# Who ate the fish? The role of fish during the Paleolithic in Western-Central Europe

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## Dedication

To my father, who always told me to keep swimming and make my dreams real.

## Acknowledgments

There are so many researchers, colleagues, and friends to thank who gave me support and help during this Ph.D.

Firstly, my Ph.D. supervisors, Prof. Dr. Nicholas J. Conard, PD Dr. Britt M. Starkovich, and Prof. Dr. Hervé Bocherens, for their crucial guidance. For their continued support and collaboration during the study of the fish remains from Gran Dolina (Atapuerca, Iberian Peninsula), I would like to thank Dr. Hugues-Alexandre Blain, Dr. Almudena Martínez-Monzón, and Dr. Gloria Cuenca-Bescós. The study of Navalmaíllo rock shelter (Pinilla del Valle, Iberian Peninsula) was possible thanks to Dr. César Laplana and Dr. Hugues-Alexandre Blain. I am very grateful to Dr. Keiko Kitagawa and Prof. Dr. Claus-Joachim Kind, who helped me substantially during my work on Hohlenstein-Stadel (Swabian Jura, Germany). I thank Dr. Ana Belén Marín-Arroyo and Dr. Manuel R. González-Morales for giving me the excellent opportunity to study the fish assemblage from the Gravettian site of Fuente del Salín cave (Cantabrian Region, Iberian Peninsula).

I want to thank Prof. Dr. Nicholas J. Conard and PD Dr. Britt M. Starkovich for allowing me to study the fish remains from Hohle Fels. Thank you to Dr. Jordi Agustí for allowing me to study the Lower Paleolithic fish material from Barranco León (Guadix-Baza, Iberian Peninsula). Of course, I appreciate the hard work of all the excavation teams who helped me excavate, water-screen, and sort all the material I studied during this Ph.D. dissertation.

Also, thank the Zooarchaeology Department team at the University of Tübingen for their essential support. I especially thank the “Micro lovers ES/IT” team during our thousands of coffee breaks. Dr. Elisa Luzi, Dr. Iván Rey-Rodríguez, and the future Dr. Mata-González help me unconditionally with their friendship and heart. This thesis has brought us closes as friends. Thanks for your patience! Of course, I want to thank Dr. Elisa Luzi, Dr. Susanne Münzel, Dr. Marta Díaz-Zorita, Dr. Wong, and Dr. Riehl for their suggestions and comments to improve this manuscript. To my husband and all my family for suffering my absence during the writing process of this manuscript at home. To Dr. María Saña-Seguí at the Autonomous University of Barcelona and Dr. Arturo Morales Muñiz at the Autonomous University of Madrid for their help and for the encouragement during my first steps in identifying and studying fish remains. Thank you all of you!

## Abbreviations

BP – years Before Present

Ma – Millions of years ago

MIS – Marine Isotope Stage

GH – Geological Horizon

NISP – Number of Identified Specimens

MNI – Minimum Number of Individuals

sp. - Species name when its identity is not clear

cf. – confer, compare with

## Summary

In Western and Central Europe, researchers described the presence of fish remains in several Paleolithic sites. Due to their long history of zooarchaeological studies in well-analyzed Paleolithic contexts, two areas such as the Iberian Peninsula and the Swabian Jura, are relevant for interpreting the role of water-related resources and fishing as part of the human subsistence strategies, from both regional and local points of view within the Western-Central European context.

Nevertheless, sometimes, archaeologists assume an anthropogenic origin for the existence of fish in faunal records when other evidence of human occupation is present, such as lithics, worked bones (organic artifacts), or animal bones with anthropogenic marks, and it is viewed as a crucial factor in evaluating human dietary changes.

To determine the potential predator of fish and reconstruct the ecosystem, we must consider the faunal assemblage, especially the mixture of fish remains and other small vertebrates. Comparative analyses of fish remains are needed to clarify the origin of their accumulations in European Paleolithic cave/rock shelter contexts to increase our knowledge of aquatic ecosystems. This thesis explores the role of fish in Paleolithic contexts, exemplified by several study cases from different sites and periods across Western and Central Europe.

## Zusammenfassung

In West- und Mitteleuropa wird das Vorkommen von Fischresten aus mehreren paläolithischen Fundplätzen beschrieben. Zwei Regionen wurden aufgrund ihrer langen zooarchäologischen Forschungsgeschichte in gut analysierten paläolithischen Kontexten als besonders relevant eingestuft, nämlich die Iberische Halbinsel und die Schwäbische Alb, um die Rolle wasserbezogener Ressourcen und der Fischerei in den Subsistenzstrategien menschlicher Gruppen zu untersuchen, sowohl was den regionalen, als auch den lokalen Aspekt im West- und Mitteleuropäischen Kontext angeht.

Allerdings, Archäologen meistens einen anthropogenen Ursprung für die Existenz von Fischen in Faunenkomplexen, wenn es andere Hinweise auf menschliche Besiedlung gibt, wie beispielsweise Steinartefakte, organische Artefakte oder Tierknochen mit anthropogenen Spuren, und es wird als entscheidendes Argument für die Bewertung menschlicher Ernährungsgewohnheiten bewertet.

Um potenzielle Predatoren von Fischen bestimmen und das Ökosystem rekonstruieren zu können, müssen wir die Faunagemeinschaft als Ganzes betrachten, insbesondere die Mischung aus Fischresten und anderen kleinen Wirbeltieren. Vergleichende Analysen von Fischresten sind erforderlich, um die Ursache ihrer Ansammlungen in Höhlen-/Felsschutzkontexten des europäischen Paläolithikums zu klären und unser Wissen über aquatische Ökosysteme zu erweitern. Diese Dissertation will die Rolle von Fischen in paläolithischen Kontextenanhand mehrerer Studien an verschiedenen Fundstellen und Epochen in West-Mitteleuropa beispielhaft untersuchen.

## List of Published articles

**(1)** Agustí, J., Blain, H-A., Lozano-Fernández, I., Piñero, P., Oms, O., Furió, M., **Blanco-Lapaz, A**., López-García, J.M., Sala-Ramos, R. 2015. Chronological and environmental context of the first hominin dispersal into Western Europe: The case of Barranco León (Guadix-Baza Basin, SE Spain). Journal of Human Evolution. 87: 87-94. https://doi.org/10.1016/j.jhevol.2015.02.014 (**Appendix 1**).

**(2) Blanco-Lapaz, A**., Martínez-Monzón, A., Blain, H-A., Cuenca-Bescós, G. 2021a. Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record. Palaeogeography, Palaeoclimatology, Palaeoecology, 574 (2): 11044. https://www.doi.org/10.1016/j.palaeo.2021.110444 (**Appendix 2**).

**(3)** Blain, H-A., Sánchez-Bandera, C., Fagoaga, A**., Blanco-Lapaz, A**., Martínez-Monzón, A., Bisbal-Chinesta, J.F., Moclán, A., Huguet, R., Laplana, C., Márquez, B., Sevilla, P., Arsuaga, J.L., Pérez-González, A., Baquedano, E. 2022. A warm and humid paleoecological context for the Neanderthal mountain settlement at the Navalmaíllo rock shelter (Iberian Central System, Madrid)**.** Quaternary Science Reviews. 293: 107727. https://doi.org/10.1016/j.quascirev.2022.107727 (**Appendix 3**).

**(4) Blanco-Lapaz, A**., Kitagawa, K., Kind, C-K. 2021b. Aquatic resource exploitation during the Paleolithic in the Swabian Jura based on fish remains from Hohlenstein-Stadel Cave. Quartär, 68: 1-14. https://doi.org/10.7485/qu.2021.68.94293 (**Appendix 4**).

**(5)** Luzi, E., **Blanco-Lapaz, A**., Rhodes, S.E., Conard, N.J. 2022. Paleoclimatic and paleoenvironmental reconstructions based on the small vertebrates from the Middle Paleolithic of Hohle Fels Cave, SW Germany. Archaeological and Anthropological Sciences 14(6): 107. https://doi.org/10.1007/s12520-022-01568-5 (**Appendix 5**).

**(6) Blanco-Lapaz, A**., Marín-Arroyo, A.B., Gutiérrez-Zugasti, I., González-Echegaray de Yarto., F., González-Morales, M.R. 2023. Coastal and Inland subsistence strategies during the Gravettian in the Cantabrian Region (northern Iberian Peninsula). Quaternary Science Advances, 12: 100106. https://doi.org/10.1016/j.qsa.2023.100106 (**Appendix 6**).

## Personal Contribution

To comply with point 6.2 of the Doctoral Degree Regulations of the Faculty of Science at the University of Tübingen, I briefly describe my contribution to any collaborative works included in this dissertation, highlighting their extent and significance.

As the first author of manuscripts 2, 4, and 6, I conceptualized and formulated the research goals and aims. I am also the primary writer of the manuscripts. As the principal author, I applied the formal analysis of the fish assemblages and conducted the research and investigation process. For manuscript 2, I studied the fish remains from Gran Dolina (Atapuerca, Iberian Peninsula) and coordinated the contributions from the other co-authors since Dr. Blain and Dr. Martínez-Monzón provided paleoecological context and Dr. Cuenca-Bescós the geological context of the site. In manuscript 4, Dr. Kitagawa provided zooarchaeological and archaeological context. Prof. Kind provided archaeological and geological contexts. Dr. Marín-Arroyo and Dr. Gutiérrez-Zugasti provided editorial input and zooarchaeological context based on molluscs and helped develop some interpretations in manuscript 6. Dr. González-Morales provided the archaeological context, and Mr. González-Echegaray de Yarto provided the zooarchaeological context based on large game.

As co-author in manuscripts 1, 3, and 5, I studied the fish assemblages from different aspects, such as taxonomy, taphonomy, and palaeoecology. I also developed interpretations based on the data from those fish assemblages.

# Chapter 1. Introduction

In Paleolithic contexts, one of the goals of zooarchaeologists is to strive to understand how humans interacted with their environment by analyzing their diets (e.g. Gaudzinski-Windheuser and Niven, 2009) following generally the optimal foraging theory (Stephens and Krebs, 1986) to determine what humans ate (prey choice model; Stephens and Krebs, 1986; Pianka, 2000) and where or when they obtained their food resources (patch model; MacArthur and Pianka, 1966).

Based on the prey choice model from the optimal foraging theory, researchers distinguish two main groups of prey: small game (such as lagomorphs, birds, tortoises, molluscs, and fish) and large game (mostly ungulates; e.g. Stiner et al., 1999; 2000; Stiner and Munro, 2002). Researchers consider the small game as a low-ranked taxon since they offer lower caloric yields and the large game as high-ranked species, given that they offer proportionally much more caloric intake (e.g. see discussions in MacArthur and Pianka, 1966; Payne, 1975; Stephens and Krebs, 1986; Pianka, 2000; Stiner et al., 2000; Nagoaka, 2002; Lupo, 2006; Stiner, 2013; Gifford-González, 2018). In addition, slow-ranked species are divided into slow-moving animals (tortoises and molluscs) and fast-moving taxa (lagomorphs, birds, and fish; e.g. Stephens and Krebs, 1986; Pianka, 2000; Stiner et al., 2000; Gifford-González, 2018).

To study prey availability, investigators used the patch model (MacArthur and Pianka, 1966) from the optimal foraging theory. This model points out that resources are present in distinct patches (for example: rivers, steppe, forest, and seasonal hunt areas) rather than evenly distributed across the environment. Based on this model, foragers evaluate the average return rate of different patches, considering travel time. They prioritize patches based on their rank and add the prey that inhabit the patch to their diet until the average foraging returns per unit decrease (e.g. Stephens and Krebs, 1986; Kelly, 2013). In ethnographic studies of hunting-fishing strategies, humans considered it less profitable when the return rates in a particular profitable patch were lower than the average return rate of other patches and tended to exploit other patches (e.g. Smith, 1991; Kelly, 2013).

