

THE LATEST RUSCINIAN AND EARLY VILLANYIAN ARVICOLINAE FROM SOUTHERN SPAIN RE-EXAMINED: BIOSTRATIGRAPHICAL IMPLICATIONS

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ABSTRACT—The Arvicolinae from the latest Ruscianian and early Villanyian sites of the section of Tollo de Chiclana (Southern Spain) are re-examined in the light of new material and exhaustive comparisons with other European populations. The uppermost Ruscianian population from TCH-1B, previously assigned to *Mimomys stehlini*, is now ascribed to *M. hassiacus*, cited for the first time from southern Spain. The populations from the lower Villanyian localities of TCH-3 and 13, assigned to *M. minor*, are considered to belong to *M. stehlini*. In addition, the material from the uppermost Ruscianian karstic level of Mo1-A, assigned to “*Mimomys*” *occitanus* is ascribed to *M. hassiacus*. The presence of different species of Arvicolinae is key for delimiting the Ruscianian–Villanyian boundary in the continental deposits of southern Spain and correlating them with European biochronological schemes. In this paper we discuss the problems associated with specific identifications of upper Ruscianian and lower Villanyian arvicolines from Spain, pointing out the invalidity of many citations, and demonstrating the need for an extensive revision of these faunas.

INTRODUCTION

Arvicolines are the most commonly micromammals used for establishing biostratigraphical schemes in the continental deposits of the upper Pliocene and Quaternary, mainly because of their high rate of morphological and biometrical change. In addition, their wide geographic distribution permits correlations among localities from distant areas. This is especially interesting in the case of the Spanish Pliocene faunas, since species of other rodent groups like Muridae and Cricetidae are frequently endemic in the Ibero-Occitan region.

On the other hand, the specific identification of Arvicolinae presents several difficulties: they show great intraspecific variability; various criteria have been used for their classification; and numerous synonymies among species have been proposed by different authors. This problem is aggravated in southern Spain because Pliocene arvicolines are scarce, and many papers dealing with this mammal group lack descriptions, measurements, or illustration of the teeth.

In the section of Tollo de Chiclana, several Pliocene localities have yielded rich rodent and insectivore faunas. The Arvicolinae, quite abundant in all these fossiliferous sites, were described in a previous paper (Minwer-Barakat et al., 2004). Some of the specific identifications of these arvicoline populations are still valid: *Dolomys adroveri* from TCH-1 (upper Ruscianian), *Kislangia ischus* from TCH-3 (lower Villanyian), and *Mimomys medaensis* from TCH-10 and 10B (upper Villanyian). Nevertheless, the specific identifications of the populations from TCH-1B (uppermost Ruscianian), TCH-3, and TCH-13 (lower Villanyian) have been demonstrated to be invalid after renewed sampling of one fossiliferous level (TCH-13) and exhaustive comparisons with a great number of European populations of arvicolines.

In this article, we re-examine the Arvicolinae from these lo-

calities, which represent the most abundant collections of arvicolines published from stratified levels of the upper Ruscianian–lower Villanyian of Spain. Correctly identifying the arvicolines of these faunas is essential to clarify the occurrence of arvicolines in the Iberian Peninsula during the Pliocene, and to compare them with other European populations. In addition, these populations allow the Ruscianian–Villanyian boundary to be delimited in southern Spain.

More information on the geological setting and the complete faunas from the localities of Tollo de Chiclana can be found in Minwer-Barakat (2005) and Minwer-Barakat et al. (2004, 2005, 2007).

The nomenclature used in the descriptions of the teeth (Fig. 1) and the measuring method for the height of the hyposinulid are those defined by Rabeder (1981); occlusal lengths and widths have been measured as defined by van der Meulen (1973). The A/L ratio is the percentage of the length of the anterior complex in relation to the total length of the m1 (after van der Meulen, 1973). Drawings were made using a Wild M8 stereomicroscope with camera lucida. Specimens are kept in the Departamento de Estratigrafía y Paleontología de la Universidad de Granada, Spain.

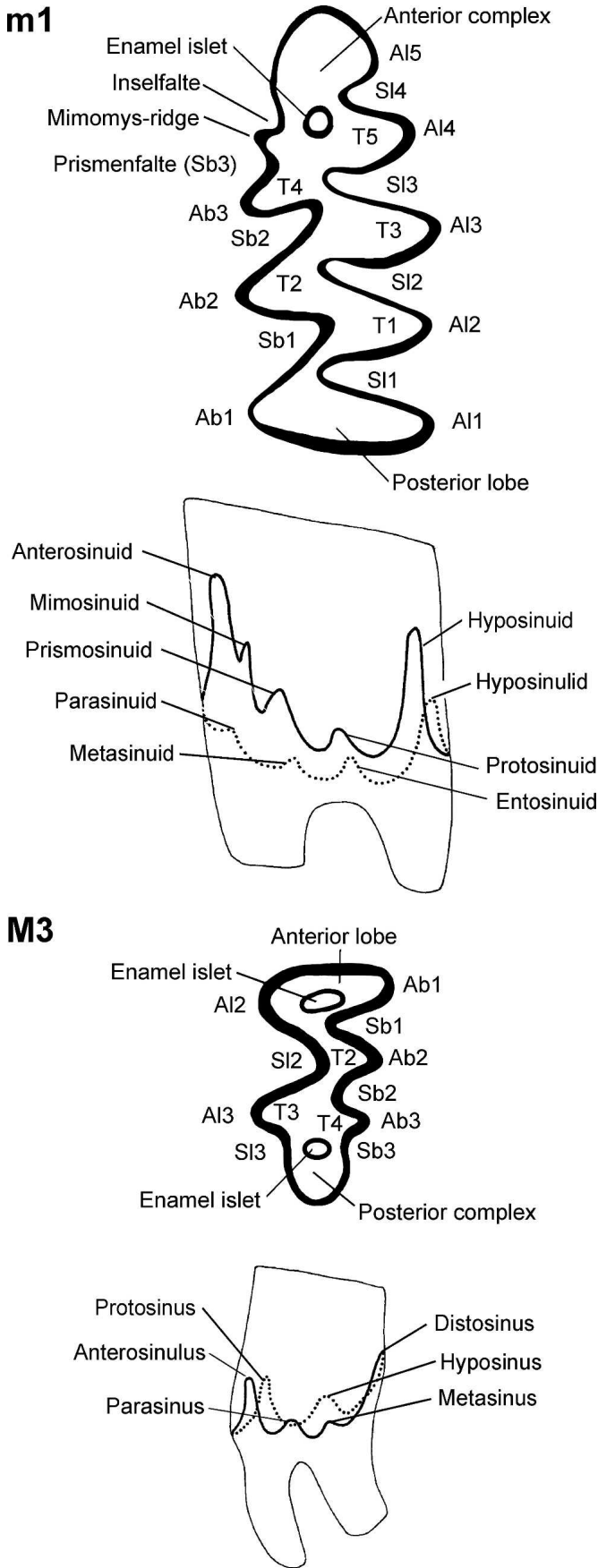
SYSTEMATIC PALEONTOLOGY

Family MURIDAE Illiger, 1811
Subfamily ARVICOLINAE Gray, 1821
Genus *MIMOMYS* Forsyth Major, 1902
MIMOMYS HASSIACUS Heller, 1936
(Fig. 2)

Occurrence—TCH-1B.

