

2D geometric morphometrics reveals temporal patterns in the evolution of modern and Pleistocene *Arvicola* (Rodentia, Cricetidae) in Europe

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ABSTRACT

This study applies a comprehensive two-dimensional (2D) geometric morphometric framework to investigate dental morphological variation in modern and Pleistocene populations of the genus *Arvicola*. A reference dataset of 390 first lower molars (m/1) representing four extant species (*A. amphibius*, *A. sapidus*, *A. italicus*, and *A. persicus*) was analysed using Elliptic Fourier Analysis combined with multivariate statistics (PCA, MANOVA, LDA, CDA, Random Forest, and Mahalanobis distances). All modern species of *Arvicola* exhibit highly significant morphological differences, demonstrating that m/1 outlines shape reliably discriminates species-specific variation. This validated classification framework was applied to fossil assemblages from five well-dated localities spanning the late Middle Pleistocene to Upper Pleistocene (MIS 6 to MIS 3). The MIS 6 assemblage from Lazaret Cave displays a heterogeneous and intermediate morphospace distribution, reflecting the presence of archaic lineages attributed to *Arvicola* ex gr. *cantianus/amphibius* and *Arvicola* ex gr. *cantianus/sapidus*. By MIS 5.5 (Baume Moula-Guercy), *Arvicola amphibius*-like morphologies dominate, although several specimens retain plesiomorphic traits. In contrast, MIS 3 assemblages (Abauntz Cave, Cova Eirós, and Trou Al'Wesse) exhibit predominantly modern morphologies, with high classification agreement (up to 100%) and clear species-level assignment. A temporal trend emerges in which discrimination accuracy and morphological distinctiveness

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increase from the late Middle Pleistocene to MIS 3, documenting the evolutionary transition from archaic *Arvicola* forms to fully differentiated modern species. The results further suggest a complex biogeographic history of *Arvicola sapidus*, involving multiple Middle and early Late Pleistocene dispersal events into Western Europe. Overall, this study demonstrates that 2D outline-based geometric morphometrics of the m/1 is a robust and informative tool for resolving *Arvicola* systematics and for reconstructing evolutionary and palaeoenvironmental patterns in the Pleistocene of Europe.

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INTRODUCTION

Voies of the genus *Arvicola* (Rodentia, Cricetidae) are among the most common and geographically widespread small mammals in Quaternary deposits across Europe. Their abundance in Middle and Upper Pleistocene archaeological and palaeontological contexts, combined with rapid evolutionary rates and ecological sensitivity, has long made them valuable indicators for biostratigraphic correlation and palaeoenvironmental reconstruction (Chaline, 1972; Koenigswald and Van Kolfschoten, 1996; Markova, 2007; Markova and Puzachenko, 2017, 2018; Mahmoudi et al., 2020; Masini et al., 2020; Krokhmal' et al., 2021, 2023; Popova et al., 2025). Traditional morphometric approaches have revealed clear temporal trends in *Arvicola* dental evolution (Hinton, 1926; Heinrich, 1978, 1982, 1987, 1990; Fejfar and Heinrich, 1983; Agadzhanyan, 1983; Rekovets, 1990, 1994; Kolfschoten, 1992; Marquet, 1993; von Koenigswald and Van Kolfschoten, 1996; Abbassi et al., 1998; Desclaux et al., 2000; Maul et al., 2000, 2020; Kalthoff et al., 2007; Escudé et al., 2008a, 2008b; Ruddy, 2011) particularly in enamel thickness differentiation, named SDQ (Schmelzband-Differenzierungs-Quotient) by Heinrich (1978), which decreases through time and reflects broader functional and ecological shifts (Koenigswald et al., 1994).

Despite this well-established biostratigraphic significance, geometric morphometric approaches have been applied only sporadically to the genus *Arvicola*. In contrast, two-dimensional geometric

morphometrics (2D GMM) have proven highly effective for quantifying continuous shape variation across a wide range of biological systems (Martín-Torres et al., 2006; Escudé et al., 2008b; Kayser et al., 2012; Evin et al., 2013; Sagonas et al., 2014; Seetah et al., 2014; Delgado et al., 2015; Gómez-Robles et al., 2015; Dykes, 2016; Cucchi et al., 2020; Matos et al., 2020; Noerwidi et al., 2020; Galli et al., 2021; Arlegi et al., 2022; Nataraajan et al., 2024; Gomez Rodriguez et al., 2025; Pelletier, 2025), including various rodent taxa (Marcolini, 2007; Escudé et al., 2013; Souto-Lima and Millien, 2014; Stoetzel et al., 2017; Montuire et al., 2019; Fox et al., 2020; Khidas et al., 2020; Moclán et al., 2023; Rey-Rodriguez et al., 2021, 2024; Arbez et al., 2026). However, landmark-based configurations may not fully capture the continuous outline variation characteristic of rootless arvicoline molars, which exhibit intricate enamel patterns and lack clear homologous landmark positions. Among outline-based methods, Elliptic Fourier Analysis (EFA) has been successfully applied to various species (Rufino et al., 2006; Bonhomme et al., 2021; Bouby et al., 2024; Machado et al., 2025) and in particular to quantify molar shape variation in rodent teeth (Renaud et al., 1996; Cucchi et al., 2002, 2005; Hurth et al., 2003; Michaux et al., 2007; Escudé et al., 2008b; Valenzuela-Lamas et al., 2011; Kimura et al., 2013; Stoetzel et al., 2013, Gomez Cano et al., 2017; Carro-Rodríguez et al., 2020; Menéndez et al., 2023). EFA is especially well-suited for rodent taxa with continuously growing teeth, such as arvicolines including

the genus *Arvicola*, as it captures global shape properties without requiring predefined anatomical landmarks. We can note that earlier morphometric studies, primarily based on outlines, demonstrated substantial intra- and interspecific variability in first lower molar (m/1) morphology, suggesting complex evolutionary dynamics within *Arvicola* (Escudé et al., 2008b).

The present study applies a comprehensive 2D outline-based geometric morphometric protocol to investigate morphological variation in modern and fossil populations of Western European *Arvicola*. We focus on the first lower molar (m/1), a tooth widely used in taxonomic and palaeobiological studies due to its diagnostic features and frequent preservation in the fossil record. A key question addressed here is whether the two modern Western European species - *Arvicola amphibius* (predominantly fossorial) and *Arvicola sapidus* (mainly aquatic) - can be reliably distinguished based solely on m/1 outline morphology. Because these species occupy distinct ecological niches, differentiating them in fossil assemblages offers important insights into past environments and habitat structure. In addition, fossil populations of the late Middle Pleistocene age often show intermediate or archaic morphologies referred to *Arvicola cantianus* Hinton, 1910 or *Arvicola mosbachensis* Schmidtgen, 1911, raising questions about evolutionary continuity and phenotypic transitions leading to modern species.

The aims of this study are threefold: (1) to test the efficacy of outline-based 2D GMM for discriminating modern *Arvicola* species based on m/1 morphology; (2) to evaluate the taxonomic composition of late Middle and Late Pleistocene fossil assem-

blages, including the identification of archaic lineages; and (3) to reconstruct temporal trends in morphological divergence and assess the evolutionary transition from archaic Middle Pleistocene forms to fully differentiated modern species. By integrating modern comparative datasets with fossil material from diverse chronological and geographic contexts, this study provides a robust methodological and evolutionary framework for understanding *Arvicola* systematics and for refining their use as palaeoenvironmental and biostratigraphic indicators.

MATERIAL AND METHODS

Material

To address these issues, we built a modern reference dataset of 390 m/1 specimens representing the four extant *Arvicola* species - *Arvicola amphibius* (AA, N = 231), subdivided into Western European (AAwest, N = 194) and Eastern European (AAeast, N = 36) populations, *Arvicola sapidus* (AS, N = 145), *Arvicola italicus* (AI, N = 5), and *Arvicola persicus* (AP, N = 9) - originate from nine countries and spanning a broad geographical range from Norway to Iran, thus capturing broad geographic and ecological variation within the genus (Table 1, Figure 1). All material derives from natural history museum collections and researchers from various institutions and includes both wild-caught individuals and remains from owl pellets with reliable taxonomic attribution. Only well-preserved m/1s with intact occlusal surfaces and clearly defined enamel outlines were selected. Full details of specimen provenance, including institu-

TABLE 1. Provenance of modern *Arvicola* m/1 specimens. Groups: AAwest = *Arvicola amphibius* (Western Europe), AAeast = *Arvicola amphibius* (Eastern Europe), AI = *Arvicola italicus*, AP = *Arvicola persicus*, AS = *Arvicola sapidus*.

	AAwest	AAeast	AI	AP	AS
Bulgaria	0	25	0	0	0
France	0	0	0	0	33
Hungary	0	5	0	0	0
Iran	0	0	0	9	0
Italy	0	0	5	0	0
Moldova	0	3	0	0	0
Norway	6	0	0	0	0
Portugal	0	0	0	0	50
Russia	0	1	0	0	0
Spain	188	0	0	0	62
Ukraine	0	3	0	0	0