In studies to reconstruct human diets through the Paleolithic based on aquatic resources in particular, researchers considered the contribution of fish (fast-moving taxa) during the Lower Paleolithic/Early Stone Age as sporadic (Stewart, 1994; Joordens et al., 2009; Zohar et al., 2022). Available data on human fish exploitation starts at Early Stone Age sites in some regions of Africa, such as East Turkana and Olduvai Gorge (e.g. Braun et al., 2010). Several characteristics supported this assumption, such as low taxonomic diversity of the fish assemblage, selective exploitation of seasonally spawning species, skewed skeletal element representation, continuous occupation, and bone modifications (Howel et al., 1987; Stewart, 1989, 1994; Hovers et al., 2008; Ashley et al., 2009; Hovers, 2012; Stewart, 2014). Moving from Africa and into the Middle East, in Israel, at Gesher Benot Ya'aqov, Zohar et al. (2022), pursued a multi-technique approach, observing that also early humans cooked fish during the Lower Paleolithic (780,000 years ago) at this site.

During the Middle Paleolithic in Europe, several authors described the Neanderthals as mainly large-game hunters (e.g. Stiner, 1994; Bocherens, 2009; Niven, 2006; Guadzinski-Windhesuer and Niven, 2009; Niven et al., 2012; Yravedra et al., 2015; Marín et al., 2017, 2019; Real et al., 2019; Rots et al., 2021, Terlato et al., 2021). Nevertheless, Neanderthals showed a more diversified diet since they also exploited small game (fast and slow-moving) as a food resource, including birds (e.g. Cochard et al., 2012; Blasco and Peris, 2009; Blasco and Fernández-Peris, 2012; Laroulandie et al., 2016; Romandini et al., 2016; Blasco et al., 2013, 2014, 2016, 2022; Gómez-Olivencia et al., 2018), leporids (e.g. Cochard et al., 2012; Carvalho et al., 2018; Pelletier et al., 2019), tortoises (e.g. Stiner et al., 1999; Stiner et al., 2000; Blasco et al., 2011, 2013; Nabais and Zilhão, 2019), and aquatic taxa such as crabs (Nabais et al., 2023), molluscs, and fish (Roselló-Izquierdo and Morales-Muñiz, 2005; Hardy and Moncel, 2011; Brown et al., 2011; Zilhão et al., 2020; Villa et al., 2020; Guillaud et al., 2021; Romandini et al., 2023).

Moving to the Upper Paleolithic contexts, several authors observed the increase of fish (small and fast-moving taxa) as part of the diet of hunter-gatherers in Europe (e.g. Stephens and Krebs, 1986; Pianka, 2000; Stiner et al., 2000; Stiner, 2001; Stiner and Munro, 2002; Aura-Tortosa, 2002; Munro, 2004; Zhilin, 2008; Hockett and Haws, 2009; Owen 2010, 2013; Cochard et al., 2012; Manne et al., 2012; Starkovich et al., 2018; Aura-Tortosa et al., 2019; Marín-Arroyo et al., 2023). Those researchers, following optimality models, considered various factors to explain this increase, such as regional human population growth, advancements in technology and catching techniques (tools like traps and specialized equipment), changes in mobility patterns, and paleoenvironmental changes (e.g. Stiner et al., 1999; Stiner et al., 2000; Stiner, 2001; Lupo and Schmitt, 2002; Stiner and Munro, 2011). In addition, Flannery (1969) proposed the idea of a Broad Spectrum Revolution (BSR) that occurred towards the Upper Paleolithic, before the genesis of food production economies. This BSR is characterized by an increase in the variety of foods consumed, especially small game, and is thought to be linked to the growth of the human population since small and fast-moving animals are more complicated to catch (Schmitt, 2002; Stiner and Munro, 2011).

In Paleolithic studies, some researchers assumed that humans were the main accumulator of fish remains in archaeological contexts such as caves and rock shelters (e.g., Reynolds et al., 2018). Nevertheless, we must consider many parameters in interpreting fish assemblages in archaeological contexts, such as spatial distribution, skeletal element representation, and anthropogenic/non-anthropogenic modifications, since other potential predators, such as small-medium size carnivores and birds of prey, since previous authors observed that they were also accumulation agents of fish (e.g. Jones 1984, 1986; Nicholson, 2000; Álvarez-Castañeda and González-Quintero, 2005; Broughton et al., 2006; Van Neer et al., 2007; Rambaud and Laroulandie, 2009; Russ 2010a-b; Russ and Jones, 2011; Guillaud et al. 2017b, 2018). In doing so, our knowledge about past aquatic ecosystems and human subsistence strategies in archaeological contexts will substantially improve.

This dissertation aims to present new and significant data about the interaction of fish and human populations based on my results of fish assemblages studies in six archaeological sites from the Iberian Peninsula (Barranco León, Guadix-Baza Basin, **Appendix 1**; Gran Dolina, Sierra de Atapuerca, **Appendix 2**; Navalmaíllo rock shelter, Meseta mountain range, **Appendix 3**; and Fuente del Salín Cave, Cantabrian Region, **Appendix 6**) and Southern Germany (Hohlenstein-Stadel, **Appendix 4**, and Hohle Fels, **Appendix 5**, both in the Swabian Jura) covering the period from the Lower Paleolithic to the Upper Paleolithic (**Figures 1** and **2**). In all these Paleolithic Iberian and Swabian Jura sites, zooarchaeologists analyzed the faunal assemblages from well-studied archaeological sequences. Nevertheless, their fish assemblages still needed detailed studies from the taxonomical, paleoenvironmental, and human diet reconstruction points of view.

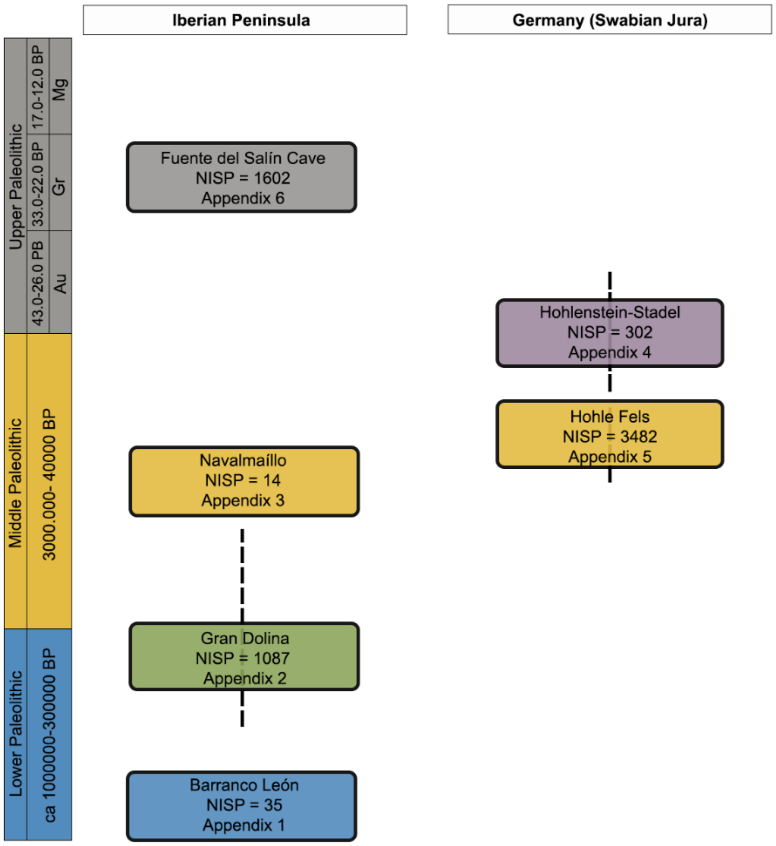

**Figure 1.** Chronological distribution of the analyzed sites for this manuscript. Au: Aurignacian; Gr: Gravettian; Mg: Magdalenian. NISP: number of identified specimens. Appendix from 1 to 6.

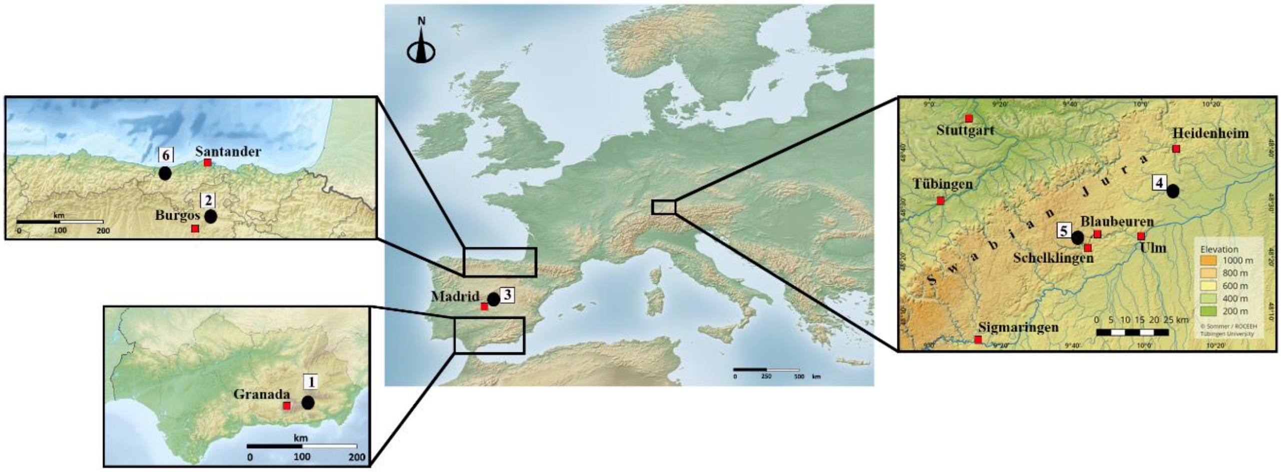

**Figure 2.** Geographical distribution of the analyzed sites for this manuscript. **1**. Barranco León (Guadix-Baza Basin, Granada, Spain; **Appendix 1**), **2**. Gran Dolina (Atapuerca, Burgos, Spain**; Appendix 2**), **3**. Navalmaíllo rock shelter (Pinilla del Valle, Madrid, Spain; **Appendix 3**), **4**. Hohlenstein-Stadel (Swabian Jura, Germany; **Appendix 4**), **5**. Hohle Fels (Swabian Jura, Germany; **Appendix 5**), **6**. Fuente del Salín Cave (Cantabria, Cantabrian Region, Spain; **Appendix 6**). Modified from © Sommer/ROCEEH Universität Tübingen and Natural Earth 2.

The geographic regions where these sites are located have a long history of Paleolithic studies and each represent an important step in the history of human groups in Europe (e.g. Fraas, 1867; Schmidt, 1912; Riek, 1934; Wetzel, 1961; Kind, 1987; Schuler, 1994; Carbonell et al., 1995, 1999, 2014; Bermúdez de Castro et al., 1997, 2008; García and Arsuaga, 1999; Münzel, 2001; Münzel and Conard, 2004; Niven, 2006; Krönneck, 2008; Conard et al., 2008, 2009, 2010, 2011; 2013, 2016; Huguet et al., 2010; Pérez-González et al., 2010; Toro-Moyano et al., 2011, 2013; Bolus and Conard, 2012; Arsuaga et al., 2012; Kitagawa, 2012, 2014, 2019; Krönneck 2012; Ollé et al., 2013; ; Márquez et al., 2013; Napierala et al., 2014; Taller et al. 2014; Boger et al., 2014; Bolus, 2015; Laplana et al., 2015; Maier, 2017; Wong et al., 2017, 2020; Campaña et al., 2017; Hess, 2019; Kind, 2019; de Lombera-Hermida et al., 2020; Bertacchi et al., 2021;Barsky et al., 2021; Baquedano et al., 2021, 2023; Moclán et al., 2021).

