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View of the entrance to the Mas d'Azil cave. Credits: photo by Marc Jarry.

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ISSN (imprimé / *print*) : 1631-0683/ ISSN (électronique / *electronic*) : 1777-571X

The small vertebrate assemblages from the Aurignacian deposits of the Mas d’Azil cave (Ariège, France): new data for the understanding of the MIS3 environmental changes in the Pyrenees

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Submitted on 21 June 2024 | Accepted on 28 October 2024 | Published on 22 January 2025

[urn:lsid:zoobank.org:pub:20D9A783-8D7C-4617-9745-512EEDC037F3](https://zoobank.org/pub:20D9A783-8D7C-4617-9745-512EEDC037F3)

Stoetzel E., Lebreton L., Pallier C., Bruxelles L., Bon F., Lejay M., Anderson L., Martin H. & Jarry M. 2025. — The small vertebrate assemblages from the Aurignacian deposits of the Mas d’Azil cave (Ariège, France): new data for the understanding of the MIS3 environmental changes in the Pyrenees. *Comptes Rendus Palevol* 24 (1): 1-18. <https://doi.org/10.5852/cr-palevol2025v24a1>

ABSTRACT

The Mas d’Azil cave, located in southwestern France in the foothills of the Pyrenees, is a major site for the study and understanding of the European Upper Palaeolithic. The early Aurignacian levels (US4 and US5) have yielded 3762 remains of small vertebrates, allowing to document the faunal communities in this border region during the MIS3 (*c.* 40-37 ky cal. BP), and to propose interpretations of the taphonomic and paleoenvironmental context of the human occupations. The accumulations from both US were mainly formed by predation, and the climatic conditions were mostly temperate, but slightly colder than the current ones. The landscape was dominated by grasslands, with wooded areas in the valley, and steppes and rocky areas on the slopes. The geographical position of the site, under the climatic influences of the Mediterranean Sea, the Atlantic Ocean and the Pyrenees, may have created proximity between faunal communities of different ecological affinities. The results obtained are placed in the broader regional context of the MIS3 in southwestern France and northeastern Spain.

KEY WORDS

Amphibiens,
birds,
micromammals,
taphonomy,
palaeoecology,
Late Pleistocene,
southwestern France.

RÉSUMÉ

Les microvertébrés des dépôts aurignaciens de la grotte du Mas d’Azil (Ariège, France) : contribution à la compréhension des changements environnementaux au SIM 3 dans les Pyrénées.

La grotte du Mas d’Azil, située dans le Sud-Ouest de la France au pied des Pyrénées, en Ariège, est un site majeur pour l’étude et la compréhension du Paléolithique supérieur européen. Les niveaux datés du début de l’Aurignacien (US4 et US5) ont livré 3762 restes de petits vertébrés, permettant de documenter les communautés fauniques de cette région pendant le SIM3 (*c.* 40-37 ka cal. BP), et de proposer des interprétations sur le contexte taphonomique et paléoenvironnemental des occupations humaines. Les accumulations des deux US ont été formées principalement par prédation, et les conditions climatiques étaient globalement tempérées, bien que légèrement plus froides que l’actuel. Le paysage était dominé par des prairies, avec des zones boisées dans la vallée, et des steppes et des zones rocheuses sur les pentes. La position géographique du site, soumise aux influences climatiques de la mer Méditerranée, de l’océan Atlantique et des Pyrénées, a pu créer une proximité entre des communautés fauniques d’affinités écologiques différentes. Nos résultats ont été replacés dans le contexte régional plus large du SIM3 dans le Sud-Ouest de la France et le Nord-Est de l’Espagne.

MOTS CLÉS

Amphibiens,
oiseaux,
micromammifères,
taphonomie,
paléoécologie,
Pléistocène supérieur,
Sud-Ouest de la France.

INTRODUCTION

The early Upper Palaeolithic in western Europe coincides with the arrival and settlement of *Homo sapiens* in an area formerly occupied by neandertal groups. In southern France, and especially the north Pyrenean range, the Aurignacian culture attributed to *Homo sapiens* and dated in between *c.* 40 and 34 Ky BP (Anderson 2019) represents a comprehensive set of social, technologic, economic and symbolic behaviors contemporaneous to this crucial shift in European Prehistory. The present study aims at providing, for the first time, information on the small vertebrate communities documented in the early Aurignacian levels of the Mas d'Azil cave (Jarry *et al.* 2017), as well as on the taphonomic and palaeoenvironmental context of the occupations. The results obtained are placed in the broader regional context of the MIS3 in the Pyrenean region.

The Mas d'Azil cave (Fig. 1) is known for its exceptional archaeological richness and gave its name to a Prehistoric chrono-cultural period, the Azilian (Piette 1889, 1895). The site is also well known for its mobiliary art, one of the richest and the most beautiful known in a Magdalenian context (e.g. Piette 1907; Péquart & Péquart 1960, 1961a, b; Chollot 1963; Clottes *et al.* 1981; Schwab 2008; Azema *et al.* 2021). Although it is less known, the Mas d'Azil cave has also shown proof of Aurignacian occupations (Jarry *et al.* 2017, 2021b), recorded in about twenty sites on the Pyrenean piedmont – including its eponymous site Aurignac – but very few in valley bottoms (Bon 2002, 2007), which makes the Mas d'Azil cave even more important for the study of European Prehistory, especially regarding our understanding of the Upper Palaeolithic.

However, the sedimentary processes are complex, and the archaeological sequence is not continuous: gaps have been observed in the human occupations of the site, both chronologically (absence of *in situ* occupation levels from the recent Aurignacian to the early Magdalenian) and spatially (differential distribution of remains, particularly during the Magdalenian) (Pallier *et al.* 2016, 2024; Pallier 2021; Jarry *et al.* 2021a). Interdisciplinary studies, including historiography, geomorphology, karstology, geoarchaeology and archaeology, have provided some answers to this issue (Pallier *et al.* 2016, 2024; Pallier 2021). For example, the sedimentary levels containing Aurignacian occupations were covered by several meters of fluvial sediment, leading to the erosion of the superficial part of the deposits (possible late/recent Aurignacian found elsewhere in secondary position), but also to the good preservation of the underlying levels of the early Aurignacian, which are the subject of this study.

The Mas d'Azil cave, crossed by the course of the river Arize, provides a high-resolution image of the hydrosedimentary responses resulting from climatic fluctuations during the last glacial cycle (Pallier *et al.* 2016, 2024; Pallier 2021). Small vertebrates are also well known to be good palaeoclimatic and palaeoenvironmental proxies (e.g. Royer *et al.* 2020; López-García *et al.* 2021), and give an interesting and

complementary view of the global climatic conditions and local landscape at the site at the moment of the deposition and can also help to better understand the timing of human occupations (Lebreton *et al.* 2021).

MATERIAL AND METHODS

STUDIED LAYERS

The two US studied in this work are only known from a 50 cm² test-pit each, and their deposition was made over several periods of time of deposits.

US4 (5 to 20 cm thick) is composed of pinkish sedimentary breccia with small calcareous elements, Aurignacian Lithic material and burnt fauna; it was dated at 34880 ± 260 BP (Beta-449 411), i.e., 40631 to 39480 cal. BP (Intcal 2020, Reimer *et al.* 2020) (Jarry *et al.* 2017; Pallier *et al.* 2024).

US5 (> 40 cm thick, base not reached) is a mixture of limestone blocks and fine brown silty-clay sediments with an increasingly dense chaos of limestone blocks, Aurignacian material and fauna; it was dated at 33260 ± 210 BP (Beta-449 412), i.e., 38954 to 37157 cal. BP (Intcal 2020, Reimer *et al.* 2020) (Jarry *et al.* 2017; Pallier *et al.* 2024).

The Radiocarbon datings were made on undeterminable burnt bone fragments, and although indicating an apparent inversion attributable to post-depositional processes, they are homogeneous and belong to the early Aurignacian (Fig. 2). The early Aurignacian is the most well-known among the different stages of the Aurignacian sequence of the northern Pyrenees, and lithic industries from US4 and US5 are perfectly similar to those described in other regional context securely attributed to the early Aurignacian, like at La Tuto de Camalhot (Ariège) or La grotte des Hyènes at Brassempouy (Landes) (Bon 2002; Anderson 2019). No difference was observed between the Aurignacian industries of US4 and US5, which have been noted as “sedimentary units” but belong to the same archaeological set.

