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Expanding the Faunal Interpretation of the Cova Eirós (NW Iberia) Middle Paleolithic–Early Upper Paleolithic Record With ZooMS

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ABSTRACT

The Cova Eirós archaeopaleontological site preserves the most comprehensive archaeostratigraphic sequence in the northwestern Iberian Peninsula, with an exceptionally rich record spanning from the Mousterian to the Upper Paleolithic. The extensive fragmentation of the faunal record and the rich taxonomic diversity at this site have limited the identifiability of the remains and led to an overrepresentation of the main taxa (*Ursus spelaeus* and *Cervus elaphus*). To refine our understanding of the site's faunal composition and to explore the subsistence strategies of both Neanderthal and Anatomically Modern Human (AMH) groups, we compared the results of traditional morphological analyses with those obtained through the application of Zooarchaeology by Mass Spectrometry (ZooMS) to the indeterminate fraction of the assemblage. While overall congruent with morphological identifications, the ZooMS data reveal two significant trends: firstly, a marked decrease in the relative abundance of *Ursus spelaeus*, previously overrepresented due to the prevalence of deciduous teeth; and secondly, an increased representation of large ungulates compared to that identified through conventional methods. The inclusion of specimens showing clear evidence of anthropogenic modification reduces the apparent dominance of *C. elaphus*, suggesting a more diversified subsistence strategy. The integration of paleoproteomic and morphological approaches thus provides a more nuanced reconstruction of the paleoenvironment and dietary patterns of the hunter-gatherer groups occupying the Eastern Mountains of Galicia during the middle to late phases of MIS 3.

1 | Introduction

The Eastern Mountains of Galicia, located on the westernmost foothills of the Cantabrian Mountain Range, contain a significant archaeopaleontological record that allows for the reconstruction of the environments inhabited by Upper Pleistocene hominins (e.g., Bal-García et al. 2025; Fernández Rodríguez 2006; Valverde Tejedor 2019). The

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zooarchaeological analysis of these sites presents a challenge shared with other Paleolithic assemblages: a high degree of bone fragmentation with the consequent difficulty in morphological identification of the remains, with ca. 70%–90% of the specimens typically classified as indeterminate. In connection with this issue, a method of faunal identification known as ZooMS (Zooarchaeology by Mass Spectrometry) has gained increasing relevance over the past few years (e.g., Buckley et al. 2017; Discamps et al. 2024; Holloran et al. 2024; Kitagawa et al. 2025; Morin et al. 2023; Oertle et al. 2025; Oldfield et al. 2025; Pothier-Bouchard et al. 2024; Raymond et al. 2024; Ruebens et al. 2022; Ruebens et al. 2024; Sinet-Mathiot et al. 2019; Sinet-Mathiot et al. 2023; Smith et al. 2024; Stevens et al. 2023; Torres-Iglesias et al. 2024; Wang et al. 2023; Wang et al. 2024; Welker et al. 2015). This method consists in a form of peptide mass fingerprinting which is used to taxonomically identify archaeological and paleontological samples (Buckley et al. 2009; Richter et al. 2022). This technique is generally applied to bones, which lack the diagnostic features necessary for macroscopic and anatomical identification (e.g., Martisius et al. 2020; Brown et al. 2022; Kitagawa et al. 2025). In these analyses, type-I collagen is extracted from each sample and compared against a reference library of known species which enables taxonomic identification.

In this study, the ZooMS identification method will be applied to the Middle and Upper Paleolithic record of Cova Eirós, with the aim of improving our knowledge about the subsistence strategies followed by both Neanderthals and Anatomically Modern Humans (AMH) throughout an extended period of occupation of roughly 20,000 years. Likewise, by comparing the results of the morphological analysis of the remains (Morpho-NISP) with those obtained through the paleoproteomic method (ZooMS-NISP), it will be possible to further discuss the advantages and limitations of this identification method, which is being supported by a growing body of evidence, both within the Iberian Peninsula (Torres-Iglesias et al. 2024) and across the broader European Paleolithic record (e.g., Brown et al. 2022; Discamps et al. 2024; Holloran et al. 2024; Kitagawa et al. 2025; Morin et al. 2023; Oertle et al. 2025; Pothier-Bouchard et al. 2024; Raymond et al. 2024; Ruebens et al. 2022; Ruebens et al. 2024; Sinet-Mathiot et al. 2019; Sinet-Mathiot et al. 2023; Stevens et al. 2023; Wang et al. 2024).

2 | Site Description and Archaeological Background

Cova Eirós is an archaeopaleontological cave site located near the village of Cancelo (Triacastela, Lugo, NW Iberia) (Figure 1A,B), on the NNW slope of Monte Penedo. The cave has a sheltered entrance where archaeological excavations are concentrated. Since 2008, the current investigation project has documented at least six main archaeoestratigraphic levels with Middle and Upper Paleolithic occupations, yielding abundant lithic industry, faunal remains, hearths, bone industry, and ornaments. Altogether, they make up an important sequence of discontinuous Paleolithic occupations spanning more than 30,000 years (de Lombera-Hermida et al. 2014; de Lombera-Hermida et al. 2021).

This study focuses on the Mousterian Levels 4 (> 41,7 ka cal BP) and 3 (41,7–39 ka cal BP) and the Early Upper Paleolithic Levels 2 (36,1–35 ka cal BP) and 2D (undated, but slightly more recent than Level 2 based on archaeoestratigraphic evidence) (Figure 1C). The detailed stratigraphy and chronology of the site have already been addressed in several publications (Bal-García et al. 2025; de Lombera-Hermida 2020; de Lombera-Hermida et al. 2021), so they will not be discussed in detail here; however, it can be summarized as an extensive occupation sequence contained within the Upper Pleistocene, specifically to the climatic phases MIS 3 and 2. The Middle Paleolithic levels (5, 4, and 3) all display typical Mousterian features, representing a period of occupation between ~60 and 39 ka. The main Upper Paleolithic occupation level corresponds to an initial arrival of AMH with expedient Aurignacian technology in Level 2; but the site also includes occupation levels attributed to the Gravettian (Level 1) and the Upper Magdalenian (level B), expanding the range of anthropic occupations in the site to approximately 14–13,8 ka BP. In any case, this sequence consists of a succession of palimpsests with alternating occupations by both carnivores and hunter-gatherers, in which human presence usually follows a short, seasonal occupation pattern characterized by high logistical mobility and a subsistence pattern based on locally abundant resources. The only exception is Level 4, where the high density of lithic artifacts, the presence of several hearths and the abundance of faunal remains exhibiting human consumption indicate a long-term occupation characterized by an intensive—yet diversified—exploitation of resources.