Description—A complete description of the material has been given in Minwer-Barakat et al. (2004). The most characteristic features of the m1 are: scarce cement in the synclinals; very high Sb3-wall (sensu Maul, 1996); enamel islet large, oval, and oblique

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to the longitudinal axis of the molar and present in early stages of wear; shallow inselfalte; well-marked prismenfalte; wide anterior complex; Sb2 oriented towards the anterior part of the tooth; T4 oriented backwards; SI4 deep in young specimens, weakening with wear. The difference in size between the labial and lingual triangles is not very accentuated, so the teeth are rather symmetrical. The mimosinuid and hyposinuid are notably lower than the anterosinuid, and the hyposinuid is very low.

The M3 bears a single enamel islet, irregular or oval, in the posterior complex. The T4 is small and sharp-pointed. The posterior complex is wide. The linea sinuosa is low.

Measurements—See Table 1.

Discussion—The material from TCH-1B was ascribed to *M. stehlini* in a previous paper (Minwer-Barakat et al., 2004). Later comparison with the material from several European localities has demonstrated that this population corresponds to *M. hassiacus*.

The species *M. hassiacus* was described from Gundersheim (Germany), a set of karstic fissure infillings that have yielded faunas of different ages. The type-population of this species corresponds to an early Villanyian infilling, whereas other fissures have provided both younger and older faunas (Fejfar, 2001). The species *M. hajnackensis* Fejfar, 1961 was considered to be a synonym of *M. hassiacus* by Fejfar et al. (1997) and Mörs et al. (1998); this opinion is now widely accepted, and many European populations ascribed to *M. hajnackensis*, including those from Teruel (Adrover et al., 1988), are now called *M. hassiacus*.

We have compared the material from TCH-1B with published data of *M. hassiacus* from Gundersheim, Hajnáčka, Beremend 3, Wölfersheim (Fejfar et al., 1997, 1998; Fejfar, 2001), Arcille (Masini and Torre, 1990), Arondelli (Michaux, 1971; Masini and Torre, 1990; Fejfar, 2001), Hambach (Mörs et al., 1998), and Concud Estación 1, 2, and 3 (Adrover et al., 1988). We have also compared the material with that of *M. hassiacus* from several European localities stored at the University of Lyon I: Arondelli, Commenaille, Concud Estación 1, 2, and 3, Uryv 1, Escorihuela, and Concud Pueblo 3.

The size of *M. hassiacus* from TCH-1B is very similar to that of the same species from Arondelli, Hambach, Arcille, Concud Estación 1, 2, and 3, and slightly larger than that from Uryv 1, Escorihuela, and Concud Pueblo 3. In Concud Pueblo 2 and 3 (Adrover et al., 1988) the mean length of the m1 is smaller than in TCH-1B; this difference is not significant, since only two specimens have been measured from each of these levels.

The occlusal morphology is practically identical in TCH-1B and the rest of the mentioned localities. In contrast, the development of the linea sinuosa varies notably in different populations of this species. The linea sinuosa is similar in TCH-1B and Gundersheim, Hambach, and Wölfersheim. In the lower first molars from Escorihuela, the linea sinuosa is slightly higher than in those from TCH-1B; this difference is more accentuated in the specimens from Commenaille and Arondelli, which also show a much better marked mimosinuid than those from TCH-1B. In the lower first molars from Concud Pueblo 3, younger than Escorihuela, the undulations of the linea sinuosa are much higher than in those from TCH-1B, especially the hyposinuid and hyposinulid. The linea sinuosa of M3 is also more developed, especially in the anterosinulus and protosinus. In the specimens from Concud Estación 1, 2, and 3, younger than Concud Pueblo 3, the linea sinuosa is even higher and has a very well marked mimosinuid; these specimens also have a notably higher crown

FIGURE 1. Terminology used in the descriptions of the occlusal morphology and the linea sinuosa of left m1 and M3 of *Mimomys* (modified from Rabeder, 1981). In buccal view, solid line represents buccal tracts of linea sinuosa and dashed line represents lingual tracts.

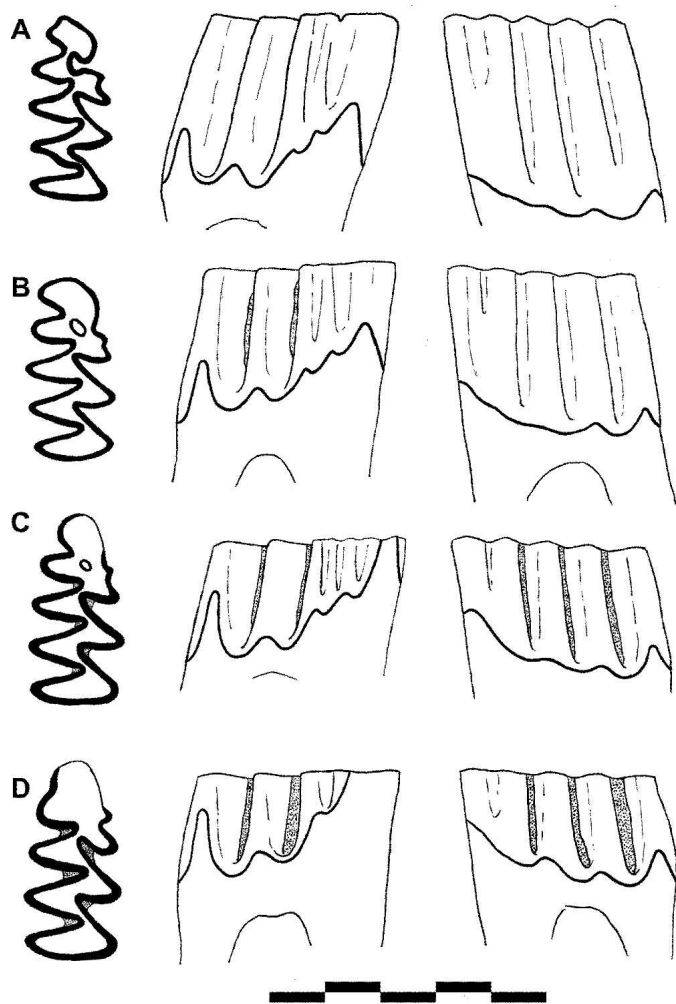


FIGURE 2. Lower first molars of *Mimomys hassiacus* from TCH-1B with different stages of wear in occlusal (left), labial (middle) and lingual (right) views. **A**, TCH-1B 513; **B**, TCH-1B 511; **C**, TCH-1B 516; **D**, TCH-1B 515. Scale bar equals 5 mm.

and a more ephemeral enamel islet than those from TCH-1B. The specimens from TCH-1B also have a clearly lower linea sinuosa than those from Hajnáčka, Beremend 3, and Arcille. In addition, the cement of the synclinals is more abundant in the teeth from Arondelli, Commenaille and Concud Estación-1 than in those from TCH-1B.