SAMPLING

A total of eight samples from US4 and ten samples from US5 were recovered for microvertebrate study from test-pit 2.2 of the “Theatre” room (Fig. 1).

Each sample represents a bucket of sediment (*c.* 10 l.) corresponding to a “spit” extracted during the 2014 and 2015 excavation campaigns, then sieved (2 mm mesh) and sorted. Each sample was numbered separately, keeping at each stage the information of its provenance (test-pit, US, z; Appendices 1; 2).

Even if it would have been preferable to consider each spit separately (Royer 2014), the quantity of material present in each spit was not sufficient to obtain reliable and representative information. Moreover, some samples appear clearly smaller than the others, probably linked to variations in the amount of sediment vs limestone blocks in each bucket, leading to a bias of species and anatomical representation between spits. Consequently, for the present study we have chosen to group the spits following the archaeological US.

TABLE 1. — Faunal list of the small vertebrates from the Aurignacian levels of the Mas d’Azil cave. Arvicolinae indet. include unidentified molars and fragmented palatum; Rodents indet. include isolated incisors, fragmented cranial remains and post-cranial remains. Abbreviations: **MNI**, minimum number of individuals; **NISP**, number of identified specimens.

Taxa	US 4		US 5		Total	
	NISP	MNI	NISP	MNI	NISP	MNI
Lagomorpha	indet.	0	2	1	2	1
Rodentia	<i>Apodemus</i> gr. <i>sylvaticus-flavicollis</i>	1	8	6	9	7
	<i>Chionomys nivalis</i> (Martins, 1842)	4	13	10	17	14
	<i>Arvicola</i> gr. <i>amphibius-sapidus</i>	21	38	26	59	40
	<i>Microtus</i> gr. <i>arvalis-agrestis</i>	42	26	98	54	140
	<i>Alexandromys oeconomicus</i> (Pallas, 1776)	10	7	7	7	14
	Arvicolinae indet.	276	24	458	66	734
	indet.	681	—	898	—	1579
Chiroptera	indet.	50	17	143	19	193
Eulipotyphla	<i>Talpa</i> gr. <i>europaea-aquitania</i>	3	1	24	6	27
	<i>Sorex</i> gr. <i>araneus-coronatus</i>	3	3	11	10	13
Anura	<i>Rana</i> cf. <i>temporaria</i>	7	4	37	17	44
	cf. <i>Rana/Pelophylax</i>	19	22	17	38	36
	indet.	151	—	282	—	433
Squamata	Lacertidae indet.	0	3	1	3	1
Aves	indet.	100	—	354	—	454
Pisces	indet.	0	0	1	1	1
Total		1368	123	2394	262	3762
						385

SPECIES IDENTIFICATION

The identification of the recovered species were made thanks to comparisons with modern specimens from the *Muséum national d’Histoire naturelle* (collection *Mammifères et Oiseaux*), as well as identification keys from the literature, notably Chaline *et al.* (1974), Quéré & Le Louarn (2011), Laplana *et al.* (2015) and Kryštufek & Shenbrot (2022) for small mammals, Bailon (1999) for amphibians, Bocheński & Tomek (2009) and Tomek & Bocheński (2009) for birds. For each taxon, we considered the number of identified specimens (NISP), the minimum number of elements (MNE) and the minimum number of individuals (MNI). Birds and bats were not precisely identified. For Arvicolines, we followed Kryštufek & Shenbrot (2022) for the nomenclature; the identification at the species level and the calculation of MNI were based on isolated and *in situ* lateralized first lower molars, representing the most discriminating element. Other elements were placed in unidentified Arvicolines.

TAPHONOMY

For the taphonomic analysis of the small mammal remains, we followed the method developed by Andrews (1990) and Fernández-Jalvo *et al.* (2016). The anatomical representation was calculated following the formula: $PR = [F_{obs} / (F_{th} \times MNI)] \times 100$, with PR = percentage of representation, F_{obs} = observed frequency of each element in the fossil assemblage, F_{th} = theoretical frequency of each element in a living individual, MNI = minimum number of individuals. Concerning the surface alteration of bones, we especially considered rodent femoral heads, isolated incisors and molars for the study of the digestion. For each considered element, the percentage of digestion (PD) was calculated as follows: $PD = (N_{dig} / N_{tot}) \times 100$, with N_{dig} = number of digested elements, N_{tot} = total number of elements. Other traces (oxids, roots, weathering, trampling, among others) were noticed but not quantified.

As bone fragmentation can be subject to various peri-mortem and post-depositional factors, the percentage of fragmentation is most often high in archaeological context and not very informative, so we have chosen not to study it here in detail. For bats, shrews, amphibians and birds the low number of remains did not allow an in-depth taphonomic analysis, and only general observations were made.

PALAEOENVIRONMENTAL RECONSTRUCTIONS

Current distribution and ecological requirements of species follow Aulagnier *et al.* (2008), Quéré & Le Louarn (2011), Lescure & Massary (2012), Nicolas *et al.* (2021), Kryštufek & Shenbrot (2022) and the IUCN database (<http://www.iucn-redlist.org>). Then several complementary methods for palaeoclimatic and palaeoenvironmental reconstructions commonly used in micromammal studies were applied:

— Climatogram: this method considers the relative proportions of rodent species (minimum number of individuals (MNI) by grouping them into climato-ecological classes according to their affinities. This method has been used by various authors (e.g. Chaline 1983; Marquet 1993; Desclaux & Defleur 1997; Barroso Ruiz *et al.* 2003; Cuenca-Bescós *et al.* 2005, 2009; Hanquet & Desclaux 2011).

— Taxonomic Habitat Index (THI): this is an approach that takes into account only the presence or absence of species (Andrews 1990, 2006; Evans *et al.* 1981). For each species, a total value of 1 is distributed between the different frequented habitats, with different values according to the intensity of frequentation. For each habitat type, the sum of the indices given for all the species present per level is calculated, allowing a dominant habitat to be determined.

— Climate Restriction Index: this method, developed by Hernández-Fernández (2001) and updated by Royer *et al.* (2020), shows some similarities with the THI. The main difference is that the score allocated to the different habitats