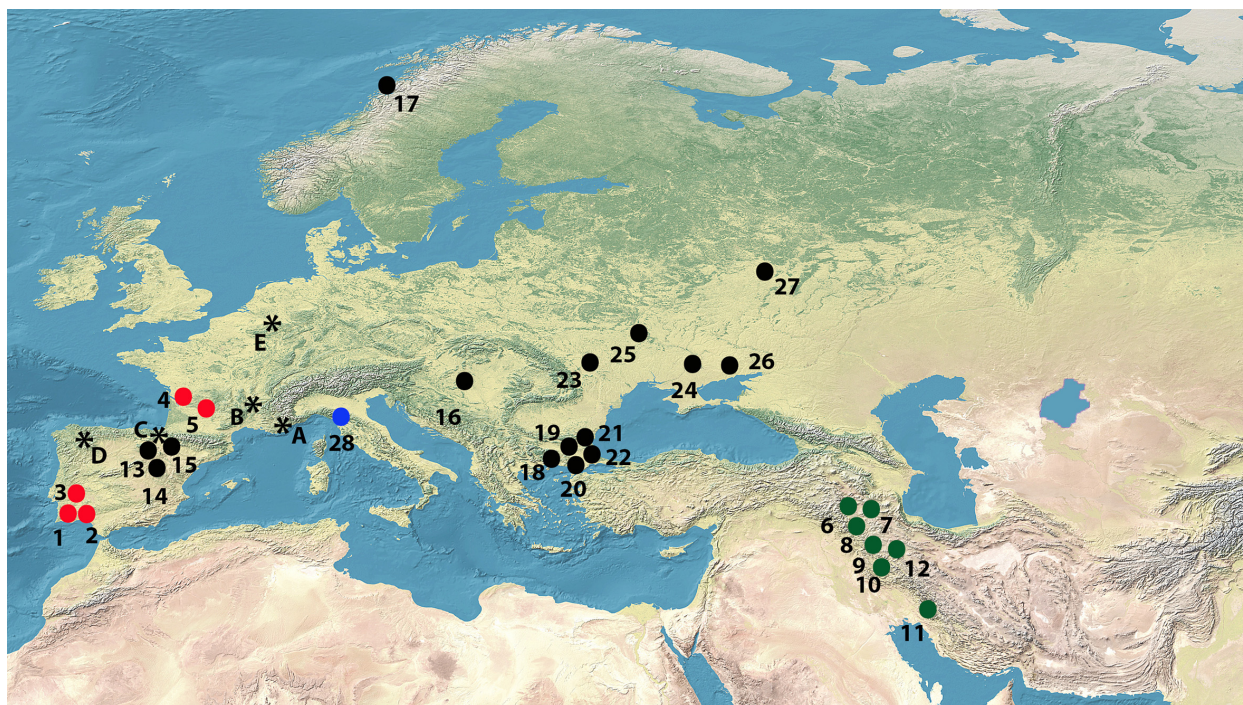


FIGURE 1. Location of modern and Pleistocene *Arvicola* samples. Modern *A. sapidus* (red points): 1, Loulé; 2, Almonte; 3, Moura; 4, Saint-Auvent; 5, Favars. Modern *A. persicus* (green points): 6, Marmisho; 7, Urmia; 8, Sarab; 9, Kurdistan; 10, Lorestan; 11, Yasuj; 12, Hamedan. Modern *A. amphibius* (black points): 13, Noceco; 14, Entrambas-mesta; 15, Barrio; 16, Pákozd; 17, islet Trolløya; 18, Ropotamo; 19, Sredetzka; 20, Aytoska; 21, Veleka; 22, Tundzha; 23, Prut River; 24, Nikopol; 25, Kyiv; 26, Voinova; 27, Dudinka. Modern *A. italicus* (blue point): 28, Pisa. Pleistocene sites: A, Lazaret Cave; B, Baume Moula-Guercy; C, Abautz Cave; D, Cova Eirós; E, Trou Al'Wesse.

tion names and inventory numbers, are provided in Appendix 1.

Using this dataset, we developed a multivariate statistical framework combining Principal Component Analysis (PCA), Multivariate Analysis of Variance (MANOVA), Linear Discriminant Analysis (LDA), Canonical Discriminant Analysis (CDA), Random Forest classification (RF), and Mahalanobis distance analysis to evaluate species-level discrimination based on molar outline shape.

This validated framework was then applied to fossil assemblages from five well-dated localities in Europe spanning the late Middle and Late Pleistocene: Lazaret Cave (France, MIS 6, ~150 ka), Moula-Guercy (France, MIS 5.5, ~125 ka), Abautz Cave (Spain, MIS 3, ~40-50 ka), Cova Eirós (Spain, MIS 3, ~30-40 ka), and Trou Al'Wesse (Belgium, MIS 3, ~30-40 ka). This chronological framework allows us to examine temporal patterns of morphological variation and reassess the taxonomic composition of key fossil populations.

The fossil dataset includes 87 m/1 specimens from five well-stratified and well-dated archaeologi-

cal sites spanning the late Middle to Late Pleistocene:

- Lazaret Cave (Nice, France): MIS 6 (~150 ka), N=24
- Moula-Guercy (Ardèche, France): MIS 5.5 (~125 ka), N=17
- Abautz Cave (Navarre, Spain): MIS 3 (~40-50 ka), N=29
- Cova Eirós (Galicia, Spain): MIS 3 (~30-40 ka), N=12
- Trou Al'Wesse (Modave, Belgium): MIS 3 (~30-40 ka), N=5

All fossil molars are well-preserved, free of digestion traces or taphonomic damage, and exhibit complete occlusal surfaces suitable for outline capture. Data concerning Pleistocene sites are provided in Appendix 2.

Methods

All first lower molars were photographed in standardized occlusal view using a Zeiss Stemi 508 stereomicroscope equipped with a 9-megapixel digital camera at 25× magnification. A

ring-light illumination system ensured uniform lighting, and a calibrated scale bar was included in each image for size standardization. Tooth outlines were digitized manually in Fresco software using a digital pen. Tracing followed the external enamel contour of the crown, from the anterior to the pos-

terior loop, capturing all triangles (T1-T5) and producing a complete closed outline curve (Figure 2).

All outlines were aligned using the algorithm developed by Bonhomme (2014), which is specifically designed for complex biological shapes lacking homologous landmarks. This procedure

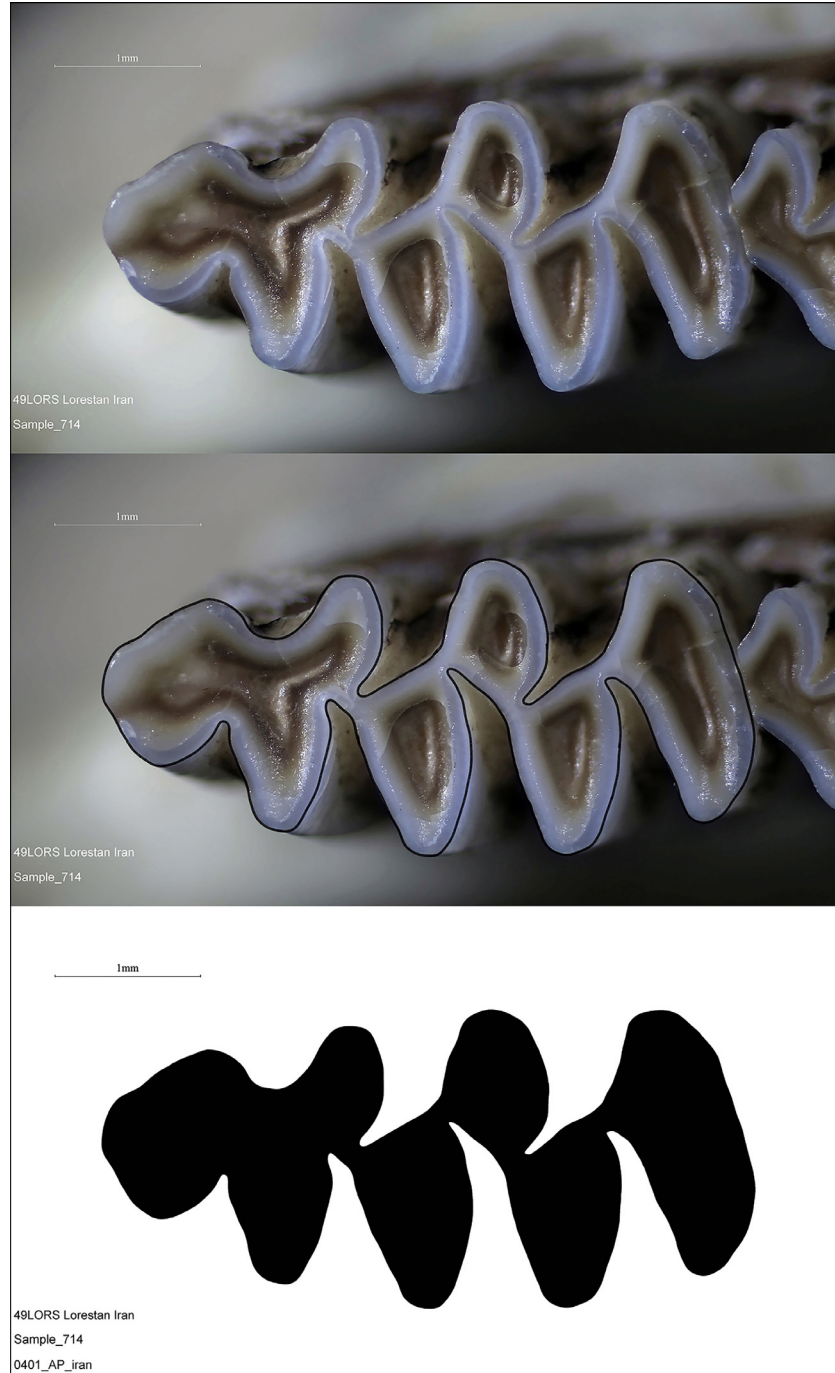


FIGURE 2. Example of a mask acquisition based on an m/1 of *Arvicola*. The specimen shown is a right m/1 of a modern *Arvicola persicus* from the Lorestan region (Iran). The original identifier is 49LORS Lorestan Iran; the sample number for genetic study is Sample 714; and the mask number is 0401_AP_iran. See complementary details in Appendix 1.

standardizes outline position, size, and orientation while preserving biologically relevant variation. The algorithm uses iterative optimization to minimize misalignment across the specimens, ensuring that subsequent analyses capture genuine morphological variation rather than artifacts of specimen positioning or digitization (Figure 3).

Aligned outlines were decomposed into harmonic components using Elliptic Fourier Transform (EFT; Kuhl and Giardina, 1982). Standard EFA was preferred over the Centered Discrete Fourier Transform (CDFT; Escudé et al., 2013), which requires identifiable biological reference points on the outline. Given that arvicoline m/1s lack clear homologous landmark positions due to their continuous, rootless growth pattern, standard EFA represents an appropriate method for capturing the full range of outline variation in these taxa. Twelve harmonics were retained, capturing 99.9% of total shape variation, yielding 48 coefficients (A, B, C, D per harmonic). However, only 13 principal components (PCs) were used in subsequent analyses (LDA, CDA), explaining 89.2% of total variance. This dimensionality reduction substantially mitigates overfitting risks, particularly for small sample sizes (Kovarovic et al., 2011). Only shape variables were analysed; size-related variables were deliberately excluded to avoid confounding effects of eco-geographic scaling (Cope's and Bergmann's rules; Bergmann, 1847; Mayr, 1956; Stanley, 1973; Meiri, 2011). All geometric morphometric analyses were conducted in R v. 4.5.1 (R Core Team, 2025) using the Momocs 1.5.0 package (Bonhomme et al., 2014).

A multivariate analytical framework was constructed to quantify morphological variation, assess species-level discrimination, and develop predictive models for fossil probabilistic assignment.

