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FEJFAR'S LEGACY: A SPANISH PERSPECTIVE ON ARVICOLINAE (RODENTIA, MAMMALIA) BIOSTRATIGRAPHY

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Abstract: In the present work, we adopt the comparative logic and methodologies used by Fejfar and colleagues, embedding Spanish faunal assemblages into continental frameworks through the evolutionary history of arvicoline rodents. Over the past three decades in Spain, extensive new collections have been made and existing materials have been re-evaluated. The present work honors the intellectual legacy of Oldřich Fejfar, whose fundamental contributions have shaped Spanish Quaternary small mammal biochronology. Fejfar's work, focused on refining arvicoline systematics, developing interregional correlation schemes, and demonstrating the biochronological power of small mammals, provides the essential framework upon which our research is built. This study applies his intellectual legacy to Iberian faunas, highlighting their continued significance for Quaternary stratigraphy and paleoecology. In the present work, the geological time selected is the Piacenzian, Gelasian, Calabrian (around 3.1–0.7 Ma), which shows a likely correlation between Central Europe and Spain, using Arvicolinae mammals during the latest Pliocene and Early Pleistocene interval.

Key words: Arvicolinae rodents, biostratigraphic correlation, latest Pliocene, Early Pleistocene, Iberian Peninsula, Central Europe

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Introduction

The late Cenozoic was a period of rapid faunal turnover events and climatic oscillation that reshaped Eurasian mammal communities. A major source of information about the period comes from the study of small mammals, particularly arvicoline rodents, whose rapid evolutionary rates and distinctive dental morphology make them potent biostratigraphic markers, and produced high-resolution opportunities for continental correlation. The work of Oldřich Fejfar (1931–2023) substantially shaped the conceptual and practical tools used to correlate Plio-Pleistocene sequences across Eurasia, and his work remains a cornerstone for Iberian Quaternary biochronology. Fejfar's pan-Eurasian syntheses established a framework for aligning regional and interregional faunal successions into a coherent temporal scheme. The influential synthesis by Fejfar et al. (1997) brought together late Cenozoic site-sequences from various regions throughout Eurasia, producing an updated correlation that enabled researchers to place local assemblages within a continental sequence. For Spanish Quaternary studies, where local faunal lists must be compared to an increasingly refined continental reference frame, this integrative approach provided essential chronological leverage, enabling Iberian faunas to be situated relative to climatic and evolutionary events documented elsewhere in Eurasia.

Complementing these correlative efforts, Fejfar's work on Arvicolinae (Cricetidae, Rodentia) origins and the evolution of its dental characters provided the taxonomic and morphological resolution needed for high-precision biochronology. The detailed study of Early Pliocene arvicolines (Fejfar and Repenning 1998) clarified the ancestry of the Lemmini and illuminated the tempo of arvicoline diversification at the Pliocene-Pleistocene transition. Later syntheses (Fejfar et al. 2011) examining "microtoid" cricetids and early arvicolines refined the knowledge of dental innovations that mark key evolutionary stages. Recent works, using different technologies like DNA (i.e., Abramson et al. 2021, Alfaro-Ibañez et al. 2024a, b, c, among others) refine and confirm Fejfar's proposals on Arvicolinae evolution and diversification. Together, these studies articulated the understanding of character change that underpins the stage-based correlations widely used in Plio-Pleistocene chronologies.

In Spain, the application of Arvicolinae biochronology has been decisive in establishing high-resolution frameworks for major Quaternary sites. That is a new point from the current database. Major aspects of investigation into the Atapuerca karst system, central to understanding human evolution in Europe, have relied on small vertebrates, mainly arvicoline successions and stage nomenclature to construct a finely resolved chronological, environmental, and paleoclimatic model (Cuenca-Bescós et al. 2003, 2005, 2010a, b, 2013, 2015, 2016, Moya-Costa et al. 2023, Alfaro-Ibáñez et al. 2024b, c, Domínguez-García et al. 2024). In Almenara-Casablanca, and in the Guadix-Baza Basin, Arvicolinae-based correlations provide the scaffolding for interpreting faunal and environmental change during the Early Pleistocene (Agustí et al. 2011, 2015), while at Quibas, rodent assemblages anchor the chronology of Mediterranean faunal turnover (Piñero et al. 2020, Agustí and Piñero 2023). At Atapuerca, Vallparadís and other Spanish sites (Duval et al. 2011), evolutionary stages of *Mimomys* and *Arvicola* are similarly used to refine correlations (Cuenca-Bescós et al. 1995, 2010a, b, Lozano-Fernández et al. 2013, 2019). In all these cases, the methodological tools we employ – dental character analysis, lineage-based stage assignments and cross-referencing with Eurasian sequences – are directly indebted to the taxonomic concepts and interregional frameworks established by Fejfar.

Recent continental reference studies continue to demonstrate the vitality of Dr. Fejfar's legacy. One of my latest works was the study of the rodent fauna of the Hasli Formation of the Irchel Plateau, Switzerland (Thew et al. 2024). The paper provided an integrated biochronological and magnetostratigraphic sequence for older Early Pleistocene interglacial deposits in northern Switzerland; such reference profiles are directly comparable to the selected sites in United Kingdom, Spain, France, Germany, Italy, Czechia, Poland, and other European sequences, when using arvicoline-based tie-points. This work was inspired by the early studies of the fossil rodents from the Hasli Formation of Fejfar, among other authors (Thew et al. 2024, and literature therein).

In the present work, we adopt the same comparative logic, embedding Spanish faunal assemblages into continental frameworks through the evolutionary history of mainly arvicoline rodents. This allows us to refine biochronological placement, test the concordance between arvicoline stages and independent stratigraphic markers, and evaluate how Iberian faunas fit into the broader narrative of Eurasian Plio-Pleistocene evolution.

Over the past three decades in Spain, extensive new collections have been established, and existing materials re-evaluated. The present work honors the intellectual legacy of Oldřich Fejfar, whose foundational contributions have shaped Spanish Quaternary biochronology. Fejfar's work – focused on refining arvicoline systematics, developing interregional correlation schemes, and demonstrating the biochronological power of small mammals – provides the essential framework upon which our research is built. That is a new point from the current database.

Our aim was accomplished by an extensive review of the selected literature (Supplementary material), which provided terrestrial localities from across Europe that are probably less known in synthetic Quaternary studies. This effort has improved faunal lists and the biostratigraphy of the region. To test the strength of our biostratigraphic framework, we focused on localities with independent dating. For ease of reading, references are compiled in online Supplementary material rather than being cited throughout the text, unless a citation is essential for context or attribution.

Material and methods

The integration of the Spanish sites into the biochronological framework of the late Cenozoic in Europe has required the analysis of scientific works focused mainly on studies of arvicoline rodents, because they are the best tool for chronostratigraphic correlation (see references in Supplementary material). Plus, there are papers solely on the ages of sites. A compilation of the over 500 scientific papers consulted has resulted in a schematic stratigraphic distribution of Arvicolinae (and other rodent) sites. The fossiliferous sites are located throughout some European regions and span the Late Pliocene to Early Pleistocene. The study's focus was specifically on this time range (around 3.1 to 0.7 Ma). We use here the Calabrian MmQ zones MmQ1–MmQ3 as defined by Agustí et al. (1987).

Literature selection

To ensure the relevance and scientific rigor of our synthesis, we applied the following criteria for literature selection: (1) inclusion of faunal lists derived from paleontological analyses; (2) a well-defined chronological framework of the site(s); (3) when available, a detailed geological and paleontological context; and (4) high-quality stratigraphic sections, with clear differentiation of fossiliferous layers.

Site selection

The selection of terrestrial localities was guided by multiple criteria: geographic coverage of Central Europe and the Iberian Peninsula; archaeological and paleontological significance; availability of reliable dating methods; a wide stratigraphic range; the presence of well-documented rodent assemblages. Localities based solely on faunal lists without analytical (geology, radiometric data) discussions were excluded to ensure the robustness of the biostratigraphic framework. The list of fossiliferous layers containing Arvicolinae rodent remains across the 3.1–0.7 Ma interval in selected European regions is presented in Table 1. The stratigraphic ordering of sites is the result of the chronological order given by the authors: biostratigraphic, radiochronologic, and magnetostratigraphic order. The sites are listed vertically, likely in chronological order from youngest (top) to oldest (bottom). Each species is mapped horizontally across the site list. The first occurrence of a species in the stratigraphic column represents its FAD in the European records. This allows for visual tracking of evolutionary and dispersal patterns through time.

