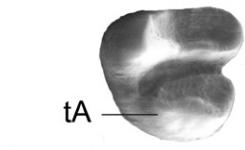
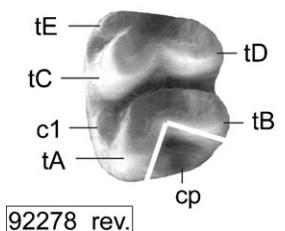
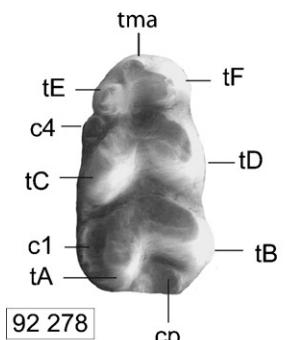
cusp t3 on M2), a careful analysis of the other molars of the Bouziès-Q sample (M1, m1, m2 and m3) allows us to recognize several more molars that can also be referred to a species different from *Apodemus sylvaticus* and *A. flavicollis*, also present in the fauna. The well-known determination difficulty of isolated teeth in the middle-sized species of *Apodemus* (as *A. agrarius*, *A. sylvaticus*, *A. flavicollis*) justifies a detailed description of the new material of Bouziès-Q, a preliminary work to any wider scope morphological and morphometrical study of the subspecies and species of the Stripe Field Mouse lineage, the phylogeography of which is now rather well established [10,11,14]. The nomenclature of the dental structure (Plate 1, left column) is that proposed by Michaux [9].

### 2.1. Lower molars

#### 2.1.1. m1

There is a small tma, little differentiated from the four anterior cusps. Connections between the pairs of cusps tE–tF and tC–tD are rather low and in between them, a small pit is present, which may disappear with wear. The labial cingular margin bears two accessory

*A. agrarius* Recent  
coll. Bonn

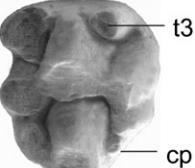
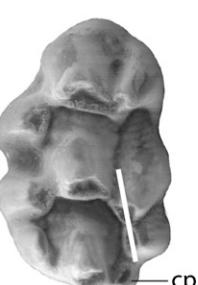
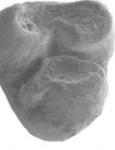
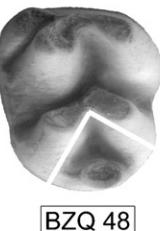


*A. cf. agrarius*  
Bouziès-Q



BZQ 17

*A. sylvaticus*  
Bouziès-Q



1 mm

Table 1

Molar length and width measurements (mm) of *Apodemus cf. agrarius* (Bouziès-Q locality, France) and *Apodemus agrarius* from a German population (Niedersachsen). L and W, mean value

Tableau 1

Mesures des longueurs et largeurs (en mm) des molaires d'*Apodemus cf. agrarius* de Bouziès-Q et d'une population allemande (Basse-Saxe). L et W, valeur moyenne

A. cf. <i>agrarius</i> , Bouziès-Q, Late Pleistocene							A. <i>agrarius</i> , Niedersachsen, Germany, Recent							
n	$L_{\min}$	L	$L_{\max}$	$W_{\min}$	W	$W_{\max}$	n	$L_{\min}$	L	$L_{\max}$	$W_{\min}$	W	$W_{\max}$	
M1	3	1.97	2.01	2.03	1.17	1.22	1.25	36	1.84	2.05	2.28	1.12	1.20	1.29
M2	4	1.20	1.22	1.25	1.06	1.08	1.11	34	1.05	1.14	1.24	1.03	1.10	1.17
M3	—	—	—	—	—	—	—	33	0.65	0.73	0.83	0.73	0.79	0.93
m1	5	1.68	1.75	1.84	1.06	1.06	1.07	33	1.61	1.72	1.82	0.92	1.02	1.14
m2	5	1.24	1.28	1.33	1.05	1.07	1.10	33	1.14	1.24	1.31	0.92	1.00	1.09
m3	2	0.95	—	0.97	0.82	—	0.82	33	0.94	1.04	1.15	0.79	0.83	0.89

cusps, the anterior one (c4) being elongated as a cingulum, and connected to cusp tE. The posterior one (c1) is as high as cusp tA and merging into the latter. In place of the posterior cingulum is a low crest starting from cusp tA, which will connect to cusp tC along with wear.