The Lower Paleolithic Guadix-Baza Basin (southeastern Iberian Peninsula) is a relevant region since its sites, such as Barranco León (37°43’28.4"N 2°27’03.7"W) and Fuente Nueva 3, contain lithic artifacts, hominin, and animal fossils dating back to approximately 1.5-1.3 Ma. (Blain et al., 2013) that bring crucial information about the first known hominin habitat and subsistence strategies in Iberia and potentially in Western Europe (e.g. Yravedra et al., 2021, 2022). For this dissertation, I described my results based on my study of the fish assemblage from layers D1 and D2 of Barranco León (**Figure 2**; **Appendix 1**; Agustí et al., 2015; Blain et al., 2016). This fish material is now hosted at the Institut Catalá de Paleoecologia Humana i Evolució Social (Tarragona, Spain).

In Central Iberia, researchers discovered several Middle Paleolithic key sites with Neanderthal presence (Buena Pinta, Camino, and Des-cubierta caves, and Navalmaíllo rock shelter) at Calvero de la Higuera Archaeological System (Meseta mountain range, Pinilla del Valle, Madrid; e.g. Huguet et al., 2010; Pérez-González et al., 2010; Arsuaga et al., 2012; Márquez et al., 2013; Laplana et al., 2015; Baquedano et al., 2012, 2021, 2023; Moclán et al., 2021). In this manuscript, I described the results of my analysis based on the fish material from the Middle Paleolithic layer F of Navalmaíllo rock shelter (40°55’26"N 3°48’33"W; **Figure 2**; **Appendix 3**, Blain et al., 2022). I sorted out the sediment to recover the fish at the Museo Arqueológico Regional de la Comunidad de Madrid (Alcalá de Henares, Spain), where the material is currently housed.

In northern Iberian Penisula, the Sierra de Atapuerca (Burgos) is well known for its prolific archaeological and paleontological sites that have a complete Quaternary record (human fossils, thousands of lithic artifacts and vertebrate remains) spanning almost one and a half million years of Earth's history and human evolution (e.g. Fernández-Jalvo, 1995; Carbonell et al., 1995, 1999, 2014; Bermúdez de Castro et al., 1997, 2008; Falguerès et al., 1999; García and Arsuaga, 1999; Sánchez-Marco, 1999; Cuenca-Bescós et al., 1999; Blasco et al., 2013; Ollé et al., 2013; Moreno et al., 2015; Galán et al., 2019; Nuñez-Lahuerta et al., 2019; de Lombera-Hermida et al., 2020). Several Atapuerca karst complex caves have internationally renowned sites, such as Galería, Sima de los Huesos, Gran Dolina, and Sima del Elefante. For my studies in Gran Dolina (42°21’00"N 3°31’10"W; **Figure 2**; **Appendix 2**, Blanco-Lapaz et al., 2021a), I analyzed the fish assemblage recovered from the layers TD4-TD8 (Lower Paleolithic) and TD10.1-4 (Middle Paleolithic). Both fish assemblages are hosted at the Institut Catalá de Paleoecologia Humana i Evolució Social (Tarragona, Spain).

Moving to southern Germany, the Swabian Jura (**Figure 2)** played a vital role in our understanding of Neanderthal and modern human occupations from the Middle to the Upper Paleolithic in Central Europe. In this area, two valleys, Ach and Lone valleys, include sites with rich assemblages and some of the oldest human artifacts, such as figurines and musical instruments from the Aurignacian (Conard, 2009). Several authors analyzed numerous sites in the Ach Valley, such as Hohle Fels, Geißenklösterle, Brillenhöhle, Große Grotte, Sirgenstein, and Kogelstein (e.g. Schmidt, 1912; Torke, 1981,1998; Münzel, 2001; Conard and Malina, 2003, 2006, 2007; Münzel and Conard, 2004; Conard and Janas, 2021; Conard, 2009, 2011; Bolus and Conard, 2012; Napierala et al., 2014; Taller et al. 2014; Bolus, 2015; Maier, 2017; Hess, 2019; Bertacchi et al., 2021; Roots et al., 2021). In the Lone Valley, archaeologists also studied several sites such as Langmahdhalde, Vogelherd, Hohlenstein-Stadel, and Bockstein (e.g. Fraas, 1867; Riek, 1934; Wetzel, 1961; Kind, 1987; Schuler, 1994; Krönneck, 2008; Niven, 2006; Soergel-Rieth, 2011; Conard and Malina, 2007; Conard and Zeidi, 2011, 2012, 2014; Conard et al., 2008, 2009, 2010, 2013, 2016; Kitagawa, 2012, 2014, 2019; Krönneck 2012; Boger et al., 2014; Wong et al., 2017, 2020; Kind, 2019; Krönneck and Hournaure-Hahnke, 2019; Rhodes et al., 2019).

In this manuscript, I analyze the results of my studies in two different Swabian Jura sites such as Hohlenstein-Stadel (48°32’57"N 10°10’21" E) and Hohle Fels (48°22’45"N 9°45’20"E; **Appendix 4** and **5**, Blanco-Lapaz, 2019; Blanco-Lapaz et al., 2021b; Luzi et al., 2022b). Nowadays, the Hohlenstein-Stadel material is housed in Landesamt für Denkmalpflege, Gesellchaft für Archäologie in Württemberg und Hohenzollern (Esslingen am Neckar, Germany) and the material of Hohle Fels, at the University of Tübingen (Germany).

During the Upper Paleolithic, scholars described several sites in the Iberian Peninsula (e.g. Straus, 1983a; González-Morales and Straus, 2009; Gutiérrez-Zugasti et al., 2012; **Supplementary Material**). However, the Cantabrian Region (**Figure 2**; Asturias, Cantabria, Basque Country, and Navarre) mainly represents a crucial area to understand subsistence strategies with rich and well-documented sites such as La Viña, Sopeña, Cueto de la Mina, Coímbre B, Llonín, Altamira Cave, Hornos de la Peña, El Castillo, El Pendo, Morín, La Garma A, El Mirón, Bolinkoba, Antoliñako, Irikaitz, Amalda, Aitzbitarte III, and Alkerdi (Straus, 1983a; Freeman, 1988; Freeman et al., 1988; Pokines, 1998; Gónzalez-Morales and Moure-Romanillo, 2000, 2008; González-Morales and Straus, 2009; Perea and Doadrio, 2009; Russ, 2010b; Roselló-Izquierdo and Morales-Muñiz, 2011; Gutiérrez-Zugasti et al., 2012; Álvarez-Fernández et al., 2011, 2022; Cuenca-Solana, 2013; Clemente-Conte et al., 2020; Marín-Arroyo et al., 2021, 2023). This manuscript presents my results from the Gravettian layers of the few studied Fuente del Salín Cave (43°21’52"N 4°28’58"W; **Appendix 6**; Blanco-Lapaz et al. 2023b). The material is currently placed at the University of Cantabria (Spain).

Analyzing the fish assemblages mentioned before, I identified the fish specimens using comparative modern material from the osteological collections housed in the Senckenberg Center for Human Evolution (University of Tübingen, Germany), the National Natural Sciences Museum of Madrid - CSIC (Madrid, Spain), and the Autonomous University of Madrid (Madrid, Spain). Also, I used osteological atlases (Lepiksaar, 1994; Watt et al., 1997; Prenda et al., 1997). The taxonomic nomenclature follows Cannon (1987). In addition, I used the term Teleostei for unidentifiable elements when it was not possible to recognize a specific taxonomical category.

I processed and sorted the fish remains using tweezers and a microscope EXACTA OPTECH model LFZ s/n 201030 20W. I have used several photographic devices, such as a Dino-Lite Edge Digital Microscope and a Zeiss Stereo Discovery.V8, to produce images for high-quality close-up pictures. For each taxonomic category, I used the standard number of identified specimens (NISP; Grayson, 1984; Lyman, 2008) and, if possible, the minimum number of individuals (MNI; Grayson, 1984; Lyman, 2008).

To study the taphonomical processes affecting the fish bones, I analyzed modifications of the bone surface such as digestion marks, compression, and bite marks (**Appendix 2** and **3**; Blanco-Lapaz et al., 2021a; Blain et al., 2022), following previous studies (e.g. Jones, 1984, 1986, 1999; Butler, 1990; Butler and Schroeder, 1998; Guillaud et al., 2015; Guillaud et al., 2018; Frontini et al., 2021; Morales-Muñiz et al., 2021), skeletal representation (**Appendix 2**, **4**, and **6**; Blanco-Lapaz et al., 2021a-b; Blanco-Lapaz et al., 2023), cutmarks and evidence of burning (**Appendix 4** and **6**; Blanco-Lapaz et al., 2021b; Blanco-Lapaz et al., 2023) using the stages of thermal-induced discoloration following Cáceres et al. (2002) for the second parameter, and spatial distribution (**Appendix 4**; Blanco-Lapaz et al., 2021b).

In addition, I conducted a seasonality study based on sclerochronometry (marginal increment analysis; MIA) using well-preserved scales (**Appendix 4**; Blanco-Lapaz et al., 2021b) and following previous studies (Beamish and McFarlane, 1983; Guillaud et al., 2017a)

To reconstruct the fish associations and the aquatic ecosystem around the archaeological sites described in this manuscript, I analyzed the body size (**Appendix 2**, **3**, **4**, and **6**; Blanco-Lapaz et al., 2021a; Blain et al., 2022; Blanco-Lapaz et al., 2021b; Blanco-Lapaz et al., 2023), also necessary for testing the Bergmann's rule (e.g. Bergmann, 1847; Mousseau, 1997; Belk and Houston, 2002; Parra et al., 2009; Gabriel et al., 2012; Rypel, 2014; Adhikari, 2015; Arranz-Urgell, 2017). I also described the habitat distribution, ecological needs (**Appendix 1-6**; Agustí et al., 2015; Blanco-Lapaz et al., 2021a; Blain et al., 2022; Luzi et al., 2022; Blanco-Lapaz et al., 2021b; Blanco-Lapaz et al., 2023), and capture areas to infer fishing strategies (**Appendix 4** and **6**; Blanco-Lapaz et al., 2021b; Blanco-Lapaz et al., 2023).

## Chapter 2. Research questions

Based on my studies mentioned before, I propose the following research questions, which will improve our knowledge about landscape reconstruction, fishing activities, and the role of non-anthropogenic agents of fish accumulation from Paleolithic contexts in Western and Central Europe.

**Research question 1**: Can aquatic ecosystems and paleoenvironments be reconstructed using fish remains in archaeological contexts? What is the relationship between the human communities and the environmental conditions they were facing?

**Research question 2**: Researchers commonly recover fish remains from Paleolithic sites that are inland caves and rock shelters. It is crucial to clarify the origin of fish assemblages. Based on taphonomic studies, could we differentiate between non-human and human agents as accumulators of fish remains?

**Research question 3:** What new evidence concerning subsistence activities during the Paleolithic in Western-Central Europe can I provide using detailed multi-spectrum studies (including spatial distribution, taphonomy, seasonality, and element representation) based on fish remains?

## Chapter 3. Results and Discussion

Based on my results (**Appendix 1** to **6**) and previous available records from other Paleolithic contexts (**Supplementary Material, Tables 1** and **2**), I observed different fish associations and an apparent increase of sites yielding fish assemblages during the Upper Paleolithic (**Figure 3**), in agreement with other researchers (e.g. Stephens and Krebs, 1986; Pianka, 2000; Stiner et al., 2000; Stiner, 2001; Stiner and Munro, 2002; Hockett and Haws, 2009; Cochard et al., 2012; Manne et al., 2012; Starkovich et al., 2018; Aura-Tortosa et al., 2019; Marín-Arroyo et al., 2023).