Data extraction

Over the past five years, we have systematically compiled faunal lists and stratigraphic data from the literature.

This process involved manual review and data entry using the FileMaker platform (File Maker Pro14), with cross-referencing applied wherever possible to enhance consistency and accuracy.

The database includes the following fields: locality name, country, radiometric age, magnetostratigraphic age, MN zone, age in Ma, latitude, longitude, age determined by alternative methods. IUGS age, geological context, and detailed species lists of small mammals (including Eulipotyphla, Chiroptera, Rodentia, and Lagomorpha), invertebrates, and large mammals. It also contains references to relevant paleontological and geological/chronological literature. A final field is reserved for observations, such as the archaeological and paleoanthropological significance of each site.

We intend to make this database available to the broader scientific community – not only to specialists in paleontology. In future stages, we aim to integrate our dataset into public platforms such as the Paleobiology Database (PBDB) and the Global Biodiversity Information Facility (GBIF). That is a new point from the current database. See the complete list of references in Supplementary material.

Comparative methods

We conducted cross-site comparisons of arvicoline rodent assemblages, focusing on species turnover, first and last appearance data (FADs and LADs), and evolutionary lineages (Lozano-Fernandez et al. 2013, 2015, 2019, Martin et al. 2018, Piñero et al. 2020, Fejfar et al. 1997, Tesakov 2003, among others). This allowed us to identify biostratigraphic markers and refine regional correlations within the Late Pliocene – Early Pleistocene interval.

Statistical tools

Previous statistics and cluster analyses were performed using FileMaker and Excel 2016. These analyses helped quantify faunal similarities and dissimilarities among sites, and detect potential chronological outliers. As it is an ongoing project, the preliminary results are presented here in tables and figures.

Chronological integration

Sites with independent dating (radiometric, magnetostratigraphic, or biostratigraphic) were prioritized to anchor the framework. We cross-referenced MN zones and IUGS stages to ensure consistency across temporal scales. Where available, we incorporated age models from published stratigraphic charts.

This multi-method approach strengthens the reliability of our biochronological framework and enhances its applicability for future paleontological and archaeological research.

Results

The compilation of the data base of fossil localities containing rodent remains across Spain and Central Europe yielded a total of 300 fossiliferous layers, each preserving small vertebrates alongside other faunal elements.

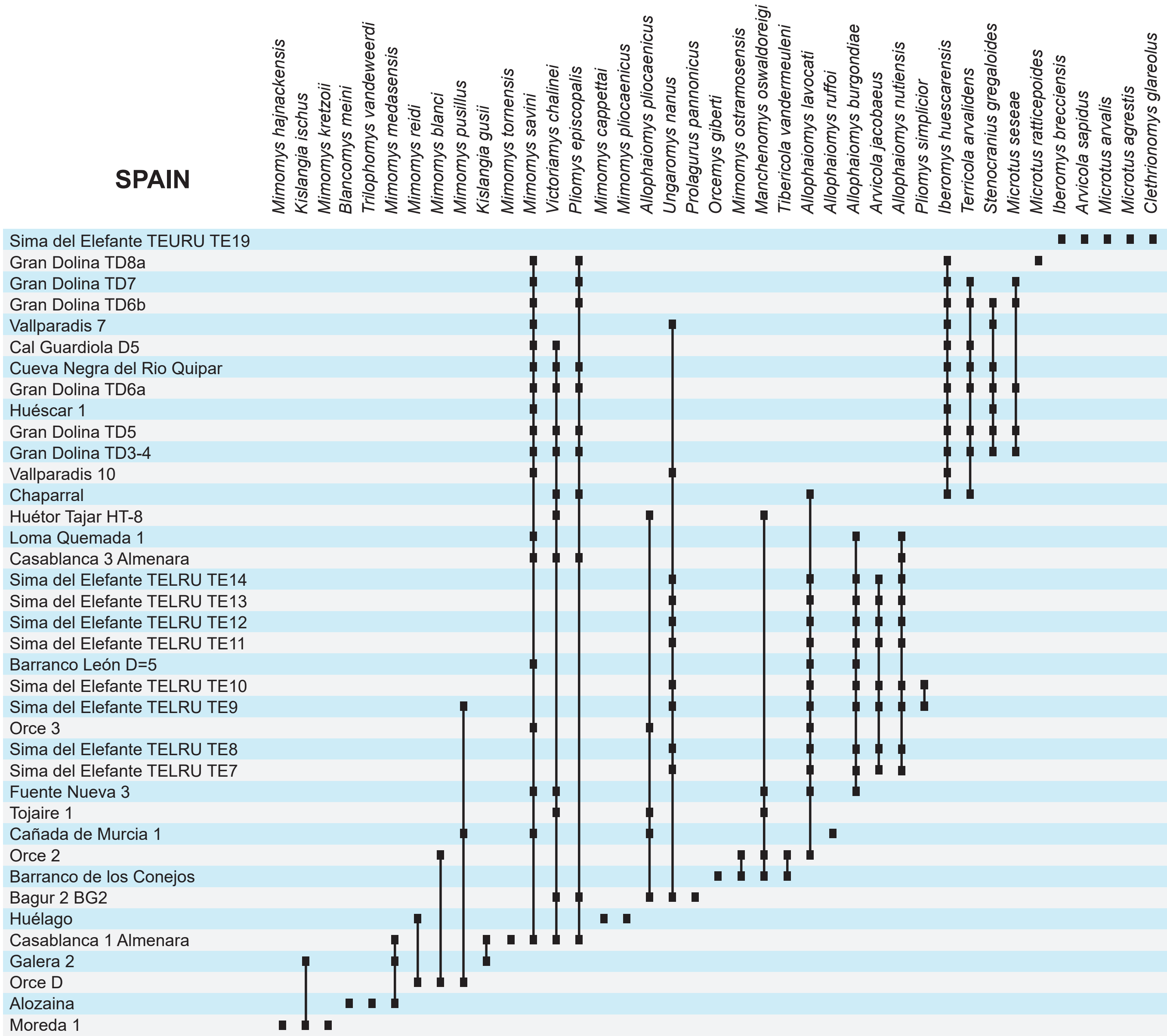
To facilitate regional comparisons and biostratigraphic synthesis, the selected fossil layers have been grouped by country (Tab. 1). This organization allows for clearer visualization of biostratigraphic patterns and temporal distribution across the Late Pliocene to Early Pleistocene interval. There are marked differences in the concentration of these sites across Europe when presenting the results by country. Nevertheless, when a comparison is made between the Iberian Peninsula and Central Europe, these differences are less marked. As a single country, Spain has the largest number of fossiliferous layers (112), suggesting a remarkable geological and paleontological richness during the Plio-Pleistocene in Spain. Despite still incomplete retrieval of fossil record from some countries (particularly Czechia, see Horáček and Ložek 1988, Fejfar and Horáček 1990, Horáček 1990), the respective asymmetry seems to be robustly supported (Tab. 1).

Table 1. Geographic distribution of fossiliferous layers containing Arvicolinae rodent remains across 3.1–0.7 Ma interval in selected European regions. Samples from Czechia still not completely retrieved.

Country	Fossiliferous layers
Czechia	15
Germany	38
Hungary	37
Poland	23
Slovakia	23
Spain	112
Switzerland	3
Total layers	**251**

The cross-site comparisons of arvicoline rodent assemblages, focusing on species first and last appearance data (FADs and LADs), allowed us to identify biostratigraphic markers and refine regional correlations within the Late Pliocene-Early Pleistocene interval. These results are synthesized in Text-figs 1, 3, 4, and 5.