3 | Materials and Methods

3.1 | Anatomical, Taxonomical, and Taphonomic Analysis

All skeletal remains analyzed in this study derive from the archaeological excavations conducted at Cova Eirós between 2008 and 2023. Fieldwork follows a traditional methodology based on 1 m^2 grids. All identifiable bone fragments or those larger than 20 mm and all dental remains are individually recorded; smaller finds are grouped by grid and fixed intervals of 5 cm in depth. The extracted sediment is processed at the field laboratory by wet sieving, employing two superimposed metal sieves with mesh sizes of 5 and 0.5 mm.

Anatomical and taxonomic identification of the assemblage was carried on a large sample of faunal remains from Level 4 ($n = 2988$), Level 3 ($n = 3665$), Level 2 ($n = 970$), Level 2D ($n = 323$), and Level 1 ($n = 229$), using comparative anatomy and zooarchaeology manuals (Davis 1987; Hillson 1992, 2005; Pales and Garcia 1981; Pales and Lambert 1971; Schmid 1972) and the reference collection from the Prehistory Laboratory at the Universidad de León (ULE). To quantify the assemblage, the Number of Identified Specimens (NISP), Minimum Number of Elements (MNE), Minimum Number of Individuals (MNI), and Minimal Animal Units (MAU) were used (Binford 1981; Lyman 2008). For MNE, an approach focused on the identification of diagnostic features was adopted (Dobney and Rielly 1988; Gifford-González and Crader 1977). NISP has also been employed as the basic unit to establish

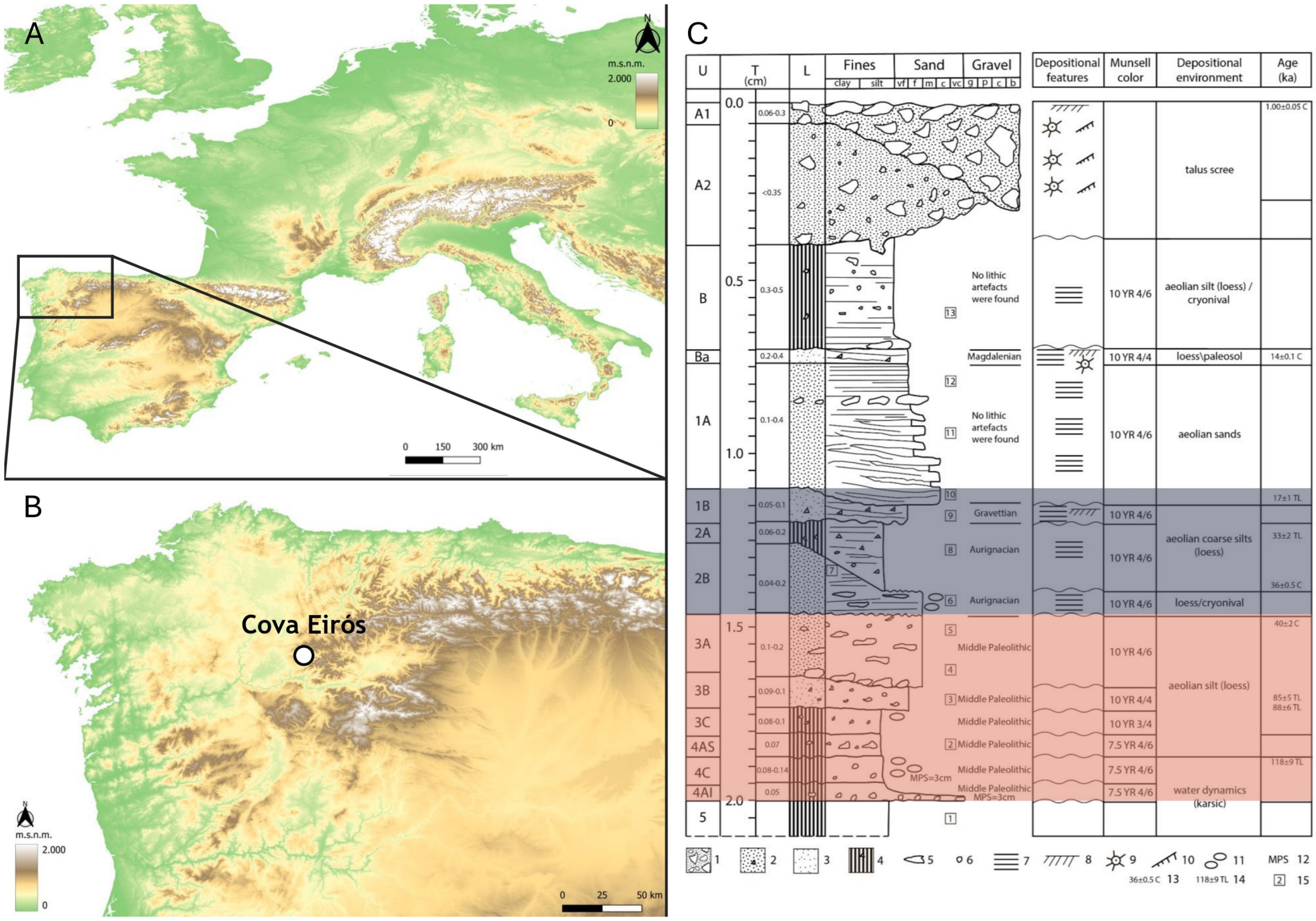

FIGURE 1 | Location of the Cova Eirós archaeological site (A, B) and detailed archaeostratigraphic description of the sequence (C). Middle Paleolithic levels are marked in red and Upper Paleolithic are marked in blue. Level 2D is not included in this classification, as it has been described from a profile in which this level is not observed. [Colour figure can be viewed at wileyonlinelibrary.com]

comparisons between the morphological sample and the ZooMS sample. For each specimen, laterality, bone portion, and ontogenetic age were recorded. Indeterminate remains were classified into size classes following Brain (1981) and Marean et al. (2000): Size 1 (< 20 kg), Size 2 (18–100 kg), Size 3 (70–300 kg), Size 4 (300–1000 kg), and Size 5 (> 1000 kg). In addition—when known—the taxonomic order was noted (e.g., Size 2 ungulate). Although ~9000 individual remains have been recovered from the site, given the scope of this study, only specimens identified to species level were considered for the methodological comparison.