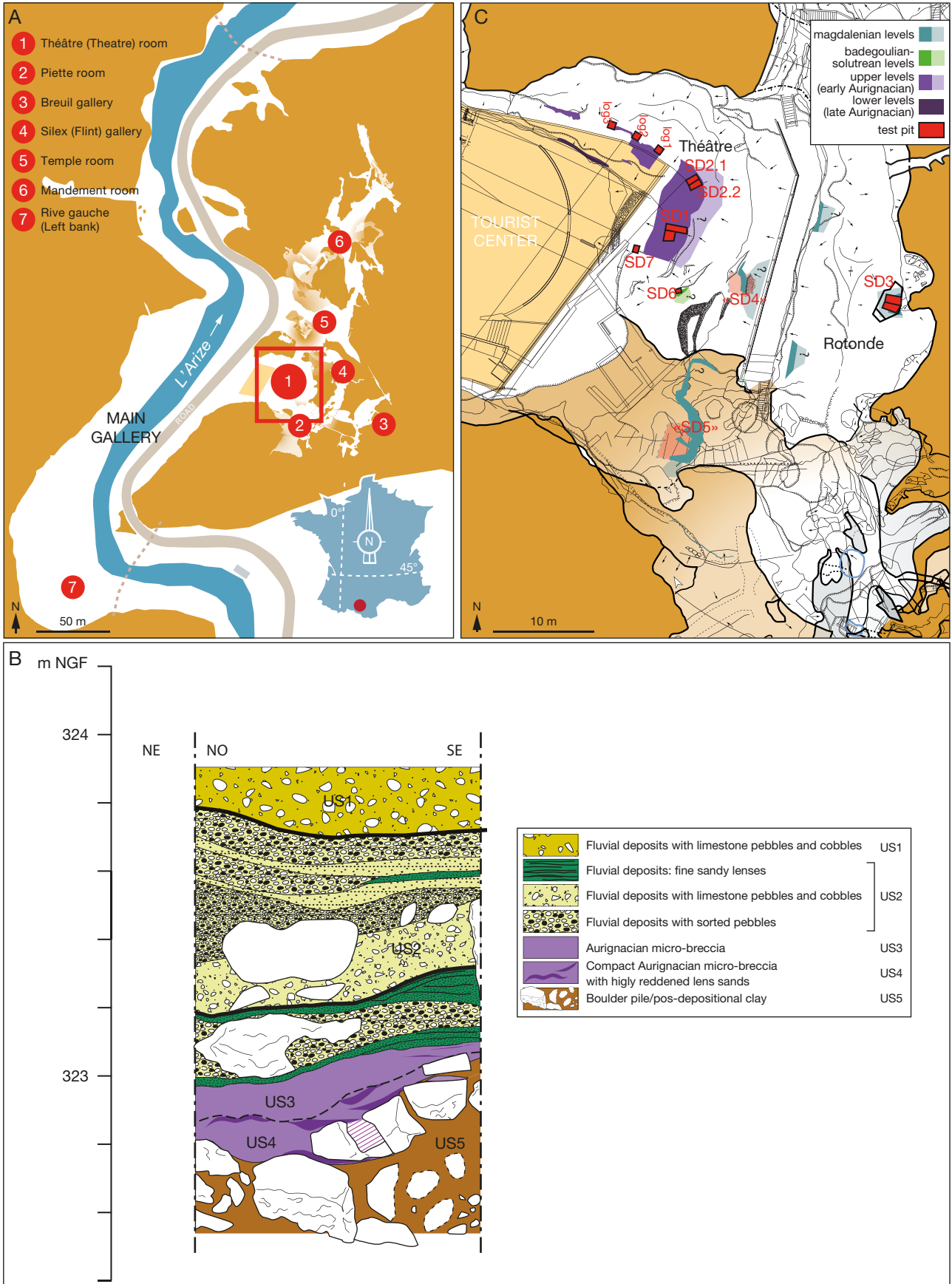


FIG. 1. — A-C, Geographical location of the Mas d'Azil cave (A), stratigraphy (B) and excavation map (C) of the "Theatre" room. Credits: drawing and credit M. Jarry and C. Pallier, Inrap-Traces.

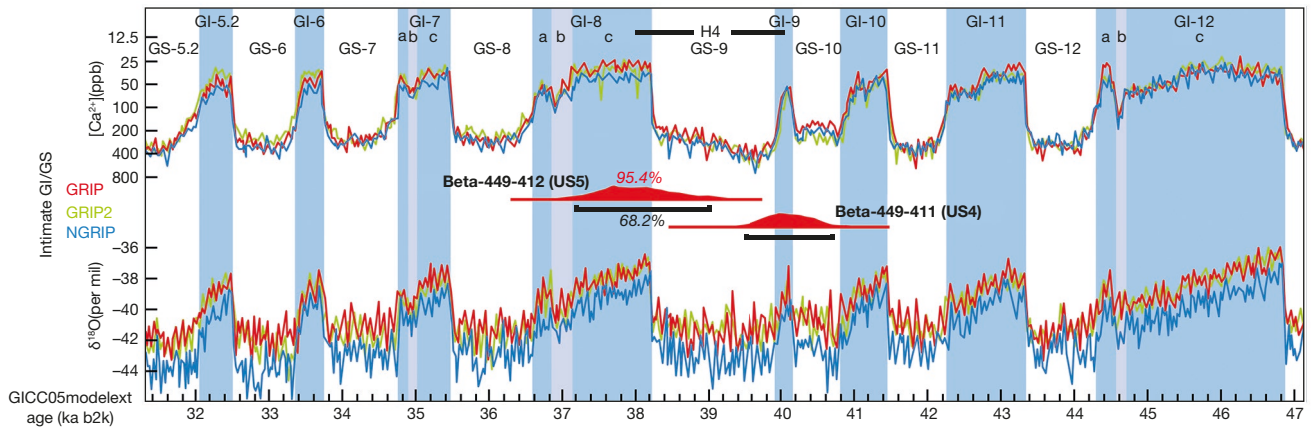


FIG. 2. — Radiocarbon dates of US4 and 5 of the Mas d'Azil cave associated with climatic curves (from Rasmussen *et al.* 2014).

frequented by a species is distributed equally, regardless of the proportions of habitats occupied. If 15% or more of a species' range is present in the climate zone, then the species is considered to inhabit that zone. As with the THI, this method makes it possible to reconstruct palaeo-landscapes, avoiding potential biases of over-representation of species. It also allows ecological preferences to be considered, but with an equitable distribution between the zonobiomes.

Two additional methods are used for the reconstruction of climate parameters, based on large databases of current species distribution and climatic parameters. The use of the two following methods makes it possible to step back from the amplitudes of variation of the climatic parameters:

— Bioclimatic Model: based on the assumption that there is a correlation between climate and mammalian communities, the Bioclimatic Model uses data from the Climate Restriction Index to determine climatic parameters using discriminant analysis and multiple linear regression (Hernández-Fernández 2001; Hernández-Fernández & Pelaez-Campomanes 2005; Royer *et al.* 2020). This method allows an initial approach to climatic parameters, particularly temperature (mean annual temperature, mean temperature of the warmest month and mean temperature of the coldest month).

— Quantified Ecology method: was developed by Jeannet (2010). For each species, quantitative climatic values are assigned (mean annual temperature, minimum and maximum annual temperature, mean annual precipitation, among others) according to its range.

RESULTS

MICROVERTEBRATE ASSEMBLAGE

A total of 3762 remains were studied in both units. Among small mammals, one lagomorph species, nine rodent species, one mole and one shrew species and several unidentified bats were recognised (Table 1; Fig. 3). Remains of amphibians (mainly frogs) and several species of small passerine birds (as well as three distal phalanges belonging to a small raptor in US5) have also been found.

The relative proportions of the major faunal groups and the faunal spectra are very similar in the two US, although the quantity of material appears more important in US5. Both units are dominated by Arvicolines, especially *Microtus gr. arvalis-agrestis* and *Arvicola gr. amphibius-sapidus*, and amphibians are also well represented (Table 1). Most species still inhabit the study region today (*Apodemus gr. sylvaticus-flavicollis*, *Arvicola gr. amphibius-sapidus*, *Microtus gr. arvalis-agrestis*, *Talpa gr. europaea-aquitania*, *Sorex gr. araneus-coronatus*, *Rana cf. temporaria*, *Pelophylax sp.*), but others are found today more in altitude or in more distant areas in the same region (*Chionomys nivalis* (Martins, 1842)), or in more eastern regions of northern and central Europe and Asia (*Alexandromys oeconomus* (Pallas, 1776)).

Several species groups occurring in the study region today display a similar bones and teeth morphology, which make them difficult to discriminate without further morphometric analyses. This is notably the case for *Apodemus gr. sylvaticus-flavicollis*, *Arvicola gr. amphibius-sapidus*, *Microtus gr. arvalis-agrestis*, *Talpa gr. europaea-aquitania* and *Sorex gr. araneus-coronatus*. Both morphotypes were recognized at the Mas d'Azil cave for *M. arvalis* (Pallas, 1779)/*M. agrestis* (Linnaeus, 1761) and *A. sapidus* Miller, 1908/*A. amphibius* (Linnaeus, 1758). For the other genera (*Apodemus* Kaup, 1829, *Talpa* Linnaeus, 1758, *Sorex* Linnaeus, 1758) it is difficult to say for the moment if one or two species are represented in the assemblage for each of them, waiting further morphometric analyses. However, *Sorex* mandibles of the Mas d'Azil appear closer to *S. coronatus* Millet, 1828. Concerning Talpidae, other European *Talpa* species are also known in Italy, Greece or Spain, but they are generally smaller than *T. europaea* Linnaeus, 1758 and *T. aquitania* Nicolas, Martinez-Vargas & Hugot, 2017.