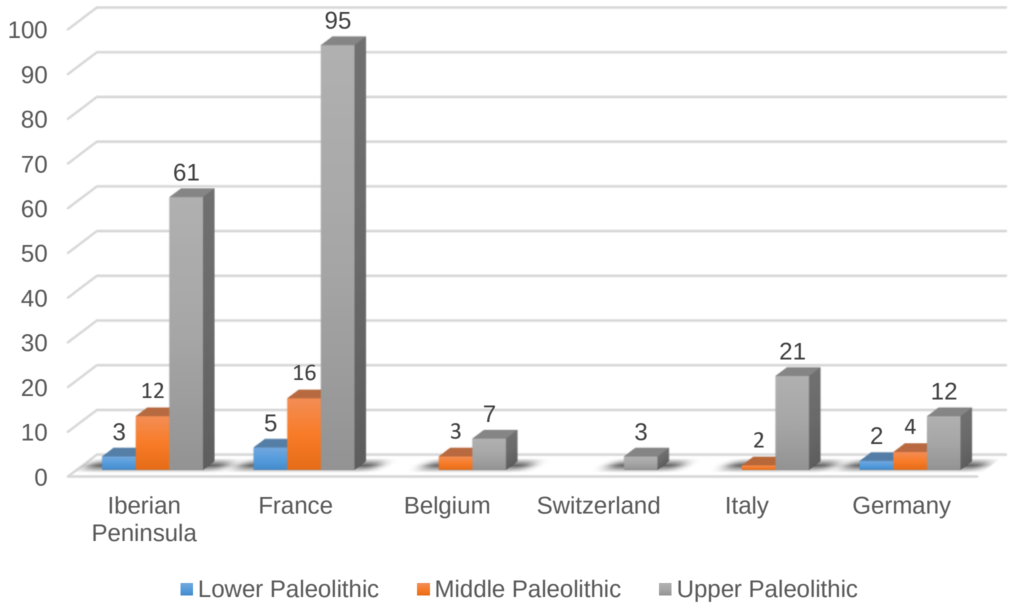

**Figure 3**. Western-Central European sites/deposits yielding fish remains by region/country and period. This record includes fish assemblages with an anthropogenic and a non-antrhopogenic origin of accumulation.

From the geographical distribution point of view, my studies confirm that fish species from the Paleolithic follow their modern distribution in Western-Central Europe (e.g. Doadrio et al., 2011; Füllner et al., 2016; Agustí et al., 2015; Blanco-Lapaz et al., 2021a-b, Blain et al., 2022; Luzi et al., 2022b, Blanco-Lapaz et al., 2023), indicating that, generally, the fish assemblages reflect the natural fish populations around the archaeological sites.

| **Taxa** | **Lower Paleolithic** | | | | **Middle Paleolithic** | | | | **Upper Paleolithic** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IB | FBS | GE | IT | IB | FBS | GE | IT | IB | FBS | GE | IT |
| *Thymallus thymallus* | | | | | | + | +* | | | + | + | |
| *Salmo trutta* | +* | + | + | | + * | + | + * | + | + | | | + |
| *Salmo salar* | | | | | + | + | | | + * | | | |
| *Salvelinus alpinus* | | + | | | | | | | | + | + | |
| *Salmo sp.* | + | | | | + * | + | | | + * | | | |
| *Hucho hucho* | | | | | | | + * | | | | + | |
| *Coregonus sp.* | | | | | | | + | | | + | | |
| *Lota lota* | | | + | | | + | + * | | | + | + | |
| *Silurus glanis* | | | | | | | | | | +? | | |
| *Anguilla anguilla* | + | + | | | + * | + | | + | + | | | |
| *Cottus gobio* | | | | | | + | + * | | | | + | |
| *Esox lucius* | | + | + | | | + | + * | + | | + | | |
| *Squalius* cf. *pyrenaicus* | * | | | | | | | | | | | |
| *Squalius* cf. *cephalus* | * | | | | | | | | | | | |
| *Leuciscus cephalus* | | | | | | + | + * | | | | + | |
| *Phoxinus phoxinus* | | | | | | + | + | | | | | |
| *Chondrostoma nasus* | | | | | | | + * | | | | + | |
| *Vimba vimba* | | | | | | | + | | | | | |
| *Barbatula barbatula* | | | | | | + | + | | | | | |
| *Chondrostoma polylepis* | | | | | + | | | | | | | |
| *Leuciscus leuciscus* | | | | | | | + | | | | | |
| *Luciobarbus cf. sclateri* | * | | | | | | | | | | | |
| *Luciobarbus cf. bocagei* | * | | | | | | | | | | | |
| *Squalius* sp. | | | | | + * | | | + | | | | |
| *Barbus* sp. | | | | | + | + | | | | | | |
| *Barbus barbus* | | + | | | | | | | + | | + | |
| *Barbus plebejus* | | | | | | | | | | | | + |
| *Tinca tinca* | | | + | | | | | | | + | | |
| *Carassius carassius* | | | + | | | | | | + | | | |
| *Rutilus rutilus* | | | + | | | + | | | | + | | |
| *Rutilus frisii* | | | | | | | | | | | + | |
| *Scardinius erythrophthalmus* | | | + | | | | | | | | | |
| *Leucaspius delineatus* | | | + | | | | | | | | | |
| *Alburnus alburnus* | | | + | | | | | | | | | |
| *Perca fluviatilis* | | + | + | | | + | | | | + | | |
| *Misgurnus fossilis* | | | + | | | | | | | | | |
| *Gasterosteus aculeatus* | | | + | | | | | | | | | |
| *Gobio gobio* | | | + | | | | | | | | | |
| *Gymnocephalus cernuus* | | | | | | | | | | | + | |
| *Pungitius pungitius* | | | + | | | | | | | | | |
| *Zingel zingel* | | | | | | | + | | | | | |
| *Acipenser sp.* | | | | | | | + | | | | | |
| *Acipenser sturio* | | | | | | + | | | | | | |
| *Alosa* sp. | | | | | + | + | | | | + | | |
| *Alosa alosa* | | | | | | | | | + | | | |
| Cyprinidae | + | + | + | | + * | + | + | + | + | + | + | + |
| Salmonidae | + | + | + | | + | + | + | + | + | + | + | + |

**Table 1.** Freshwater and anadromous families, genera, and species of fish recovered from Paleolithic Western-Central European sites based on both previously published work (+) and my studies (*). IB, Iberian Peninsula; FBS, France, Belgium, Switzerland; GE, Germany; IT, Italian Peninsula.

| **Taxa** | **Lower Paleolithic** | | | | **Middle Paleolithic** | | | | **Upper Paleolithic** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IB | FBS | GE | IT | IB | FBS | GE | IT | IB | FBS | GE | IT |
| *Melanogrammus aeglifinus* | | | | | | | | | + * | | | |
| *Trisopterus minutus* | | | | | | | | | + | | | |
| Labridae | | + | | | | | | | | + | | |
| *Labrus merula* | | | | | | | | | + | | | |
| Pleuronectidiae | | | | | + | | | | | | | |
| *Platichtys flesus* | | | | | | | | | + | | | |
| *Solea* sp. | | | | | | | | | + | | | |
| Sparidae | | + | | | + | | | | + | + | | |
| *Diplodus sargus/vulgaris* | | | | | + | | | | | | | |
| *Diplodus vulgaris* | | | | | | | | | + | | | |
| *Sparus aurata* | | | | | + | | | | + | | | + |
| *Pagellus erythrinus* | | | | | | | | | + | | | |
| *Pagellus pagrus* | | | | | | | | | + | | | |
| *Phycis* sp. | | | | | | | | | + | | | |
| *Belone* | | | | | | | | | + | | | |
| *Trachurus trachurus* | | | | | | | | | | | | |
| *Alosa* sp. | | | | | + | + | | | | | | |
| Clupeidae | | | | | + | | | | | | | |
| *Conger conger* | | | | | + | | | | | | | |
| *Trachurus trachurus* | | | | | | | | | + | | | |
| *Dentex gibosus* | | | | | | | | | + | | | |
| *Epinephelus guaza* | | | | | | | | | + | | | |
| *Blennius* sp. | | | | | | | | | + | | | |
| Elasmobranchii (sharks) | | | | | | | | | + | | | |
| *Raja* sp. | | | | | | | | | + | + | | |

**Table 2.** Marine families, genera, and species of fish recovered from Paleolithic Western-Central European sites based on both previously published work (+) and my studies (*). IB, Iberian Peninsula; FBS, France, Belgium, Switzerland; GE, Germany; IT, Italian Peninsula.

## 3.1. Lower Paleolithic

My studies in Barranco León (**Appendix 1**; **Figure 4**; Blanco-Lapaz et al., 2015; Agustí et al., 2015; Blain et al., 2016) described the presence of several endemic cyprinid species such as Bocage barbel (*L*. cf. *bocagei*), Andalusian barbel (*L.* cf. *sclateri*), and Pyrenian chub (*S*. cf. *pyrenaicus*; **Table 1**) and based on more recent studies, also gobids (Přikryl et al. 2022).

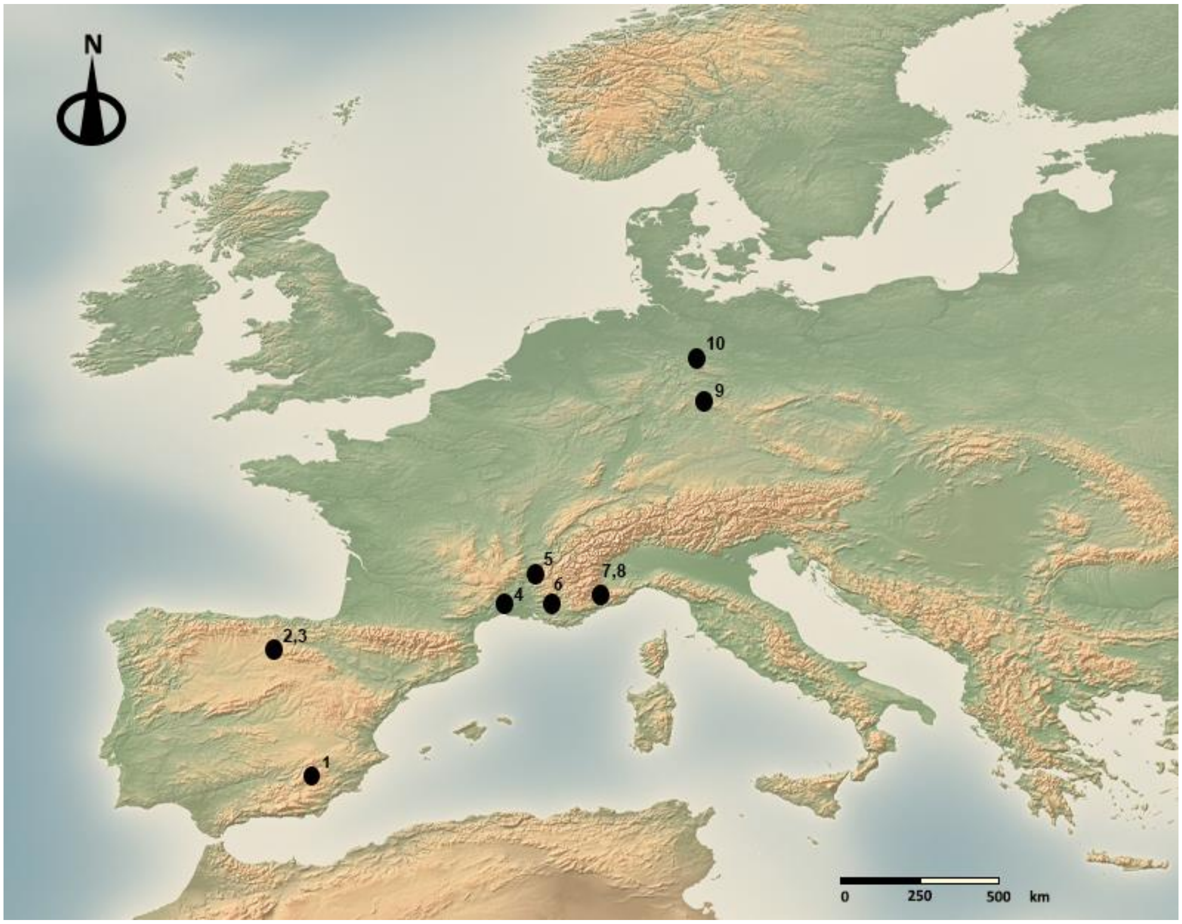

**Figure 4.** General locations of Western-Central European Lower Paleolithic sites with fish remains: 1. Guadix-Baza basin (Granada, Spain), 2. Gran Dolina (Sierra de Atapuerca, Burgos Spain), 3. Sima del Elefante (Sierra de Atapuerca, Burgos, Spain), 4. Grottes du Mas de Caves (Occitanie, France) 5. Durfort (Bourdieu, France), 6. Orgnac (Auvergne-Rhone-Alpes, France), 7. Lazaret (Alpes-Maritimes, France), 8. Grotte du Vallonnet (Alpes-Maritimes, France). 9. Bilzingsleben (Thuringia, Germany), 10. Schöningen (Niedersachsen). Modified from Natural Earth 2.