### 2.1.2. *m2*

Cusp tE appears more or less as a cingulum connected to the mesial side of cusp tC. In upper view, the angle defined by cusps tA and tB is clearly obtuse. The size of the accessory cusp c1 is highly variable and this cusplet is even no more than a crest connected to tC. The posterior cingulum is a crest more developed than on m1.

### 2.1.3. *m3*

The two specimens have a simple crown made of two practically parallel and transversal chevrons connected on their labial side by a small crest.

## 2.2. Upper molars

### 2.2.1. *M1*

They have slender outline, being relatively narrow. Cusp t1 is settled rather posteriorly to cusp t2 and along with wear, it will connect to cusps t4 and t5. The anterior face of cusp t2 has a strong dip. Cusp t3 has a posterior spur directed toward cusp t4. In lateral view, cusps t4 and t8 are rather vertical. Connections t6–t9 and t4–t7 are

developed. The molar is stephanodont, as there is a continuous connection between cusps t4–t5–t6–t7–t8–t9. The valley or sinus delimited by cusps t4 and t5 is at least of 90°, as is the sinus made by cusps t5 and t6. Cusps t4, t7, and t9 are similar in size and are slightly smaller than cusp t6. The weakly differentiated posterior cingulum (cp) is as a thickening of the posterolabial side of t8, whose posterior flank, together with the mesial part of the second molar, forms a transversal gutter.

### 2.2.2. *M2*

The lack of a cusp t3 is the diagnostic character of *A. agrarius*, the anterolabial side of the molar being almost vertical. Cusp t1 is rather well developed, but is rather lower than cusp t2 to which it is more or less connected. As on M1, connections between cusps t4–t7 and t6–t9 are clearly differentiated, but the size of the cusps is variable, cusp t9 being the more weakly developed. There is no posterior cingulum.

## 3. Comparison with *A. sylvaticus* from Bouziès-Q and *A. agrarius* (Central Europe)

Tables 2 and 3 summarize respectively the special features of the teeth useful for discriminating the Bouziès-Q's Stripe Field Mouse from both the Bouziès-Q *Apodemus sylvaticus* (and/or *A. flavicollis*) and the Recent *A. agrarius* (Plate 1 and Table 1). This mor-

Plate 1. Morphological comparison between *Apodemus agrarius*, Recent (German population), *A. cf. agrarius*, and *Apodemus sylvaticus* from Bouziès-Q locality (Lot, France), Late Pleistocene. Characters of interest are indicated, cusp nomenclature as in Michaux [9]. Collection numbers of specimens are indicated.

Planche 1. Comparaison de *Apodemus agrarius*, récent (population allemande), *A. cf. agrarius* et *Apodemus sylvaticus* de Bouziès-Q (Lot, France), Pléistocène terminal. Certains caractères discutés dans le texte sont indiqués, et la nomenclature des cuspides suit Michaux [9]. Les numéros des spécimens sont reportés.