Principal Component Analysis (PCA) was performed on the EFT coefficient matrix to visualise morphospace structure. Multivariate Analysis of Variance (MANOVA) assessed overall morphological differentiation among species. Post-hoc univariate ANOVAs and Tukey HSD tests identified the principal components contributing most strongly to interspecific differentiation. Complementary MANOVA statistics (Pillai's trace, Wilks' lambda, Hotelling-Lawley trace, Roy's greatest root) were used to ensure robust inference.

Three probabilistic assignment approaches were applied:

1. Linear Discriminant Analysis (LDA) identified linear combinations of shape variables that best separate species. Classification accuracy assessed using leave-one-out cross-validation (LOOCV). Confusion matrices were used to quantify interspecific misclassifications.
2. Canonical Discriminant Analysis (CDA) provided complementary results by incorporating within-group covariance. Mahalanobis distances between species centroids quantified morphometric divergence (Appendix 3).
3. Random Forest (RF) implemented via the *caret* package with 5-fold cross-validation in R (Kuhn, 2008). RF is a non-parametric ensemble method capturing nonlinear shape relationships. Variable importance scores identified the most influential principal component.

Pairwise Mahalanobis distances between specimens and modern species centroids were used to evaluate proximity and identify potentially ambiguous or intermediate morphologies. Hierarchical clustering (Ward's method) using Euclidean

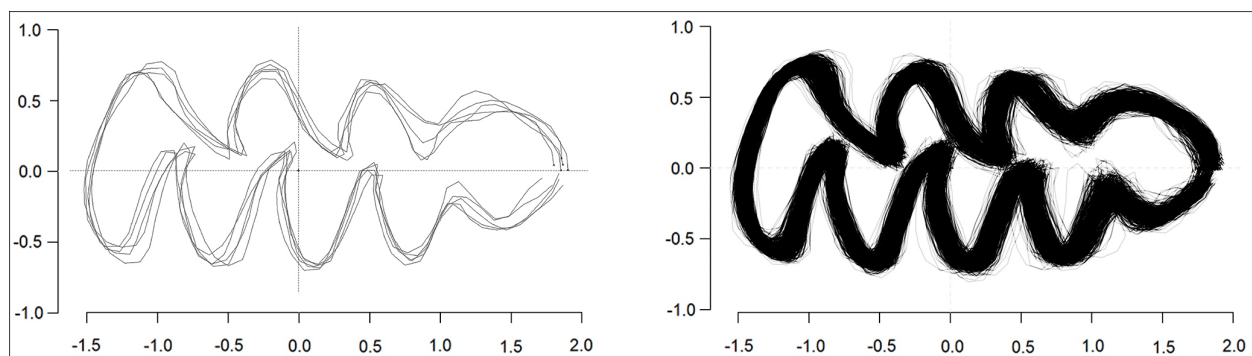


FIGURE 3. **A**, example of outline alignment for an m/1 of *Arvicola italicus*. **B**, alignment of m/1 outlines for modern *Arvicola* specimens.

and Mahalanobis distances was used to visualise interspecific relationships; cophenetic correlation coefficients assessed clustering robustness. Heatmaps of Mahalanobis distances were generated into patterns of morphological similarity and divergence. The results and interpretations are in Appendix 3.

The classification protocol developed for modern species was adapted for fossil assemblages, with two key modifications to accommodate both the palaeontological context and potential morphological intermediacy characteristic of late Middle Pleistocene and Late Pleistocene populations. Because *Arvicola italicus* and *A. persicus* occur in peripheral geographic ranges and have small sample sizes, fossil probabilistic assignment used a two-species reference framework restricted to modern *Arvicola amphibius* (AA) and *A. sapidus* (AS). Western and Eastern European AA populations were pooled, consistent with their demonstrated conspecific status. For each fossil assemblage, the following analytical sequence was applied:

1. Fossil specimens were projected onto PCA axes defined by modern specimens. MANOVA assessed morphological affinities among fossils and modern groups.
2. LDA, RF, and Mahalanobis distance approaches were applied to each fossil specimen. Posterior probabilities and distance values quantified classification confidence.
3. Agreement among the three classification methods (LDA, RF, Mahalanobis) was assessed for each fossil specimen. Consistent results indicated clear affinities; discordant classifications flagged potentially intermediate or archaic morphologies.
4. Canonical Variate Analysis (CVA) was conducted for Lazaret Cave as a collective group to evaluate its morphometric position relative to modern species (Appendix 3).

RESULTS

Modern Specimens

Because the taxonomic status of some modern *Arvicola* forms, especially concerning *Arvicola scherman*, is not consensual (Mahmoudi, 2020; Chevret et al., 2021; Kryštufek and Schenbrot, 2022; Balmori-de la Puente et al., 2022; Somoano, 2024; Roman et al., 2025), this study follows the

nomenclature established in the Mammal Diversity Database (ASM), retaining four widely accepted species: *A. amphibius*, *A. sapidus*, *A. italicus*, and *A. persicus* (Figure 4).

For this study, *A. amphibius* has been separated in two groups (AAeast = Eastern European *Arvicola amphibius* and AAwest = Western European *Arvicola amphibius*). Indeed, the conspecific status of Western and Eastern European *A. amphibius* populations is supported by ancient and modern DNA analyses, which confirm their belonging to the same species while revealing a clear genetic structuring between Eastern and Western European lineages derived from distinct glacial refugia (Brace et al., 2016).

Principal Component Analysis (PCA) of Elliptic Fourier coefficients shows clear species-level structuring. Although PC1 and PC2 together explain 53.3% of variance, MANOVA indicates that higher-order components contribute substantially to discrimination, particularly PC3 (7.3% of variance), which yields the highest F-statistic ($F = 45.29$). This highlights that interspecific differences are distributed across multiple axes and not captured solely by the first two PCs. Species occupy distinct regions of morphospace (Figure 5, Table 2): *Arvicola amphibius* from Western Europe (AAwest) forms a compact homogeneous cluster; *Arvicola sapidus* (AS) plots on the opposite side of PC1 with limited overlap; *Arvicola amphibius* from Eastern Europe (AAeast) occupies an intermediate position between AAwest and other species, suggesting geographical structuring; *Arvicola persicus* (AP) displays higher variation along PC2; *Arvicola italicus* (AI) forms a small, discrete cluster with intermediate PC1 values.

MANOVA confirms highly significant differences among all species ($p < 2.2e-16$; Wilks' $\lambda = 0.1445$). Tukey's post-hoc tests show that *Arvicola sapidus* and *A. persicus* are consistently well differentiated, whereas AAwest and AI show expected similarity (AI, $N = 5$). A multifactor MANOVA indicates significant species $\times$ geography interactions, supporting geographic differentiation within modern species belonging to the genus *Arvicola*.

Overall, 2D outline-based GMM provides strong species-level discrimination in modern *Arvicola*, including subtle east-west differentiation within *A. amphibius*.

Linear Discriminant Analysis (LDA) shows strong separation among species (Figure 6), with LD1 explaining 81.91% of between-group variance. Leave-one-out cross-validation (Figure 7) reveals high classification accuracy: AAwest - 98%

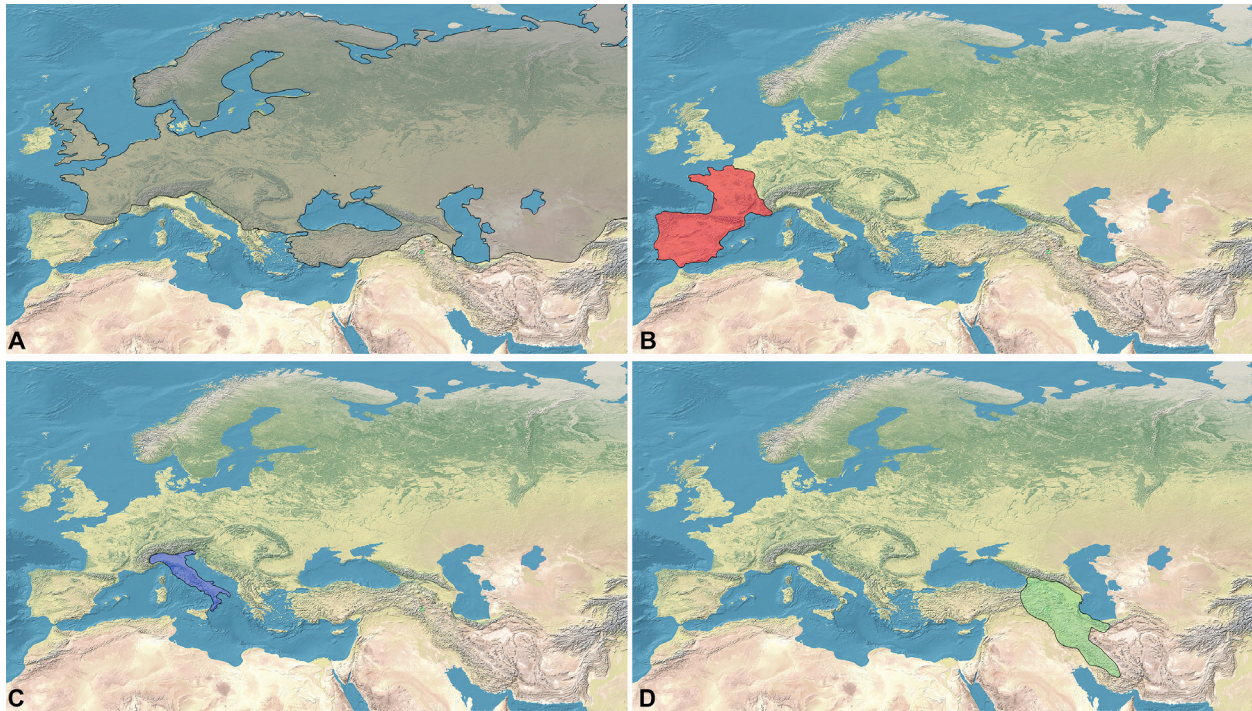


FIGURE 4. Modern geographic distribution of each of the four *Arvicola* species included in the reference dataset (**A**, *Arvicola amphibius*; **B**, *Arvicola sapidus*; **C**, *Arvicola italicus*; **D**, *Arvicola persicus*). After Kryštufek and Shenbrot (2022), modified.

(192/194 specimens correctly classified) AS - 93% (135/144), AAeast - 63% (24/36, with misclassifications occurring with AAwest and AS), AP - 56% (5/9), and AI - 40% (2/5). Misclassifications occur within *A. amphibius*, reflecting east-west clinal variation. All other species remain well separated.