Those taxa indicate high temperatures, dissolved oxygen, and salinity tolerances compatible with a seasonal saline lake characterized by low-running waters (Doadrio and Casado, 1989). This record is consistent with previous interpretations and paleoenvironmental reconstructions of the Guadix-Baza Basin since researchers described this area as an endorheic continental basin with the presence of fauna associated with a paleolake denominated Baza Lake (Anadón et al., 1994; Martínez-Navarro et al., 2003, 2010; Anadón et al., 2015; Anadón and Gabàs, 2009; Blain, 2005, 2009; Blain and Bailon, 2010; Bailon, 2010; Abbazi, 2010; Blain et al., 2011, 2016; Oms et al., 2016; Sánchez-Bandera et al., 2020; Titton et al., 2021; Barsky et al., 2021). In addition, my studies indicate no evidence of digestion or gnawing marks, suggesting natural mortality and accumulation *in situ*, probably during very harsh conditions (Přikryl et al., 2016, 2022).

Moving to northern Iberia (Gran Dolina), I described more cold-temperate fish species, such as brown trout (*S. trutta*) and common European eel (*A. anguila*) during the Lower Paleolithic (**Appendix 2**, Blanco-Lapaz et al., 2021a). Nevertheless, the record also indicates the presence of cyprinids, mostly in layers TD6-1 and TD6-3. This observation suggests sporadic warmer-temperate peaks (between 10 and 25ºC) during the Lower Paleolithic at this site (Doadrio et al., 2011; Tissot and Souchon, 2010; Blanco-Lapaz et al., 2021a). Those data indicate a difference in temperatures and freshwater ecosystems between the southern (warmer and drier conditions) and the northern Iberian Peninsula (more cold-temperate environment).

The presence of both brown trout (*S. trutta*) and common European eel (*A. anguilla*) is only observed in the northern region of Iberia (Aguirre, 1995; Cuenca-Bescós et al., 1997; Huguet et al., 2015; Blanco-Lapaz et al., 2021a) and France (Desse and Granier, 1976; Cleyet-Merle, 1990; **Table 1**, **Figure 4**, **Supplementary Material**). Salmonids are the most common taxa in mostly Lower Paleolithic sites of Western-Central Europe except Barranco León, where they are not present. In general, the second most represented taxon in Lower Paleolithic contexts is cyprinids (**Table 1**, **Figure 4**, **Supplementary Material**; Desse and Granier, 1976; Cleyet-Merle, 1990; Aguirre, 1995; Cuenca-Bescós et al., 1997; Böhme, 1998, 2015; Huguet et al., 2015; Blanco-Lapaz et al., 2021a).

A broad predator spectrum is present in Paleolithic sites, such as humans, birds of prey, and carnivores. In Gran Dolina, my taphonomy analysis described the Eurasian eagle owl (*B. bubo*) as the most probable agent of fish accumulation (**Appendix 2**; Blanco-Lapaz et al., 2021a) based on their specific taphonomic signal (predator category three; Andrews, 1990; Rambaud, 2004; Fernández-Jalvo et al., 2016; Guillaud et al., 2018), coinciding with previous studies on Paleolithic archaeological contexts (Le Gall, 1999; Sanchís-Serra, 2000; Laroulandie, 2002; Rambaud, 2004; Rambaud and Laroulandie, 2009; De Cupere et al., 2009; Russ, 2010a; Guillaud et al., 2018; Lebreton et al., 2020). Although previous authors observed a broad spectrum of prey (Blasco et al., 2011) and wild plant consumption (Allué et al., 2015) by hominids at Gran Dolina, my results determined that fish were not part of the human diet during the Lower Paleolithic in this site.

Moving to other Lower Paleolithic sites in Western-Central Europe, Huguet et al. (2015) described the white-tailed sea eagle (*Haliaeetus albicilla*) as the principal accumulation agent of the fish remains at Sima del Elefante (Sierra de Atapuerca, Iberian Peninsula; **Table 1**, **Figure 4, Supplementary Material**). In France, Desse and Granier (1976) described a natural accumulation of fish assemblages at Lazaret, Organic, and Durfort (**Table 1, Figure 4**). The authors also recovered mainly remains of salmonids such as brown trout (*S. trutta*) and char (*Salvelinus* sp.), common European eel (*A. anguilla*), and cyprinids such as common barbel (*Barbus barbus*). Later, Cleyet-Merle (1990) enlarged the number of fish assemblages from other Lower Paleolithic sites by publishing those found in Grotte du Vallonnet and Grottes du Mas de Caves (**Table 1**, **Figure 4**), indicating also a non-anthropogenic origin of the fish assemblage. In Central-Northern Germany, two important Lower Paleolithic sites stand out. Bilzingsleben (Thuringia, **Figure 4**) Schöningen (Niedersachsen; **Figure 4**; **Table 1**). In both cases, cyprinids are the most represented taxa on the assemblages, followed by burbot (*L. lota*) and salmonids, among others (Böhme, 1998, 2015), and the authors described no evidence of anthropogenic fish accumulation, suggesting a natural deposit.

In conclusion, my results in both sites, Barranco León and Gran Dolina, are similar to previous studies in other archaeological contexts (e.g. Desse and Granier, 1976; Cleyet-Merle, 1990; Böhme, 1998, 2015; Huguet et al., 2015), suggesting no evidence of anthropogenic exploitation of fish during the Lower Paleolithic in Central and Western Europe.

On the other hand, outside Europe, previous authors noticed that during the Early Stone Age in sites such as Gogo Falls, White Paintings, Ishango, Kom Ombo, Khor Musa, Wadi Kubbaniya, and Isna (East Turkana and Olduvai Gorge), hominins sporadically exploited fish, mainly catfish (*Clarias* sp.) and tilapias (Cichlidae; Howel et al., 1987; Stewart, 1989, 1994). Moving to the Levant, Zohar et al. (2022) described fish exploitation by hominids at Gesher Benot Ya'aqov (Israel) during the Lower Paleolithic. At this site, archaeologists observed that humans fished and cooked mainly large-size individuals of two species of cyprinids, the Jordan barbel (*Luciobarbus longiceps*) and the Jordan himri (*Carasobarbus canis*). In addition, archaeologists also recovered catfish (*Clarias* sp.) and tilapias (Cichlidae).

It has been described by Antón et al. (2002) that changes in the ecosystem structure could have caused changes in foraging and diet, which in turn, promoted the dispersal of *Homo erectus* from Africa since several African/ Levantine sites were located close to freshwater habitats, which could have been a possible dispersal route for hominins (e.g. Antón et al., 2002; Zohar et al., 2022). These aquatic habitats provided abundant and stable food sources, which could have been easily acquired without advanced technology.

In this context, researchers described the sporadic fish exploitation in the African and Levantine sites, being no evidence of anthropogenic fish accumulation in Western and Central European sites, suggesting the presence of different factors that probably played a role in Africa/Levant for the incorporation of the fish as part of the hominin diets. I could propose that one factor would be the presence of catfish (*Clarias* sp.) and tilapias (Cichlidae), taxa not present in the European sites during the Lower Paleolithic. Following the optimal foraging theory, and being high-ranked preys, previous authors suggested that these taxa were more accessible to catch during spawning or lethargy seasons with no specific tools (e.g. Howel et al., 1987; Stewart, 1989, 1994).

### 3.2. Middle Paleolithic

Comparing fish associations of Middle Paleolithic in Southern Germany and the Iberian Peninsula, I observed a higher number of species in the first region (Hohlenstein-Stadel; **Appendix 4**; Blanco-Lapaz, 2019; Blanco-Lapaz et al., 2021b and Hohle Fels; **Appendix 5**; Luzi et al., 2022b) than in Iberia (Gran Dolina; **Appendix 2**, Blanco-Lapaz et al., 2021a; and Navalmaíllo rock shelter; **Appendix 3**; Blain et al., 2022). Based on my results, the grayling (*T. thymallus*) is the most common species in the Swabian Jura sites, followed by the burbot (*L. lota*). Bullhead (*C. gobio*) and cyprinids are also present in both sites (Blanco-Lapaz et al., 2021b; Luzi et al., 2022a-b; **Table 1**). Northern pike (*E. lucius*), Danubian salmon (*H. hucho*) and brown trout (*S. trutta*) completed the list in Hohle Fels (Luzi et al., 2022a-b). Previously, researchers recovered similar fish associations from other Middle Paleolithic deposits in this region, such as Kogelstein and Geißenklösterle (Böttcher et al., 2001; Conard et al., 2013; Böhme, 2019; **Supplementary Material**, **Figure 5**).

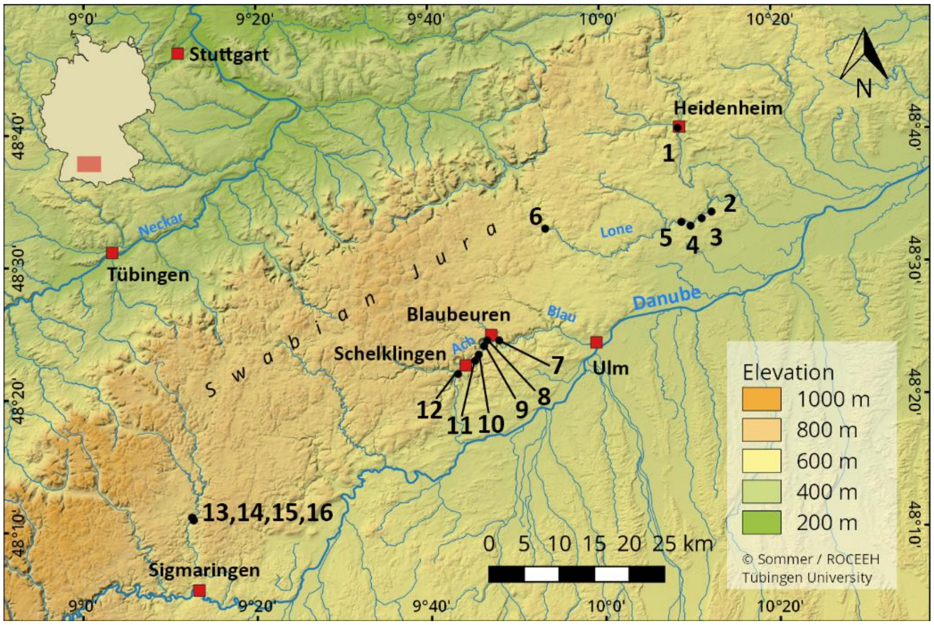

**Figure 5.** General location of the MP Swabian Jura sites. 1. Heidenschmiede, 2. Langmahdhalde, 3. Vogelherd, 4. Hohlenstein-Stadel, 5. Bockstein, 6. Haldenstein, 7. Große Grotte, 8. Brillenhöhle, 9. Geißenklösterle, 10. Sirgenstein, 11. Hohle Fels, 12. Kogelstein, 13. Annakapelienhöhle, 14. Göpfelsteinhöhle, 15. Schafstallhöhle, 16. Nikolaushöhle. Modified from © Sommer/ROCEEH Universität Tübingen.