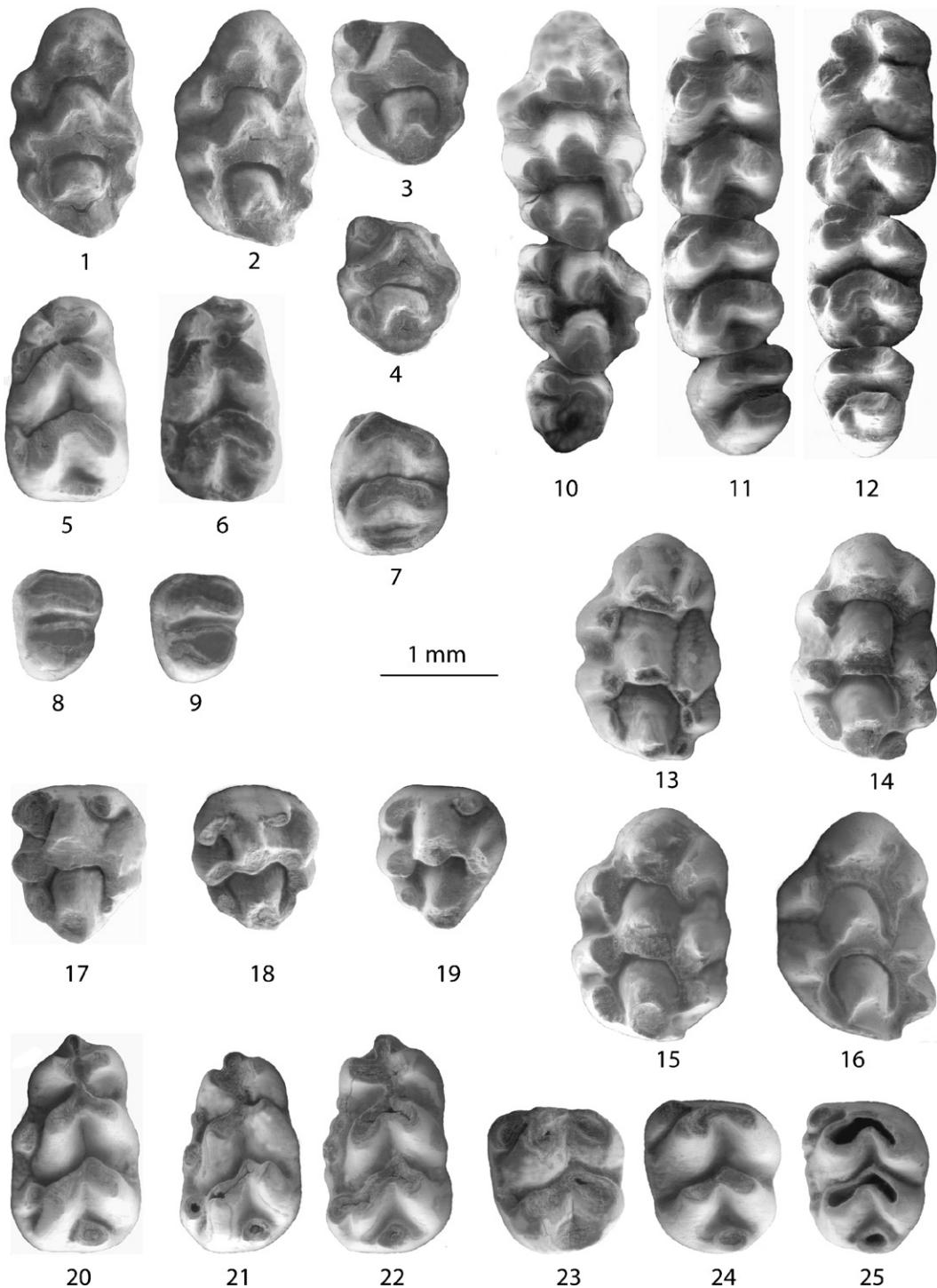


Table 2

Characters differentiating *Apodemus cf. agrarius* and *Apodemus sylvaticus* from Bouziès-Q

Tableau 2

Comparaison *Apodemus cf. agrarius*–*Apodemus sylvaticus* de la localité de Bouziès-Q