Text-fig. 1 provides a synthetic scheme of the stratigraphic distribution of the Arvicolinae rodents from the Plio-Pleistocene interval in the fossiliferous sites in Spain (López-Martínez et al. 1976, Gil and Sesé 1984, Agustí and Galobart 1986, Esteban and López-Martínez 1990, Aguilar et al. 1993, Laplana 1999, Sesé et al. 2001, Minwer-Barakat et al. 2004, 2011, García-Alix et al. 2009, Madurell-Malapeira et al. 2010, Agustí et al. 2011, 2013, 2015, López-García et al. 2012, Cuenca-Bescós et al. 2013, 2016, Walker et al. 2016, Piñero et al. 2020, Agustí and Piñero 2023). This interval shows the first appearance (FAD) of 40 species of Arvicolinae. Observe that an important number of the arvicoline species appear for the first time during the Late Pliocene-Early Pleistocene interval, in the localities of Moreda 1, Alozaina, the Orce complex, other localities of Guadix-Baza, in the south of Spain, and the Bagur and Casablanca-Almenara karst complex in the eastern Mediterranean part of Spain. The rest are the rich fossiliferous layers of the Atapuerca karst complex in the Central-North region (Burgos) of Spain. For the sake of comparison, we include five of the 40 species that are drawn



Text-fig. 1. Stratigraphic distribution of Arvicolinae rodents from Plio-Pleistocene interval in Spain. There are 40 species in total. Sima del Elefante Lower Red Unit (TELRU, TE) and Gran Dolina (TD) are two of eight cave localities from Atapuerca karst complex. We have included Middle Pleistocene level of upper red unit from Sima del Elefante (TEURU, TE) to observe FAD of modern species.

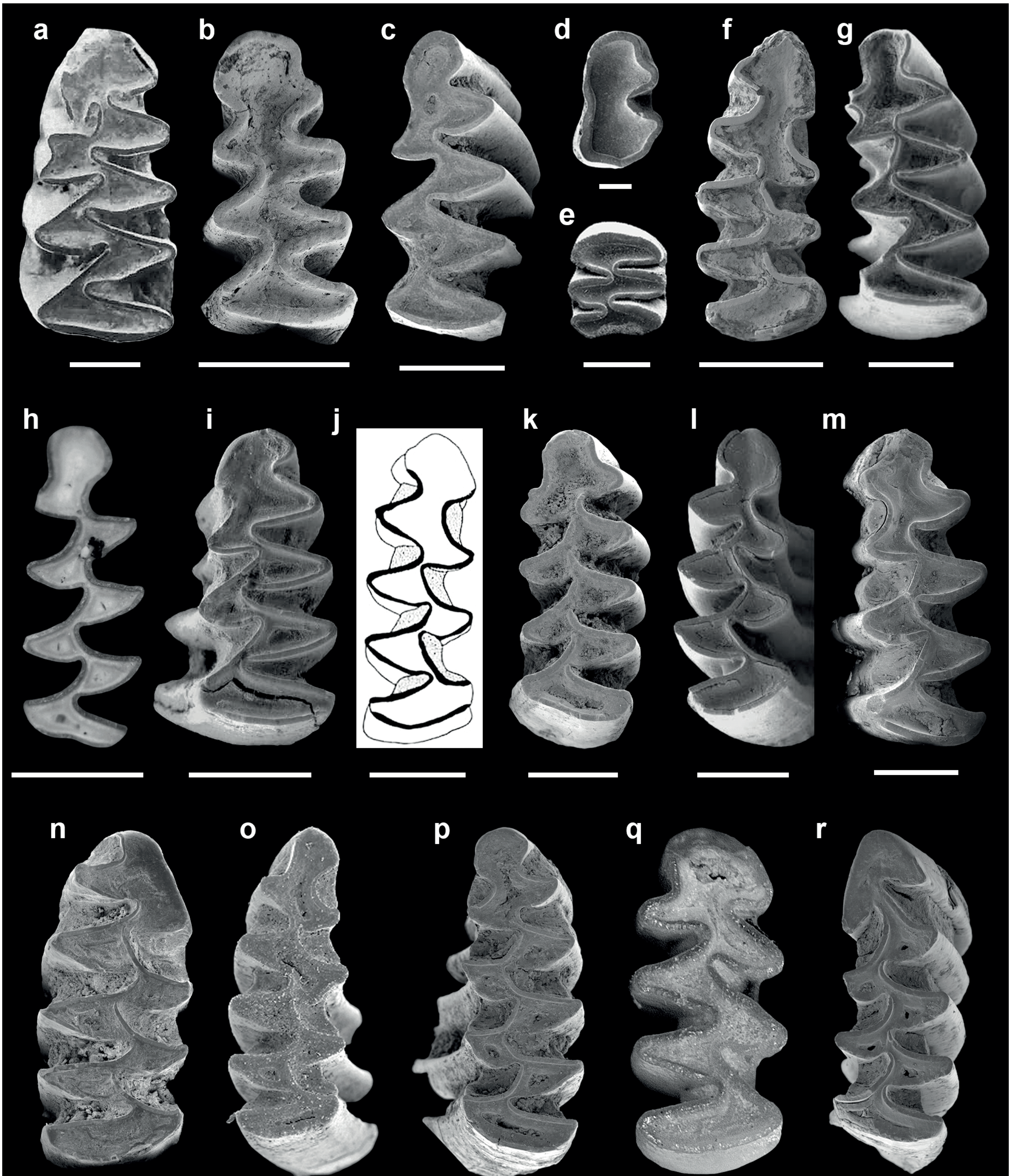
in the figure, of Middle Pleistocene age. In the figure, these are represented by the Middle Pleistocene of the Upper Red Unit from Sima del Elefante, in the Atapuerca karst complex (TEURU, TE19).

We present a selection of Arvicolinae rodent species from Spain in Text-fig. 2. They are primarily represented by their lower first molars (m1), except for *Trilophomys vandeweerdi* from Tollo de Chiclana 1, which depicts a second lower molar (m2).