In the localities from the Teruel area, whose stratigraphic position is well documented (Mein et al., 1990), one can observe an increase in the height of the crown and in the development of the linea sinuosa from older to younger populations. The linea sinuosa is lower in TCH-1B than in Escorihuela; therefore, we interpret TCH-1B as older than all the localities from Teruel we have compared with. We can also deduce that TCH-1B is older than Commenaille and Arondelli. This conclusion is consistent with the whole faunal association of TCH-1B, which indicates a late Ruscinian age.

Mimomys hassiacus from TCH-1B is notably larger than *M. vandermeuleni* (see data in Fejfar et al., 1990) and *M. davakosi* (see van de Weerd, 1979; Chaline et al., 1981; Fejfar et al., 1990). In addition, the latter two species have a much lower crown than *M. hassiacus*, and a less developed linea sinuosa with very subtle undulations.

Dolomys adroveri from Orrios 3, 4, and 7, Villalba Alta Corral

TABLE 1. Measurements (mm) of *Mimomys hassiacus* from Tollo de Chiclana-1B.

| Parameter | n | min. | mean | max. |
|---------------------------------|----|------|------|------|
| Occlusal length of m1 | 21 | 2.92 | 3.23 | 3.48 |
| Occlusal width of m1 | 27 | 1.27 | 1.44 | 1.55 |
| Length of the anterior complex | 21 | 1.34 | 1.46 | 1.60 |
| A/L | 21 | 40.8 | 45.1 | 49.5 |
| Height of the hyposinulid of m1 | 20 | 0.43 | 0.53 | 0.69 |
| Occlusal length of M3 | 30 | 1.84 | 2.12 | 2.35 |

The A/L ratio is the percentage of the length of the anterior complex in relation to the total length of the m1 (after van der Meulen, 1973).

(Fejfar et al., 1990), and TCH-1 (Minwer-Barakat et al., 2004) is larger than *M. hassiacus* from TCH-1B. Morphological differences are obvious: the m1 of *D. adroveri* have a very low linea sinuosa and lack a *Mimomys*-ridge. The enamel islet appears in *D. adroveri* in a more advanced stage of wear than in *M. hassiacus*.

Mimomys gracilis, which coexists with *M. hassiacus* in several European localities, is much smaller. The maximum lengths of the m1 of *M. gracilis* from Csarnota (type-locality), Wèze, Nîmes (Michaux, 1971), and Ortalica (Ünay and de Bruijn, 1998) are notably smaller than the minimum from TCH-1B. The few specimens from Escorihuela B assigned to "*Mimomys*" *occitanus* by Fejfar et al. (1990) and now ascribed to *M. gracilis* are also clearly smaller than those of *M. hassiacus* from TCH-1B. Direct comparison with specimens of *M. gracilis* from Wèze, Ivanovce, Escorihuela, Escorihuela B, and Poblado Ibérico has shown that the linea sinuosa is much lower in this species than in *M. hassiacus*.

The measurements from TCH-1B fit the size range of *Dolomys occitanus* from its type locality (Sète) and the mean length of the m1 is larger in TCH-1B, according to the data of Chaline and Michaux (1975). We have directly compared the material from TCH-1B with the collection of *D. occitanus* from Sète kept at the University of Lyon I. The m1s from both localities share several morphological characters: wide anterior complex; oval, oblique enamel islet; Sb2 oriented forwards; T4 oriented backwards; and deep SI4. The occlusal morphology is, in general, quite similar in specimens from both localities, although some specimens from Sète have a very shallow prismenfalte, and the *Mimomys*-ridge is therefore scarcely present. In contrast, in lateral view, the differences between both populations are very noticeable. The crown is notably lower in the specimens from Sète, and the linea sinuosa is much less developed. The anterosinulid and hyposinulid are clearly lower in the m1s from Sète than in those from TCH-1B; the mimosinulid is very low or even absent in some specimens, and the hyposinulid is almost inappreciable. The height of the Sb3-wall is very similar in all the specimens from TCH-1B, close to the entire height of the crown in unworn specimens; therefore, the enamel islet occurs in early stages of wear. In the specimens from Sète, however, the height of the Sb3-wall is quite variable, but always lower than in TCH-1B; in many specimens, this wall is very far from the apex of the tooth, so the enamel islet appears in very advanced stages of wear. In fact, this feature allowed Maul (1996) to transfer the species *Mimomys occitanus* to the genus *Dolomys*, since the height of its Sb3-wall is notably lower than in all the species of *Mimomys*. The new combination, *Dolomys occitanus*, is now widely accepted.

Mimomys hassiacus from TCH-1B is notably larger than *M. stehlini* from San Giusto (type-locality), Seynes, Balaruc 2 (Michaux, 1971; Bachelet et al., 1991), Moreda (Castillo, 1990; Bachelet et al., 1991), Grand Serre (Aguilar et al., 1993), Concud Estación 1 (Adrover et al., 1988), and TCH-3 and 13. We have compared the specimens from TCH-1B with those of *M. stehlini* from Seynes, Balaruc 2, Moreda1-B, Rambla Seca-Ab, TCH-3, and TCH-13. The molars of *M. stehlini* are notably narrower and

somewhat higher. In m1, the enamel islet is smaller and more rounded, the anterior complex is more compressed, and the asymmetry between the labial and lingual triangles is more accentuated than in the specimens from TCH-1B. In contrast to *M. hassiacus*, the T4 and the Sb2 in *M. stehlini* are oriented transversally to the longitudinal axis of the molar. The linea sinuosa, especially the hyposinuid, is somewhat higher in *M. stehlini* than in *M. hassiacus* from TCH-1B. The M3 of *M. stehlini* has two enamel islets.

Mimomys hassiacus from TCH-1B is smaller than *M. polonicus* from Rebielice Krolewskie (type-locality; Kowalski, 1960) and Magny-les-Auxonnes (Michaux, 1971), and similar in size to *M. polonicus* from Cessey-sur-Tille and Chagny II (Michaux, 1971). The linea sinuosa is notably higher, with a much higher and thinner hyposinuid, and the cement is more abundant in the molars of *M. polonicus* than in those of *M. hassiacus* from TCH-1B. *Mimomys hassiacus* can be distinguished from *M. pliocaenicus* and *M. medasensis* by its smaller size, its lower crown height, and its much lower linea sinuosa.