Visualisation of LDA scores (Figure 8) confirms that (i) AS is rather homogeneous, compact and distinct but we also can note that AS shows a visible contact with AAeast, (ii) AP and AI, despite small sample sizes, form identifiable groups, and

(iii) there is no overlap between AAwest and AAeast and they remain distinguishable from other species.

Canonical Discriminant Analysis (CDA), see Appendix 3, strongly supports these results (prediction accuracy >99% for species with large sample sizes), and Mahalanobis distances confirm the close affinity of AAwest and AAeast, reinforcing their conspecific status. A detailed discussion on that topic is available in Appendix 3. Random Forest (RF) achieves overall accuracy of 91.4%; vari-

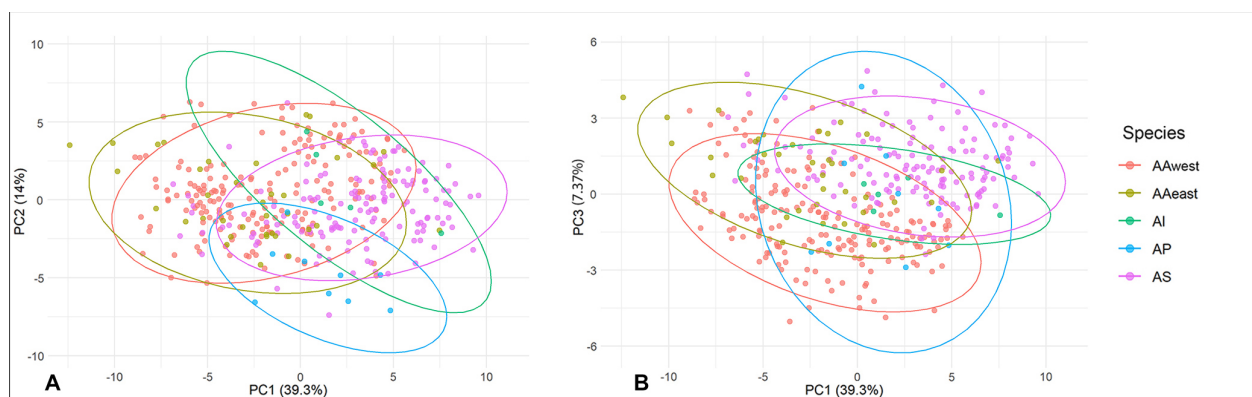


FIGURE 5. Principal component analysis (PCA) of modern *Arvicola* with 95% confidence ellipses. **A**, PC1 vs PC2. **B**, PC1 vs PC3. Groups: AAwest = *Arvicola amphibius* (Western Europe), AAeast = *Arvicola amphibius* (Eastern Europe), AI = *Arvicola italicus*, AP = *Arvicola persicus*, AS = *Arvicola sapidus*.

TABLE 2. Percentage of variance explained by the first ten principal components (PC1-PC10) of the PCA.

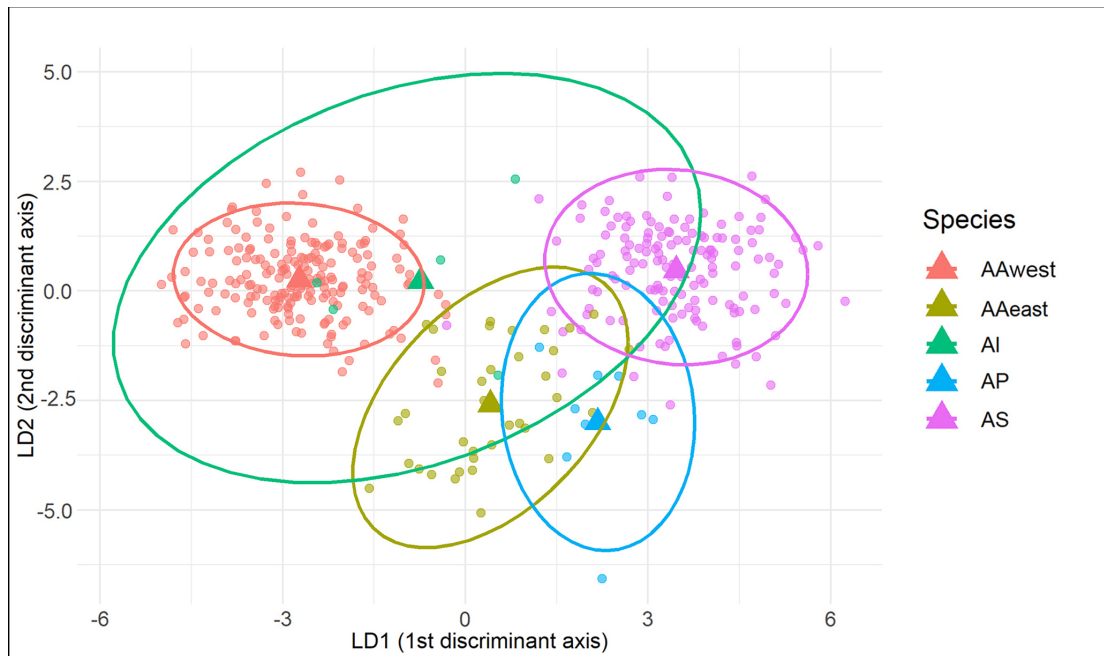
Axis	Eigenvalue	% variance	% cumulative variance
1	18.8431033	39.256465	39.25647
2	6.7420835	14.046007	53.30247
3	3.5155760	7.324117	60.62659
4	2.8030684	5.839726	66.46631
5	2.3630221	4.922963	71.38928
6	1.5773435	3.286132	74.67541
7	1.4448400	3.010083	77.68549
8	1.1610436	2.418841	80.10433
9	1.0738199	2.237125	82.34146
10	0.9760544	2.033447	84.37491

able importance identifies PC1 and PC3 as the strongest contributors. KNN performs well (86.45% at $k=1$), whereas K-medoids show limited discrimination (ARI = 0.195). Collectively, these methods demonstrate that modern *Arvicola* species can be reliably discriminated based on m/1 outline morphology.

Fossil Specimens

Among the four modern species included in this study, only *A. amphibius* and *A. sapidus* were retained as reference taxa for the classification of fossil specimens, for two complementary reasons. First, the sample sizes of *A. italicus* (N=5) and *A.*

persicus (N=9) are too limited to ensure reliable individual-level classification, as explicitly acknowledged throughout the modern specimen analyses. Second, and independently, neither *A. italicus* nor *A. persicus* has been reported, to our knowledge, from any Pleistocene or Holocene fossil site within the geographic area covered by the five prehistoric localities studied here - spanning southern France, northern Spain, and Belgium. The exclusion of these two peripheral species from the fossil classification framework is therefore both statistically and biogeographically justified, and the two-species AA/AS reference framework should be understood

**FIGURE 6.** Linear discriminant analysis (LDA) of modern *Arvicola* with individual points, centroids, and 95% confidence ellipses in the LD1-LD2 plane. Groups as in Figure 5.

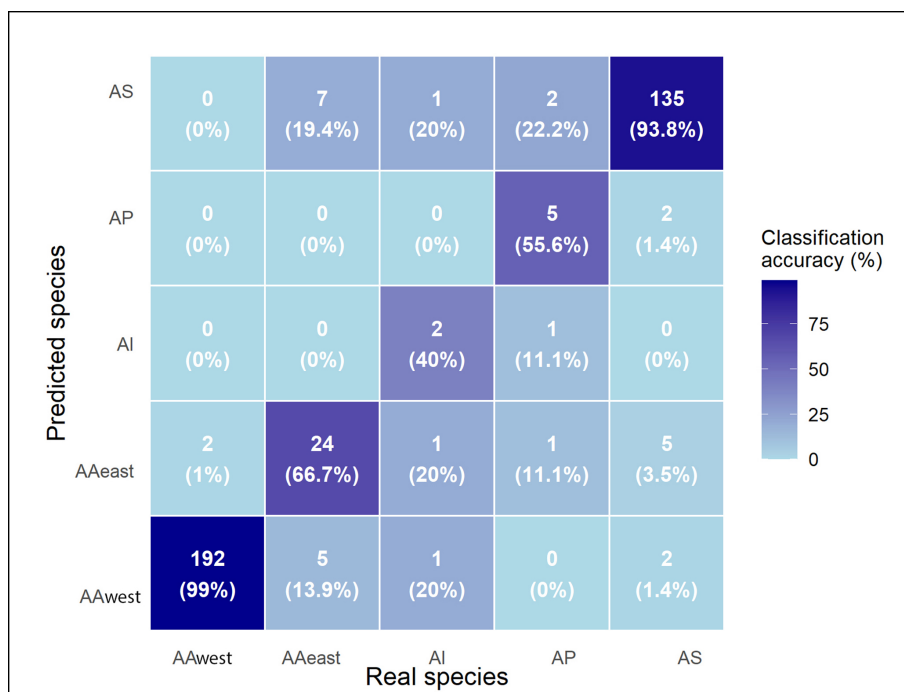


FIGURE 7. Confusion matrix from LDA cross-validation for modern *Arvicola*. Groups as in Figure 5.

as an assessment of morphological affinities rather than a strict taxonomic classification.