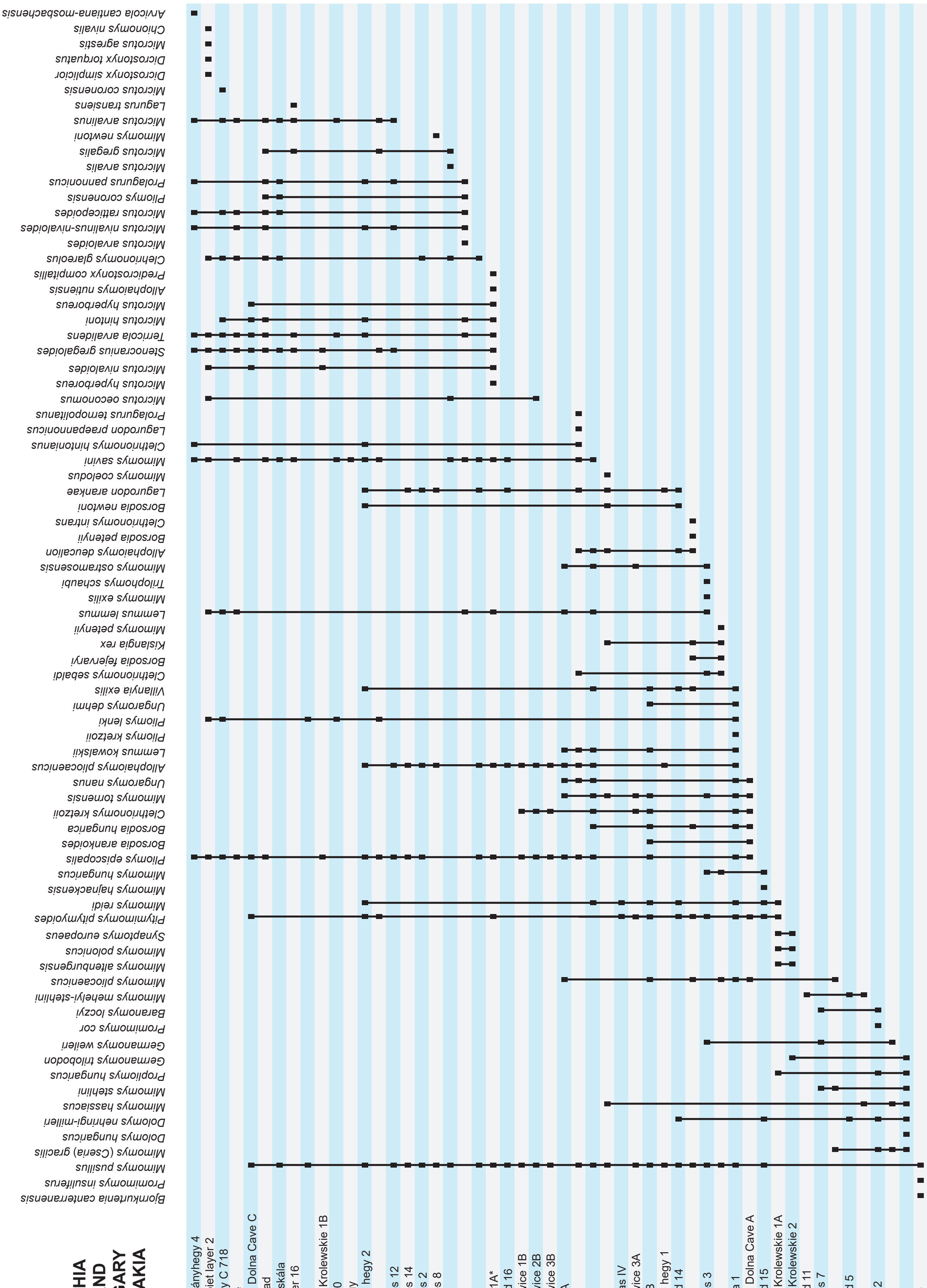
Text-fig. 3 shows that the fossiliferous layers of Czechia, Poland, Hungary, and Slovakia present higher taxonomic diversity than in Spain. They are the arvicoline rodents identified across multiple fossil localities in Czechia, Poland, Hungary, and Slovakia, spanning the Late Pliocene to Early Pleistocene. The assemblage includes representatives from 12 key genera shared with localities from Spain: *Allophaiomys*, *Arvicola*, *Clethrionomys*, *Kislangia*, *Microtus*, *Mimomys*, *Pliomys*, *Stenocranius*, *Terricola*, *Ungaromys*, *Prolagurus*, and *Trilophomys* (see Tab. 2). In general, these taxa reflect a range of ecological adaptations and biochronological significance, offering insights into faunal turnover and climatic shifts, which may be analyzed in the future. In the present work, we analyze only the importance of the species in the correlation in the European biostratigraphy (see Tab. 2).

There are 79 distinct arvicoline species listed across the regions of Czechia (Cz), Poland (Pl), Hungary (Hu) and Slovakia (Slk). These species belong to 28 genera, reflecting the well-known rich diversity of Quaternary arvicoline fauna in Central Europe. This interval sees the appearance (FAD) of several species. It is interesting to note that the species are grouped by 18 genera in Spain and by 28 in Cz-Pl-Hu-Slk, half again as many in almost the same time span.

The localities – ranging from Podlesice to Rębielice Królewskie in Poland, Osztramos and Beremend in Hungary, and Stránská Skála in Czechia – provide a robust framework for comparative analysis. The presence of trans-



Text-fig. 2. Selected Arvicolinae rodent species from Spain. They are represented by their lower first molars (m1) except for 2e, which is a m2. a: *Kislangia capettai* de Balaruc II. b: *Ungaromys nanus* from Sima del Elefante, Atapuerca TELRU TE9c. c: *Mimomys savini* from Gran Dolina, Atapuerca, TD6. d: *Blancomys meini* from Tollo de Chiclana1B. e: m2 of *Trilophomys vandeweerdi* from Tollo de Chiclana 1B. f: *Allophaiomys lavocati* from Sima del Elefante, Atapuerca TELRU TE9b. g: *Orcemys giberti* from Barranco de los Conejos. h: *Prolagurus* (= *Lagurus*) *pannonicus* Süttő 21 (it is present in Bagur 2). i: *Manchenomys* (= *Tcharinomys*) *oswaldoreigi* from Barranco de los Conejos. j: *Victoriamys chalinei* from Gran Dolina TD4-6. k: *Pliomys* sp. Gran Dolina TD10. l: *Tibericola vandermeuleni* from Barranco de los Conejos. m: *Arvicola* sp. Gran Dolina TD10. o: *Iberomys cabrerae*, extant. p*:* *Terricola atapuerquensis* from Trinchera Galería TG, Atapuerca. q: *Microtus agrestis* from Gran Dolina TD10, Atapuerca. r: *Clethrionomys acrorhiza* from Sima de los Huesos, Atapuerca. s: *Chionomys nivalis* from the Late Pleistocene from Aguilón, Zaragoza. Figures taken from Cuenca-Bescós and Morcillo-Amo (2022), except Text-fig. 2g, i from Agustí and Piñero (2023), 2h from Pazonyi et al. (2023) and 2r from Arsuaga et al. (2014).



Text-fig. 3. Stratigraphic distribution of Arvicolinae rodents from Plio-Pleistocene interval in Czechia, Poland, Hungary and Slovakia.

Table 2. Arvicolinae genera by region: 12 genera shared in both regions (excluding Austria). In the right column to the genera, there are the numbers of species per genus.

Spain		Central Europe (Cz-Pl-Hu-Slk)	
Genus	**Number of species**	**Genus**	**Number of species**
Allophaiomys	5	*Allophaiomys*	3
Arvicola	2	*Arvicola*	1
Clethrionomys	1	*Clethrionomys*	5
Kislangia	2	*Kislangia*	1
Microtus	4	*Microtus*	13
Mimomys	12	*Mimomys*	19
Pliomys	2	*Pliomys*	4
Stenocranius	1	*Stenocranius*	1
Terricola	1	*Terricola*	1
Ungaromys	1	*Ungaromys*	2
Prolagurus	1	*Prolagurus*	2
Trilophomys	1	*Trilophomys*	1
Tibericola	1	*Chionomys*	1
Blancomys	1	*Dicrostonyx*	2
Orcemys	1	*Dolomys*	2
Iberomys	2	*Germanomys*	2
Manchenomys	1	*Lagurodon*	2
Victoriamys	1	*Lagurus*	1
Total genera 18	**TS 40**	*Borsodia*	5
		Lemmus	2
		Bjornkurtenia	1
		Baranomys	1
		Pitymimomys	1
		Predicrostonyx	1
		Promimomys	2
		Propliomys	1
		Synaptomys	1
		Villanyia	1
		Total genera 28	**TS 79**

regional (e.g., *Mimomys savini*) forms and endemic taxa (e.g., *Borsodia fejervaryi*, *Lagurodon praepannonicus*) underscores the complexity of evolutionary dynamics in Central Europe during this interval (Tabs 2, 3). The references in this section, too extensive to be listed here, are provided in Thew et al. (2024) as well as in Supplementary material.

Text-figs 4 and 5 show the fossiliferous layers of Austria, Switzerland and Germany with fossil Arvicolinae. They share taxa with localities in the Iberian Peninsula, Czechia, Poland, Hungary and Slovakia. The fossil record from Austria during the latest Pliocene to Early Pleistocene reveals a rich assemblage of arvicoline taxa distributed across multiple stratigraphic layers. Sites like Deutsch-Altenburg, Krems and Stranzendorf contribute multiple fossiliferous layers. Also note that in Austria, some taxa are exclusive to a single fossil layer, indicating localized temporal occurrences: *Cseria carnutina*, *Dolomys milleri*, *Ungaromys altenburgensis*, *Pusillomimus stenokorys*, among others. The same observations apply to Germany and Switzerland.

Table 3. Arvicolinae species shared in both regions, Spain and Central Europe (Czechia, Poland, Hungary and Slovakia, excluding Austria).