References to *M. hassiacus* in the Iberian Peninsula are very scarce (Adrover et al., 1988). Esteban and López Martínez (1990) reported the presence of a medium-sized arvicoline in Moreda that was labelled as *M. cf. hajmackensis* (now considered a synonym of *M. hassiacus*). We have studied the specimens from the level Moreda1-A (Mo1-A), assigned by Castillo (1990) to "*M. occitanus*". Despite the sparse material (only five complete molars), one can observe that these teeth are notably larger and clearly have a higher crown and a more developed linea sinuosa than *D. occitanus* from Sète. On the other hand, the specimens from Mo1-A are very similar in size and morphology to those of *M. hassiacus* from TCH-1B. Therefore, the material from Mo1-A must be assigned to *M. hassiacus*. This determination confirms the datum of Esteban and López Martínez (1990), although these authors did not consider the subdivision of the karstic locality of Moreda in several infillings of different ages, as pointed out by Castillo (1990). According to the data of this latter author, *M. hassiacus* is only present in the oldest level, Mo1-A, whereas in younger infillings, other arvicolines appear (*M. stehlini*, *Kislangia cappetai*, *K. ischus*).

As in the cases of TCH-1B and Mo1-A, it is probable that other populations from southern Spain ascribed to other species (specially *D. occitanus* and *M. stehlini*) in fact correspond to *M. hassiacus*. Therefore, the lack of citations of this species from southern Spain may be due to incorrect determinations more than to a real absence of this form in the region. This problem will be discussed later.

MIMOMYS STEHLINI Kormos, 1931
(Fig. 3)

Occurrence—TCH-3, TCH-13.

Description—The material from TCH-13 was first described by Minwer Barakat et al. (2004). Renewed sampling expanded the collection to 197 molars including 28 m1 and 23 M3 (Minwer-Barakat, 2005).

The most characteristic features of m1 are: moderate hypsodonty; scarce cement in the synclinals; poorly differentiated enamel; small and round enamel islet; shallow inselfalte and prismenfalte; narrow anterior complex; Sb2 transverse to the longitudinal axis of the tooth; T4 small; deep S14, delimiting a distinct T5. The labial triangles are notably smaller than the lingual ones, so the teeth are clearly asymmetrical. The anterosinuid is high, the hyposinuid is rather lower, and the height of the hyposinuid is less than one third of the crown height.

M3 has two enamel islets: one, small and circular, between the anterior lobe and the T2, and the other one, larger and oval, in the posterior complex. The posterior islet appears in earlier stages of wear than the anterior one. The posterior complex is

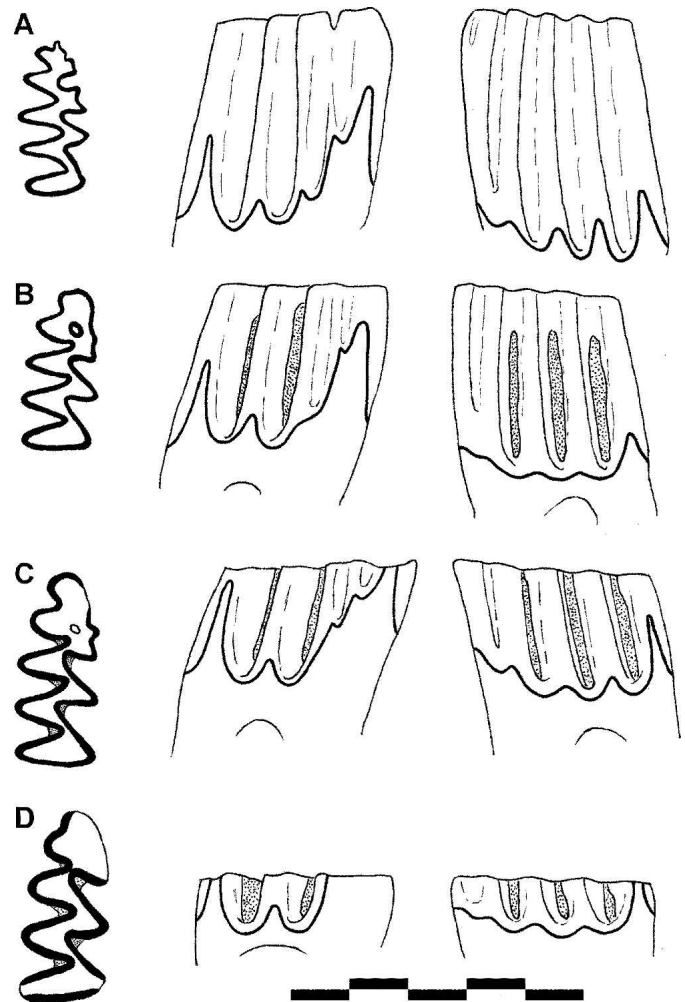


FIGURE 3. Lower first molars of *Mimomys stehlini* from TCH-13 with different stages of wear in occlusal (left), labial (middle) and lingual (right) views. **A**, TCH-13 111; **B**, TCH-13 39; **C**, TCH-13 110; **D**, TCH-13 114. Scale bar equals 5 mm.

narrow. The T4 is small and sharp-pointed. The linea sinuosa is relatively low.

The scarce material from TCH-3 (one fragment and one complete M3; eight incomplete m1) is described in Minwer-Barakat et al. (2004). No significant differences can be observed between these specimens and the material described from TCH-13.

Measurements—See Table 2.

Discussion—The populations from TCH-3 and 13 were assigned to *Mimomys minor* in a previous paper (Minwer-Barakat et al., 2004). In the present article, we acknowledge the syn-

TABLE 2. Measurements (mm) of *Mimomys stehlini* from Tollo de Chiclana-13.

| Parameter | n | min | mean | max |
|--------------------------------|----|------|------|------|
| Occlusal length of m1 | 9 | 2.63 | 2.94 | 3.26 |
| Occlusal width of m1 | 20 | 1.07 | 1.21 | 1.29 |
| Length of the anterior complex | 9 | 1.15 | 1.25 | 1.47 |
| A/L | 9 | 35.7 | 42.6 | 45.8 |
| Height of the hyposinuid of m1 | 12 | 0.70 | 0.95 | 1.19 |
| Occlusal length of M3 | 15 | 1.55 | 1.73 | 1.95 |

The A/L ratio is the percentage of the length of the anterior complex in relation to the total length of the m1 (after van der Meulen, 1973).

onymy between *M. minor* and *M. stehlini*, as proposed by Fejfar and Heinrich (1990a); therefore, these populations are ascribed to *M. stehlini*.

M. stehlini, described from the Italian locality of San Giusto, is characterized by its small size and by several morphological characters including intermediate development of the linea sinuosa. The emended diagnosis given by Bachelet et al. (1991) compiles other diagnostic characters like the disappearance of the enamel islet at approximately half of the height of the crown, the shallow prismenfalte, and the scarcity of cement. Other characteristic features are the accentuated asymmetry between the labial and lingual triangles in the m1 and the existence of two enamel islets in the M3.

We have compared our material with published data of *M. stehlini* from Seynes, Balaruc 2 (Michaux, 1971; Bachelet et al., 1991), Moreda (Castillo, 1990; Esteban and López Martínez, 1990; Bachelet et al., 1991), Grand Serre (Aguilar et al., 1993), Concud Estación 1 (Adrover et al., 1988), Hajnáčka, and San Giusto (Fejfar et al., 1998; Fejfar, 2001). We have also compared it with material of *M. stehlini* from Balaruc 2, Seynes, Concud Estación 1 (stored at the University of Lyon I), Moreda1-B, and Rambla Seca-Ab (kept at the University of Granada).