The taphonomic study was conducted on all identifiable skeletal remains and on indeterminate bones larger than 20 mm from Level 4 ($n = 1997$), Level 3 ($n = 2494$), Level 2 ($n = 558$), Level 2D ($n = 207$), and Level 1 ($n = 124$), using Olympus SZ-51 and ZEISS Stemi-508 binocular stereomicroscopes, up to 50X magnification. The surfaces of all bone remains were examined for evidence of anthropogenic exploitation (cutmarks, intentional breakage, and burning), carnivore activity and fossil diagenetic alterations (trampling, weathering, chemical dissolution, abrasion, manganese and iron coatings, etc.) following standard zooarchaeological criteria for the identification (Andrews and Cook 1985; Behrensmeyer 1978; Behrensmeyer et al. 1986; Binford 1981; Courtenay et al. 2020; Domínguez-Rodrigo et al. 2009; Fernández-Jalvo and Andrews 2016; Fisher 1995; Gifford-Gonzalez 2018; Gümrükçü and Pante 2018; Kos 2003; López-González et al. 2006; Pineda et al. 2019; Shipman and Rose 1984; Olsen and Shipman 1988; Thompson et al. 2011).

The identification of cutmarks followed the criteria of Domínguez-Rodrigo et al. (2009). In addition, the anatomical position of the marks has been recorded to infer the activities undertaken (Binford 1981; Soulier and Costamagno 2017; Trolle-Lassen 1990). Regarding fragmentation, fracture patterns were assessed for all large bone remains following the model of Villa and Mahieu (1991), recording the percentage of surviving circumference for each specimen and the morphology of fracture surfaces (orientation, angle, and texture). Likewise, features indicative of green-bone breakage were recorded, such as impact platforms, impact points, hackle marks, notches, flake scars, adhering flakes, presence of cortical flakes, and peeling (Blumenschine and Selvaggio 1988; Capaldo and Blumenschine 1994; Coil et al. 2020; Moclán et al. 2019; Pickering and Egeland 2006; Vettese et al. 2020). Thermal alteration was evaluated by color changes and classified into five stages: S0 (unburned), S1 (brown), S2 (black), S3 (gray/blue), and 4 (white) (Etxebarría 1994; Shipman et al. 1984; Stiner et al. 1995).

3.2 | ZooMS Sampling and Extraction Protocol

A total of 114 bone specimens (Figure 2) measuring ≥20 mm were selected from Level 4 ($n = 43$), Level 3 ($n = 56$), Level 2 ($n = 8$), Level 2D ($n = 6$), and a single piece from Level 1, but as it yielded a negative result, no further reference will be made to this level. Most specimens correspond to long bones, although mandibles, ribs, vertebrae, and compact bones were also included (Data S1). Most of this material (91.2%) could not be assigned to any species using morphological identification methods. The remaining 8.8% comprised elements that had been only tentatively attributed to a species.

Three criteria guided the selection of material: (1) Bones attributed to small ungulates (size 2) where a distinction between cervids (*Capreolus capreolus*) and bovids (*Rupicapra pyrenaica*) could not be made on morphological terms. (2) Bones from size 3/4 ungulates. (3) Selection of indeterminate long bones to obtain a random sample indicative of the site's potential taxonomic diversity. From a taphonomic perspective, part of the selected material exhibits evidence of anthropogenic exploitation, as well as carnivore activity (toothmarks and corroded specimens), making them excellent indicators of the respective subsistence strategies followed by either agent. Burned remains were excluded to optimize the number of identified samples (Smith et al. 2024), no additional taphonomic criteria were employed to exclude remains from the sample.

ZooMS analysis was carried out following established protocols (Buckley et al. 2009). In brief, bone chips were demineralized in 0.6 M hydrochloric acid and rinsed to a neutral (7.5) pH using 50 mM ammonium bicarbonate. The demineralized bone was then gelatinized for 1 h at 65°C and allowed to digest in 0.4 μg of trypsin overnight at 37°C. The resulting supernatant was de-salted and concentrated using C18 ZipTips and eluted in 50 μL 0.1% trifluoroacetic acid and 50% acetonitrile.

Samples were spotted in triplicate on an MTP384 groundsteel plate and analyzed on a Bruker Autoflex maX LRF MALDI-MS System. Data analysis of the results was carried out following an in-house protocol for mammal identifications (following the baseline, smoothing, and signal-to-noise thresholds recorded in Brown (2021) via mMass version 6.0.2 by Niedermeyer and Strohalm (2012)). The comparative reference library was compiled from previously published literature (Buckley et al. 2009; Welker et al. 2016) following established nomenclature (Brown et al. 2021) and based on known species at the site and within the region.

4 | Results

4.1 | Morphological Analysis

The morphological analysis across the four levels considered (4, 3, 2, 2D) enabled the taxonomic assignment of 1472 remains, with a clear predominance of *Ursus spelaeus* (52.5%) and *Cervus elaphus* (21.8%). In Level 4 ($n = 342$) (Table 1), in addition to the predominance of red deer (36.5%) and cave bear (35.1%), a relatively high number of *R. pyrenaica* (7.9%) and *C. capreolus* (6.1%) remains were identified. The other taxa are rare, all of them representing <5% of the total identified NISP. Anthropogenic exploitation in this level is concentrated on red deer (78.9%) and complemented by roe deer (10.5%), horse (5.3%), and birds (5.3%). Nonetheless, it should be noted that the proportion of taxonomically identified remains with anthropogenic modifications is extremely low (9.3%), resulting in a relatively wide margin of uncertainty.