Lazaret Cave (Nice, France): MIS 6 (~150 ka). Specimens from this site were previously assigned to *A. cantianus* morphotype *amphibius* and *A. cantianus* morphotype *sapidus* (Desclaux et al., 2000). The 24 Lazaret m/1 specimens occupy an intermediate position between modern AA and AS in PCA

space, showing broad dispersion (Figure 9A). MANOVA confirms strong differentiation among three groups. All statistical tests (Pillai = 0.818, Wilks λ = 0.267, Hotelling-Lawley = 2.429, Roy = 2.291) show extremely significant results ($p < 2.2e-16$), indicating clear morphological differentiation. Tukey tests indicate that Lazaret specimens align more closely with AA on PC1 and PC3, but with AS

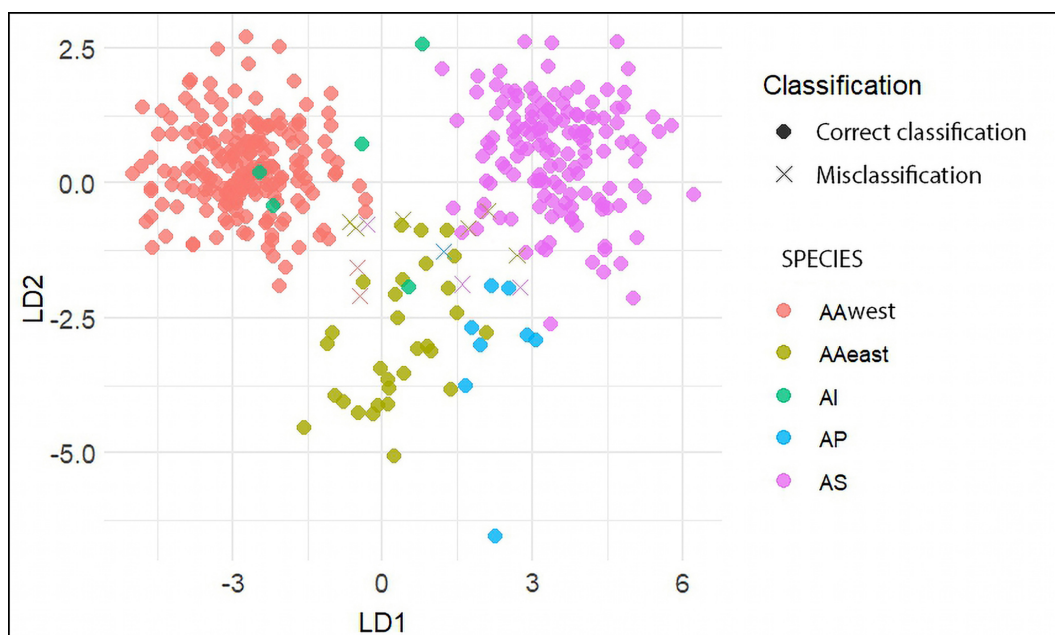


FIGURE 8. Linear discriminant analysis showing classification errors in the LD1-LD2 plane. Groups as in Figure 5.

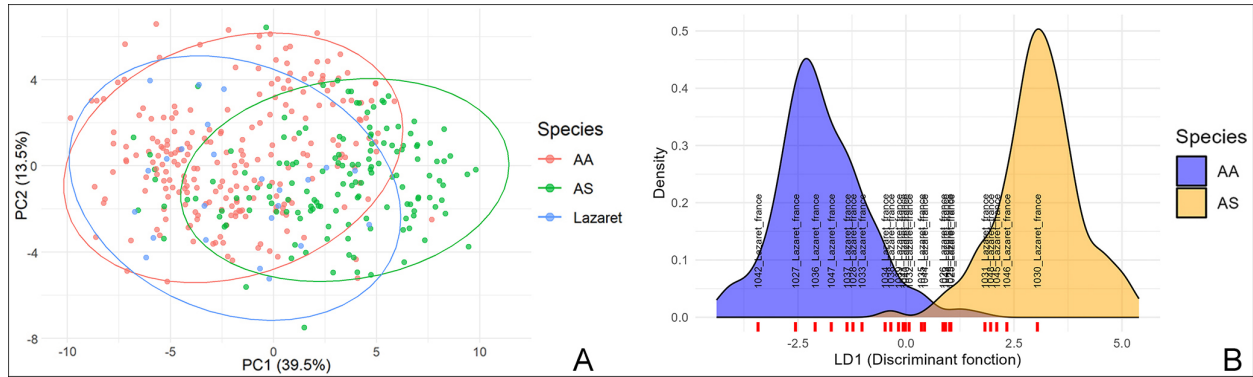


FIGURE 9. A, Principal component analysis (PCA) of modern *Arvicola* and fossil specimens from Lazaret Cave (MIS 6) with 95% confidence ellipses (PC1-PC2). **B**, LDA classification of Lazaret specimens along LD1, plotted with modern reference distributions (Kernel density curves). Groups: AA = *Arvicola amphibius*, AS = *Arvicola sapidus*, lazaret = fossil specimens.

on PC2, and show unique characteristics on PC5. LDA probabilistic assignment yields 15 AA-like specimens (62.5%) and nine AS-like specimens (37.5%). Three specimens show probabilities <80%, indicating intermediate morphologies. Morphospace range along LD1 nearly spans the full AA-AS separation observed in modern specimens. Random Forest assigns 17 specimens (70.8%) to AA and seven (29.2%) to AS. Mahalanobis distances match LDA exactly (62.5% AA; 37.5% AS). The three probabilistic assignment methods show different levels of concordance (Table 3): LDA vs Mahalanobis - complete agreement (24/24 specimens; 100%); LDA vs RF - partial agreement (14/24; 58.3%); RF vs Mahalanobis - partial agreement (14/24; 58.3%). Discordant cases likely reflect archaic, transitional morphologies typical of MIS 6 populations. The results indicate the presence of two co-occurring *Arvicola* lineages, with AA-like morphotype dominant (ratio ~ 1.7:1). These results strongly support the interpretation that Lazaret specimens represent archaic lineages belonging to *Arvicola* ex gr. *cantianus/amphibius* and *Arvicola* ex gr. *cantianus/sapidus*. This pattern is consistent with expected evolutionary complexity of MIS 6 refugial contexts and with previous findings of transitional morphologies in late Middle Pleistocene *Arvicola*. In conclusion, the MIS 6 assemblage at Lazaret Cave already shows a degree of morphological differentiation allowing partial discrimination between *A. amphibius*-like and *A. sapidus*-like morphotypes, despite their archaic character.

Baume Moula-Guercy (Ardèche, France): MIS 5.5 (~125 ka). Seventeen specimens were analysed. Specimens from Baume Moula-Guercy were previously assigned to *A. amphibius* and *A. sapidus* (Desclaux et al., 2000). PCA indicates strong

morphometric differentiation among groups, with the first three components explaining 60.6% of total variance (PC1: 40.0%, PC2: 13.3%, PC3: 7.3%). Visual inspection shows clear AA-AS separation, with Moula-Guercy specimens plotting mostly within the AA morphospace (Figure 10A). MANOVA confirms highly significant group differences (Pillai's trace = 1.016, $p < 2.2e-16$). Individual ANOVAs identify significant separation across multiple PCs, particularly PC1 ($F = 90.23$, $p < 2e-16$), PC3 ($F = 71.02$, $p < 2e-16$), and PC6 ($F = 25.65$, $p = 3.47e-11$). Post-hoc Tukey tests consistently show significant differences between AA and AS across most axes. LDA probabilistic assignment of the Moula-Guercy specimens (Figure 10B) yields 13 specimens assigned to *Arvicola amphibius*, and four specimens assigned to *A. sapidus*. Random Forest probabilistic assignment indicates a more strongly AA-dominated assemblage: 16 AA specimens, and a single AS specimen. LDA and Mahalanobis distance show perfect concordance (100%), and the agreement between LDA and RF is moderate (70.6%; Table 4).

Most Moula-Guercy specimens can be confidently assigned to *A. amphibius* (13/17 by LDA and Mahalanobis; 16/17 by RF), indicating that this species dominated the MIS 5.5 assemblage. A small set of specimens (1071, 1072, 1081, 1082, 1085) shows ambiguous assignments, likely due to retention of plesiomorphic dental traits, similar to MIS 6 patterns but less pronounced. The larger Lazaret sample size allowed LDA and RF to discriminate more effectively between morphotypes, suggesting that the limited Moula-Guercy sample ($n=17$) may constrain probabilistic assignment confidence for borderline specimens. Such configuration supports the interpretation that MIS 5.5

TABLE 3. Mahalanobis distances, LDA and RF probabilities, and taxonomic predictions for each *Arvicola* m/1 specimen from Lazaret Cave.

Specimen	Probability LDA	LDA	Probability RF	RF	Agreement	Mahalanobis	Previous determination
1027_Lazaret_france	99.99%	AA	91.00%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>
1028_Lazaret_france	99.99%	AA	79.60%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1032_Lazaret_france	94.69%	AA	52.60%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1033_Lazaret_france	99.98%	AA	89.00%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>
1034_Lazaret_france	99.67%	AA	100.00%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1035_Lazaret_france	80.32%	AA	50.80%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1037_Lazaret_france	100.00%	AA	93.40%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1039_Lazaret_france	98.39%	AA	92.60%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1041_Lazaret_france	97.30%	AA	88.00%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1042_Lazaret_france	100.00%	AA	72.20%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1047_Lazaret_france	100.00%	AA	80.00%	AA	TRUE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1029_Lazaret_france	85.84%	AS	60.80%	AS	TRUE	AS	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>
1045_Lazaret_france	99.93%	AS	97.60%	AS	TRUE	AS	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1048_Lazaret_france	99.86%	AS	94.00%	AS	TRUE	AS	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>
1036_Lazaret_france	100.00%	AA	53.00%	AS	FALSE	AA	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>
1038_Lazaret_france	99.34%	AA	77.80%	AS	FALSE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1040_Lazaret_france	96.48%	AA	98.20%	AS	FALSE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1044_Lazaret_france	75.33%	AA	87.80%	AS	FALSE	AA	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1025_Lazaret_france	87.58%	AS	98.20%	AA	FALSE	AS	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1026_Lazaret_france	72.93%	AS	72.20%	AA	FALSE	AS	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1030_Lazaret_france	100.00%	AS	80.20%	AA	FALSE	AS	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>
1031_Lazaret_france	99.72%	AS	72.60%	AA	FALSE	AS	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>
1043_Lazaret_france	78.40%	AS	98.80%	AA	FALSE	AS	<i>Arvicola</i> morphotype <i>cantianus/amphibius</i>
1046_Lazaret_france	99.98%	AS	56.40%	AA	FALSE	AA	<i>Arvicola</i> morphotype <i>cantianus/sapidus</i>

watervoles are still close to archaic lineages (*A. cantianus* sensu lato, syn. *A. mosbachensis*) that have been observed, for example, at Lazaret Cave (MIS 6).