The length of the holotype of *M. stehlini* (2.93 mm; van de Weerd, 1976) is almost identical to the mean length of the m1 from TCH-13. The measurements of TCH-13 are slightly larger than those of *M. stehlini* from Seynes and Balaruc 2, and very similar to those from Moreda. The few specimens from Concud Estación 1 are somewhat smaller than those from TCH-13. The length of the single m1 of *M. stehlini* from Grand Serre fits the size range of the population from TCH-13.

The occlusal morphology of m1 from TCH-13 is very similar to that of the holotype of *M. stehlini*. The only difference with the specimens from Hajnáčka is the shallower prismenfalte in the molars from TCH-13. The height of the linea sinuosa is, for most specimens from TCH-13, intermediate between that of the specimens from San Giusto (holotype) and Hajnáčka.

There is no significant morphological difference between the specimens from TCH-3 and 13, Balaruc 2, Seynes, Concud Estación, Moreda1-B, and Rambla Seca-Ab; in all of them, m1 has a narrow anterior complex, a small and rounded enamel islet that disappears in senile specimens, a very accentuated asymmetry between the labial and lingual triangles, a deep SI4, and a T4 oriented transversally to the axis of the molar. The height of the crown, the persistence of the enamel islet, and the morphology of the linea sinuosa (with the anterosinuid higher than the hypsinuid), are also similar in the indicated populations. The M3 is also similar in all these localities; it is a small tooth with two enamel islets, a narrow posterior complex and a relatively low linea sinuosa. The existence of cement in the synclinals is a variable character in all the populations.

Although *Dolomys occitanus* has been considered by different authors to be a synonym of *M. stehlini* (see next section), the differences between these two species are very clear: *D. occitanus* from Sète (Michaux, 1971; Chaline and Michaux, 1975) is larger than *M. stehlini* from all the localities we have compared with. In addition, m1 of *D. occitanus* is lower-crowned and has a larger anterior complex and a clearly lower linea sinuosa than that of *M. stehlini*; the enamel islet appears in much more advanced stages of wear and the T4 is oriented posteriorly.

Mimomys gracilis from Nîmes, Wèze, Csarnota (Michaux, 1971), and Ortaica (Ünay and de Bruijn, 1998) is much smaller than *M. stehlini*. Through direct comparison of our material with that of *M. gracilis* from Wèze, Sarrión, Escorihuela, and Escorihuela B, we observed that the molars of *M. gracilis* are lower-crowned and have a less-developed linea sinuosa than those of *M. stehlini*. *Mimomys reidi* from Rebielice, Kadzielnia, Cessey-sur-Tille (Michaux, 1971), and Tegelen (Tesakov, 1998) is also clearly smaller than *M. stehlini* from Tollo de Chiclana. Morpho-

logically, *M. stehlini* can be distinguished from *M. reidi* by its lower crown, its less developed linea sinuosa, its more persistent enamel islet, and its deeper SI4. The M3 of *M. reidi* is more elongated and has a single enamel islet.

Mimomys hassiacus is clearly larger than *M. stehlini*. We have directly compared the material from TCH-3 and 13 with *M. hassiacus* from Arondelli, Escorihuela, Concud Pueblo 3, Concud Estación 1, 2, and 3, and TCH-1B, and have observed the following morphological differences: m1 of *M. stehlini* is narrower and has a smaller and more rounded enamel islet than that of *M. hassiacus*; the asymmetry between the lingual and labial triangles is more accentuated and the anterior complex is considerably more compressed in *M. stehlini* than in *M. hassiacus*. The T4 and Sb2 of *M. stehlini* from TCH-3 and 13 are transverse to the longitudinal axis of the molar, in contrast to the corresponding features of *M. hassiacus*. The inselfalte is somewhat deeper in *M. hassiacus*. M3 of *M. stehlini* has a narrower posterior complex and a more pronounced SI3 and Sb3 than that of *M. hassiacus*, which has only one enamel islet. The height of the crown and the development of the linea sinuosa are variable in the different populations of *M. hassiacus* we have examined; the specimens from the oldest populations of *M. hassiacus* (TCH-1B, Escorihuela) have a lower crown and a less developed linea sinuosa than those of *M. stehlini* from TCH-3 and 13, whereas the teeth from the youngest localities (Concud Pueblo, Concud Estación) are more hypsodont and have a notably higher linea sinuosa than those of *M. stehlini* from TCH-3 and 13.

Mimomys stehlini differs markedly from other upper Pliocene species (i.e., *M. medasensis*, *M. polonicus*, *M. pliocaenicus*, *Kislangia cappetai*, *K. ischus*, and *K. gusii*) by its clearly smaller size.

REMARKS ON THE SPECIES OF *MIMOMYS* FROM THE RUSCINIAN AND LOWER VILLANYIAN OF SOUTHERN SPAIN

The presence of different species of Arvicolinae in the Ruscinian and lower Villanyian in Spain has been problematic for several reasons, primarily the lack of agreement in the criteria employed by several authors for distinguishing and naming the species. Several European populations of small-sized Arvicolinae have been assigned to *M. stehlini* or to other species by different authors, resulting in confusion in their specific identification. In recent decades, different synonymies have been proposed between *M. stehlini* and other species, although not all of them have been widely accepted. At present, populations have been referred to *M. stehlini* that clearly differ from the one from San Giusto. It is therefore necessary to clarify several questions regarding this species, and to reconsider the validity of the identifications of several Pliocene populations of arvicolines from southern Spain.

First, the population from Sète, described by Thaler (1955) as the type-population of "*Mimomys occitanus*", has been assigned to *M. stehlini* in several papers (Michaux, 1971; Chaline and Michaux, 1975). Later, those and other authors recognized the distinctiveness of these two species, and included *M. stehlini* in the evolutionary lineage "*M. occitanus*–*M. ostramosensis*", which they considered an example of phyletic gradualism (Chaline and Mein, 1979; Rabeder, 1981; Chaline and Laurin, 1986). According to this hypothesis, the species of this lineage show several morphological changes that follow a unidirectional trend, without apparent interruptions in time: increase of the hypsodonty and the development of the linea sinuosa, and progressive disappearance of the enamel islet and the roots. If this is true, the forms belonging to *M. stehlini* should show intermediate morphological features between those of "*M. occitanus*" and *M. polonicus* (see Chaline and Laurin, 1986). The invalidity of these phylogenetic relationships has subsequently been demonstrated.

On the one hand, *occitanus* has been referred to *Dolomys* by Maul (1996), so obviously it is not the ancestor of *M. stehlini*. On the other hand, *M. hassiacus* is today considered to be the ancestor of *M. polonicus* (Fejfar et al., 1997, 1998; Mörs et al., 1998), whereas *M. stehlini*, clearly small-sized, belongs to a different phylogenetic lineage. The inclusion of *M. stehlini* in the lineage *occitanus-ostromosensis* has been very frequent in the literature, even in recent papers (Hurth et al., 2003). Several populations with an occlusal morphology similar to that of *M. polonicus* (but lower crowned, with a less developed linea sinuosa, and a more persistent enamel islet) erroneously have been assigned to *M. stehlini*; these forms must be attributed to *M. hassiacus* (as in the case of the population from TCH-1B).