In the Middle Paleolithic sequences of Hohle Fels, I observed the occurrence of cyprinids such as the nase (*C. nasus*) and the common chub (*L. cephalus*) in GHs 15-13 (MIS 5 layers). On the other hand, during MIS 3-4 (GHs 12-9), those taxa disappear, suggesting more temperate-warm water conditions during MIS 5 (Tissot and Souchon, 2010; Doadrio et al., 2011; Tissot and Souchon, 2010; Füllner et al., 2016). This data supported the paleo-environmental and -climatic reconstructions based on small mammals, indicating a more temperate setting during MIS 5 (**Appendix 5**; Luzi et al., 2022b)

At Hohle Fels, both small mammals and fish remains display two significant climatic oscillations: the first one, more temperate, during MIS 5, corresponding to relatively high-intensity Neanderthal occupations, and a second one, during MIS 3-4, colder and more arid, characterized by low-intensity Neanderthal occupations and harsher conditions (Luzi et al., 2022b). I observed the same in the Middle Paleolithic layers of Hohlenstein-Stadel, where cyprinids are exclusively in layers F and E, which points to a more temperate environment. Ziegler (2019) indicated a relative decrease in the tundra environment in both layers based on the recovered micromammal species. Micromammals and cyprinids could point to a likely interstadial condition during the sedimentation of these layers at Hohlenstein-Stadel (**Appendix 4**; Blanco-Lapaz et al., 2021b).

Outside the Swabian Jura, in Bavaria (**Figure 6**), Bötcher (2001) also described the presence of bullhead (*C. gobio*), grayling (*T. thymallus*), and burbot (*L. lota*) at Höhlenruine Hunas. Böttcher (2014) described the same taxa in association with northern pike (*E. lucius*), Danubian salmon (*H. hucho*), nase (*C. nasus*), and the common chub (*L. cephalus*) at Sesselfelsgrotte VI. In addition, Böttcher (2014) indicated that the high diversity and small size of the Sesselfelsgrotte VI assemblage and the taphonomy could indicate a non-anthropogenic origin of the fish accumulation.

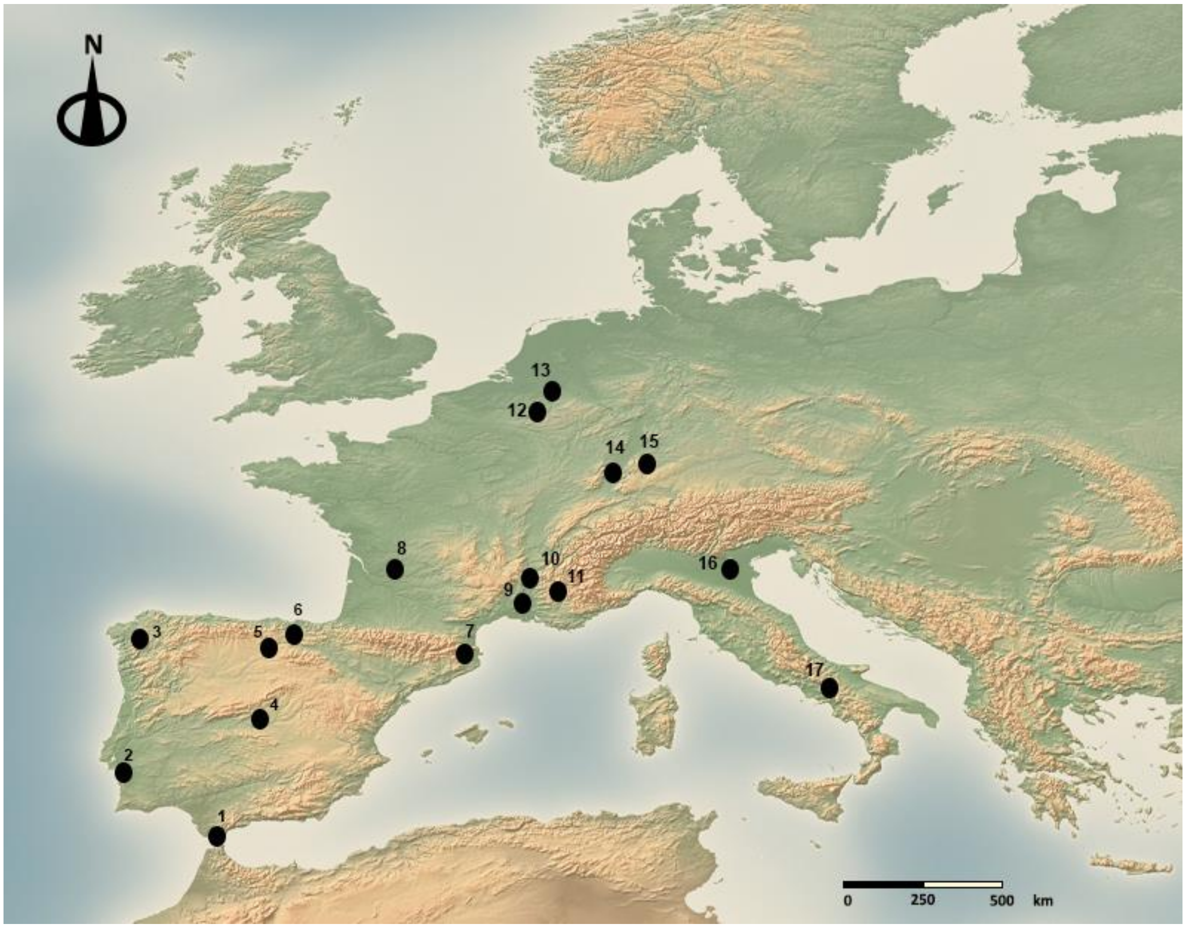

**Figure 6.** General location of the Middle Paleolithic sites with fish remains from Western-Central Europe. Iberian Peninsula: 1. Gibraltar (Vanguard Cave), 2. Figueira Brava Cave, 3. Eirós Cave, 4. Navalmaíllo rock shelter, 5. Sierra de Atapuerca (Gran Dolina, Sima del Elefante, Sima de Los Huesos), 6. Caves of Tito Bustillo, del Castillo, Millán, and Amalda, 7. Arbreda and Ermitons caves. France: 8. Vaufrey Cave, 9. Baume Moula-Gercy, 10. Barrasses II Cave, 11. Abri des Pécheurs. Belgium: 12. Walou Cave, 13. Marie-Jeanne Cave. Germany: 14. Swabian Jura sites, 15. Baviera (Höhlenruine Hunas and Sesselfelsgrotte VI). Italy: 16. Riparo del Broion and 17. Castelcivita. Modified from Natural Earth 2.

In my studies of Iberian sites (Gran Dolina and Navalmaíllo rock shelter; **Appendix 2** and **3**; Blanco-Lapaz et al., 2021a; Blain et al., 2022), I described assemblages dominated by the brown trout (*S. trutta*).

In both Iberian and Swabian Jura sites (Blanco-Lapaz, 2019; Blanco-Lapaz et a., 2021a-b; Blain et al., 2022; Luzi et al., 2022b), I observed that salmonids dominate the fish associations, following previous studies in the Iberian Peninsula sites such as the caves of Cova Eirós, Tito Bustillo, del Castillo, Millán, Amalda, Arbreda, and Ermitons (Roselló-Izquierdo and Morales-Muñiz, 2005; Rey-Rodríguez et al., 2016; **Figure 6**), and the Swabian Jura sites such as Hohle Fels and Geißenklösterle (Conard et al., 2013; Böhme, 2019; **Figure 5** and **6**). My results also are similar to other locations, such as the French and Belgian sites of Vaufrey Cave, Baume Moula-Gercy, Barrasses II Cave, Abri des Pécheurs, Walou Cave, and Marie-Jeanne Cave (Van Neer and Wouters, 2010; Hardy et al., 2013; Guillaud et al., 2021; **Figure 6**) and the Italian site of Castelcivita (Cassoli et al., 1997; Russ, 2010b; **Figure 6**). Riparo del Broion (Italy) represents an exception since researchers only identified remains of northern pike (*E. lucius*) and cyprinids (Romandini et al., 2023).

The associations of the brown trout (*S. trutta*) and common European eel (*A. anguilla*) in Iberian sites (Gran Dolina and Navalmaíllo rock shelter; **Appendix 2** and **3**; Blanco-Lapaz et al., 2021a; Blain et al., 2022), and the grayling (*T. thymallus*), Danube salmon (*H. hucho*), burbot (*L. lota*), and bullhead (*C. gobio*) in the Swabian Jura (Hohle Fels and Hohlenstein-Stadel), are typical of the salmonids zones (Huet, 1949, 1954; Doadrio et al., 2011), indicating permanent, oxygen-rich, and relatively cold running waters (**Appendix 4** and **5**; Blanco-Lapaz et al., 2021b; Luzi et al., 2022b). Previous studies based on herpetofauna, birds, and mammals also support the indication of presence of well-developed freshwater ecosystems in Gran Dolina and Navalmaíllo rock shelter (Marco-Sánchez, 1999; Bochenski, 2007; Rofes et al., 2009, 2011; Rey-Rodríguez et al., 2016; Moya-Costa et al., 2019; Moya-Costa et al., 2019; Blanco-Lapaz et al., 2021a; Blain et al., 2022), and in Hohle Fels and Hohlenstein-Stadel (Conard et al., 2013; Ziegler, 2019; Bertacchi et al., 2021; Beattie, 2022).

The presence of similar freshwater ecosystems around the archaeological contexts in the Iberian Peninsula and the Swabian Jura (and other central European regions such as France and Belgium) during the Middle Paleolithic is relevant because it would suggest that any incorporation of fish as part of the human diet would not be dictated by different aquatic habitat or resources. Still, it must be related to other factors such as population pressure, changes in the technology used to fish, or regional decries of the high-ranked animal species.

Knowing the accumulation agent of fish remains in archaeological sites is crucial to avoid problems when interpreting the hominin diet. In this context, I observed that in the Middle Paleolithic layers of Gran Dolina (Atapuerca, Spain; Blanco-Lapaz et al., 2021a; **Appendix 2**) and Navalmaíllo rock shelter site (Pinilla del Valle, Spain; Blain et al., 2022; **Appendix 3**), the main accumulation agent was the European eagle owl (*B. bubo*), based on his specific signature (**Appendix 2** and **4**; Blanco-Lapaz et al., 2021a; Blain et al., 2022).

My results emphasize the underestimation of non-human faunas' role in the fish's deposition in both Middle Paleolithic archaeological contexts. Previously, researchers observed a broad spectrum of resources in the human diet during the Middle Paleolithic in Gran Dolina (layers TD10), indicating the exploitation of large game joined with fast-moving small game such as rabbits (Blasco et al., 2013). However, my taphonomic studies at those layers exclude the fish as a food resource for the hominids at this site (**Appendix 2**; Blanco-Lapaz et al., 2021a). The accumulation of fish by the European eagle owl (*B. bubo*) at Navalmaíllo rock shelter also disagrees with previous studies since researchers argued that the Iberian lynx (*Lynx pardinus*) was the main responsible for the accumulation of the small animals at the site (Arriaza et al., 2017).