We note the absence of forest species such as *Sciurus vulgaris* Linnaeus, 1758 or Glirids, occurring today in the area, as well as Mediterranean voles of the sub-genus *Terricola* Fatio, 1867, today represented in southwestern France notably by *Microtus duodecimcostatus* (Selys-Longchamps, 1839), *M. lusitanicus* (Gerbe, 1879) or *M. gr. pyrenaicus-gerbei*. We observed a very large morphological variability within the *Microtus gr. arvalis-agrestis* and *Chionomys nivalis* species

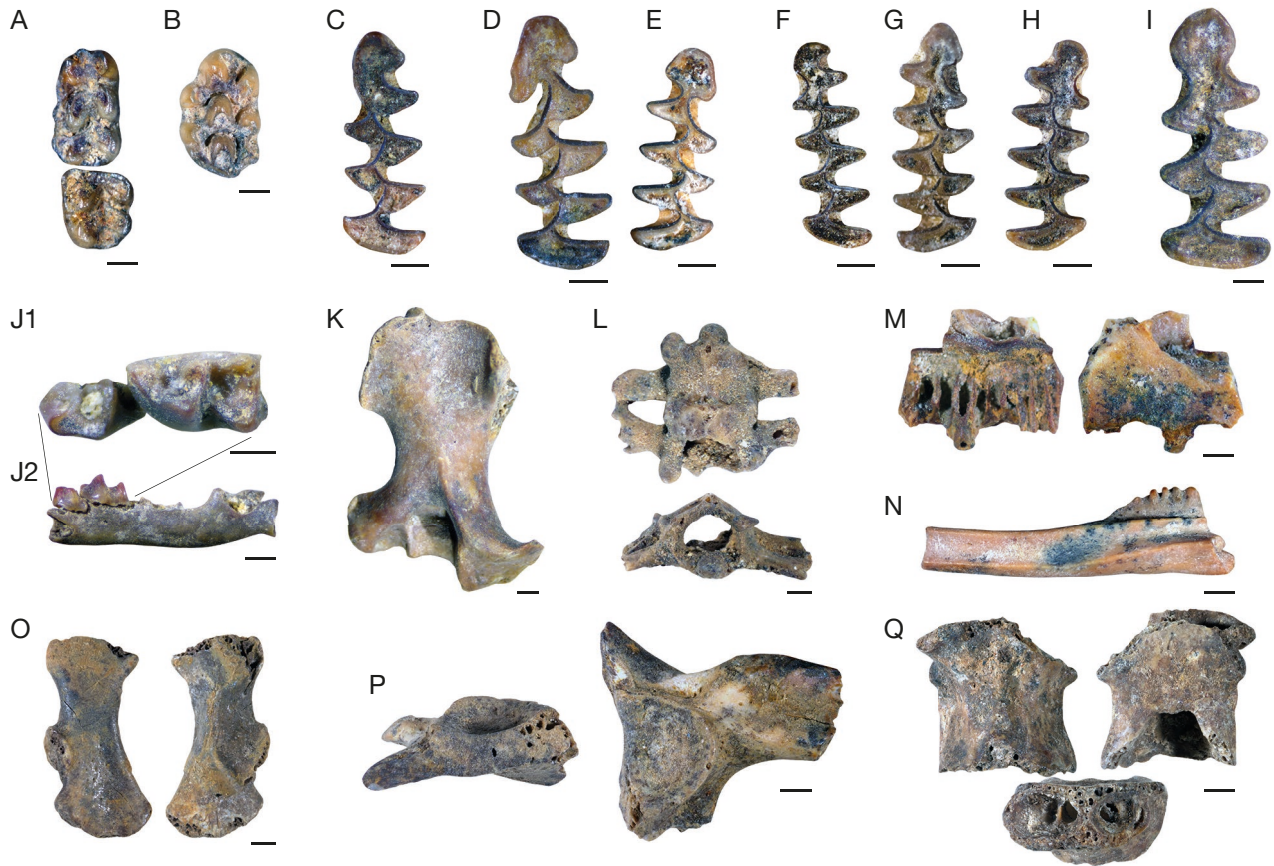


FIG. 3. — Examples of small vertebrate remains from the Aurignacian levels of the Mas d'Azil cave: **A**, *Apodemus gr. sylvaticus-flavicollis*, left lower m1-m2 (MA_S2.2_US5_z9-10); **B**, *Apodemus gr. sylvaticus-flavicollis*, left upper M1 (MA_S2.2_US5_z10-11); **C**, *Alexandromys oeconomus* (Pallas, 1776), left lower m1 (MA_S2.2_US5_z10-11); **D**, **E**, two morphotypes of *Chionomys nivalis* (Martins, 1842), left (**D**) and right (**E**) lower m1 (MA_S2.2_US5_z14-15); **F-H**, three morphotypes of *Microtus gr. arvalis-agrestis*, one left (**F**) and two right (**G**, **H**) lower m1 (MA_S2.2_US4_z12-13; MA_S2.2_US5_z10-11; MA_S2.2_US5_z16-17); **I**, *Arvicola gr. amphibius-sapidus*, left lower m1 (MA_US5_S2.2_z10-11); **J**, *Sorex gr. araneus-coronatus*, left mandible in lateral view, with *in situ* u2-m1 in occlusal view (MA_US5_S2.2_z10-11); **K**, *Talpa gr. europaea-aquitania*, right humerus, ventral view (MA_US5_S2.2_z10-11); **L**, Lacertidae Opperl, 1811, sacral vertebrae, dorsal and posterior views (MA_US5_S2.2_z15-16); **M**, Lacertidae, premaxillary, posterior and anterior views (MA_US5_S2.2_z16-17); **N**, *Rana/Pelophylax* sp., left angular, lateral view (MA_S2.2_US4_z14-15); **O**, *Rana cf. temporaria*, right scapula, dorsal and ventral views (MA_US5_S2.2_z16-17); **P**, *Rana cf. temporaria*, right ilion, distal and lateral views (MA_US5_S2.2_z10-11); **Q**, *Rana cf. temporaria*, sphenethmoïde, ventral, dorsal and anterior views (MA_US4_S2.2_z13-14). Scale bars: A-J1, L, M, 0.5 mm; J2, K, N-Q, 1 mm.

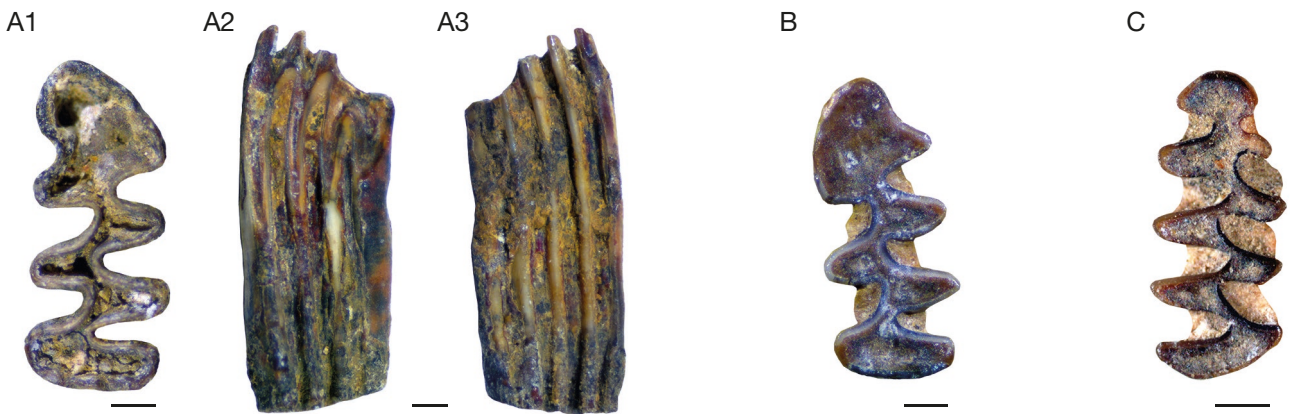


FIG. 4. — Anomalous vole specimens: **A**, *Arvicola* sp., lower m1: **A1**, apical; **A2**, **A3**, lateral views (MA_US5_S2_z11-12); **B**, *Arvicola* sp., lower m1, occlusal view (MA_US5_S2_z10-11); **C**, *Microtus/Chionomys?*, lower m1, occlusal view (MA_US5_S2.2_z10-11). Scale bars: A1, B, C, 0.5 mm; A2, A3, 1 mm.