Second, many early Villanyian populations of small sized arvicoline have been ascribed to *M. minor* Fejfar, 1961, described from Hajnácka as a subspecies of *M. pliocaenicus* and later elevated to species rank. The synonymy between *M. minor* and *M. septimanus* Michaux, 1971, has been noted by Michaux and Chaline (1982); populations like Seynes and Balaruc II, first ascribed to *M. septimanus*, were therefore assigned later to *M. minor*. Fejfar and Heinrich (1982) considered *minor* to be a subspecies of *M. stehlini*; they alluded to the specimens from Arondelli, Seynes, Beremend-3, and Hajnácka as *Mimomys stehlini minor*, reserving the name *M. stehlini stehlini* for younger populations like Osztramos 7. Later on, these authors admitted the synonymy between these species, accepting the oldest name, *M. stehlini* (Fejfar and Heinrich, 1990a). Nevertheless, there are frequent later references to *M. minor* (Aguilar et al., 1993; Erbajeva and Alexeeva, 2000; Erbajeva et al., 2003; Hurth et al., 2003). Moreover, Bachelet et al. (1991) explicitly recognized differences between *M. stehlini* and *M. minor* from Hajnácka. We think that the differences between the material from Hajnácka and the other populations assigned to *M. stehlini* are not sufficient to justify their referral to two different species. We therefore accept the synonymy proposed by Fejfar and Heinrich, 1990a, and assign the populations from TCH-3 and 13, previously ascribed to *M. minor* (Minwer-Barakat et al., 2004), to *M. stehlini*.

Likewise, several populations assigned to *M. kretzoi* Fejfar, 1961 (e.g., Deutsch-Altenburg 9 and 20; Rabeder, 1981), have been ascribed to *M. stehlini* in later papers (Bachelet et al., 1991). The small-sized arvicoline found in Moreda, initially identified as *M. stehlini* (Gmelig-Meyling and Michaux, 1973; Ruiz Bustos and Sesé, 1985), was considered to belong to *M. kretzoi* by Esteban and López Martínez (1990). However, as argued by Bachelet et al. (1991), the subtle difference in size between the specimens from Moreda and those of populations of *M. stehlini* like Seynes and Balaruc 2 are not enough to assign the material from Moreda to a different species; this population certainly corresponds to *M. stehlini*.

Finally, we must indicate the problems related to the synonymy proposed by Ruiz Bustos and Sesé (1985) and Ruiz Bustos (1987) between the species *M. stehlini*, "*M. occitanus*", *M. gracilis*, *M. septimanus*, *M. kretzoi*, *M. polonicus*, *M. hassiacus*, and *M. hajnackensis*. As we have argued in previous paragraphs, the synonymies between *M. septimanus* and *M. stehlini* and between *M. hassiacus* and *M. hajnackensis* are widely accepted. Nevertheless, biometrical and morphological differences between the species *M. stehlini*, *D. occitanus*, *M. gracilis*, *M. polonicus*, and *M. hassiacus* are very clear (see above). The cited authors have continued using these synonymies in later papers, most of them referring to localities from the Guadix-Baza Basin; even in recent papers (Sesé et al., 2001; Ruiz Bustos, 2002) all the representatives of *Mimomys* found in this basin in the upper Ruscinian and lower Villanyian are assigned to *M. stehlini*. This situation has created great confusion concerning the presence of *Mimomys* in southern Spain in the Pliocene, given that many of the references to *M. stehlini* must correspond in fact to other species. Thus, the few specimens from Huéscar-3 (Mazo et al.,

1985) and Barranco de Cañuelas-3 (Sesé, 1989) are clearly larger than *M. stehlini* from San Giusto, Seynes, Balaruc 2, Moreda, and TCH-13; in addition, the faunal association from Huéscar-3, with *Apocricetus* and *Paraethomys*, indicates that this locality is older than the European sites in which *M. stehlini* is present. The arvicoline from Huéscar-3 and Barranco de Cañuelas-3 must should correspond to another species, probably *D. occitanus* or *M. hassiacus*. Likewise, the citations of *M. stehlini* from Nuca-1 (Ruiz Bustos, 1991), Santa, and Cómodo (Guerra Merchán and Ruiz Bustos, 1991) seem to be incorrect. Although these papers include no descriptions, measurements or figures of the teeth, the faunal associations of these sites, with representatives of *Occitanomys*, *Paraethomys*, and *Apocricetus*, are indicative of the late Ruscinian and, therefore, predate the appearance of *M. stehlini*.

For all these reasons, special caution must be taken in comparisons between several populations assigned to *M. stehlini*, because the observed biometrical and morphological differences may be due to incorrect or obsolete determinations.

Figure 4 summarizes different interpretations of the phylogenetic relationships between the most common species of *Mimomys* from the Pliocene of Europe. The origin of *M. hassiacus* has been controversial; several authors (Fejfar and Heinrich, 1982; Viriot et al., 1990; Neraudeau et al., 1995) saw its ancestor in "*Mimomys*" *occitanus*. Later on, the latter species was transferred to *Dolomys* by Maul (1996); *Mimomys davakosi*, present in localities of the lowermost upper Ruscinian, was considered to be the ancestor of *M. hassiacus* (see Fejfar et al., 1997). Nevertheless, Fejfar (2001) recently maintained that *M. hassiacus* may be an oriental immigrant.

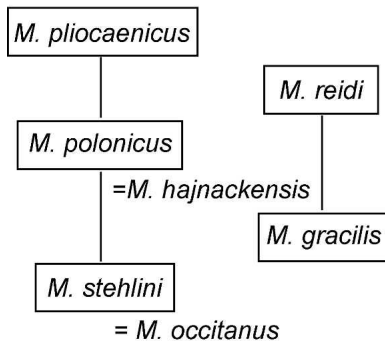
With regard to *M. stehlini*, after different interpretations, the most recent hypothesis (Fejfar, 2001) points to its origin from *M. gracilis*. This opinion is the most reliable, given the similarity between these species and their biostratigraphical distribution; all the localities where *M. gracilis* has been identified are older than those yielding remains of *M. stehlini*. We therefore accept the phylogenetic relationships proposed by Fejfar (2001).

BIOSTRATIGRAPHICAL CORRELATIONS

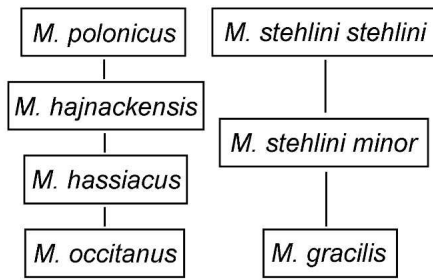
The faunal associations from TCH-1B, 3, and 13 allow them to be assigned to both MN units (Mein, 1990) and European Land Mammal Ages (Sen, 1997). The presence of widespread species of Arvicolinae in the studied levels also makes their correlation with other (even distant) European localities possible. Figure 5 synthesizes these biostratigraphical correlations.