In Level 3 ($n = 854$) (Table 2), bears reach their highest predominance (60.2%), followed again by *C. elaphus* (17.3%) and a lower proportion of *R. pyrenaica* (7.9%) and *C. capreolus* (5%). All other identified species fall below 5% of NISP. Human subsistence in this level is clearly focused on the processing of red deer (83.3%), with incidental contributions of *Ursus spelaeus* (11.1%) and *Bos/Bison* (5.6%). The percentage of taxonomically identified remains modified by humans remains low (14.6%).

FIGURE 2 | Some of the sampled bone specimens selected for palaeoproteomic analysis at Cova Eirós, recovered from Levels 4, 3, 2 and 2D of the site's stratigraphic sequence. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | Faunal composition of Cova Eirós Level 4 identified through both morphological (Morpho-NISP) and palaeoproteomic (ZooMS-NISP) analysis, along with the total abundance of each species derived from the integration of both identification methods (ZNISP).

Taxa	Morph-NISP	Morph-NISP%	ZooMS-NISP	ZooMS-NISP%	ZNISP	ZNISP%
C. elaphus	125	36.5	16	42.1	141	37.1
C. capreolus	21	6.1	3	7.9	24	6.3
Bos/Bison	4	1.2	2	5.3	6	1.6
R. pyrenaica	27	7.9	2	5.3	29	7.6
C. pyrenaica	2	0.6	2	5.3	4	1.1
S. scrofa	2	0.6	0	0.0	2	0.5
E. ferus	12	3.5	12	31.6	24	6.3
Rhinocerotidae	5	1.5	0	0.0	5	1.3
C. lupus	3	0.9	0	0.0	3	0.8
V. vulpes	12	3.5	0	0.0	12	3.2
U. spelaeus	120	35.1	1	2.6	121	31.8
O. cuniculus	9	2.6	0	0.0	9	2.4
Total ID	342	100	38	100	380	100

TABLE 2 | Faunal composition of Cova Eirós Level 3 identified through both morphological (Morpho-NISP) and palaeoproteomic (ZooMS-NISP) analysis, along with the total abundance of each species derived from the integration of both identification methods (ZNISP).

Taxa	Morph-NISP	Morph-NISP%	ZooMS-NISP	ZooMS-NISP%	ZNISP	ZNISP%
C. elaphus	148	17.3	14	37.8	162	17.9
C. capreolus	43	5.0	0	0.0	43	4.9
Bos/Bison	11	1.3	3	8.1	14	1.6
R. pyrenaica	67	7.8	6	16.2	73	8.1
C. pyrenaica	1	0.1	1	2.7	2	0.1
S. scrofa	4	0.5	0	0.0	4	0.5
E. ferus	12	1.4	3	8.1	15	1.6
C. antiquitatis	7	0.8	2	5.4	9	1.0
C. lupus	9	1.1	0	0.0	9	1.0
V. vulpes	21	2.5	0	0.0	21	2.4
C. crocuta	8	0.9	0	0.0	8	0.9
P. pardus	3	0.4	0	0.0	3	0.3
Ursidae	514	60.2	8	21.6	522	59.1
O. cuniculus	6	0.7	0	0.0	6	0.7
Total ID	854	100	37	100	891	100

In Level 2 ($n = 177$) (Table 3), bears continue to predominate (51.4%), while the importance of *C. elaphus* declines slightly (13%). There is a growing presence of small ungulates, with *R. pyrenaica* reaching 10.2% of the identified NISP and *C. capreolus* the 5.6%. In addition, this level shows a marked increase in *Oryctolagus cuniculus* remains (9.6%). All other taxa occur at frequencies below 5% of the NISP. Human activity at this level is virtually absent; despite 3.1% of the assemblage exhibiting cutmarks, impacts, and thermal alteration, only two specimens could be identified to species level, being *C. elaphus* and *Ursus spelaeus*.

In Level 2D ($n = 77$) (Table 4), bears continue to dominate (48.1%) and red deer regain prominence (26%); these are followed by *Vulpes vulpes* (6.5%) and *C. capreolus* (5.2%). The remaining taxa are sparsely represented. Evidence of anthropogenic activity in this level is very limited, with only five specimens exhibiting

TABLE 3 | Faunal composition of Cova Eirós Level 2 identified through both morphological (Morpho-NISP) and palaeoproteomic (ZooMS-NISP) analysis, along with the total abundance of each species derived from the integration of both identification methods (ZNISP).

Taxa	Morph-NISP	Morph-NISP%	ZooMS-NISP	ZooMS-NISP%	ZNISP	ZNISP%
C. elaphus	23	13.0	2	33.3	25	13.7
C. capreolus	10	5.6	0	0.0	10	5.5
Bos/Bison	0	0.0	1	16.7	1	0.5
R. pyrenaica	18	10.2	2	33.3	20	10.9
E. ferus	1	0.6	1	16.7	2	1.1
C. lupus	7	4.0	0	0.0	7	3.8
V. vulpes	3	1.7	0	0.0	3	1.6
Mustelidae	4	2.3	0	0.0	4	2.2
P. pardus	1	0.6	0	0.0	1	0.5
U. spelaeus	91	51.4	0	0.0	91	49.7
O. cuniculus	17	9.6	0	0.0	17	9.3
Lepus sp.	2	1.1	0	0.0	2	1.1
Total ID	177	100	6	100	183	100

TABLE 4 | Faunal composition of Cova Eirós Level 2D identified through both morphological (Morpho-NISP) and palaeoproteomic (ZooMS-NISP) analysis, along with the total abundance of each species derived from the integration of both identification methods (ZNISP).