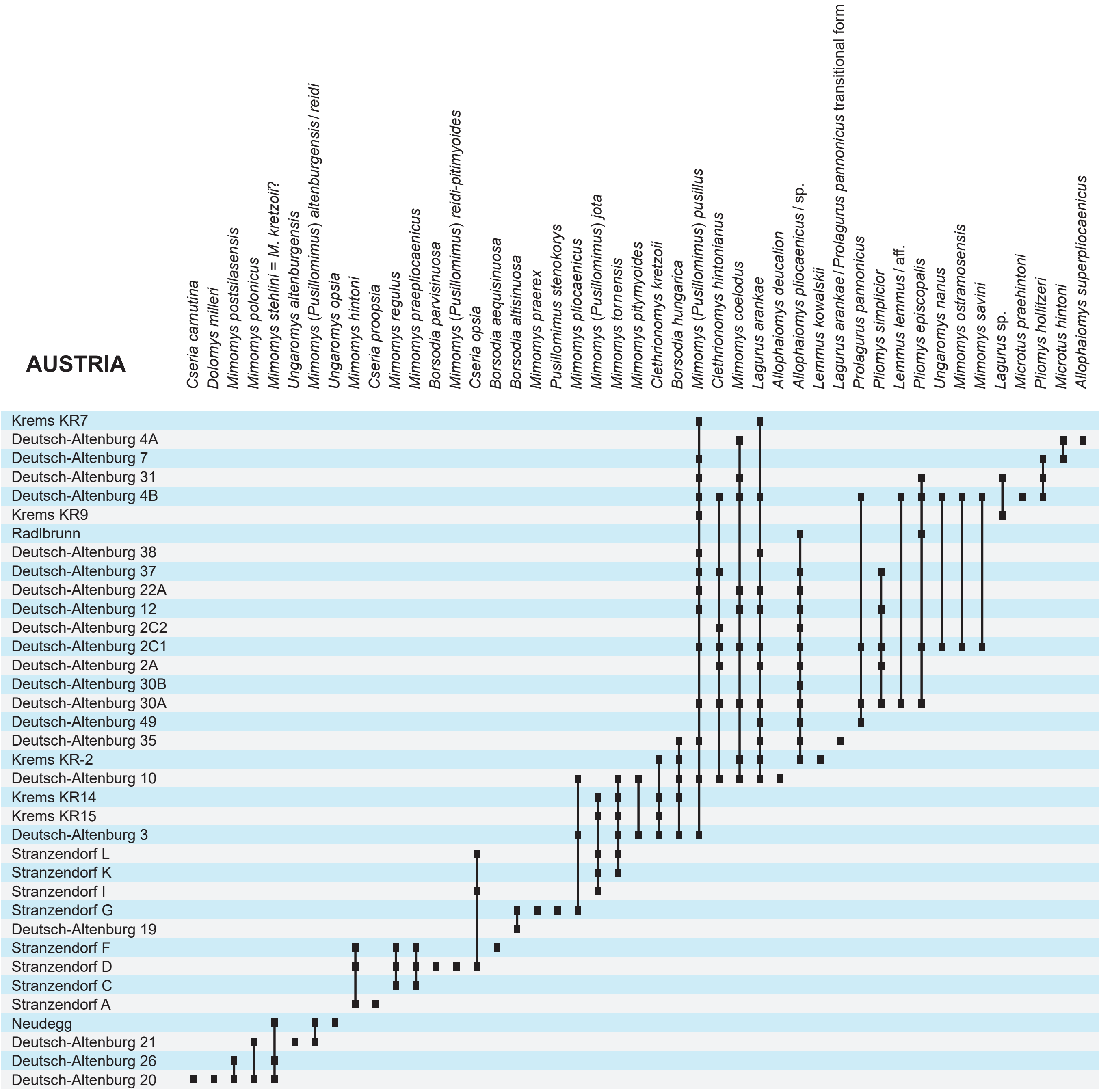
Arvicolinae species	Spain	Central Europe (Cz-Pl-Hu-Slk)
Mimomys hajnackensis	+	+
Mimomys reidi	+	+
Mimomys pusillus	+	+
Mimomys tornensis	+	+
Mimomys savini	+	+
Mimomys ostramosensis	+	+
Mimomys pliocaenicus	+	+
Allophaiomys pliocaenicus	+	+
Allophaiomys nutiensis	+	+
Microtus ratticepoides	+	+
Microtus arvalis	+	+
Microtus agrestis	+	+
Stenocranius gregaloides	+	+
Terricola arvalidens	+	+
Prolagurus pannonicus	+	+
Pliomys episcopalis	+	+
Clethrionomys glareolus	+	+
Ungaromys nanus	+	+

Discussion

The variation in the number of sites could be attributed to several factors, including geology, research and exploration, and preservation conditions. In Spain, the presence of rock formations from the suitable lithological units with karstification potential (such as the Mesozoic, well represented in Spain) is a determining factor. The research and exploration highlight the level of paleontological activity and the number of excavations conducted in each country. Funding trends are not negligible; the Atapuerca localities are probably so well studied for the implications for paleoenvironmental reconstructions and human evolution studies. Another important issue is the preservation conditions, that is, the taphonomy, in any of its phases, the biostratinomic and fossildiagenetic processes. In short, the distribution of localities in Europe reflects the differences in paleontological potential of each European country, providing a valuable resource for studying the large-scale distribution of fossil remains. Another reason may be the ecological and paleoclimatic conditions in which the arvicoline rodents may thrive and survive.

To discuss the problem of correlation among the Central Europe and the Spanish faunas, we have built chronostratigraphic charts with the distribution of the main localities in both regions. For the discussion on the distribution and correlation of the localities in the charts, we use the species distribution as well as other chronological proxies.

Text-fig. 1 shows the steady FAD of the arvicoline species in the 112 localities selected for the Late Pliocene to Early Pleistocene age from Spain. The Sima del Elefante Lower Red Unit (TELRU) and the Gran Dolina lower levels TD3-4