Abauntz Cave (Navarre, Spain): MIS 3 (~40-50 ka). The Abauntz Cave assemblage (MIS 3, ~40-50 ka, N=29) presents a markedly different pattern from the Middle Pleistocene Lazaret sample. Specimens from Abauntz cave were previously

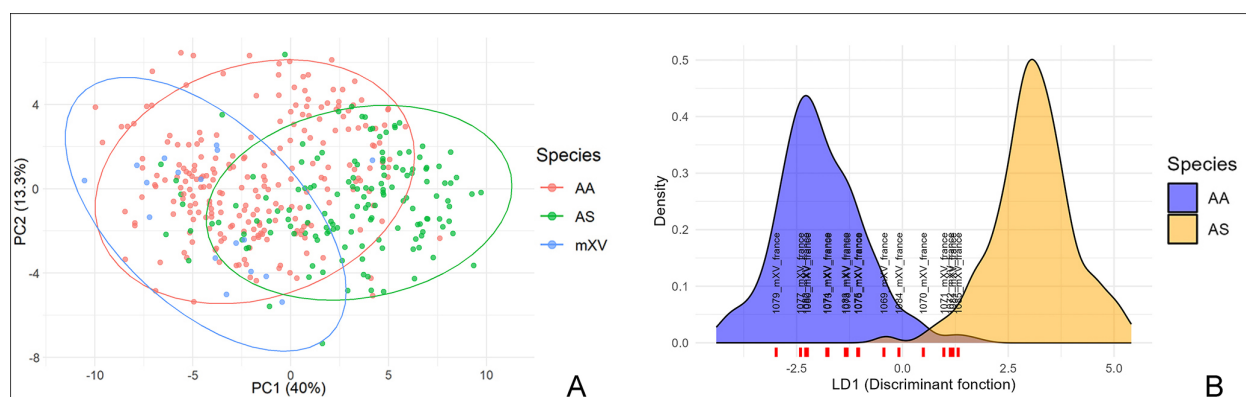
**FIGURE 10.** **A**, PCA of modern *Arvicola* and fossil specimens from Baume Moula-Guercy (MIS 5.5) in the PC1-PC2 plane. **B**, LDA classification of Moula-Guercy specimens along LD1 relative to modern species. Groups: AA = *Arvicola amphibius*, AS = *Arvicola sapidus*, mXV = Moula-Guercy (level XV) specimens.

TABLE 4. Mahalanobis distances, LDA and RF probabilities, and taxonomic predictions for each *Arvicola* m/1 specimen from Baume Moula-Guercy (level XV).

Specimens	Probability LDA	LDA	Probability RF	RF	Agreement	Mahalanobis	Previous determination
1069_mXV_france	99.60%	AA	71.20%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1070_mXV_france	70.15%	AA	82.80%	AA	TRUE	AA	<i>Arvicola sapidus</i>
1073_mXV_france	99.99%	AA	70.60%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1074_mXV_france	99.99%	AA	69.20%	AA	TRUE	AA	<i>Arvicola sapidus</i>
1075_mXV_france	99.99%	AA	87.00%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1076_mXV_france	99.99%	AA	95.00%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1077_mXV_france	99.99%	AA	59.20%	AA	TRUE	AA	<i>Arvicola sapidus</i>
1078_mXV_france	99.99%	AA	96.40%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1079_mXV_france	99.99%	AA	71.20%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1080_mXV_france	99.99%	AA	93.20%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1083_mXV_france	99.99%	AA	89.60%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1084_mXV_france	97.67%	AA	80.40%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1085_mXV_france	96.63%	AS	80.00%	AA	FALSE	AS	<i>Arvicola amphibius</i>
1071_mXV_france	82.92%	AS	50.20%	AA	FALSE	AS	<i>Arvicola sapidus</i>
1072_mXV_france	91.24%	AS	74.20%	AA	FALSE	AS	<i>Arvicola amphibius</i>
1081_mXV_france	93.48%	AS	70.20%	AA	FALSE	AS	<i>Arvicola amphibius</i>
1082_mXV_france	99.99%	AA	85.60%	AS	FALSE	AA	<i>Arvicola sapidus</i>

assigned to *A. amphibius* (Arteaga-Briebe et al., 2024). PCA shows that Abauntz specimens occupy an intermediate position in morphospace (Figure 11A), overlapping substantially with modern *A. amphibius* but shifted leftward along PC1 (mean PC1 = -2.59 relative to modern AA), indicating subtle morphological differences. MANOVA confirms significant differences from both reference species (Wilks λ = 0.241, p < 2.2e-16), with strong discrimination on PC1 (F = 101.6, p < 2e-16) and PC3 (F = 74.04, p < 2e-16). Post-hoc Tukey tests show that Abauntz differs significantly from both AA (p = 0.0008) and AS (p < 0.0001) on PC1, confirming its distinct morphometric signature. Classification

results demonstrate exceptional convergence across methods. LDA assigns 28/29 specimens (96.6%) to *A. amphibius* and only 1/29 (3.4%) to *A. sapidus* (Figure 11B) with most specimens showing very high posterior probabilities (>99%). Random Forest probabilistic assignment is nearly identical: 27/29 (93.1%) as AA and 2/29 (6.9%) as AS. LDA-RF agreement reaches 96.6% (28/29 specimens), much higher than the 58.3% observed at Lazaret, and LDA-Mahalanobis concordance is perfect at 100% (Table 5). This high methodological agreement indicates well-defined, unambiguous morphologies characteristic of fully evolved Late Pleistocene *Arvicola*, contrasting sharply with

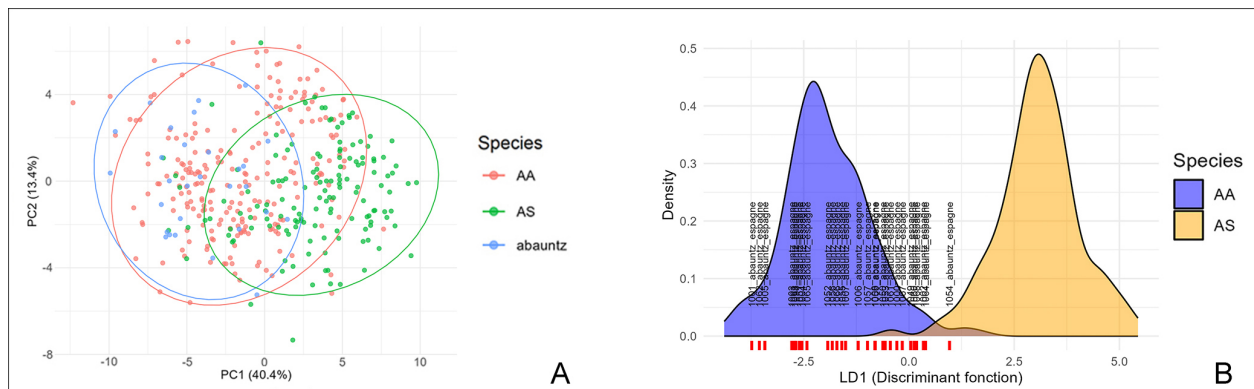
**FIGURE 11. A,** PCA of modern *Arvicola* and fossil specimens from Abauntz Cave (MIS 3) in the PC1-PC2 plane. **B,** LDA classification of Abauntz specimens along LD1 relative to modern species. Groups: AA = *Arvicola amphibius*, AS = *Arvicola sapidus*, abauntz = Abauntz specimens.

TABLE 5. Mahalanobis distances, LDA and RF probabilities, and taxonomic predictions for each *Arvicola* m/1 specimen from Abauntz Cave.

Specimen	Probability LDA	LDA	Probability RF	RF	Agreement	Mahalanobis	Previous determination
1000_abauntz_spain	99.16%	AA	80.00%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1001_abauntz_spain	100.00%	AA	73.40%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1002_abauntz_spain	83.64%	AA	89.20%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1003_abauntz_spain	100.00%	AA	99.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1004_abauntz_spain	100.00%	AA	93.20%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1005_abauntz_spain	100.00%	AA	96.40%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1006_abauntz_spain	99.99%	AA	64.40%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1007_abauntz_spain	100.00%	AA	90.60%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1008_abauntz_spain	99.94%	AA	71.00%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1049_abauntz_spain	95.83%	AA	88.00%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1051_abauntz_spain	100.00%	AA	93.40%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1052_abauntz_spain	100.00%	AA	82.00%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1053_abauntz_spain	99.79%	AA	87.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1055_abauntz_spain	100.00%	AA	99.60%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1056_abauntz_spain	100.00%	AA	96.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1057_abauntz_spain	99.97%	AA	81.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1058_abauntz_spain	100.00%	AA	69.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1059_abauntz_spain	99.93%	AA	87.20%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1060_abauntz_spain	93.94%	AA	78.60%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1061_abauntz_spain	99.61%	AA	98.20%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1062_abauntz_spain	100.00%	AA	99.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1063_abauntz_spain	100.00%	AA	87.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1064_abauntz_spain	79.69%	AA	89.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1065_abauntz_spain	100.00%	AA	98.20%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1066_abauntz_spain	100.00%	AA	99.00%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1067_abauntz_spain	98.43%	AA	98.60%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1068_abauntz_spain	91.93%	AA	56.80%	AA	TRUE	AA	<i>Arvicola amphibius cantabriae</i>
1054_abauntz_spain	81.37%	AS	77.80%	AS	TRUE	AS	<i>Arvicola amphibius cantabriae</i>
1050_abauntz_spain	99.84%	AA	97.80%	AS	FALSE	AA	<i>Arvicola amphibius cantabriae</i>

the transitional forms observed in MIS 6. Mean Mahalanobis distances (AA: 8.477, AS: 8.649, difference: 0.172) confirm overall affinity with *A. amphibius*, while maintaining a slightly intermediate position consistent with MIS 3 chronology. The single specimen (1054_abauntz_espagne) identified as *A. sapidus* is consistently classified across methods: LDA assigns it to AS with 81.37% probability, RF with 77.8%. Mahalanobis distances place it marginally closer to AS. Although probabilities are lower than those of typical AA specimens (95%), the probabilistic assignment is robust and likely reflects genuine taxonomic presence rather than ambiguity. Its slightly intermediate position may indicate retention of plesiomorphic traits.