Taxa	Morph-NISP	Morph-NISP%	ZooMS-NISP	ZooMS-NISP%	ZNISP	ZNISP%
C. elaphus	20	26.0	2	40.0	22	26.8
C. capreolus	4	5.2	0	0.0	4	4.9
R. pyrenaica	3	3.9	1	20.0	4	4.9
E. ferus	1	1.3	1	20.0	2	2.4
C. lupus	1	1.3	0	0.0	1	1.2
V. vulpes	5	6.5	0	0.0	5	6.1
Mustelidae	1	1.3	0	0.0	1	1.2
P. pardus	1	1.3	0	0.0	1	1.2
U. spelaeus	37	48.1	1	20.0	38	46.3
O. cuniculus	3	3.9	0	0.0	3	3.7
Lepus sp.	1	1.3	0	0.0	1	1.2
Total ID	77	100	5	100	82	100

marks; among the latter only a burned tibia of *O. cuniculus* could be identified at species level.

4.2 | ZooMS Analysis

Of the 114 specimens analyzed by ZooMS, 75.4% ($n=86$) yielded positive results, albeit with variable taxonomic precision (Data S1). Among those from which taxonomic information could be obtained, 45.3% were identified to family level, while the remaining 54.7% could only be narrowed to a range encompassing several families (i.e., Cervidae/Gazella/Saiga). Nevertheless, the latter were subsequently assigned to a specific taxon based on morphological reassessment. The most frequent categories identified were Ovis/Cervidae/Gazella/Saiga ($n=26$), followed by Equidae ($n=17$), Cervidae/Gazella/Saiga ($n=14$), and Ursidae ($n=10$); the remaining categories being represented by fewer specimens. Species-level correspondence within these categories is provided in the supporting material (Data S2). Raw data for all specimens are available in Mendeley Data (Brown 2026) and are available at: https://data.mendeley.com/datasets/wz6zpxrnjm/1.

Level 4 (Table 1) showed a clear predominance of *C. elaphus* (42.1%) and *Equus ferus* (31.6%), followed by *C. capreolus* (7.9%). Other species exhibit a more limited distribution. Sixteen sampled specimens exhibited evidence of anthropogenic exploitation, indicating processing of horse, red deer, and large bovid. In Level 3 (Table 2), the most abundant taxa were *C. elaphus* (37.8%), Ursidae (21.6%), and *R. pyrenaica* (16.2%), with *Bos/Bison* and *E. ferus* also present. The application of ZooMS further enabled the identification of additional specimens of *Coelodonta antiquitatis* and *Capra pyrenaica*, both being taxa that were already present at the site, but very rare. The sample from this level included 17 specimens bearing evidence of anthropogenic exploitation. Of these, only 68.7% could be identified, indicating the exploitation of red deer, horse, chamois, large bovid, and cave bear.

In Level 2 (Table 3), the most frequent taxa were *C. elaphus* (33.3%) and *R. pyrenaica* (33.3%), followed by *E. ferus* (16.7%) and *Bos/Bison* (16.7%). Nevertheless, the small number of analyzed specimens ($n = 8$) limits the representativeness of these results, even more considering that not all the samples allowed identification. The sample included a chamois tibia bearing cutmarks. In Level 2D (Table 4), the highest NISP was again provided by *C. elaphus* (40%); *R. pyrenaica* (20%), *E. ferus* (20%), and *Ursus spelaeus* (20%) are also present. Once more, the small sample size ($n = 6$) constrains interpretation. From a taphonomic point of view, despite the limited sample size at this level, two specimens exhibiting evidence of anthropogenic exploitation were included and identified as *C. elaphus* and *E. ferus*.

4.3 | Comparison Between Both Methods

These results indicate substantial variation in species composition across all levels considered (Figure 3). In Level 4, comparison between the two identification methods showed that the ZooMS-NISP approach overrepresents *E. ferus* (+28.1%) and, to a lesser extent, *C. elaphus* (+5.6%), *C. pyrenaica* (+4.7%) and *Bos/Bison* (+4.1%); whereas all carnivores exhibit a clear decline, most notably *Ursus spelaeus* (−32.5%). A chi-square test confirms that this differentiation is statistically significant ($\chi^2 = 68.9$; df = 11; $p < 0.0001$), with a moderate effect size (Cramér's V = 0.4). In Level 3, the largest increases are observed for *C. elaphus* (+20.5%), *R. pyrenaica* (+8.4%) and *E. ferus* (+6.7%), reflecting a general upward trend among ungulates except for *C. capreolus* (−5%). By contrast, carnivores show again a marked decline, with *Ursus spelaeus* experiencing the greatest loss (−38.6%). As in the previous case, application of the chi-square test indicates that the distinction between the two identification methods—although slightly smaller—is statistically significant ($\chi^2 = 62.2$; df = 13; $p < 0.0001$) and exhibits a moderate effect size (Cramér's V = 0.3).

Comparison at Level 2 reveals a substantial overrepresentation among most ungulates, especially *R. pyrenaica* (+23.2%), *C. elaphus* (+20.3%), *Bos/Bison* (+16.7%), and *E. ferus* (+16.1%). In contrast, all carnivores exhibit marked declines in representativeness (i.e., *Ursus spelaeus*: −51.41%). As in the Mousterian levels, this differentiation is statistically significant ($\chi^2 = 52.45$; df = 11; $p < 0.0001$) and is associated with a moderately large effect size (Cramér's V = 0.5). Lastly, in Level