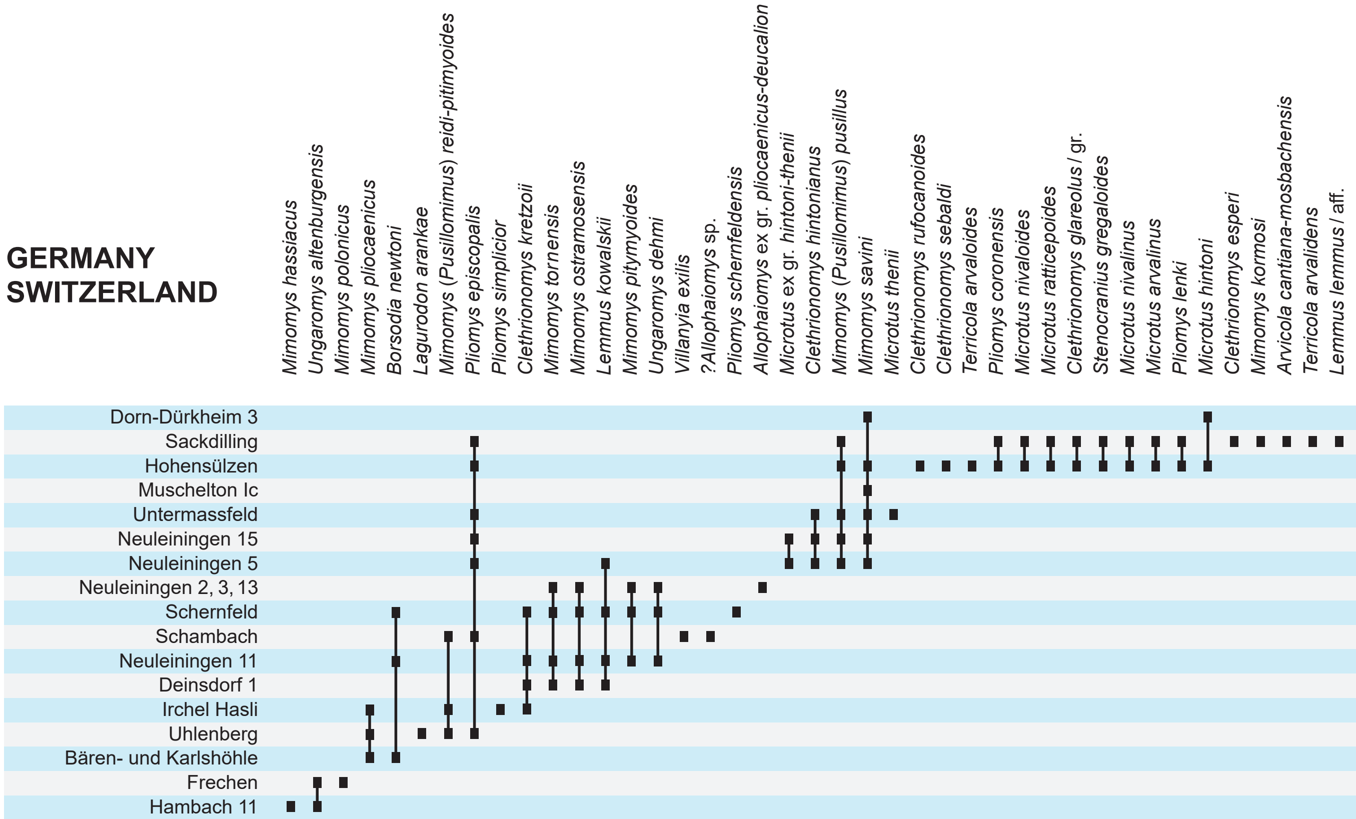


Text-fig. 4. Stratigraphic distribution of Arvicolinae rodents from Plio-Pleistocene interval in Austria.

to the bottom of TD7 are Early Pleistocene in age (Berger et al. 2008, Falguères et al. 2013, Arnold et al. 2015). This composite stratigraphic section is one of the most complete records of the late Early Pleistocene transition in the terrestrial record of Western Europe. There are magnetostratigraphic markers: Gran Dolina layers TD3-4 and Gran Dolina TD7 are located between the Jaramillo subchron and the Brunhes-Matuyama boundary (0.99–0.78 Ma; Carbonell et al. 1995, Cuenca-Bescós et al. 1995, Alvarez-Posada et al. 2018) in biostratigraphic and geochronological terms. The other chronological anchor is the burial dating based on terrestrial cosmogenic nuclides (TCN) Al-Be measured in quartz grains that yielded an age of 1.22 ± 0.16 Ma for level TE9, and 1.13 ± 0.18 Ma for level TE7 located a few meters below. These two ages are internally consistent and cannot be statistically differentiated. They are in good agreement with the Matuyama chronology of the deposits, and might suggest a pre-Jaramillo age for the deposits (Berger et al. 2008, Carbonell et al. 2008, Cuenca-Bescós et al. 2015).

The species' appearance is faster and diverse during the time interval represented in the localities of Moreda 1 to Cañada de Murcia 1. There are two to four FADs at each fossiliferous layer. From this locality upwards, the number of FADs decreases, having no FADs in several layers. The next FAD is the one at the Chaparral and Gran Dolina TD3-4 layers, though its numbers are reduced. There are no more FADs up to the Sima del Elefante Middle Pleistocene layer TEURU TE19, when first extant genus begins to appear.

Text-fig. 3 shows that much more frequent and diverse are the FADs in the Central European countries Czechia, Poland, Hungary and Slovakia (CE). Some fossiliferous layers such as Węże 1 show seven FADs. The frequency



Text-fig. 5. Stratigraphic distribution of Arvicolinae rodents from Plio-Pleistocene interval in Switzerland and Germany.

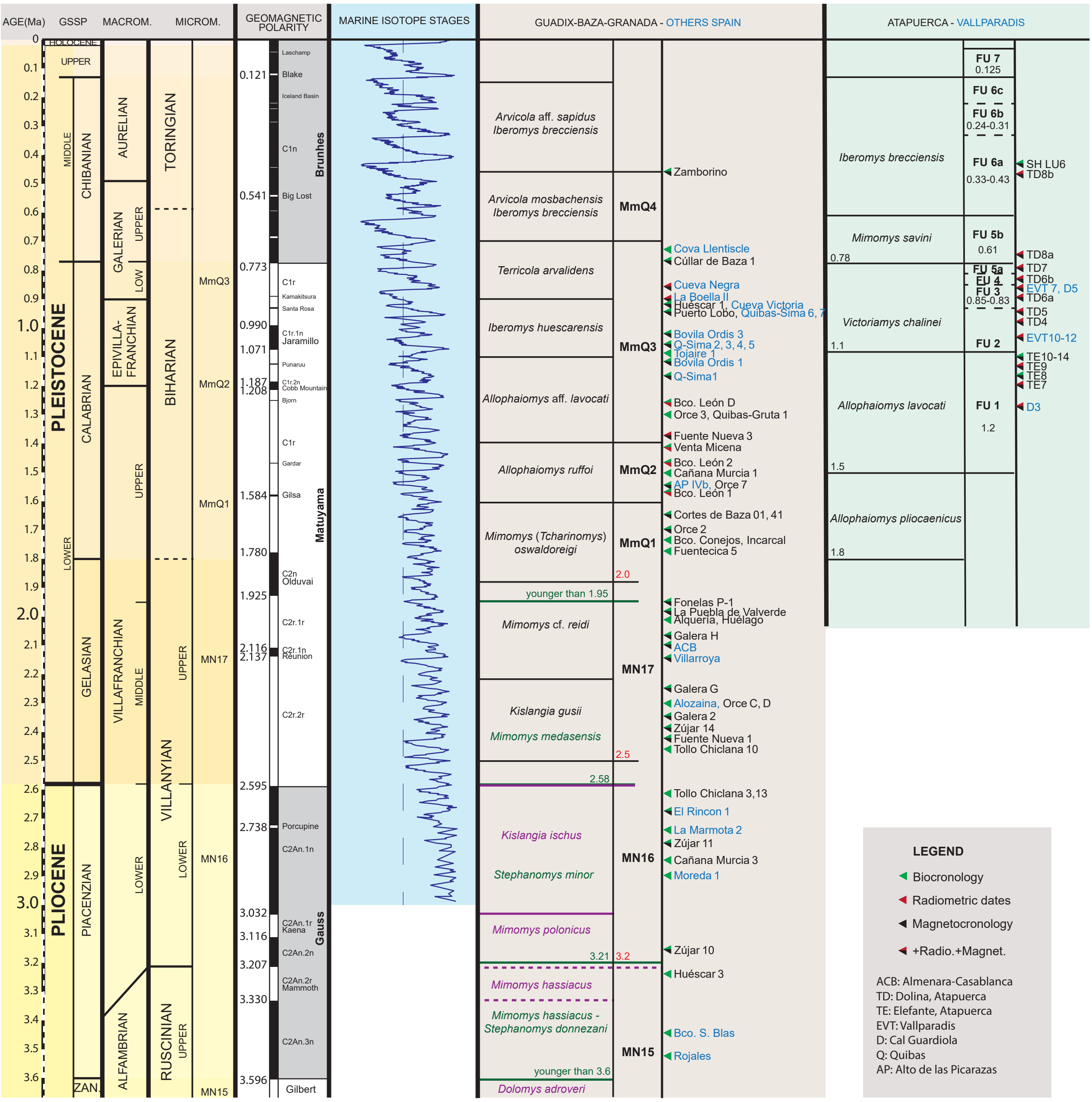
of FADs is also steady during the time represented by the 139 localities of Central Europe. Remarkable are the 25 FADs during the Gelasian Zone MN 17, characterized by rodent assemblages in Zamkowa Dolna Cave A, Kadzielnia, Villány 3, Osztramos 3, and Villány 5 (Early Pleistocene; see Text-figs 6, 7). From these localities upward, the first appearance of arvicoline species in Central European countries is less relevant until the short interval of younger age (Zones MmQ 1 to MmQ 3, Calabrian), represented by the localities of Zalesiaki 1A, Chlum 6, Chlum 4, Hajnóczy and Osztramos 8.