The locality of TCH-1B can be correlated with the karstic level of Mo1-A (Castillo, 1990); the faunal lists of both sites are very similar and share *Mimomys hassiacus*, among other species; in fact, these are the only two localities in southern Spain that have yielded this species. The site of TCH-1B is younger than TCH-1 and Galera-C (Agustí et al., 1997), in which *Dolomys adroveri* has been identified. Besides the above mentioned sites, we cannot correlate TCH-1B accurately with other upper Ruscinian localities from the Guadix-Baza Basin. The scarcity of remains of Arvicolinae in Gorafe 2, 3, and 5 does not allow a precise determination, and there are no representatives of this family in Cañada del Castaño-1 (Martín-Suárez, 1988). It is also impossible to correlate TCH-1B with the sites of Huéscar 3 (Mazo et al., 1985), Barranco de Quebradas 1, Barranco de Cañuelas 2, 3, and 5 (Sesé, 1989), Nuca-1 (Ruiz Bustos, 1991) or Santa, and Cómodo (Guerra Merchán and Ruiz Bustos, 1991). In the cited papers, *D. occitanus*, *M. gracilis*, and *M. hassiacus* are considered synonyms of *M. stehlini*. As we argue above, we don't support the synonymy of these species because they show significant differences. Moreover, according to various authors (Mein et al., 1990; Fejfar and Heinrich, 1990b; Fejfar et al., 1998), the oldest record of *M. stehlini* corresponds to the lowermost Villanyian, so

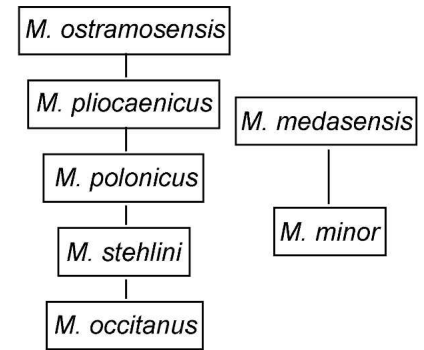
Chaline and Michaux (1975)



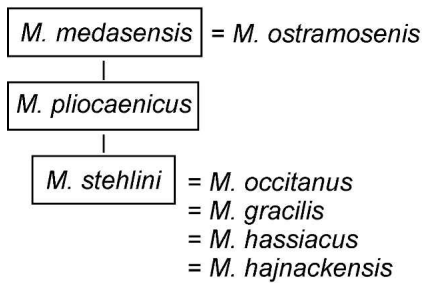
Fejfar and Heinrich (1982)



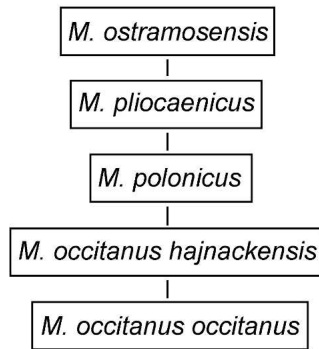
Chaline and Laurin (1986)



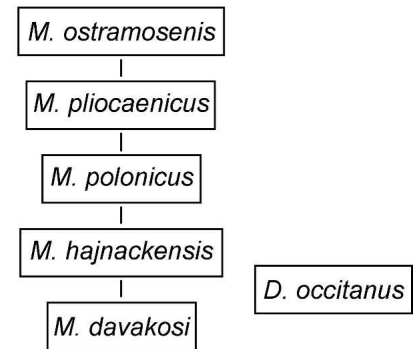
Ruiz Bustos (1987)



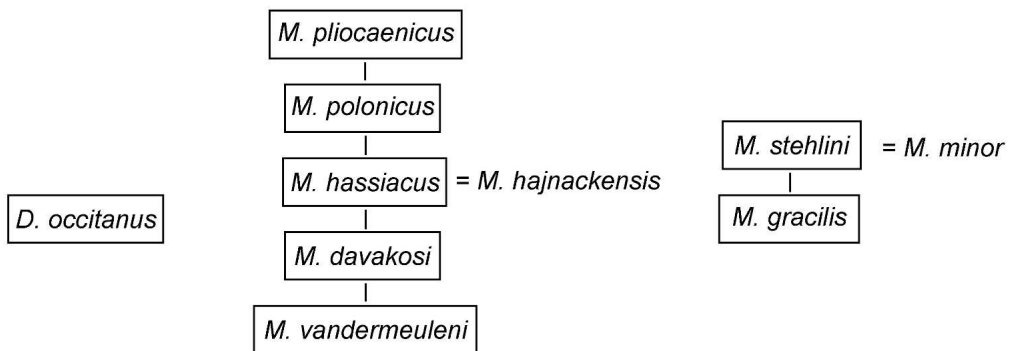
Neraudeau et al. (1995)



Maul (1996)



Fejfar et al. (1997, 1998)



Fejfar (2001)

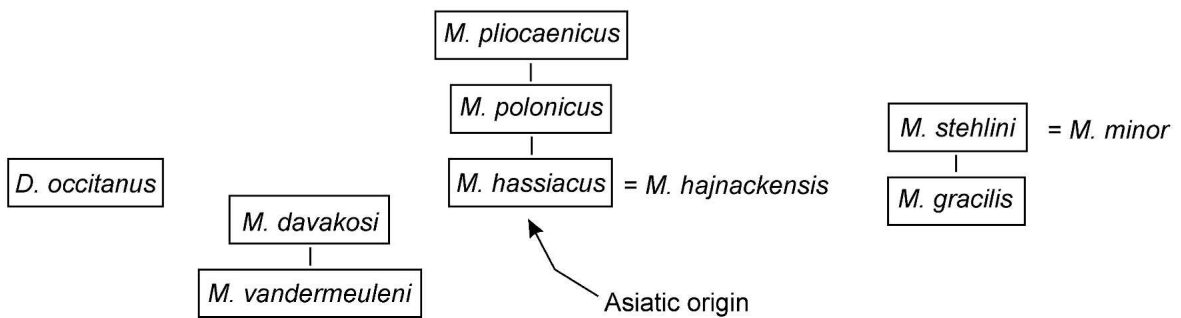


FIGURE 4. Different interpretations of the phylogenetic relationships between the most common species of *Mimomys* in the Pliocene of Europe.