	<i>A. cf. agrarius</i> , Bouziès-Q	<i>A. sylvaticus</i> , Bouziès-Q
m1	tma on m1, small, nearly undistinct from first pair of cusps	tma on m1 well-differentiated, and distinct from the cusps of the anterior lobe
m2	Labial cingular margin of m1 reduced with 2 cusplets, cusplet c4, as a crest Posterior cingulum (cp) of m1–m2 as a crest	External cingular margin of m1 with 3 or 4 accessory cusps, c4, tubercular Posterior cingulum (cp) of m1–m2, as cusp or crest, rather developed
M1	Cusp t1 in a posterior position relative to cusp t2  Connection t6–t9 parallel to tooth axis or lingually directed Cusp t7 connected to t4 cp present.	Cusp t1 near cusp t2 ; posterior cingulum (cp) rather well developed Cusp t9 in lingual position, connection t6–t9 oblique labially Cusp t7 usually not connected to t4
M2	Without cusps t3, cusp t9, small	Cusp t3 well developed on M2, cusp t9, usually as large as t6

phological analysis demonstrates that it is possible to recognize the heterogeneity of an assemblage of middle-sized *Apodemus* molars, even if the variation of some dental structures is difficult to appreciate, as for example, the size of accessory cusps. However, the Stripe Field Mouse of Bouziès-Q is still not determined as *A. agrarius*, because of several small, but meaningful differences in tooth morphology with the German population used for comparison. Differences affect the relative size of main and accessory cusps, and the shape of the chevrons. These differences are frequently used for the discrimination of species or subspecies in extant as well as in extinct species of Murinae (for example, see Darviche and Orsini [5] for the mice *Mus spretus* and *Mus musculus*). The inescapable conclusion is that a small amount of morphological evolution occurred during the two last tens of millenniums (replacement of populations?). Musser et al. [13] have given an account about taxonomy and distribution records of some oriental and European *Apodemus* and provide some data and pictures of their molars. The lack of a comparison with western populations that should involve lower molars prevents any further discussion. However, the sinus or valleys between cusps t4 and t5, as well as

t5 and t6 on M1 and M2, and t4–t5 on M2, which are wider in the Late Pleistocene population, would likely be characters worth to notice (Fig. 4B–D in Musser et al. [13]).

The present analysis also stresses the interest of a study of the populations referred to the lineage of *Apodemus agrarius* as *A. cf. agrarius*, whose occurrence is indicated in several Middle and Late Pleistocene localities in Europe. As the separation time of the Stripe Field Mouse from other *Apodemus* lineages is estimated to have occurred ca. 6 Ma ago [10], it cannot be excluded that the *agrarius* lineage or lineages related to this one expanded towards the west at several times in the past, but these events were not followed by a rather long-lasting settlement. The presence of this Middle Pleistocene *Apodemus* cf *agrarius* may be correlated with such events. Even more, *Apodemus leptodus* Kretzoi 1962, present in a Lower Pleistocene locality in central Europe [8], might similarly be linked to an occasional extension of this lineage. However, data are scarce and, considering the difficulty in determining *Apodemus* species on dental material due to variation, only an association of morphologic and biometric analyses would be efficient.