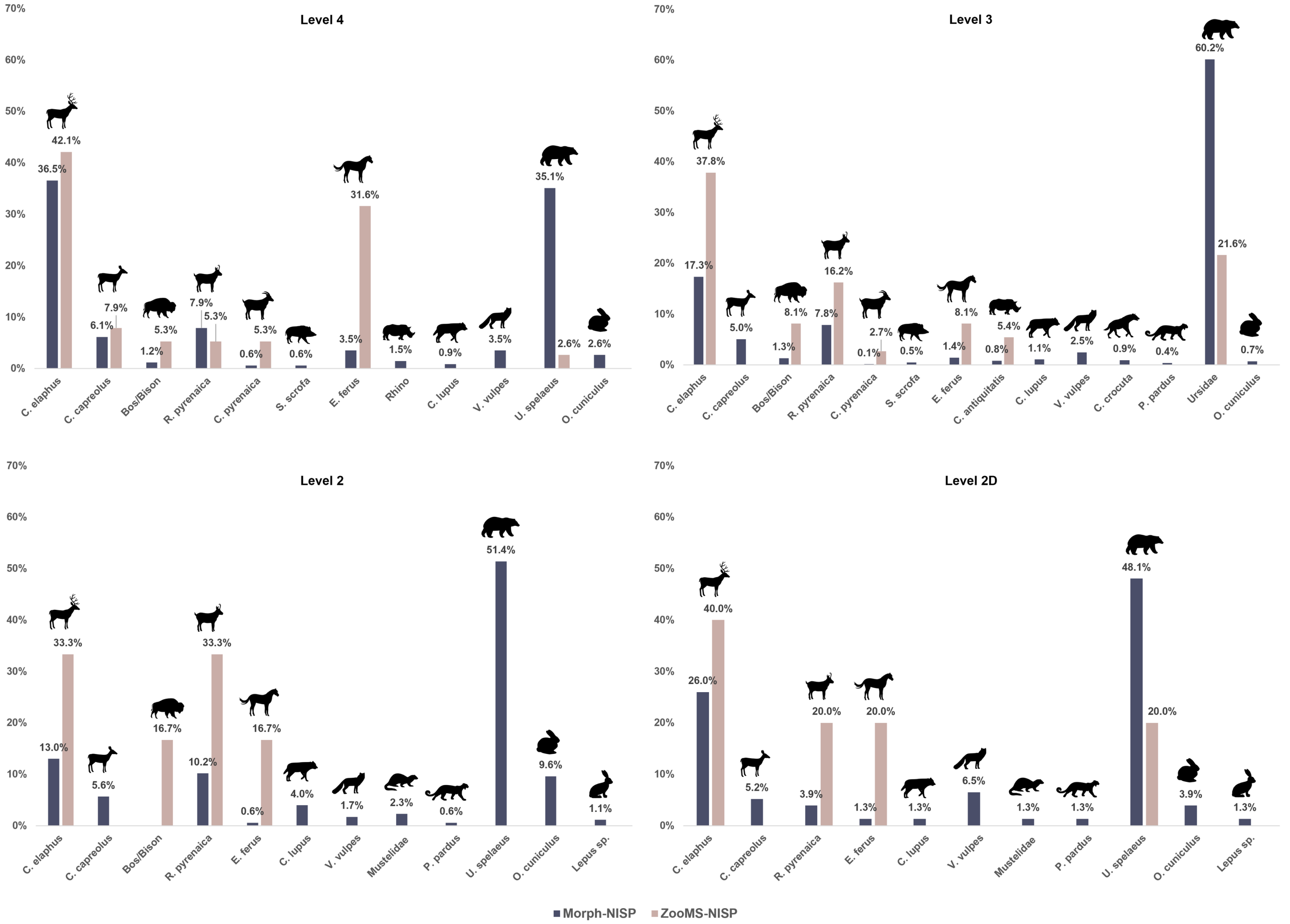

FIGURE 3 | Faunal composition of Levels 4, 3, 2 and 2D of Cova Eirós, as shown by morphological (Morpho-NISP) and paleoproteomic identifications (ZooMS-NISP). [Colour figure can be viewed at wileyonlinelibrary.com]

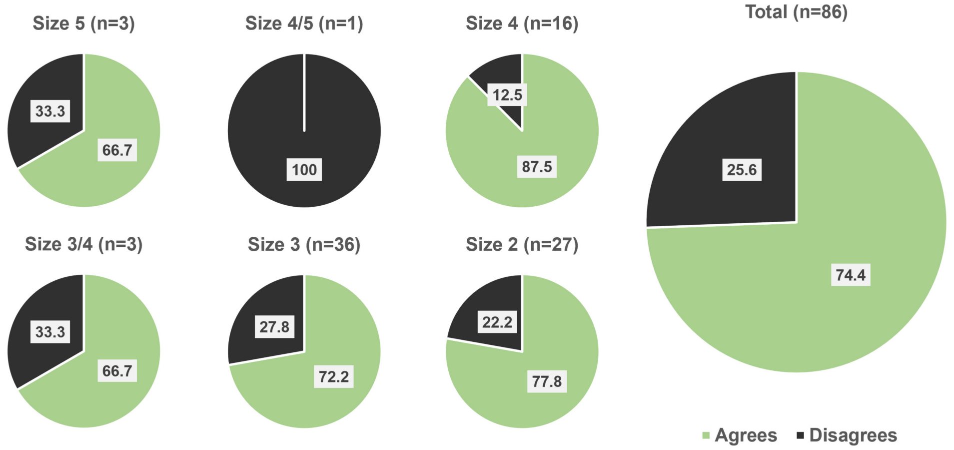

FIGURE 4 | Percentage of remains correctly assigned to a size class based on the ZooMS identification. [Colour figure can be viewed at wileyonlinelibrary.com]

2D the divergence in %NISP between the two identification methods continues the trend observed throughout the sequence. Ungulates are more strongly represented under the ZooMS-NISP, with substantial increases in *E. ferus* (+18.7%), *R. pyrenaica* (+16.1%), and *C. elaphus* (+14%), whereas *C. capreolus* declines (−5.2%). Among carnivores, all taxa decrease markedly in terms of ZooMS-NISP, with *Ursus spelaeus* once again exhibiting the greatest divergence (−28.05%). However, for this level the chi-square test indicates that the results are not statistically significant, most notably given the high p value for this sample ($\chi^2 = 11.41$; df = 10; $p = 0.3$), as well as a moderate effect size (Cramér's V = 0.4).

The percentage of agreement between the morphological and ZooMS identifications was relatively high in this sample, with 74.4% of the specimens yielding positive ZooMS results being concordant with the broad taxonomic categories assigned through morphological analysis (Figure 4). In any case, the correct identification rate varies by category. Among the control samples, specimens identified as *C. capreolus* ($n = 1$) and *R. pyrenaica* ($n = 1$) were also correctly assigned by ZooMS to these species. Of the morphologically identified *C. elaphus* samples ($n = 4$) one was re-identified as *Ursidae*. In the case of the pre-identified cf. *E. ferus* remain, ZooMS indicated that it actually belonged to *Bos/Bison*.