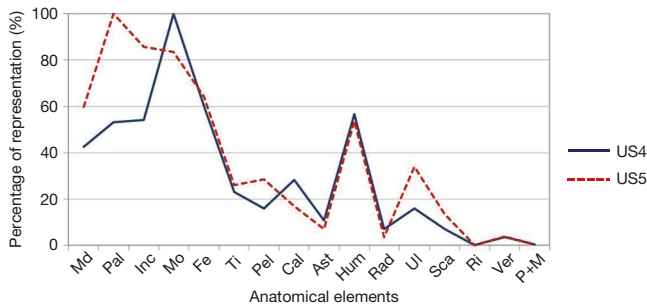


Fig. 5. — Percentage of anatomical representation (PR) of the micromammals from the Aurignacian levels of the Mas d'Azil cave.

TABLE 2. — Percentage of digested elements (PD) of the rodents from the Aurignacian levels of the Mas d'Azil cave based on femoral heads (with epiphysis), isolated incisors (with tips) and isolated molars (m1).

Elements	US	N	No dig.	Light	Moderate	Heavy	PD
Femoral heads	4	13	11	2	0	0	15.4
	5	35	29	6	0	0	17.1
	Total	48	40	8	0	0	16.7
Incisors	4	8	3	3	2	0	62.5
	5	17	3	14	0	0	82.4
	Total	25	6	17	2	0	76.0
Molars	4	75	65	8	2	0	13.3
	5	73	84	6	1	0	9.6
	Total	148	149	14	3	0	11.5

(Fig. 3). Moreover, three lower m1 display unusual morphological characters in the US5: specimen of *Microtus* size from sample US5-Sond2.2-z10-11 (Fig. 4C) with a reduced T6 and presence of a BRA4 re-entrant angle (aberrant *Microtus arvalis/agrestis* or *Chionomys nivalis* specimen?); cf. *Arvicola* sp. from sample US5-Sond2.2-z10-11 (Fig. 4B) with a relatively small size and absence of T4 (reduced to a simple “bulge” of the anterior lobe); cf. *Arvicola* sp. from sample US5-Sond2-z11-12 (Fig. 4A) with an exceptionally high crown and an asymmetrical wear in occlusal view (probably related to an occlusal defect resulting in abnormal growth and wear of the tooth, perhaps accentuated by digestion).

Concerning amphibians, *Rana temporaria* Linnaeus, 1758 is probably the most common frog species found in current and fossil communities. But today in the study region, we can also find several other species belonging to the genera *Rana* Linnaeus, 1758 (*R. pyrenaica* Serra-Cobo, 1993, *R. dalmatina* Fitzinger, 1838) and *Pelophylax* Fitzinger, 1843 (*P. ridibundus* (Pallas, 1771), *P. perezi* (López-Seoane, 1885)), for which the osteological anatomy remains poorly known. Thus, their presence in the site is not impossible, but difficult to demonstrate for now, especially considering the high rate of fragmentation of the bones in the site. No specimen belonging to the genus *Bufo* Garsault, 1764 could have been identified at the Mas d'Azil cave, but we cannot exclude that remains belonging to this genus can be present among the amphibian indet. material.

TAPHONOMIC REMARKS

The material is highly fragmented in both US, and almost all the molars are dislocated (leading to their over-representation in the anatomical profile; Fig. 5), and no element was found complete, which limits certain identifications, especially for amphibians.

Regarding the anatomical representation of micromammals (Fig. 5), we see that both US display a similar pattern, with however a higher representation of cranial bones (mandibles, palatum) in the US5, whereas in US4 the isolated molars are better represented. Most skeletal elements are well represented, except for the smallest and/or most fragile elements such as phalanges, ribs and radius, most likely due to the relatively large mesh size of the sieves (2 mm). For the same reason, Murinae and other small taxa may be under-represented (molar size frequently < 2 mm). Apart from that, no sorting by size/density/shape seems to have occurred by the action of a water flow or other natural process, reinforced by the fact that no element rounded by water action was observed.

The presence of digested elements for all taxa (rodents, bats, amphibians, birds) attests that at least part of the assemblage is due to the action of predators. The percentage and intensity of digestion of rodent elements are relatively low (Table 2; Fig. 6), considering femoral heads (15.4% and 17.1% for US4 and US5 respectively) and isolated molars (13.3% and 9.6% for US4 and US5 respectively). Values are higher for isolated incisors (62.5% and 82.4% for US4 and US5 respectively). *In situ* incisors and molars were too scarce to be considered (Table 2). In comparing with modern referentials (e.g. Andrews 1990; Denys *et al.* 2018; Royer *et al.* 2019; Lebreton *et al.* 2021), our results argue for a nocturnal raptor of category 1 (e.g. Barn owl, Short eared owl) based on femoral heads, but rather of category 3 (e.g. Eagle owls, Tawny owl, Fox) based on isolated incisors and molars. Such discrepancies were previously observed for the Snowy owl for example (Royer *et al.* 2019), and the differences observed between US may be related to a sample effect rather than a difference in the predator species. Moreover, considering the large size of the cave, it is not impossible that several predator species could have occupied the site simultaneously. Concerning bats, even if some remains display traces of digestion, a natural *in situ* accumulation is also to be considered.

Post-depositional alterations were observed in low proportion, only few root marks, weathering effects and spots of Manganese oxids.

PALAEOENVIRONMENTAL RECONSTRUCTIONS

Current distribution and ecological requirements of species
Among rodents, the wood mice of the *Apodemus* gr. *flavicollis-sylvaticus* group (*Sylvaemus* sub-genus) are today widespread in the European continent, frequenting mostly forested and bushy areas. During cold periods of the Quaternary, these rodents would have found refuge in certain Mediterranean regions and in southwestern France, allowing the maintenance of populations and their re-expansion from these regions during more temperate periods.



FIG. 6. — Examples of digestion marks observed on small vertebrate remains from the Aurignacian levels of the Mas d'Azil cave: **A, B**, rodent femoral heads with light digestion (MA_S2.2_US5_z10); **C**, rodent incisor with light digestion (MA_S2.2_US4_z17); **D**, *Alexandromys oeconomus* (Pallas, 1776) lower m1 with light digestion (MA_S2.2_US4_z15); **E**, *Alexandromys oeconomus* lower m1 with moderate digestion (MA_S2.2_US4_z15); **F**, digested Anuran ilion (MA_US5_S2.2_z10-11); **G**, digested Anuran humerus (MA_US5_S2.2_z10-11). Scale bars: A-E, 0.5 mm; F, G, 1 mm.

TABLE 3. — Definition and values of the Climatic Restriction Index (CRI) applied to the micromammals of the Aurignacian levels of the Mas d’Azil cave (according to Royer *et al.* 2020).

Climate		Biome			
IV	winter rain and summer drought	IV	Sclerophyllous woodland-shrubland		
VI	Typical temperate	VI	Nemoral broadleaf-deciduous forest		
VII	Arid-temperate	VII	Steppe to cold desert		
VIII	Cold-temperate (Boreal)	VIII	Boreal coniferous forest (Taïga)		
IX	Arctic	IX	Tundra		
	IV	VI	VII	VIII	IX
US 4 and 5	0.75	3.583	0.5	1.583	0.583

TABLE 4. — Climatic parameters obtained from the small vertebrates of the Aurignacian levels of the Mas d’Azil cave with the quantified ecology method; and the bioclimatic model. Abbreviations: **Nb Frost**, number of days of frost per year; **Pmoy**, mean annual precipitations, expressed in cm/year; **T°max**, mean temperature of the warmest month; **T°min**, mean temperature of the coldest month; **T°moy**, mean annual temperature; **T°range**, seasonal temperature range between summer and winter, all T° expressed in °C.

	T°moy	T°max	T°min	T°range	Nb Frost	Pmoy
Quantified ecology method						
Present - St Girons	11.5	16.8	6.4	10.4	30.6	98.0
Present - Toulouse	12.8	20.8	4.5	16.3	50.0	66.0
US4 and 5	6.7	20.8	-7.3	28.1	156.2	54.6
Bioclimatic model						
US4 and 5	10.0	20.4	-0.5	20.9	-	58.9

Two species of Water voles are today recognized, which can all be found in Europe (e.g. gr. *A. terrestris*): *Arvicola amphibius* and *A. sapidus*. They share the common trait of digging extensive burrows, especially around rivers, streams and marshes. But they do not have exactly the same geographical distribution and are more or less aquatic or burrowing according to the species.