On the other hand, moving to Hohlenstein-Stadel (Swabian Jura), since no gnawing or digestion marks are present in the fish assemblage, I conducted a preliminary spatial distribution study, observing that most fish remains were recovered from two squares (193/172 and 194/172) located in the center of the excavation area (**Figure 7**), indicating a preferential distribution of accumulation (see discussion in Rambaud et al., 2011). Additionally, and based on my estimations, it appears that the majority of grayling (*T. thymallus*) and burbot (*L. lota*) specimens are approximately 30 cm in length (**Appendix 4**, Blanco-Lapaz et al., 2021b).

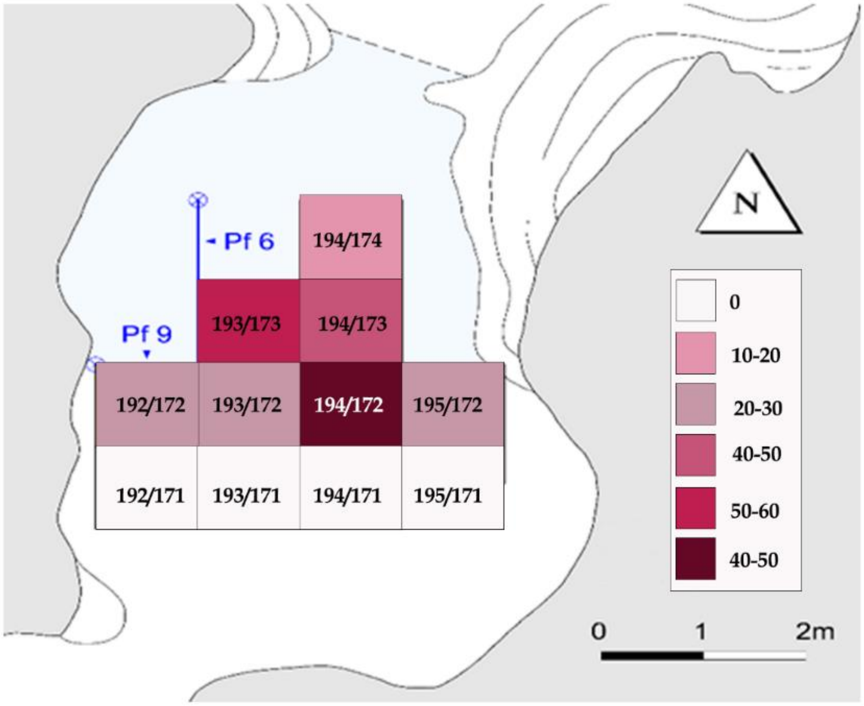

**Figure 7.** Hohlenstein-Stadel. The distribution map of fish remains based on NISP. Pf, profiles 6 and 9. Modified from Kind (2019).

At this site, based on my seasonality studies, I detected that most of the grayling scales indicated a death season for the grayling (*T. thymallus*) of spring/summer-beginning fall (**Appendix 4**; Blanco-Lapaz et al., 2021b), excluding deaths during winter, the most common season for natural death due to decreased food availability (Barret 1997; Roselló-Izquierdo and Morales-Muñiz 2005; Doadrio et al. 2011). These data and the abundance of scales probably indicate the fish processing by humans through the removal of scales for consumption at this site (**Appendix 4**, Blanco-Lapaz et al., 2021b).

Neanderthals in Hohlenstein-Stadel exploited mainly ungulates (Kitagawa, 2014, 2019; **Figure 8**), incorporating sporadically fish (mainly medium-large individuals of grayling and burbot) into their diets (Blanco-Lapaz et al., 2021b) during the most common hunting season of large game, spring-summer (Kitagawa, 2014, 2019).

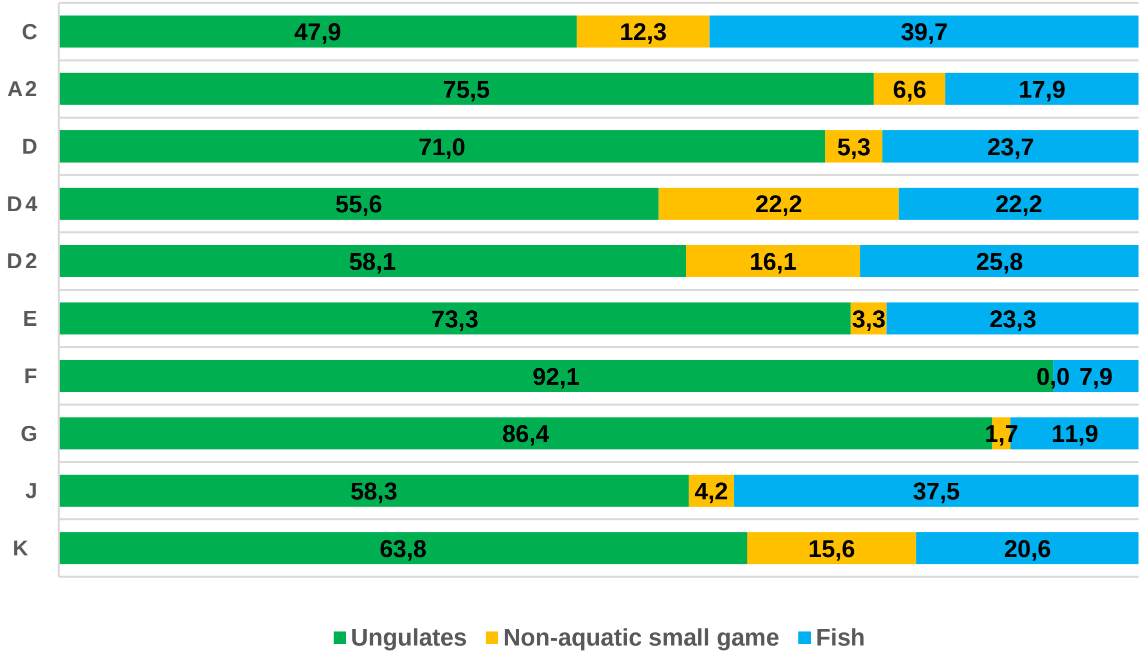

**Figure 8.** Hohlenstein-Stadel. Prey representation (%) in Middle Paleolithic layers for ungulates, non-aquatic fast-moving small game and fish (aquatic and fast-moving small game), based on NISP.

My results at Hohlenstein-Stadel support previous studies mentioning a more diversified Neanderthal diet including aquatic resources and fish (Antunes, 1991; Stiner, 1993, 2013; Cassoli et al., 1997; Henshilwood and Marean, 2003; Roselló-Izquierdo and Morales-Muñiz, 2005; Stringer et al., 2008; d'Errico et al., 2009; Van Neer and Wouters, 2010; Cortes-Sánchez et al., 2011; Marean, 2014, 2015; Villa and Roebroeks, 2014; Roebroeks and Soressi, 2016; Zilhão et al., 2010, 2020; Villa et al., 2020; Guillaud et al., 2021; Blasco et al., 2022; Nabais et al., 2023; Romandini et al., 2023) and add broader dimensions to our understanding of the role of fish resources in the subsistence of the Neanderthals in the Swabian Jura and, by extension, the rest of Western-Central Europe.

Based on those previous studies, we can distinguish two different fish exploitation groups in Neanderthal locations: 1. Inland sites such as Ermitons, and Arbreda caves (Iberian Peninsula), Walou Cave (Belgium), Vaufrey Cave, Baume Moula-Gercy, Barrasses II Cave, and Abri des Pécheurs (France), and Caselcivita and Riparo del Broion caves (Italy) with freshwater exploitation (**Table 1**; **Figure 6**; Cassoli et al., 1997; Izquierdo and Morales-Muñiz, 2005; Van Neer and Wouters, 2010; Guillaud et al., 2021; Romandini et al., 2023) and 2. Coastal sites such as Tito Bustillo, Millán, del Castillo, Amalda, Figueira Brava, and Vanguard caves (all of them located in the Iberian Peninsula), with the presence of marine species (**Table 1**; **Figure 6**; Izquierdo and Morales-Muñiz, 2005; Stringer et al., 2008; Brown et al., 2011; Zilhão et al., 2020). My study of the fish assemblage of Hohelnstein-Stadel (**Appendix 4**; Blanco-Lapaz et al., 2021b) indicates that the fish exploitation in this site was exclusively based on freshwater species, integrating this context as part of the inland sites in Western-Central Europe.

Therefore, we can say that, in terms of aquatic resource exploitation, Neanderthals fished/caught the species present close to their camps. Their subsistence strategies and diet were directly dependent on the close surroundings such as seafood (Roselló-Izquierdo and Morales-Muñiz, 2005; Stringer et al., 2008; Zilhão et al., 2010, 2020; Brown et al., 2011; Nabais et al., 2023; Romandini et al., 2023) or inland resources exploitation (Roselló-Izquierdo and Morales-Muñiz, 2005; Van Neer and Wouters, 2010; Guillaud et al., 2021; Blanco-Lapaz et al., 2021b), using nearby patches and following the patch model (MacArthur and Pianka, 1966).

### 3.3. Upper Paleolithic

In Fuente del Salín Cave, I observed an evident abundance of fish remains, followed by the slow-moving small game (molluscs; Gutiérrez-Zugasti et al., 2011, 2012) and large game (Blanco-Lapaz et al., 2023; **Figure 9**).

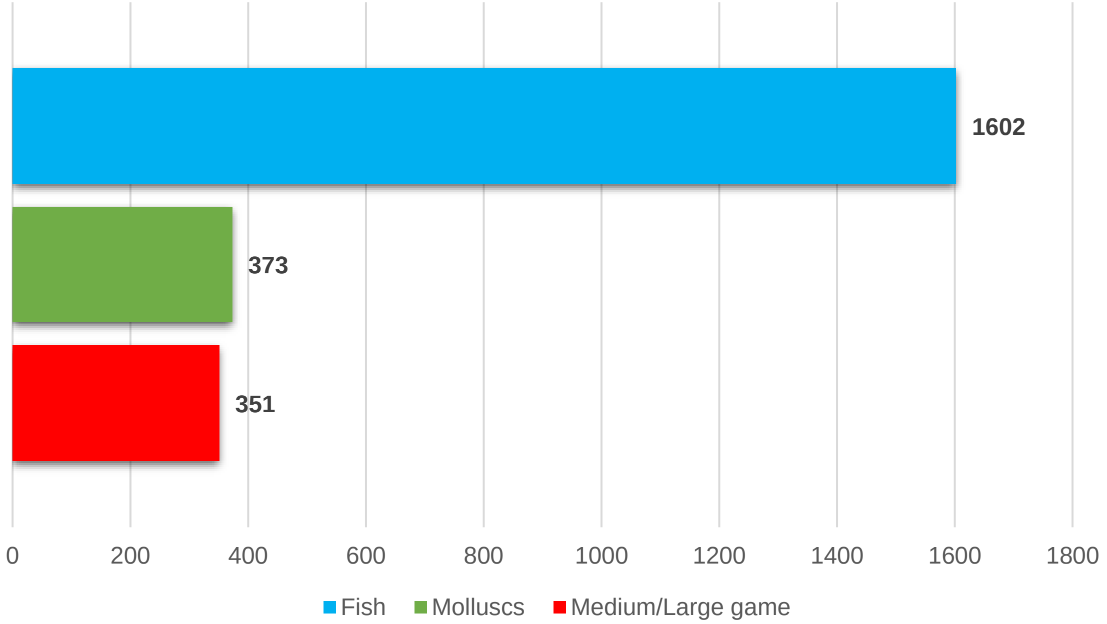

**Figure 9.** Fuente del Salín Cave. Preys in Gravettian level 2. NISP for medium/large game, fish (fast-moving small game), and molluscs (slow-moving small game). Based on Table 4 (Blanco-Lapaz et al., 2023).