Our conclusions are graphically drawn in Text-figs 6, 7, showing the chronologic framework of the Spanish sites. With the information given by the biostratigraphic distribution of rodent species, magnetostratigraphic relative position, and radiometric ages, we have built a robust and novel chronostratigraphic chart, in which anchoring of localities is robust, including age (in Ma), GSSP ages, macro- and micromammal zones of Europe, geomagnetic polarity, marine isotope stages and the localities. In Text-fig. 6 of Spanish sites, for the sake of geographic situation and chronologies, we have divided the column of localities into two: one of older chronologies and majority in the Guadix-Baza-Granada basins, and the other with younger chronologies and from the North and Mediterranean regions of Iberia.

Text-fig. 6 represents the temporal frame in which the Spanish localities are situated according to the temporal background, where the vertical axis represents geological time from approximately 3.6 million years ago (Ma) to the present. It is subdivided into epochs (Pliocene, Pleistocene, Holocene), stages (e.g., Piacenzian, Gelasian, Calabrian, Chibanian), and regional biochronological units (e.g., Villanyian, Biharian, Galerian, Aurelian). The chart includes the magnetostratigraphic zones (magnetic polarity zones).

These are aligned with radiometric ages and marine isotope stages (MIS), offering a multi-layered correlation. The fossil Units (FU 1–7) are plotted vertically with their estimated age ranges. The key rodent taxa are listed alongside their temporal ranges, including the zones *Mimomys savini*, *Iberomys brecciensis*, *Victoriamys chalinei*, *Allophaiomys lavocati* and *Arvicola mosbachensis*. The zones are based on the key taxa distributed across different fossil sites in Spain, such as Atapuerca, Vallparadís, Guadix-Baza and Granada. The correlation of sites is linked to specific fossil units and taxa assemblages, allowing for regional biochronological comparison. The dating methods are radiometric, magnetostratigraphic, biostratigraphic and combinations thereof. This figure serves as a powerful integrative tool for correlating Iberian small-mammal assemblages with global chronostratigraphic markers.

Text-fig. 7 also presents a high-resolution biochronological and magnetostratigraphic synthesis this time of rodent-bearing sites across Central and Eastern Europe. As in Text-fig. 6, the temporal (vertical) axis spans from 3.6 Ma to the present, structured according to the International Chronostratigraphic Chart, including the Piacenzian, Gelasian, Calabrian. Magnetostratigraphic boundaries are indicated by named polarity zones and reversals (e.g., Gauss, Matuyama, Brunhes), calibrated against Global Boundary Stratotype Sections and Points (GSSPs) and radiometric age constraints. The figure organizes fossil localities by geographic region – Germany, Switzerland, Hungary, Czechia, Slovakia and Poland – grouped vertically and

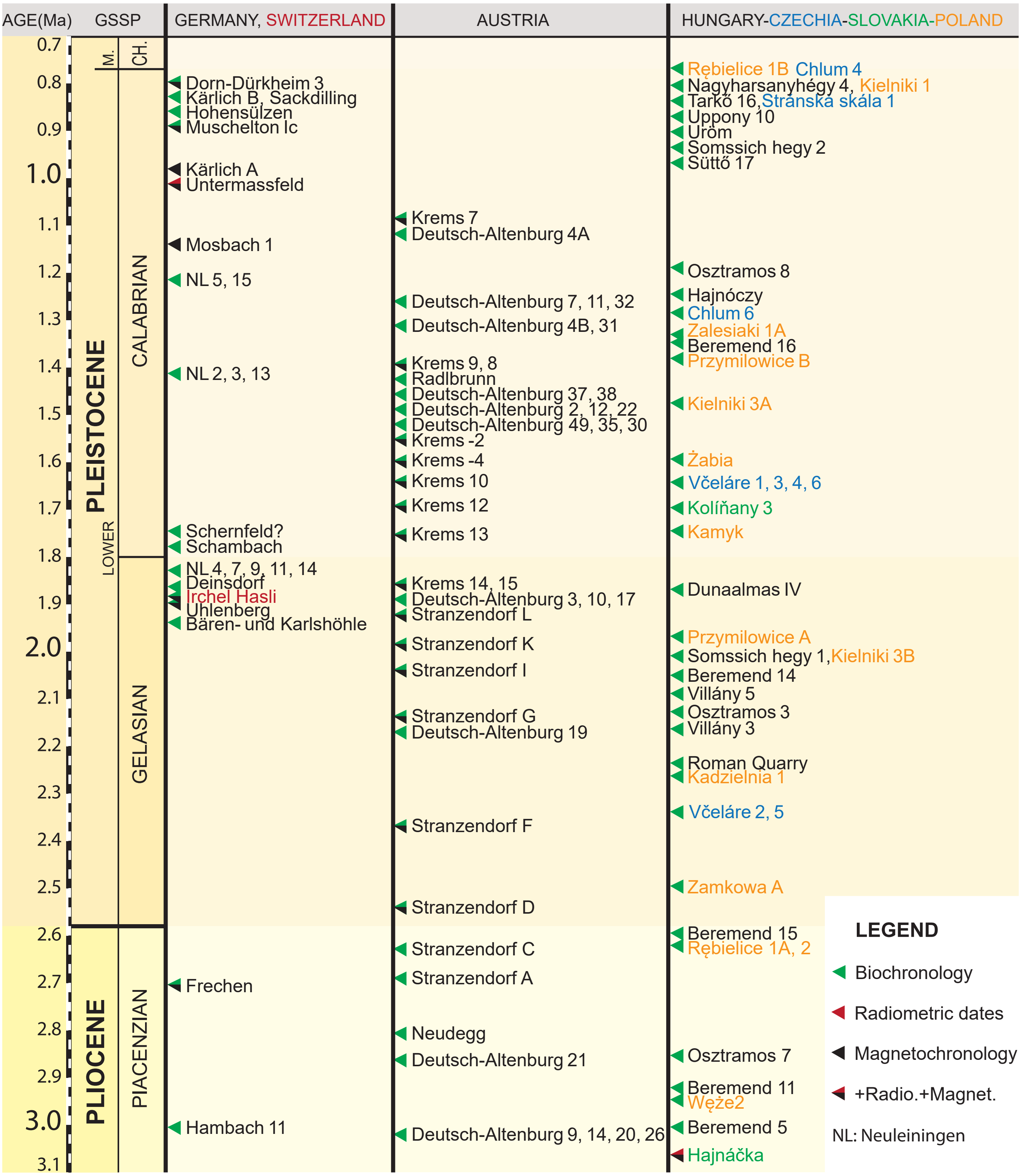


Text-fig. 6: Comprehensive biochronological and magnetostratigraphic chart synthesizes data from Iberian fossil sites, particularly focusing on small mammals, mainly Rodentia, across Plio-Pleistocene.

aligned with their respective chronostratigraphic positions. Sites such as Kärlich, Mosbach, Neuleiningen (Germany), Beremend, Villány, Osztramos (Hungary) and Kielniki, Rebielice, Zamkowa (Poland) are plotted according to their inferred ages and associated fossil units. Each locality is annotated with its dating method (radiometric, magnetostratigraphic, biostratigraphic or combined), facilitating cross-validation of temporal assignments. The chart serves as a comparative framework for correlating Spain and Central Europe rodent successions and fossil units, supporting broader interpretations of faunal turnover, dispersal events, and paleoenvironmental transitions during the Plio-Pleistocene. It complements Iberian sequences by extending the biostratigraphic resolution across continental Europe, contributing to the refinement of small mammal-based chronologies and their integration with global stratigraphic standards.

Fossil sites during the late Piacenzian

From the Piacenzian, Spain has fossiliferous layers only in the South of the country. The north lacks Piacenzian arvicolines. In Granada and Murcia, there are rich stratigraphic sequences such as Tollo de Chiclana, Zújar and Huéscar, which reveal rich faunal assemblages, though less rich in arvicolines in comparison with the Gelasian and



Text-fig. 7: Comprehensive biochronological and magnetostratigraphic chart synthesizes data from Germany, Switzerland, Hungary, Czechia, Slovakia and Poland fossil sites, particularly focusing on small mammals, mainly Rodentia, across Plio-Pleistocene.