The voles of the *Microtus* sub-genus (*Microtus arvalis* and *M. agrestis*) are common in current and past environments of western Europe. They both leave mostly in open habitats (grasslands, meadows, marshes), but the Field vole (*M. agrestis*) apparently need more humidity and vegetation cover than the Common vole (*M. arvalis*). They both avoid strictly Mediterranean areas.

The Snow vole (*Chionomys nivalis*) still inhabits western Europe and southwestern Asia. It is a heliophilous species that frequents open and rocky habitats and is today found in the Pyrenean region, but more in altitude (above the tree-line).

The Tundra vole (*Alexandromys oeconomus*) is today widespread in eastern and northern Europe and Asia. It typically inhabits damp, densely-vegetated areas along the edges of lakes, streams and marshes, and is mostly found in tundra, taiga and forest-steppe.

Among eulipotyphlans, the medium-sized red-toothed shrews of the *Sorex* gr. *araneus-coronatus* group are today well represented in Europe. They are both found in a wide

variety of habitats with dense vegetation at ground level (meadows, marshes, shrubs, riparian forests). Even if they display a similar size, morphology and ecology, they currently show different geographical distribution (*S. coronatus* in the West; *S. araneus* in the North and the East, but also in the Pyreneans) and *S. araneus* would prefer more humid and cool habitats than *S. coronatus*.

The common mole *Talpa europaea* and the recently described *T. aquitania* are both strictly burrowing species mostly found in forests and meadows. But they do not share the same geographical distribution, and the Loire River seems to represent today an ecological and geographical barrier for these species.

Concerning amphibians, all species need the proximity of water for their survival and reproduction, in a more or less drastic way. *Rana temporaria* displays a very large geographic range in European non-Mediterranean regions, while the distribution of other frog species is generally more restricted.

Palaeoecological indices

The landscape and climatic parameters displayed by the US4 and US5 are similar, and few differences are observed between the two units.

The Taxonomic Habitat Index (THI; Appendix 3; Fig. 7A) shows a predominance of deciduous forests and humid meadows, with also the presence of tundra and rocky (mountainous) habitats. The climatogram (Fig. 7B) shows a similar trend, with a dominance of humid meadows and vegetated water pounds. The slight differences observed between US4 and US5 could be due to a sampling effect (mesh size and number of studied samples).

The Climatic Restriction Index (CRI; Table 3; Fig. 7C) is also in line with the two previous indices, with a predominance of biome VI (temperate meadows and deciduous forests) and biome VIII (Boreal coniferous forest).

The climatic parameters (Table 4) deduced from the bioclimatic model, and especially from the quantified ecology, show lower temperatures and precipitations than today, with a wider seasonal temperature range and more days of frost per year. According to Jeannet (2010), the difference in temperature between the warmest month and the coldest month indicates a continental phase (periglacial) if the variation is higher than 25°, a temperate period for 15 to 20°,

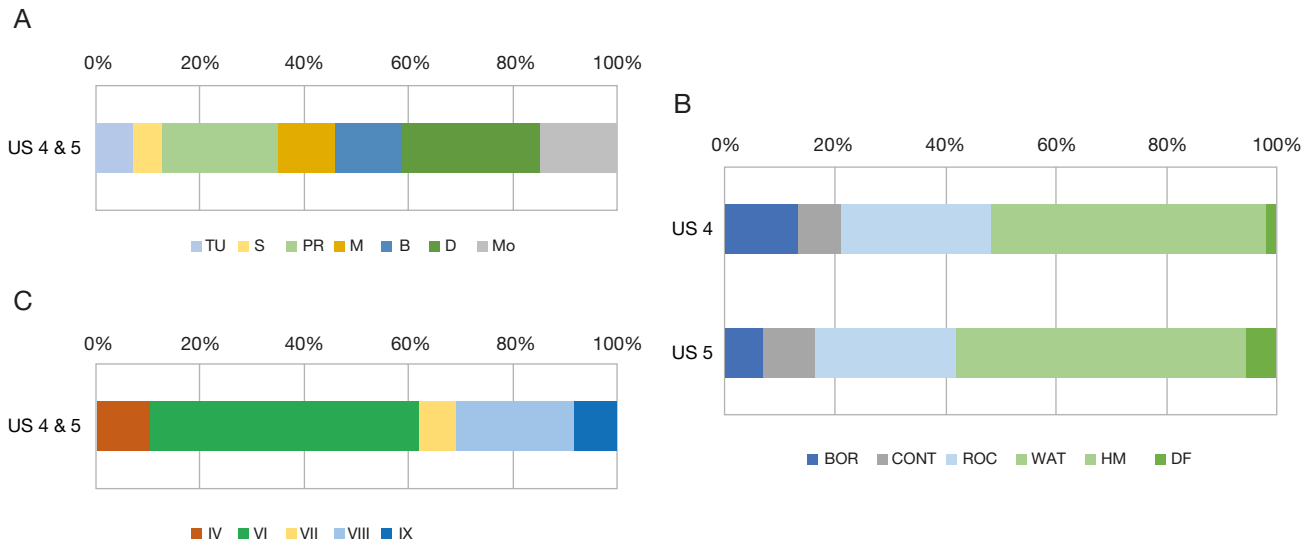


FIG. 7. — Palaeoecological indices applied to the small mammals of the Mas d'Azil cave: **A**, Taxonomic Habitat Indices (**TU**, Tundra; **S**, Arid steppe; **HM**, Humid meadow; **M**, Mediterranean; **B**, Boreal forest; **D**, Deciduous forest; **Mo**, Mountain); **B**, Climatogram (**BOR**, Boreal cold-humid habitats; **CONT**, Continental arid steppes; **ROC**, Rocky habitats; **WAT**, Vegetated water pounds; **HM**, Humid meadow; **DF**, Deciduous forests); **C**, Climatic Restriction Index (see Table 3).

and Mediterranean and semi-desert conditions for smaller values (8° to 12°). In US4 and US5 of Mas d'Azil, the climate thus appears more continental (periglacial) than today (temperate to Mediterranean).

DISCUSSION

COMPARISON TO OTHER PALAEOENVIRONMENTAL PROXIES IN THE MAS D'AZIL CAVE

Throughout the Quaternary climatic fluctuations, the Arize river experienced several phases of alluvial filling (periglacial context) and re-excavation (more temperate context). The sedimentary sequence of the Mas d'Azil cave reflects these environmental changes and has recorded at least two aggradation phases (Pallier *et al.* 2016, 2024; Jarry *et al.* 2021a; Pallier 2021). The oldest fluvial fillings (Mandement and Temple rooms) show an important sedimentary aggradation in this part of the cavity, which has been entirely filled in by the alluvium of the Arize during an earlier period of the Pleistocene (MIS6). Then the Arize river resumed a free flow dynamic and dug this filling, emptying a part of the rooms and galleries of the cave, and allowing humans or faunas to reach the cave. It is in this context that the Aurignacians have occupied a part of the cavity, during a more favorable climatic period of MIS3. The last fluvial sequence (Theatre/Rotonde room) dates to the last glacial period (from the end of MIS3) and covers the Aurignacian occupation levels with over several meters of deposits. This event blocked part of the Mas d'Azil cave and prevented any access to the human populations for several thousand years, between the Gravettian and the Solutrean. Human populations started to settle back in the cave in the Solutrean/Badegoulian period (MIS2), and then massively occupied it during the Magdalenian period (Pallier *et al.* 2016, 2024; Pallier 2021).

Concerning faunal data from the Aurignacian levels of the Mas d'Azil cave (US5-3), unfortunately the number of determined remains of large mammals is quite low, due to significant bone fragmentation and burning (Martin *in* Jarry *et al.* 2014, 2015; Jarry *et al.* 2017). The identified taxa are mainly equids, reindeer (*Rangifer tarandus* (Linnaeus, 1758)) and bovines, with the occasional presence of birds and carnivores (*Vulpes* sp., large canids). Although limited, these results confirm the idea of an open environment of grassland or steppe under a cooler climate than the present one, especially through the presence of reindeer. However, this latter is less represented than in the Magdalenian levels, characterized by more marked cold conditions.