Cova Eirós (Galicia, Spain): MIS 3 (~30-40 ka). Twelve specimens were analyzed. Specimens from Cova Eirós were previously assigned to *A. amphib-*

ius and *A. sapidus* (Rey-Rodriguez et al., 2011, 2016; Bal-Garcia et al., 2026). PCA revealed strong morphometric differentiation among modern groups, with the first three components explaining 60.2% of total variance (PC1: 39.4%, PC2: 13.6%, PC3: 7.3%). Cova Eiros specimens plot across both AA and AS morphospaces, indicating a mixed assemblage (Figure 12A). MANOVA indicates strong group differentiation (Pillai's trace = 0.897, $p < 2.2e-16$). ANOVAs show significant separation across nine PCs, especially PC1 ($F = 77.37$, $p < 2e-16$), PC3 ($F = 68.88$, $p < 2e-16$), and PC9 ($F = 18.43$, $p = 2.26e-08$). This robust discrimination across multiple axes provides a solid foundation for fossil classification. LDA probabilistic assignment (Figure 12B) identifies eight specimens as *A. amphibius* and four specimens as *A. sapidus*. RF probabilistic assignment yields nine AA specimens

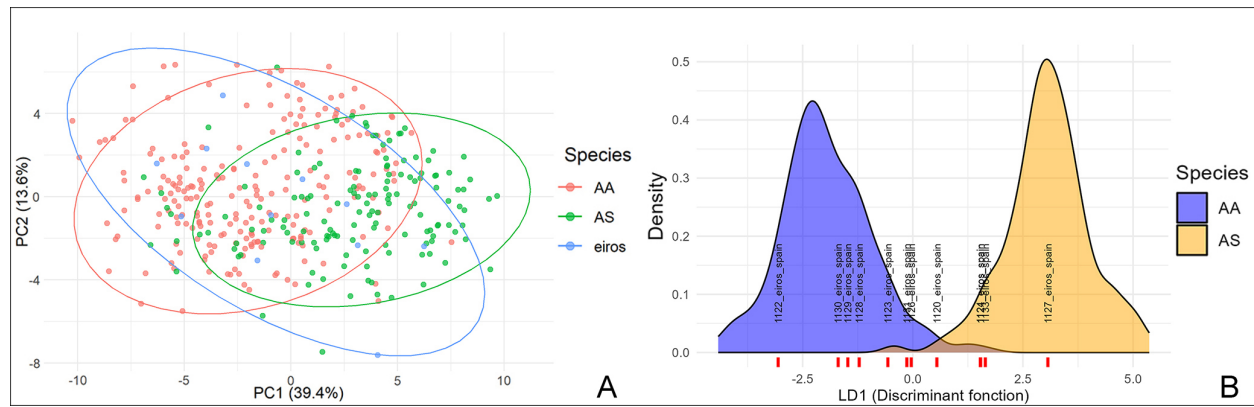


FIGURE 12. A, PCA of modern *Arvicola* and fossil specimens from Cova Eirós in the PC1-PC2 plane. **B,** LDA classification of Cova Eirós specimens along LD1 relative to modern species. Groups: AA = *Arvicola amphibius*, AS = *Arvicola sapidus*, eiros = Cova Eirós specimens.

and three AS specimens. Thus, Cova Eiros shows a relatively balanced co-occurrence of both species, contrasting with the predominantly monospecific assemblages at Moula-Guercy (MIS 5.5) and Abauntz (MIS 3). Concordance statistics are as follows: LDA-RF agreement: 9/12 (75%), LDA-Mahalanobis agreement: 12/12 (100.0%). Three specimens (1121_eiros_spain, 1131_eiros_spain and 1133_eiros_spain) show disagreement between LDA and RF, although Mahalanobis distances consistently support the LDA assignments. The Cova Eirós assemblage therefore exhibits a clear bimodal taxonomic structure, with both *A. amphibius* and *A. sapidus* well represented (Table 6). Mean Mahalanobis distances to modern centroids are nearly identical (AA: 10.388 ± 3.45 ; AS: 10.427 ± 3.58), indicating that the fossils occupy

intermediate positions consistent with their MIS 3 age.

Trou Al'Wesse (Modave, Belgium): MIS 3 (~30-40 ka). This assemblage represents a small but highly informative Late Pleistocene sample. All specimens from Trou Al'Wesse were previously assigned to *A. amphibius* (Miller et al., 2007). Despite the small number of specimens, results are exceptionally clear, and strong convergence across analytical methods. PCA (Figure 13A) places the Trou Al'Wesse specimens in an intermediate position between modern *A. amphibius* and *A. sapidus* along PC1, with a pronounced leftward shift (mean PC1 = -3.61 relative to modern AA). MANOVA confirms highly significant group differentiation (Wilks $\lambda = 0.267$, $p < 2.2e-16$), with the strongest discrimination on PC1 ($F = 89.48$, $p < 2e-$

TABLE 6. Mahalanobis distances, LDA and RF probabilities, and taxonomic predictions for each *Arvicola* m/1 specimen from Cova Eirós.

Specimens	Probability LDA	LDA	Probability RF	RF	Agreement	Mahalanobis	Previous determination
1120_eiros_spain	62.41%	AA	74.80%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1122_eiros_spain	100%	AA	100.00%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1123_eiros_spain	99.76%	AA	65%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1126_eiros_spain	96.77%	AA	86.00%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1128_eiros_spain	99.99%	AA	100%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1129_eiros_spain	99.99%	AA	94.80%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1130_eiros_spain	99.99%	AA	60.40%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1124_eiros_spain	98.84%	AS	57.00%	AS	TRUE	AS	<i>Arvicola amphibius</i>
1127_eiros_spain	99.99%	AS	91.80%	AS	TRUE	AS	<i>Arvicola amphibius</i>
1121_eiros_spain	98.87%	AS	69.60%	AA	FALSE	AS	<i>Arvicola amphibius</i>
1131_eiros_spain	98.03%	AA	94.00%	AS	FALSE	AA	<i>Arvicola sapidus</i>
1133_eiros_spain	99.33%	AS	89.20%	AA	FALSE	AS	<i>Arvicola sapidus</i>

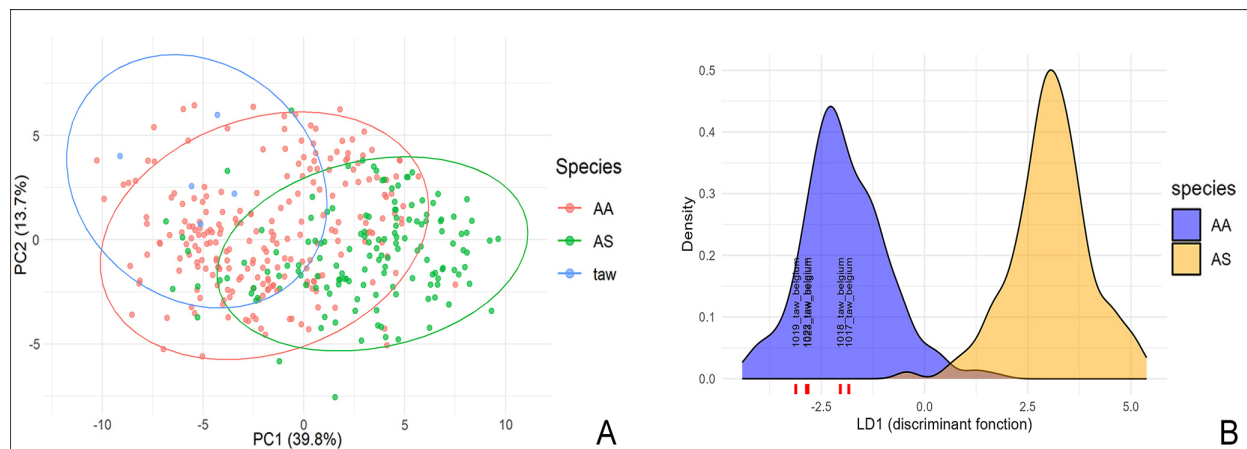


FIGURE 13. A, PCA of modern *Arvicola* and fossil specimens from Trou Al'Wesse in the PC1-PC2 plane. **B**, LDA classification of Trou Al'Wesse specimens along LD1 relative to modern species. Groups: AA = *Arvicola amphibius*, AS = *Arvicola sapidus*, taw= Trou Al'Wesse specimens.

16) and PC3 ($F = 61.82$, $p < 2e-16$). Notably, post-hoc Tukey tests indicate that Trou Al'Wesse differs significantly from AS ($p < 0.0001$), whereas the difference from AA approaches but does not reach significance ($p = 0.070$), suggesting closer morphological affinity with *A. amphibius*. Probabilistic assignment results show perfect methodological agreement (Figure 13B; Table 7).

All five specimens are consistently assigned to *A. amphibius* by LDA (100%), RF (100%), and Mahalanobis distances (100%). LDA posterior probabilities are extremely high ($\geq 99.99\%$), and RF probabilities range from 84.6% to 99.2%, confirming unambiguous morphological signatures. This complete concordance reflects the well-defined Late Pleistocene morphology characteristic of fully evolved *A. amphibius*. Mean Mahalanobis distances (AA: 9.319; AS: 9.561; difference: 0.242) further support the close affinity of the Trou Al'Wesse specimens to modern *Arvicola amphibius*, while maintaining a slightly intermediate position consistent with MIS 3 chronology.

DISCUSSION

This study demonstrates that two-dimensional geometric morphometric study of the first lower molar (m/1) outlines provides a robust and highly informative framework for assessing taxonomic boundaries, evolutionary trends, and temporal transitions within the genus *Arvicola*.

By integrating a large modern reference dataset with fossil specimens spanning MIS 6 to MIS 3, our results reveal clear morphological differentiation among modern species, substantial structuring within *Arvicola amphibius*, and a progressive evolutionary trajectory from archaic Middle Pleistocene forms to fully modern and differentiated modern species *A. amphibius* and *A. sapidus*.

Analyses of modern specimens confirm that m/1 morphology provides strong discriminatory power across *Arvicola*. Multivariate exploratory analyses (PCA, MANOVA) show significant inter-specific differences, enabling reliable species-level discrimination.

Among probabilistic assignment approaches, LDA achieved an overall accuracy of 91%, driven

TABLE 7. Mahalanobis distances, LDA and RF probabilities, and taxonomic predictions for each *Arvicola* m/1 specimen from Trou Al'Wesse. Agreement column indicates concordance between LDA and RF classifications.

Specimen	Probability LDA	LDA	Probability RF	RF	Agreement	Mahalanobis	Previous determination
1017_taw_belgium	99.99%	AA	99.20%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1018_taw_belgium	99.99%	AA	84.60%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1019_taw_belgium	100%	AA	98.60%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1022_taw_belgium	100%	AA	96.80%	AA	TRUE	AA	<i>Arvicola amphibius</i>
1023_taw_belgium	100%	AA	92.20%	AA	TRUE	AA	<i>Arvicola amphibius</i>

primarily by the robust performance on the well-sampled groups *A. amphibius* and *A. sapidus*; classification accuracy for *A. italicus* and *A. persicus* was more limited, consistent with their small sample sizes and the associated statistical constraints discussed above. The strong separation of *A. amphibius* and *A. sapidus* validates long-standing ecological and morphological distinctions between fossorial and aquatic forms. The heterogeneity observed within *A. amphibius* - especially east-west differentiation - illustrates ecogeographic structuring likely influenced by climatic gradients, habitat variation, or historical population dynamics. Despite small sample sizes, *A. italicus* and *A. persicus* remain distinct, highlighting the sensitivity of the method even for peripheral species. While consistent morphometric signals are detectable for *A. italicus* and *A. persicus* across multiple methods - particularly the strongly negative LD4 scores for *A. italicus* and the Mahalanobis distances placing both species as morphometrically divergent - the degree of morphospace overlap observed and the limited classification accuracy precludes strong claims of distinctiveness. The sensitivity of the method for these peripheral species should be understood as preliminary and in need of confirmation with larger samples.