Calabrian. In Central Europe, especially in Czechia, Slovakia, Hungary and Poland, there are rich reference localities, such as Hajnáčka, Węże, Beremend. The Czech localities such as Měňany 3, with *Germanomys* sp., *Mimomys* cf. *gracilis*, *Mimomys hassiacus*, are older. One of the best stratigraphic sequences with fossil arvicolines is Deutsch-Altenburg in Austria, with rich and diverse faunal assemblages of other mammals as well (Rabeder 1981, Döppes and Rabeder 1997).

Fossil sites during the Gelasian

During the Gelasian period, fossil sites are densely concentrated in southeastern Spanish basins such as Granada, Guadix-Baza and Orce, including key localities like Fonelas P-1, Fuente Nueva 1, and several others in the Orce area. In contrast, Gelasian fossil evidence across Central Europe appears more scattered, distributed over much broader regions that include countries such as Germany, Switzerland, Poland, Hungary, Slovakia, and Czechia. Interestingly, it includes sites with early *Allophaiomys* and *Mimomys* taxa, but fewer in number and density. Notable patterns indicate that Spain presents a richer and more continuous fossil record during the Gelasian, with numerous sites gathered in two basins. In contrast, Central Europe lack the spatial clustering observed in Spanish basins. Moreover, Spanish sites tend to span broader biozones (MmQ1–MmQ2) and encompass a greater diversity of taxa relevant to Early Pleistocene transitions.

Fossil sites during the Calabrian

As in the Gelasian, Spain has a notably high concentration of Calabrian localities in southeastern basins like Guadix-Baza, and Orce. The difference with the Gelasian is that fossil Calabrian localities appear at the north of Spain, such as the Atapuerca localities of Sima del Elefante Lower Red Unit and Gran Dolina lower stratigraphic layers (Cuenca-Bescós et al. 2016). Central Europe shows fewer sites, though they are well-distributed across biostratigraphic zones. Notably, the Spanish localities span a broader range of biozones and often have more detailed magneto- and biostratigraphic data.

Conclusions

The integration of over 500 scientific publications into a unified biochronological framework underscores the enduring impact of Fejfar's legacy in European Arvicolinae research. His foundational work in rodent biostratigraphy laid the groundwork for refined chronological correlations across the continent, particularly during the critical Late Pliocene-Early Pleistocene transition. By focusing on well-documented Spanish and selected Central European localities, and employing a multi-layered analytical approach, encompassing stratigraphy, radiometric and magnetostratigraphic dating, and detailed faunal assessments, this study reinforces the central role of arvicoline rodents as biochronological markers.

The resulting database, systematically compiled and cross-referenced, provides an essential tool for future paleoenvironmental and paleoanthropological research. It also opens new avenues for integrative studies within broader platforms such as the Paleobiology Data Base (PBDB) and GBIF. Ultimately, this synthesis not only reflects the scientific rigor of contemporary research, but also honors Fejfar's pioneering contributions, by extending his vision into a more connected and data-rich future for Quaternary biostratigraphy.

The compilation of 300 fossiliferous layers from Spain and Central Europe confirms the pivotal role of arvicoline rodents as tools for biostratigraphic correlation across the Late Pliocene and Early Pleistocene. As emphasized in previous continental syntheses (Fejfar et al. 1997), the comparison of geographically distant but temporally overlapping assemblages reveals both asymmetries in the density of the fossil record and common evolutionary markers that anchor interregional chronologies.

Spain emerges as one of the richest European regions for this interval, with 112 fossiliferous layers documenting the first appearances of arvicoline lineages, such as the small sized unrooted arvicolines, the endemic taxa *Victoriamys chalinei*, *Orcemys giberti*, *Manchenomys oswaldoreigi*, *Tibericola vandermeuleni*, *Allophaiomys lavocati*, *Arvicola jacobaeus* and *Iberomys huescarensis* (the origin of the extant species *Iberomys* (= *Microtus*) *cabrerae*). These sites, concentrated in the Guadix-Baza Basin, Atapuerca and the Mediterranean karst complexes provide the Iberian record of evolutionary events that are also traceable in Central European localities with important shared taxa. In parallel, the assemblages from Czechia, Poland, Hungary and Slovakia display higher overall taxonomic diversity, with 79 species distributed across 28 genera, nearly twice that of Spain. This contrast reflects both the exceptional richness of Central Europe as a center of arvicoline diversification and the differing depositional and paleogeographic histories of these regions.

Despite these differences, the presence of twelve shared genera, including *Mimomys*, *Allophaiomys*, *Prolagurus*, *Trilophomys* and *Terricola* demonstrates a common evolutionary and biogeographical foundation that enables interregional correlation. Shared first and last appearance data (FADs and LADs) for several of these genera underline the value of arvicolines as continent-wide chronological markers. The interplay of shared lineages and endemic forms illustrates both the unity and the complexity of European arvicoline evolution during the Plio-Pleistocene transition.

In line with Fejfar's conclusions, the present synthesis reinforces the need for integrated continental databases and comparative analyses. The Iberian and Central European records, while unequal in density and diversity, together provide a powerful framework for understanding faunal turnover, climatic shifts, and the tempo of arvicoline evolution. These results highlight the continuing relevance of cross-regional correlations for refining European biochronology, and underscore the lasting influence of Fejfar's comparative vision in Quaternary paleontology.

Concluding remarks of Text-figs 6, 7

Text-figs 6, 7 together provide an integrated temporal framework for the Plio-Pleistocene arvicoline record in Spain and Central Europe. This is the most updated scheme. The Spanish sequences are characterized by dense clusters of localities, particularly in Guadix-Baza, Orce and Atapuerca, with high-resolution correlations anchored by magnetostratigraphy and radiometric ages. These sites record key evolutionary events, including the first appearances of *Mimomys* species, *Allophaiomys* species, *Pliomys* species and *Arvicola* species, which serve as benchmarks for European biochronology. Central Europe, in contrast, preserves a broader taxonomic spectrum and a more geographically even distribution of sites, especially during the Chibanian, when the Galerian succession became well established. Although Spanish localities are fewer in number during the Middle Pleistocene, they often provide deeper stratigraphic and chronological resolution. Conversely, Central European records, while less densely clustered, extend across wider regions and offer greater taxonomic breadth. Together, the two regions complement one another:

Spain delivers continuity and chronological precision, while Central Europe contributes diversity and broader biogeographic coverage. This dual perspective refines the European biochronological framework and reinforces the pivotal role of arvicoline rodents in correlating regional successions with global stratigraphic standards.

In synthesis, the present study is that, having different assemblages of faunas, the Iberian and the Central European regions can be correlated by means of their shared arvicoline rodent fossil contents, notably, with the 12 shared genera, *Allophaiomys*, *Arvicola*, *Clethrionomys*, *Kislangia*, *Microtus*, *Mimomys*, *Pliomys*, *Stenocranius*, *Terricola*, *Ungaromys*, *Prolagurus* and *Trilophomys*, shared by both regions (Tab. 2), and the 18 shared species, *Mimomys hajnackensis*, *Mimomys reidi*, *Mimomys pusillus*, *Mimomys tornensis*, *Mimomys savini*, *Pliomys episcopalis*, *Mimomys pliocaenicus*, *Allophaiomys pliocaenicus*, *Ungaromys nanus*, *Prolagurus pannonicus*, *Mimomys ostramosensis*, *Allophaiomys nutiensis*, *Terricola arvalidens*, *Stenocranius gregaloides*, *Microtus ratticepoides*, *Microtus arvalis*, *Microtus agrestis* and *Clethrionomys glareolus* (Tab. 3). Anchoring the arvicolinae sites, in good stratigraphic successions, with reliable chronological proxies helps in building the chronostratigraphic charts presented for Spain and Central Europe.

The future of biostratigraphic studies in Europe

This synthesis contributes to ongoing efforts to refine biochronological frameworks and supports the integration of Spain and Central European data into broader Eurasian paleontological models. This framework might support future analysis, digitization, and AI-based pattern recognition in biochronology.

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Supplementary material

Complete list of references of the compiled bibliography on fossil localities from Europe.