To summarize, both sedimentary record and large mammals argue for cool, but not glacial conditions during the early Aurignacian occupations of the Mas d'Azil cave, and thus agree with the results of the microvertebrates. Moreover, it has been hypothesized that US4 may be an indurated facies of the same deposit as US5, or that US5 may be an open scree deposit into which the matrix has been subsequently inserted (Pallier 2021), which could partly explain the proximity of both microvertebrate assemblages.

THE MIS 3 IN THE PYRENEAN REGION:

A SYNTHESIS OF THE MICROVERTEBRATE DATA

The emergence of the early Aurignacian culture, to which are attributed the human occupations of the US4 and US5 of the Mas d'Azil, would have been contemporaneous of cold and dry climatic conditions across the European continent (Heinrich Event 4), leading notably to a change in the large mammal faunas (e.g. Discamps *et al.* 2011) and a geographic expansion of the human populations (Banks *et al.* 2013). However, anthracological data (Allué *et al.* 2018) have shown the persistence throughout MIS3 to MIS1 of *Pinus sylvestris* L. type forests in northeastern Spain, and in southwestern

Europe in general (Fletcher *et al.* 2010). This indicates that in this region, the climatic changes were not so extreme as to prevent the development of trees, and that the conditions were milder compared to those of more northern regions. But what are the indications given by the small faunas concerning the MIS3 climatic changes in the region?

Few references are available for the Pyrenean region (either in France or in Spain). We avoided older works with few materials, for which the chrono-stratigraphic context can be dubious and for which sieving and sorting of microvertebrate remains were not systematic, or even absent. Moreover, we focused on cave sites, allowing for the recovery of large amounts of microvertebrate remains (contrary to most of open-air sites).

In the considered area, most studies on small vertebrates dating to the MIS3 focus on older cultural periods, i.e., the Mousterian (Marquet *et al.* 1998; López-García *et al.* 2012; Discamps & Royer 2017; Fernández-García *et al.* 2018, 2020, 2022) or the Mousterian-Aurignacien transition (López-García *et al.* 2011; Álvarez-Vena *et al.* 2021). The synthesis of Royer *et al.* (2016) on micromammals from southwestern France includes few sites in the study area (central-eastern Pyrenees), which are dated to more recent periods. Very few studies cover the Aurignacian chrono-cultural period.

To our knowledge, only one other study deals with small vertebrate assemblages dating to MIS3 in the Ariège region, at the site of Portel-Ouest. Only few micromammal material was collected from the former Upper Palaeolithic Ensemble (levels B-B1) and was attributed to *Alexandromys oeconomus*, *Stenocranius gregalis* (Pallas, 1779), *Microtus arvalis-agrestis*, *Microtus (Terricola) subterraneus* (de Selys-Longchamps, 1836), *Arvicola amphibius* and *Chionomys nivalis* (Marquet 1993; Marquet *et al.* 1998). However, the level B was subsequently dated to MIS 2 by the Electron Paramagnetic Resonance method (23.1 ± 3.5 ka; Tissoux 2004) and thus associated to the Gravettian, while the level B1a was dated to MIS 3 (36.6 ± 5.4 ka; Tissoux 2004) but associated to a Chatelperronian industry. The intermediate level B1, which could have potentially corresponded to the chrono-cultural period of the Aurignacian, has apparently not been dated. Some of the underlying levels were also dated to MIS 3 (Ensemble F, c. 44-45 ka; Tissoux 2004) but associated to Mousterian industries.

The syntheses provided by López-García *et al.* (2014, 2015) and Fernández-García *et al.* (2016) allow us to make some comparisons with other sites contemporaneous of the US4 and US5 of the Mas d'Azil cave (c. 40-37 ky cal. BP), such as Teixoneres cave, Level II (c. 60-30 ky BP) and Arbreda cave, Level I (40-32 ky BP), both located in northeastern Spain. In the considered levels of both sites, the mid-European species *Microtus arvalis* and *M. agrestis* are dominant, while “forest species” (*Apodemus sylvaticus* (Linnaeus, 1758), *Glis glis* (Linnaeus, 1766), *Eliomys quercinus* (Linnaeus, 1766)) are present in much lower proportions, which would indicate cold, open humid conditions. *Chionomys nivalis* is also represented in both sites. Palaeoclimatic reconstructions (López-García *et al.* 2012, 2015) and isotopic analyses (Fernández-García *et al.* 2022) indicate colder mean annual temperatures than

today, but higher mean annual precipitations. The results that we obtained at the Mas d'Azil cave fit well with these data for the temperatures (but not for precipitation). However, one major difference is the permanent presence of Mediterranean vole species in the Spanish sites (e.g. *Microtus duodecimcostatus*, *Microtus (Iberomys) cabreræ* Thomas, 1906), together with Glirids (e.g. *Eliomys quercinus*), while both are absent in the Mas d'Azil assemblages. The absence of *M. duodecimcostatus* would be in line with the hypothesis of Royer *et al.* (2016), who stated that this species was absent from southwestern France during a large part of the Late Pleistocene and became widespread only from the beginning of the Holocene in the region. Moreover, the Mas d'Azil is located at the border of the current distribution of the species, which could also explain its absence in the site. *Microtus (Iberomys) cabreræ* is no longer recorded North of the Pyrenean Mountains, though its distribution extended further North in the past (López-García & Cuenca-Bescós 2012; Stoetzel 2022). Concerning the absence of Glirids, Fernández-García *et al.* (2016) indicate that the Mediterranean coast of the Iberian Peninsula has experienced the most pronounced forest development, which could explain a better representation of typical forest species compared to the Mas d'Azil cave, which is located in a more continental area of the Pyrenean foothills. More generally, Fernández-García *et al.* (2016) noticed differences in the faunal communities from MIS4 and MIS3 sites from northeastern Spain, and those from contemporaneous sites located in southwestern France, which generally show a colder and drier palaeoecological signal. However, in this region, Royer *et al.* (2016) highlighted the absence of typical “cold” species such as *Dicrostonyx torquatus* (Pallas, 1778) between 50 and 38 ky BP. Moreover, these authors have shown that despite changes in faunal distributions in response to abrupt and brief climatic events between MIS3 and MIS1 (Heinrich events), the rodent communities were not mandatory impacted on a regional scale. In southwestern France, the MIS3 recorded the concomitant presence of *Apodemus sylvaticus*, *Eliomys quercinus*, *Arvicola sapidus*, *Microtus* gr. *arvalis-agrestis*, *Alexandromys oeconomus*, *Spermophilus* sp., and *Stenocranius gregalis* is also well represented during MIS3 and MIS2. If most of these species are also represented in our study assemblages, *E. quercinus*, *Spermophilus* sp. and *S. gregalis* are not. But it has to be noticed that no site located in the eastern part of Pyrenean Mountains has yielded *E. quercinus* (Royer *et al.* 2016). The absence of taxa related to cold steppic habitats such as *Spermophilus* sp. and *S. gregalis* may be linked to the occurrence of more temperate climatic conditions, although cooler than today, in the Aurignacian levels of the Mas d'Azil cave. *Lagurus lagurus* (Pallas, 1773) is rare in Late Pleistocene sites from southern France but was recorded in the neighbouring site of Portel-Ouest, although in an older, Mousterian, level (Marquet 1993; Marquet *et al.* 1998), which may traduce more continental conditions. For the moment, it is difficult to decipher whether all these differences are due to geographical differences (Atlantic vs Mediterranean, coastal vs continental, plains vs mountains) and/or chronological discrepancies.

Moreover, it is acknowledged that the altitude gradient favors specific diversity, notably through the geographical proximity between ecotones, but also through the existence of habitat heterogeneity (Grytnes & McCain 2007). The presence of species with different ecological affinities can be explained by the site's proximity to a variety of habitats (grasslands, riparian forests, rocky slopes).