Among the specimens classified as Size 2 ungulate ($n = 7$), for which an identification as roe deer or chamois was expected, only 57.1% belonged indeed to one of these taxa. The remaining three samples were identified by ZooMS as *C. elaphus*, *C. pyrenaica*, and *Bos/Bison*. However, all three had previously been noted as deriving from infant or immature individuals; thus, the attribution to size class was not incorrect. For Size 4 ungulates ($n = 3$), two specimens were correctly assigned to *E. ferus*, whereas the third—a rib fragment—was against expectation assigned to *C. elaphus*. In the case of Size 3 carnivores ($n = 4$), all samples were assigned to Ursidae. One of these specimens had been observed to belong to an immature individual, which accounts for the smaller body size; the other three had been regarded as adult animals in the morphological analysis, which does indicate a misattribution to the size class.

Finally, among the randomly selected long-bone fragments, clear trends emerge by weight class. In Size 2 sample ($n = 17$), 88.2% of the remains belong to ungulates; primarily *R. pyrenaica* (41.2%), but with a relatively high number of *C. elaphus* specimens (29.4%), including both immature and adult individuals; thus, the morphological analysis failed in assigning these to their size class. In Size 3 sample ($n = 29$), *C. elaphus* clearly dominates (79.31%), although several specimens of *E. ferus* and single remains of Rhinocerotidae and Ursidae were also identified. In all these cases the individuals are presumed to have been ontogenetically adults, indicating that the misassignment to weight class reflects an observational error rather than an age-related criterion. For Size 4 samples ($n = 12$), all specimens identified by ZooMS fit the size class given by the morphological analysis, with *E. ferus* being the most represented species (58.3%). Among Size 5 remains ($n = 3$), two were identified as *Bos/Bison*—which is compatible with the size class—whereas a third one was identified as *E. ferus*, implying an overestimation of body size based on diaphyseal thickness. In the ambiguous Size 3/4 or Size 4/5 remains *E. ferus* is the predominant species. Finally, at a global scale, the presence of carnivores in the random sample is minimal, representing only 7.7% of the specimens in terms of ZooMS-NISP compared to 54.7% under Morpho-NISP. In any case, the exclusive identification of *Ursus spelaeus* within this order is in concordance with the taxonomic spectrum documented across the four levels considered, where no carnivore exceeds 5% of the NISP except for red fox in Level 2D.

Among the 31 samples for which ZooMS failed, there are elements from all levels and all size classes, encompassing long bones, axial elements, and compact bones; thus, none of these factors appears to have contributed to a higher error rate. Application of the chi-square test across the size classes considered in this study indicated that differing success rates of ZooMS identifications are not statistically significant ($\chi^2 = 1.79$; df = 4; $p = 0.77$) and the effect size is small (Cramér's V = 0.1). The provenance of samples by archaeoestratigraphic level likewise returned a negative and statistically weak result ($\chi^2 = 8.83$; df = 3; $p = 0.03$), although with a slightly more moderate effect size (Cramér's V = 0.3).

5 | Discussion

The application of ZooMS at Cova Eirós, while based on a relatively small sample ($n = 114$), has improved our understanding of the faunal composition of the Mousterian and Early Upper Paleolithic levels, revealing marked contrasts between Morpho-NISP and ZooMS-NISP that have served to somehow homogenize the faunal composition across levels. The ZooMS success rate at this site (74.5%) aligns well with other results from Paleolithic sites where this methodology has been employed (Morin et al. 2023; Oertle et al. 2025; Raymond et al. 2024; Ruebens et al. 2022; Stevens et al. 2023; Wang et al. 2024, 2023).

In terms of taxonomic identification, this study offers new perspectives on the balance between *C. elaphus* and *Ursus spelaeus* across the last half of the MIS 3 at the site. Both taxa emerge as the main constituents of the analyzed levels, with cave bear predominating over red deer in all levels except for Level 4, where they are relatively balanced in terms of Morpho-NISP. ZooMS identifications, by contrast, entail a substantial reduction in the relative importance of *Ursus spelaeus* in all levels considered that likely reflects the fact that the high abundance of isolated dental elements (especially decidual teeth) and small bone elements (phalanges, carpal/tarsal, etc.) identified in all levels is not matched by an equivalent abundance of long-bone fragments, confirming that the skeletal representation of this species is clearly biased and points towards an accumulation mainly driven by an attritional profile typical of denning sites (Andrews and Turner 1992; Weinstock 2000), as has already been pointed out for this site in previous publications (Bal-García et al. 2025; Grandal d'Anglade 1993; Valverde Tejedor 2019). The large proportion of reabsorbed deciduous teeth implies a probable survival of the cubs, which in turn explains the pronounced underrepresentation of the postcranial skeleton.

By contrast, the abundance of *C. elaphus* in the Morpho-NISP sample is corroborated by a similarly high percentage of remains identified in terms of ZooMS-NISP, allowing for two clear inferences. Firstly, in this case the abundance of red deer dental remains is indeed accompanied by an abundance of bone splinters, suggesting that these animals were transported to the site for processing, producing a large amount of bone remains by the deliberate breakage of these elements for marrow extraction. Secondly, the abundance of *Ursus spelaeus* derived from Morpho-NISP likely reflects the true abundance of this species in the assemblage, since scarcely any remains of this species have been identified in the random sample; on the other hand, the abundance of *C. elaphus* remains is underestimated given the large volume of previously indeterminate remains assigned to red deer by ZooMS.

Another important outcome of this study is that large ungulates increased their representation at the site, especially in the case of the horse. This taxon shows a rise in NISP of between 20% and 50% depending on the level, making it one of the main ungulates species in terms of remains. Nevertheless, the marked increase in large ungulates in ZooMS analysis is a common issue that has already been addressed by other authors (e.g., Discamps et al. 2024; Holloran et al. 2024; Morin et al. 2023; Oertle et al. 2025; Pothier-Bouchard et al. 2024; Raymond et al. 2024; Ruebens et al. 2024; Sinet-Mathiot et al. 2023; Wang et al. 2024). This raise has been interpreted primarily as the result of a greater number of bone splinters originated by the fragmentation of these species remains; as opposed to smaller taxa, which yield fewer remains from the same processing. Therefore, the pronounced increase of these animals in Cova Eirós should not necessarily be taken to indicate their natural abundance in the surroundings, but rather the result of the taphonomic processes to which the assemblage was subjected. In this regard, counts of MNE or MNI again emerge as better indicators of the abundance of different taxa at the site.