| ELMAS | MN UNITS | RODENT ZONES | DISTRIBUTION OF ARVICOLINE SPECIES | VERTEBRATE LOCALITIES | | |
|------------|----------|--|---|--|---|--|
| | | | | Guadix-Baza Basin | Iberian Peninsula | Central and Eastern Europe |
| VILLANYIAN | MN 17 | <i>Mimomys pliocaenicus</i> | | Cortes de Baza 1 Galera 2, G TCH-10, 10B | Almenara 1 Islas Medas Valdeganga 7, 10 | Osztramos 3 Villany 3 Saint Vallier |
| | MN 16 | <i>Mimomys polonicus</i> <i>Mimomys hassiacus</i> + <i>M. stehlini</i> | <i>M. davakosi</i> <i>D. adroveri</i> <i>M. gracilis</i> <i>M. hassiacus</i> <i>M. stehlini</i> <i>K. ischus</i> | Zújar 11 TCH-13 TCH-3 Moreda1-B | Concud Estación Concud Pueblo Villarroya Valdeganga 9, 16 La Marmota Valdeganga 14, 15 | Osztramos 7 Les Étouaires Hajnacka Seynes San Giusto Aronelli Balaruc 2 |
| RUSCINIAN | MN 15 | <i>Mimomys hassiacus</i> + <i>M. gracilis</i> <i>Mimomys davakosi</i> | | Moreda1-A TCH-1B Galera-C TCH-1 | Escorihuela Escorihuela B Layna Orrios 3, 7 Asta Regia 3 Villalba Alta 1 Arquillo 3 | Wölfersheim Weze Ivanovce Sète Csarnóta 2 Ptolemais 3 Serrat d'en Vacquer |

FIGURE 5. Correlation of the studied localities with the corresponding European Land Mammal Ages (Sen, 1997), MN units (Mein, 1990), Rodent Zones (Fejfar et al., 1998), and with different European vertebrate localities. The biostratigraphic ranges of several species of Arvicolinae are also shown. Solid lines indicate species occurrences in the Iberian Peninsula, dashed lines indicate occurrences in Central and Eastern Europe.

the citations from Ruscinian localities seem to be incorrect. Therefore, we cannot provide correlations more precise for these sites than the upper Ruscinian (which is established based on the presence of *Stephanomys donnezani*).

According to Fejfar et al. (1998), *M. hassiacus* is present in Europe from the upper Ruscinian (MN 15, *M. hassiacus* + *M. gracilis* zone) to the lower Villanyian (MN 16, *M. hassiacus* + *M. stehlini* zone). Thus, in this case, *M. hassiacus* is not useful to assign TCH-1B to a specific MN unit. The presence of *Occitanomys brailloni* and *Stephanomys donnezani* in this site does permit referral to the upper Ruscinian (MN 15), however, since these two species do not pass the Ruscinian–Villanyian boundary (Mein, 1990; Agustí et al., 2001).

This assignment opposes that of Fejfar (2001), who suggested that the apparition of *M. hassiacus* indicates the beginning of the Villanyian; this author places some localities with the association *M. hassiacus*–*M. gracilis* (e.g., Wölfersheim) in MN 16. However, the sites of Wèze and Ivanovce were also assigned to the upper Ruscinian (Fejfar, 2001), despite the presence of *M. hassiacus* (Kowalski, 1990; Fejfar et al., 1997). We therefore believe that *M. hassiacus* appears at least by the latest Ruscinian and passes the Ruscinian–Villanyian boundary without significant morphological changes, as indicated by other studies (Fejfar et al., 1997, 1998; Lindsay et al., 1997; Mörs et al., 1998). According to this interpretation, this species cannot be used to establish this boundary. On the contrary, the occurrence of *M. stehlini* is a clear indicator of the beginning of the Villanyian, because this species does not co-occur with *M. gracilis* or other typically Ruscinian species.

The localities from Teruel where *M. hassiacus* and *M. gracilis* are present (i.e., Escorihuela, Escorihuela A and C, Gea 0), as-

signed by Mein et al. (1990) to the Villanyian, would correspond to the Ruscinian according to the biozonation of Fejfar et al. (1998), which is accepted in the present paper. These sites are similar in age to TCH-1B, where *M. gracilis* has not been recorded, but other typically Ruscinian taxa are present together with *M. hassiacus*. The molars from TCH-1B have a lower crown and a less developed linea sinuosa than those of *M. hassiacus* from Escorihuela; thus, we infer that TCH-1B is slightly older. Other upper Ruscinian localities where *M. hassiacus* is also present are Wölfersheim (Germany), Wèze (Poland), and Ivanovce (Slovakia).

The localities of TCH-3 and 13 can be correlated with Moreda1-B (which has a very similar faunal list) and Zújar-11 (Oms et al., 1999); this latter site has not yielded *M. stehlini*, but other species have been identified that enable the correlation with TCH-3 and 13, including *Kislangia ischus*, *Stephanomys thaleri*, and *S. minor*.

The presence of *Mimomys stehlini* in TCH-3 and 13 allows these localities to be assigned to the MN 16. According to Fejfar et al. (1998), the occurrence of this species indicates the beginning of the Villanyian, and its stratigraphic range is restricted to the lower Villanyian. Nevertheless, it is impossible to assign TCH-3 and 13 to one of the two biozones in which Fejfar et al. (1998) divide the MN 16 (*M. stehlini* + *M. hassiacus* zone and *M. polonicus* zone), because *M. stehlini* is present in both zones, coexisting with *M. polonicus* in localities like Osztramos 7 and Les Étouaires.

Mimomys stehlini has a very wide distribution, and permits a precise correlation between TCH-3 and 13 and many European sites: Concud Pueblo and Concud Estación 1 and 2 in the Teruel region, Balaruc 2, Seynes, Les Étouaires (France), Hajnácka

(Slovakia), San Giusto, Arondelli (Italy), Osztramos 7 (Hungary), and Uryv 1 (Russia). *Kislangia ischus*, present in TCH-3, has also been found in other Spanish localities like La Marmota 1 and 2, El Carrasco, El Rincón 2 (Esteban and Martínez-Salanova, 1987), Valdeganga 14 and 15 (Opdyke et al., 1997), and Villarroya (Agustí and Oms, 2001).

CONCLUSIONS

The specific identifications of the Arvicolinae from TCH-1B, 3, and 13 have been revised: the population of *Mimomys* from TCH-1B is assigned to *M. hassiacus*; those from TCH-3 and 13 are attributed to *M. stehlini*. The medium-sized arvicoline from Mo1-A, identified as "*Mimomys*" *occitanus* by Castillo (1990), is also considered to belong to *M. hassiacus*. These are the first records of the species in southern Spain.

The synonymy of *M. stehlini*, "*M.*" *occitanus*, *M. gracilis*, *M. polonicus*, and *M. hassiacus* proposed by Ruiz Bustos and Sesé (1985) and Ruiz Bustos (1987) has created great confusion about the presence of these species in the Pliocene deposits of the Guadix-Baza Basin, and is no longer valid. An exhaustive revision of the Ruscinian and Villanyian arvicolines from South Spain is necessary. Quite probably, some upper Ruscinian populations erroneously assigned to *M. stehlini* belong to *M. hassiacus* or to other species found in other Iberian basins (e.g., *M. davakosi*, *M. vandermeuleni*, *M. gracilis*); the presence of these species would be very interesting in order to establish the relative stratigraphic position of the localities in the Guadix-Baza Basin.

The species *M. stehlini* is restricted to the lower Villanyian; it is a very appropriate indicator for delimiting the Ruscinian-Villanyian boundary and for correlating southern Spanish localities with other European sites.

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