CONCLUSIONS

The small vertebrate assemblages from the Aurignacian levels of the Mas d'Azil cave revealed the occurrence of at least 15 taxa. The accumulations from both US were mainly formed by predation, as indicated by the digestion traces observed on rodent, amphibian and bird bones. Both US are characterized by a landscape dominated by grasslands with wooded areas in the valley and steppes and rocky areas on the slopes, during a period of climatic transition, or during an interstadial within a glacial period of the Late Pleistocene. Similarities have been observed with small faunas of contemporaneous sites from northeastern Spain, but comparative data are lacking for the “French side” of the central-eastern Pyrenean Mountains for this period, further enhancing the interest of the Mas d'Azil cave for the understanding of climatic changes during MIS3 and their impact on small faunas and contemporary Aurignacian human populations.

Acknowledgements

This study was carried out within the framework of the *Prospection thématique “La grotte du Mas d'Azil - Cartographie archéologique et géoarchéologique”* (2013-2017, dir. Marc Jarry, Céline Pallier, Laurent Bruxelles & François Bon) and the *Programme Collectif de Recherche “Archives d'une grotte - Des archives paléoenvironnementales et archéologiques aux archives de fouilles (grotte du Mas d'Azil, Ariège)”* (2018-2020 and 2021-2023, dir. Marc Jarry, Céline Pallier, Laurent Bruxelles and François Bon). Our thanks go to Hélène Tissoux for discussions about the Portel-Ouest context, to Violaine Nicolas for giving us access to the small mammal collections of the *Muséum national d'Histoire naturelle* (Paris), to Salvador Bailon for his help with the identification of the Anuran angular, and to Emmanuel Desclaux for discussions about the “strange” vole specimens. Finally, we sincerely thank the two reviewers, and the associated editor, Nicolas Teyssandier, for their constructive comments.

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Submitted on 21 June 2024;
accepted on 28 October 2024;
published on 22 January 2025.

APPENDICES

APPENDIX 1. — Detailed faunal list of the small vertebrates from the US4, in separating each spit. Abbreviations: **MNI**, minimum number of individuals; **NISP**, number of identified specimens.

US		US 4																	
		7-8		11-12		12-13		13-14		14-15		15-16		16-17		17-18		Total US 4	
Spit (z)		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Lagomorpha	indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Rodentia	<i>Apodemus gr. sylvaticus-flavicollis</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1
	<i>Chionomys nivalis</i>	-	-	-	-	1	1	-	-	-	-	2	2	1	1	-	-	4	4
	<i>Arvicola gr. amphibius-sapidus</i>	-	-	1	1	-	-	1	1	1	1	2	1	9	5	7	5	21	14
	<i>Microtus gr. arvalis-agrestis</i>	-	-	-	-	1	1	2	2	5	3	5	3	20	12	9	5	42	26
	<i>Alexandromys oeconomicus</i>	-	-	-	-	1	1	-	-	-	-	3	2	6	4	-	-	10	7
	Arvicolinae indet. (molars indet. + palatum)	7	2	3	1	16	2	15	3	22	3	32	2	94	6	87	5	276	24
	indet. (inc. + fragm. cranial + post-cranial)	13	-	8	-	21	-	34	-	34	-	41	-	126	-	404	-	681	-
Chiroptera	indet.	6	1	-	-	-	-	2	1	3	1	4	2	19	7	16	5	50	17
Eulipotyphla	<i>Talpa gr. europaea-aquitania</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	3	1
	<i>Sorex gr. araneus-coronatus</i>	1	1	-	-	-	-	-	-	-	-	-	-	2	2	-	-	3	3
Anura	<i>Rana cf. temporaria</i>	-	-	-	-	-	-	1	1	1	1	-	-	3	1	2	1	7	4
	cf. <i>Rana/Pelophylax</i>	-	1	1	1	2	1	2	1	4	1	4	2	6	8	-	7	19	22
	indet.	10	-	2	-	8	-	10	-	6	-	13	-	44	-	58	-	151	-
Squamata	Lacertidae indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Aves	indet.	8	/	-	-	7	-	16	-	11	-	7	-	33	-	18	-	100	-
Pisces	indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0
Total		45	5	15	3	57	6	83	9	87	10	113	14	364	47	604	29	1368	123

APPENDIX 2. — Detailed faunal list of the small vertebrates from the US5, in separating each spit. Abbreviations: **MNI**, minimum number of individuals; **NISP**, number of identified specimens.

		US		US 5																TOTAL US 5			
				9-10		10-11		11-12		12-13		13-14		14-15		15-16		16-17				17-18	
Spit (z)		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Lagomorpha	indet.	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	2	1
Rodentia	<i>Apodemus gr. sylvaticus-flavicollis</i>	1	1	2	1	-	-	-	-	2	1	1	1	1	1	1	1	-	-	-	-	8	6
	<i>Chionomys nivalis</i>	1	1	5	4	1	1	-	-	-	-	2	1	-	-	2	1	1	1	1	1	13	10
	<i>Arvicola gr. amphibius-sapidus</i>	7	5	9	6	3	2	1	1	1	1	4	2	4	3	6	4	2	1	1	1	38	26
	<i>Microtus gr. arvalis-agrestis</i>	16	8	29	16	8	6	3	2	3	2	6	4	8	5	21	8	3	2	1	1	98	54
	<i>Alexandromys oeconomicus</i>	1	1	1	1	-	-	1	1	-	-	-	-	1	1	1	1	1	1	1	1	7	7
	Arvicolinae indet. (molars indet. + palatum)	73	8	172	25	5	7	4	2	12	2	41	5	24	3	76	8	30	4	21	2	458	66
	indet. (inc. + fragm. cranial + post-cranial)	166	-	269	-	75	-	20	-	30	-	55	-	47	-	158	-	49	-	29	-	898	-
Chiroptera	indet.	38	3	37	7	10	1	1	1	5	1	7	1	6	1	25	2	7	1	7	1	143	19
Eulipotyphla	<i>Talpa gr. europaea-aquitania</i>	3	1	10	1	-	-	-	-	1	1	1	1	-	-	8	1	1	1	-	-	24	6
	<i>Sorex gr. araneus-coronatus</i>	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	2	1	1	-	-	11	10
Anura	<i>Rana cf. temporaria</i>	4	2	14	5	2	1	1	1	1	1	5	2	1	1	6	2	2	1	1	1	37	17
	cf. <i>Rana/Pelophylax</i>	5	5	2	9	1	2	-	2	1	1	-	3	2	3	4	10	2	1	-	2	17	38
	indet.	42	-	88	-	16	-	8	-	7	-	24	-	16	-	62	-	7	-	12	-	282	-
Squamata	Lacertidae indet.	-	-	-	-	-	-	-	-	-	-	-	-	2	1	1	1	-	-	-	-	3	1
Aves	indet.	47	-	90	-	22	-	20	-	14	-	33	-	29	-	66	-	14	-	19	-	354	-
Pisces	indet.	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Total		406	37	729	76	144	21	60	11	78	11	183	22	142	20	439	41	120	14	93	10	2394	263

APPENDIX 3. — Distribution of the taxonomic habitat indices (THI) used for the micromammals of Aurignacian levels of the Mas d'Azil cave. Abbreviations: **B**, Boreal forest; **D**, Deciduous forest; **HM**, Humid meadow; **M**, Mediterranean; **Mo**, Mountain; **S**, Arid steppe; **TU**, Tundra (modified from Hanquet 2011).

Species	TU	S	HM	M	B	D	Mo
<i>Apodemus</i> gr. <i>sylvaticus-flavicollis</i>	–	0.10	0.20	0.20	–	0.50	–
<i>Chionomys nivalis</i> (Martins, 1842)	–	–	0.15	0.15	–	0.10	0.60
<i>Arvicola</i> gr. <i>amphibius-sapidus</i>	–	–	0.25	0.20	0.15	0.20	0.20
<i>Microtus</i> gr. <i>arvalis-agrestis</i>	0.10	0.20	0.20	0.10	0.10	0.15	0.15
<i>Alexandromys oeconomicus</i> (Pallas, 1776)	0.40	–	0.10	–	0.50	–	–
<i>Talpa</i> gr. <i>europaea-aquitania</i>	–	0.10	0.15	0.10	0.15	0.40	0.10
<i>Sorex coronatus</i> Millet, 1828	–	–	0.50	–	–	0.50	–