Plate 2. **1–9.** *Apodemus cf. agrarius* from Bouziès-Q. **1**, M1 sen. (1.97 × 1.17) BZQ 12; **2**, M1 sen. (2.03 × 1.23) BZQ 13; **3**, M2 sen. rev. (1.25 × 1.11) BZQ 15; **4**, M2 sen. (1.20 × 1.06) BZQ 17; **5**, m1 sen. (1.78 × 1.07) BZQ 5; **6**, m1 sen. (1.72 × 1.06) BZQ 3; **7**, m2 sen. rev. (1.24 × 1.09) BZQ 8; **8**, m3 sen. rev. (0.97 × 0.82) BZQ 9; **9**, m3 sen. (0.95 × 0.82) BZQ 10. **10–12.** Present-day *Apodemus agrarius* coll. Bonn. **10**, Maxillary sen. rev. No. 92278; M1 (2.01 × 1.23), M2 (1.16 × 1.17), M3 (0.76 × 0.78). **11**, Mandible sen. rev. No. 92278; m1 (1.76 × 1.03), m2 (1.23 × 0.97), m3 (0.97 × 0.84). **12**, Mandible sen. rev. No. 95277; m1 (1.78 × 1.09), m2 (1.22 × 1.03), m3 (0.95 × 0.83). **13–25.** *Apodemus sylvaticus* from Bouziès-Q. **13**, M1 sen. rev. (1.96 × 1.22) BZQ 73; **14**, M1 sen. rev. (1.95 × 1.20) BZQ 74; **15**, M1 sen. rev. (2.00 × 1.29) BZQ 77; **16**, M1 sen. (1.97 × 1.33) BZQ 78; **17**, M2 sen. (1.36 × 1.22) BZQ 93; **18**, M2 sen. (1.25 × 1.23) BZQ 95; **19**, M2 sen. rev. (1.24 × 1.17) BZQ 102; **20**, m1 sen. (1.88 × 1.14) BZQ 22; **21**, m1 sen. rev. (1.73 × 1.06) BZQ 24; **22**, m1 sen. rev. (1.88 × 1.13) BZQ 26; **23**, m2 sen. (1.26 × 1.14) BZQ 47; **24**, m2 sen. (1.32 × 1.11) BZQ 48; **25**, m2 sen. rev. (1.31 × 1.09) BZQ 55. Photos: SEM, UM2 Montpellier, France (C. Grill). Planche 2. **1–9.** *Apodemus cf. agrarius* de Bouziès-Q. **10–12.** *Apodemus agrarius* actuel coll. Bonn. **13–25.** *Apodemus sylvaticus* de Bouziès-Q. Photos : MEB, UM2 Montpellier (C. Grill).

Table 3

Tooth characters discriminating the Bouziès-Q's Stripe Field Mouse from the Recent *Apodemus agrarius* (Germany)

Tableau 3

Différences morphologiques entre l'*Apodemus cf. agrarius* de Bouziès-Q et l'*A. agrarius* actuel (Allemagne)

	<i>A. cf. agrarius</i> , Bouziès-Q	<i>A. agrarius</i> Recent, Germany
m1	tma on m1, small, nearly indistinct from first pair of cusps  Accessory cusp c1 closing the sinus between tA and tC Cusplet c1 as high and merged into tA Posterior cingulum (cp) of m1 (and m2) as a crest	tma on m1 rather well developed and distinct from anterior cusps  Accessory cusp c1 in a more posterior position Cusplet c1 lower than cusp tA and more isolated Posterior cingulum (cp) of m1 (and m2) as a cusp or a much larger crest
m2	Loph tA–tB widely open ( $>90^\circ$ ) c1 rather high and associated to tA	Loph tA–tB less open ( $\leq 90^\circ$ ) c1, rather low and isolated from tA
M1	Cusp t1 in a relatively posterior position Mesial side of t2 and t4, more vertical Anterolingual valley between cusp t4–t5: $\geq 90^\circ$ Enamel-free area of cusp t8 concave and with a transversal direction	Cusp t1 more anterior, closer to t2 t7 cusp like, weak connection with t4. Anterolingual valley t4–t5: $\leq 90^\circ$ Enamel-free area of cusp t8 more or less concave and no transversal direction
M2	Cusp t2, with mesial face nearly vertical Cusp t4–t7 usually connected Cusp t9 small	Cusp t2, with oblique mesial face Cusp t4–t7 usually not connected Cusp t9 less reduced

#### 4. Conclusion

A third lineage of Field Mouse was present in southwestern France besides *A. sylvaticus* and *A. flavicollis* at the end of the last glacial episode, between 17,417 and 17,044 cal BC. The recent arrival in Europe of the Stripe Field Mouse advocated by Kowalski is supported, and by the way the lineage had at a time a wider distribution. The discovery and the  $^{14}\text{C}$  dating of the population of Bouziès-Q nevertheless support the interest of the Igue-des-Rameaux locality, where the lineage was first acknowledged, the taphonomic status of the specimens from this locality as their age being still uncertain. Tooth morphology indicates that a morphological change likely occurred between the Bouziès-Q Stripe Field Mouse and a present-day population, supporting the fact that careful morphological analysis can trace population renewal, and still may be worth to develop in parallel with other morphometrical analyses.

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