These morphometric results provide a robust basis for comparison with ongoing genetic analyses and forthcoming phylogenetic models. Multivariate distance analysis further refines species affinities, strengthening in applying this framework to fossil material. These results confirm that 2D outline-based GMM is methodologically reliable and biologically meaningful, capturing both species-level differences and fine-scale geographic variability.

The Lazaret Cave assemblage displays the most complex morphological pattern among the fossil samples. PCA, LDA, and Mahalanobis distances all reveal a pronounced intermixed distribution, with fossils spanning nearly the full morphospace between modern *A. amphibius* and *A. sapidus*. High dispersion and discordance between LDA and RF probabilistic assignments indicate the presence of intermediate or transitional morphotypes rather than discrete modern-like species. These results strongly support the interpretation that Lazaret specimens represent archaic lineages belonging to *Arvicola* ex gr. *cantianus*/*amphibius* (60-65%) and *Arvicola* ex gr. *cantianus*/*sapidus* (35-40%). This pattern is consistent with expected evolutionary complexity of MIS 6 refugial contexts in southeastern France (Hanquet et al.,

2010; Lopez-Garcia et al., 2021; Barakat et al., 2025). The mosaic nature of these specimens underscores the importance of multivariate classification approaches: parametric methods (LDA, Mahalanobis) capture broad shape affinities, whereas RF is more sensitive to localised or non-linear variation, which may explain its greater tendency to identify ambiguous morphotypes. The MIS 6 assemblage at Lazaret Cave already shows a degree of morphological differentiation allowing partial discrimination between *A. amphibius*-like and *A. sapidus*-like morphotypes, despite their archaic character - demonstrating that EFA can detect lineage differentiation even in pre-modern forms.

The MIS 5.5 assemblage at Baume Moula-Guercy shows reduced variability compared to Lazaret and a predominantly *A. amphibius*-like signal, consistent with the persistence of archaic lineages close to *A. cantianus* sensu lato at this time.

Molecular clock analyses place the split between *A. amphibius* and *A. sapidus* at ~1.5 Ma (Mahmoudi et al., 2020), with palaeontological evidence of *sapidus*-type morphology in *Arvicola jacobaeus* from the Early Pleistocene of Atapuerca (~1.2-1.5 Ma; Cuenca-Bescós et al., 2010). The presence of archaic *sapidus*-type morphology at Lazaret Cave (MIS 6) and Baume Moula-Guercy (MIS 5.5) suggests that *A. sapidus* reached southern France well before the 62-ka colonization date estimated from modern genomes (Centeno-Cuadros et al., 2009). While ancient DNA analysis could theoretically reveal morphological convergence rather than true phylogenetic affinity, our morphometric results suggest early *A. sapidus* presence in southern France, at least during MIS 6 and MIS 5.5. Our morphometric data indicates a more complex and dynamic biogeographic history involving multiple immigration waves from Iberia during the Middle and early Late Pleistocene, with subsequent local extinction(s) likely during MIS 4. The 62-ka estimate represents the most recent successful colonisation, not the first, highlighting the complementary value of morphological and genetic approaches in reconstructing evolutionary history.

Furthermore, the results obtained for Lazaret Cave and Baume Moula-Guercy are in accordance with previous studies, based on morphology and SDQ (Schmelzband-Differenzierungs-Quotient) values, which have highlighted the presence of transitional morphologies in late Middle Pleistocene and early Upper Pleistocene *Arvicola* (Heinrich, 1978, 1982, 1990, 1997; Fejfar and Heinrich, 1983; Agadzhanian, 1983; Rekovets, 1990, 1994;

Kolfschoten, 1992; Marquet, 1993; von Koenigswald and Van Kolfschoten, 1996; Abbassi et al., 1998; Desclaux et al., 2000; Maul et al., 2000; Kalthoff et al., 2007; Escudé et al., 2008a, 2008b; Ruddy, 2011).

The MIS 3 sites - Abauntz, Cora Eirós, and Trou Al'Wesse - showed a marked shift toward fully modern morphologies. In Abauntz, nearly all (96-97%) specimens are confidently classified as *Arvicola amphibius* sensu stricto, with rare occurrences of *A. sapidus* (3-4%). The low discordance rate (3.4%) and high classification probabilities indicate that by MIS 3, dental morphology had largely stabilised into modern species phenotypes, in sharp contrast to the 41.7% discordance observed at MIS 6 Lazaret. These results support the evolutionary transition from archaic *A. cantianus* forms in the Middle Pleistocene to fully differentiated modern species in the Late Pleistocene. The Cova Eirós assemblage documents sympatry between *A. amphibius* and *A. sapidus*, while Trou Al'Wesse yields a clearly monospecific *Arvicola amphibius* with perfect probabilistic assignment concordance. These results demonstrate that by MIS 3, modern *Arvicola* phenotypes had become fully established across Western and Central Europe, with morphological ambiguity almost entirely absent. The strong convergence among probabilistic assignment methods (up to 100% agreement) at these sites contrasts sharply with the mixed morphologies at MIS 6, underscoring evolutionary transition between the late Middle or Late Pleistocene. From MIS 3 onwards, morphotypes become fully congruent with modern species, as demonstrated by the near-perfect classification rates at Abauntz Cave (LDA: 96.6% AA), Cova Eiros (mixed AA/AS assemblage confirmed) and Trou Al'Wesse (LDA and RF: 100% AA).

This temporal progression is independently validated by the increasing convergence between LDA and RF probabilistic assignments through time - from partial concordance at MIS 6 to full concordance at MIS 3 - which we interpret as reflecting the progressive morphological stabilization of modern *Arvicola* phenotypes. This pattern constitutes one of the most original evolutionary findings of the present study.

Our outline-based EFA framework demonstrates that, despite the considerable individual variability species in *Arvicola* m/1 morphology that complicated interspecific discrimination, which has been already mentioned by Escudé et al. (2008b), species-level discrimination remains highly reliable when global outline shape is captured in its

entirety. This suggests that outline methods are particularly well suited to taxa with high intraspecific morphological variation such as *Arvicola*.

Our work shows a highly consistent picture: at four out of five sites (Lazaret Cave, Baume Moula-Guercy, Cova Eiros and Trou Al'Wesse), 2D morphometric results are fully concordant with prior identifications, providing independent validation of both the paleontological determinations and our methodological framework. The most significant result in this respect concerns Abauntz Cave: while the assemblage had been previously identified as monospecific (*A. amphibius*), our EFA-based analysis suggests the possible presence of a single *A. sapidus* specimen (specimen 1054_abauntz_spain, LDA: AS 81.37%; RF: AS 77.8%; Mahalanobis closer to AS). This finding, supported by the convergence of three independent methods, illustrates precisely the added value of outline-based morphometrics over traditional qualitative identification: it can detect minority taxa that might otherwise be overlooked in monospecific assemblages.

CONCLUSION

A comprehensive 2D geometric morphometric protocol based on m/1 outline analysis was applied to a modern reference dataset of 390 specimens representing four *Arvicola* species: *A. amphibius* (N = 231), *A. sapidus* (N = 145), *A. italicus* (N = 5), and *A. persicus* (N = 9). Using a multivariate analytical framework combining PCA, MANOVA, LDA, CDA, Random Forest probabilistic assignment, and Mahalanobis distance analysis, we show that all modern species exhibit significant and diagnostic differences in molar outline shape. These findings confirm that species-level discrimination based on m/1 morphology is reliable across the genus.

Applying this validated framework, with minor specific adaptations, to fossil assemblages spanning MIS 6 to MIS 3 reveals a clear temporal evolutionary trajectory. The MIS 6 assemblage from Lazaret Cave displays high morphological variability, with intermediate morphotypes and complex morphologies characteristic of archaic *Arvicola* lineages (*A. cantianus* sensu lato, syn. *A. mosbachensis*). Specimens fall into two morphological groups - *Arvicola* ex gr. *cantianus/amphibius* and *Arvicola* ex gr. *cantianus/sapidus* - representing transitional forms ancestral to modern species. Comparison with other MIS 6 assemblages and forthcoming aDNA data will help refine this terminology. By MIS 5.5 (Baume Moula-Guercy), assemblages are dominated by *A. amphibius*-like

morphologies, although several specimens retain plesiomorphic traits. In contrast, MIS 3 assemblages (Abauntz, Cova Eirós, Trou Al'Wesse) show predominantly or entirely modern phenotypes, with high concordance among probabilistic assignment methods and minimal ambiguity. Together, these results document the progressive morphological divergence and eventual stabilization of the modern *Arvicola amphibius* and *A. cantianus* lineages during the late Middle to Late Pleistocene.

The data also supports a more complex biogeographic history for *Arvicola sapidus* than previously inferred from modern genetic evidence alone, suggesting multiple dispersal events into Western Europe during the Middle and early Late Pleistocene, followed by local extinctions and later recolonization. Overall, this study demonstrates that m/1 outline based geometric morphometrics is a powerful and cost-effective tool for resolving taxonomic identities and exploring evolutionary processes in both modern and fossil contexts (Rekovets and Kovalchuk, 2017). By integrating modern and Pleistocene datasets within a unified framework, we provide new insights into the morphological evolution, lineage differentiation, and biogeographic dynamics within the genus *Arvicola* across the European Pleistocene.

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DATA AVAILABILITY STATEMENT

The R script used for statistical analyses is publicly available on Huma-Num: <https://shared-ocs.huma-num.fr/wl/?id=SlauouFJjYm2dsYg6zEU9qDKALn3qd3kl>

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APPENDIX 1.

Inventory of modern and fossil *Arvicola* specimens included in this study, with collection details and repository information. (Appendices are available for download as zipped file at <https://palaeo-electronica.org/content/2026/5941-temporal-evolution-of-arvicola-molar-morphology>.)

APPENDIX 2.

Summary of the Pleistocene sites from which fossil specimens were sampled, including stratigraphic context and chronological attribution. (Appendices are available for download as zipped file at <https://palaeo-electronica.org/content/2026/5941-temporal-evolution-of-arvicola-molar-morphology>.)

APPENDIX 3.

Raw results for all statistical analyses performed on the modern and fossil datasets, including complementary analyses (CDA, CVA, and distance analysis). (Appendices are available for download as zipped file at <https://palaeo-electronica.org/content/2026/5941-temporal-evolution-of-arvicola-molar-morphology>.)