Similarly, just as the overrepresentation of large-bodied ungulates reflects both sample-selection criteria and the taphonomic processes affecting the bone assemblages, the absence of Size 1 animals in the ZooMS sample does not imply that these taxa were not present at the site. In fact, both *V. vulpes* and *O. cuniculus* have moderately high NISP, especially in the upper strata (Levels 2 and 2D). In both cases, the application of a 20 mm minimum length cutoff for sampled material entails the near-total exclusion of remains attributable to these species: fox remains on the Morpho-NISP sample at the site have a mean length of 19.5 mm, whereas in the case of rabbit the size is even smaller (17.7 mm).

Moreover, although no previously unknown taxa have been identified at the site in this study, the application of ZooMS has allowed for the recognition of a greater number of remains belonging to elusive taxa in NW Iberia, such as *C. pyrenaica* and Rhinocerotidae. Where ZooMS has genuinely contributed new perspectives is in documenting anthropogenic exploitation of additional taxa in the whole sequence, namely *Bos/Bison* in Level 4; *R. pyrenaica* and *E. ferus* in Level 3; *R. pyrenaica* in Level 2, and both *C. elaphus* and *E. ferus* in Level 2D. Likewise, this analysis has made it possible to rule out an alleged *P. spelaea* rib with cutmarks previously identified by another author (Valverde Tejedor 2019); being identified by ZooMS as Ursidae. Although this result still supports discussing the anthropogenic exploitation of a large carnivore at the site, cutmarks on bone remains of cave bear were already well attested here, especially in Level 3 (Bal-García et al. 2025).

Likewise, the proportions contributed by each species to subsistence activities vary markedly across the sequence. In Level 4, the presumed predominance of red deer exploitation is tempered by the striking increase of cutmarks and broken horse remains revealed by ZooMS, reinforcing the interpretation of a diversified hunting pattern for this occupation level. In Level 3, *C. elaphus* still predominates—albeit reduced from 83.3% to 75% of the identified NISP—with the remaining secondary taxa distributed evenly. Finally, in both Levels 2 and 2D, the small sample size precludes statistically robust conclusions, although a presumptively diversified procurement pattern is observed in both episodes.

Finally, one last point remains to be considered. Since the proliferation of paleoproteomic identification of faunal assemblages in the last decade the ongoing debate over the feasibility of attributing indeterminate remains to size classes has resurfaced. In other ZooMS studies published, high error rates have been observed when morphologically indeterminate remains are grouped by size classes (Discamps et al. 2024; Ruebens et al. 2024; Sinet-Mathiot et al. 2023, 2019). Nevertheless, in this work, as in many others (Ruebens et al. 2024; Torres-Iglesias et al. 2024), a large part of the specimens identified by ZooMS had been correctly assigned to a size class during the morphological examination (74.4%). Although this is not an exceptionally high percentage, we contend that classification by size class is broadly reliable. However, as with any observational method depending on the analyst's expertise and lacking a strictly defined criteria, large margins of error may be expected, especially if the age of the specimens is not considered; an aspect that is not addressed in several of the cited publications.

6 | Conclusions

In recent decades, ZooMS as a taxonomic identification method has become a crucial tool for addressing research questions that cannot be resolved with traditional approaches. In the case presented here, applying this method to the MIS 3 levels of Cova Eirós has revealed a greater representation of most ungulates in the faunal assemblage than that previously estimated through morphological analysis alone. It has also brought to light a higher abundance of large ungulates, as in *E. ferus*, which shifts from a residual species to a more prominent one across all levels. Moreover, sampling of bone remains bearing evidence of anthropogenic exploitation has allowed a deeper examination of Neanderthal and AMH subsistence strategies at the site, indicating a reduction in the dominance of red deer in favor of greater dietary diversification.

Despite the relatively small proportion of analyzed samples ($n = 114$) in relation to the total number of specimens recovered at the site, the low margin of error linking ZooMS identifications to the taxonomic categories (i.e., size class) proposed during the morphological analysis of the remains, supports the reliability of the remainder of the assemblage. This also demonstrates that, although not completely unproblematic, classifying bone material by size classes is a robust method for retrieving information from remains that would otherwise yield no data. In any case, in small samples such as the one presented here, given the disparity between the nature of the morphological identified assemblage (mainly teeth, long-bone epiphyses and small elements) and that sampled by ZooMS (mainly long-bone diaphyseal fragments), palaeoproteomic data should be regarded as a complement to -rather than a substitute for- morphological analysis.

Author Contributions

Hugo Bal-García: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Samantha Brown:** conceptualization, formal analysis, investigation, methodology, writing – original draft, writing – review and editing. **Iván Rey-Rodríguez:** investigation, writing – review and editing. **Mikel Díaz-Rodríguez:** investigation, writing – review and editing. **Carlos Fernández-Rodríguez:** investigation, writing – review and editing. **Álvaro Ibáñez-Encinas:** investigation, writing – review and editing. **Arturo de Lombera-Hermida:** funding acquisition, investigation, project administration, writing – review and editing. **Tania Mosquera-Castro:** investigation, writing – review and editing. **Xosé Pedro Rodríguez-Álvarez:** funding acquisition, investigation, project administration, writing – review and editing. **Ramón Fábregas-Valcarce:** funding acquisition, project administration, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Cova Eiros ZooMS Dataset, Mendeley Data, V1 at https://data.mendeley.com/datasets/wz6zpxrnjm/1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Supplementary Data 1** TAXONOMIC IDENTIFICACION BASED ON PEPTID RANGES. **Data S1:** Excel file containing the raw data of the analyzed specimens, the possible taphonomic alterations observed, and the peptide markers identified in the ZooMS analysis. **Data S2:** expanded explanation of the taxonomic identification criteria followed on specimens with ambiguous characterization by ZooMS. **Data S3:** Supporting Information.