The fish assemblage of Fuente del Salín Cave is characterized by a mixture of freshwater/anadromous taxa such as *Salmo* sp. and cyprinids, and marine species such as the haddock (*M. aeglifinus*; **Appendix 6**; Blanco-Lapaz et al., 2023). Based on these taxa, I reconstructed the aquatic landscape around the site, characterized by cold waters, since, for example, the haddock (*M. aeglifinus*) mostly prefers a range of temperatures between 4 to 10 ºC (Withehead et al., 1986). Previously, archaeologists also observed this mixture during the Upper Paleolithic in several sites of the Cantabrian and Southeast regions such as Chufín, Hornos de la Peña, El Castillo, El Pindal, La Cuevona, El Otero, La Chora, Coímbre B, El Mirón, Aitzbitarte III, Cobrante Cave, Nerja, Ambrosío, and Gorham's Cave (Straus, 1983a, Morales-Muñiz et al., 1994; Rodrigo, 1994; Roselló-Izquierdo et al., 1995, 2017; Pokines, 1998, Morales-Muñiz and Roselló-Izquierdo, 2004, 2008; Carrión et al., 2008; Pere and Doadrio, 2009; Adán et al., 2009; Gabriel and Béarez, 2009; **Figure 10**).

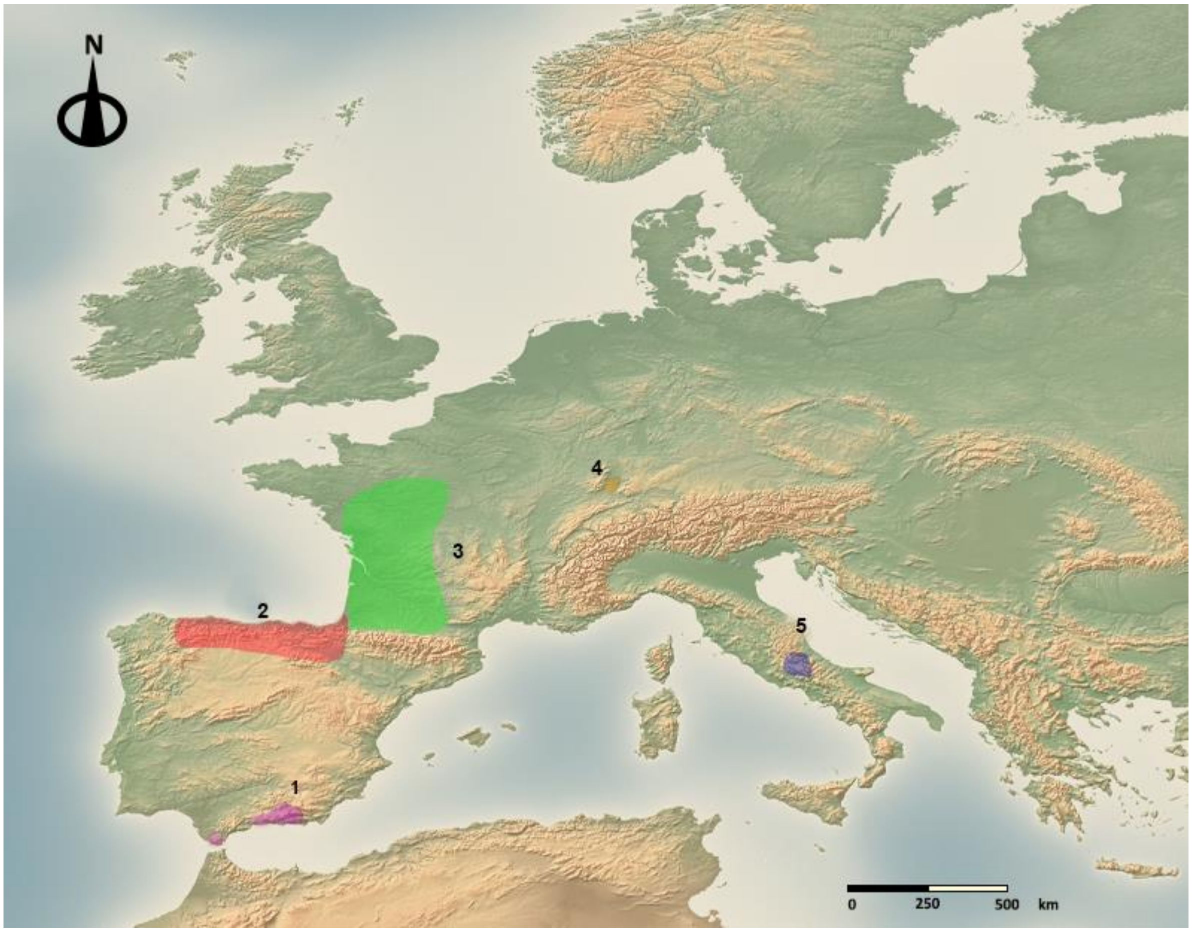

**Figure 10.** General location of the main Upper Paleolithic areas from Western-Central Europe with fish remains. Iberian Peninsula: 1. Southeast Region (Nerja, Ambrosío, Gorham), 2. Cantabrian Region (Altamira, El Juyo, La Garma A, El Castillo, Rascaño, Fuente del Salín, Chufín, Hornos de la Peña, El Pindal, La Cuevona, El Otero, La Chora, Coímbre B, El Mirón, Aitzbitarte III, Cobrante). France: 3. Southwest Region (Grotte du Pape, Gatzarria, Pont d'Ambon, Grotte des Eyzies, Abri Pataud, Lachaud, Bevis, Les Peyrugues, Laugerie Haute, Bruniquel, Bois Ragot, Grotte de Harpons, Taillis des Coteaux). Germany: 4. Swabian Jura (Brillenhöhle, Geißenklösterle, Spitzbubenhöhle, Malerfels, Höhle Fels, Hohlenstein-Stadel, Felsställe, Buttentalhöhle, Zigeunerfels, Burghöhle). Italy: 5. Fucino Basin (Grotta delle Mura, Grotta Romanelli, Riparo Slavini, Grotta della Serratura, Riparo di Biarzo, Achille Graziani, and Riparo Soman). Modified from Natural Earth 2.

At Fuente del Salín Cave, the taphonomic analysis indicated a high fragmentation of the mammal remains. Due to this, it was not possible to classify them specifically. Additionally, fresh breaks on the bones characterized the faunal assemblage, indicating intensive exploitation of the marrow by its inhabitants (González-Echegaray de Yarto, 2020; Blanco-Lapaz et al., 2023). In addition, my studies based on the thermal discoloration stages indicated that most (75.1%) of the fish remains fit into stage 1 and were fired at temperatures between 100 and 300ºC (**Appendix 6**; Blanco-Lapaz et al., 2023). During the fall and winter seasons, the Gravettians primarily hunted large ungulates (mostly red deer, *Cervus elaphus*) and focused on fishing from fall to summer. They collected limpet shells in the spring, summer, and late fall-early winter. These findings provide valuable insight into the seasonal occupation patterns during the Gravettian at this site, indicating the high variety of prey that Fuente del Salín Cave inhabitants depended on for survival, even though their short-term occupations (**Appendix 6**; Blanco-Lapaz et al., 2023).

Based on my size body estimations, most fish in Fuente del Salín Cave correspond to large-size individuals (salmonids, 60-70 cm in total length, and haddock, more than 50 cm in total length). Previously, Russ (2010b) studied large fish in the Cantabrian Region (up to 129 cm in total length, around 22 kg), suggesting that anthropogenic agency also has played a role in fish accumulation at other Cantabrian sites such as El Juyo, Altamira, and Rascaño caves.

Consuming marine fish such as haddock (*M. aeglefinus)* suggests, for the first time during the Gravettian in the Cantabrian Region, fishing and navigation far from the coastline since this species is demersal and can be found at depths between 80 to 200 m (Withehead et al., 1986). The evidence of seafaring is still uncommon in Europe during the Paleolithic. However, several archaeological sites in the Aegean archipelago suggest the earlier development of sea crossing capability during the Paleolithic and before the Gravettian (Ferentinos et al., 2014, 2023). In addition in other parts of the world such as Indonesia (Morwood et al., 1998; O'Connell et al., 2018), the island of Flores (Brown et al., 2004), Australia and New Guinea (Balme, 2013; Clarkson et al. 2017; Kealy et al. 2018), and Red Sea (Petraglia and Rose 2009; Rose et al., 2011; Armitage et al., 2011), also indicate that during the Paleolithic, human populations traveled by sea, involving great distances, only surmountable by the use of boats or canoes (Balme, 2013; Ferentinos et al., 2014; Clarkson et al. 2017; Kealy et al. 2018; O'Connell et al. 2018).

Moving to Germany and the Swabian Jura (**Figure 10**), in the Aurignacian layers of Hohlenstein-Stadel, I observed the presence of grayling (*T. thymallus*), burbot (*L. lota*), bullhead (*C. gobio*) and chub (*S*. cf. *cephalus*; Blanco-Lapaz et al., 2021b, **Appendix 4**). Previously, several authors also observed a similar fish association in other Upper Paleolithic sites in this region, such as Geißenklösterle, Spitzbubenhöhle, Brillenhöhle, Malerfels, Höhle Fels, Felsställe, Buttentalhöhle, Zigeunerfels, and Burghöhle (**Figure 5**; Lepiksaar, 1973; Torke, 1981, 1987, 1998; Hahn, 1988; Torke, 1998; Münzel, 2001; Münzel and Conard, 2004; Böhme, 2019), and other German sites such as Gönnersdof (Rhineland; Bosinski, 1979; Street and Turner, 2013).

Based on my results from conducting MIA analysis, spring would be the most common season for fishing at this site (**Appendix 4**; Blanco-Lapaz et al., 2021b). At Hohlenstein-Stadel, studies based on large game indicate no drastic changes in the subsistence practices between the Middle Palaeolithic and the Aurignacian (Kitagawa 2014, 2019). In both periods, the large game dominated the faunal assemblage (horse and reindeer during the Middle Paleolithic and mainly reindeer during the Aurignacian). However, the fish assemblage of the Aurignacian layers is reduced (NISP=10), and I cannot determine the existence of no significant changes in fish exploitation between Middle Paleolithic and Aurignacian at this site, being further studies necessary to update those results (**Appendix 4**; Blanco-Lapaz et al., 2021b).

Archaeologists described many other Upper Paleolithic sites in Western and Central Europe yielding fish assemblages, such as in France (Grotte du Pape, Gatzarria, Pont d'Ambon, Grotte des Eyzies, Abri Pataud, Lachaud, Bevis, Les Peyrugues, Laugerie Haute, Bruniquel, Bois Ragot, Grotte de Harpons, and Taillis des Coteaux among others), Switzerland (Munroz, Champréveyres, and Hollenberg-Höhle 3), and Italy (Grotta delle Mura, Grotta Romanelli, Riparo Slavini, Grotta della Serratura, Riparo di Biarzo, Achille Graziani, and Riparo Soman, among others; **Table 1**, **Figure 10**), and in Belgium (Néviau, Grotte Walou, Frotte de la Princesse, Bois de Laterie, Trou de Chaleaux, Trou du Sureau, and Trou du Frontal).

In all sites, salmonids such as brown trout (*S. trutta*) and grayling (*T. thymallus*) are the most taxa present in the assemblages, followed by burbot (*L. lota*) and cyprinids. Additionally, other species such as pike (*E. lucius*), European perch (*P. fluviatilis*), and whitefish (*Coregonus* sp.), are also present in most of the sites mentioned before (e.g. MacCurdy, 1924; Giltay, 1931; Desse and Desse, 1976; Bosinski, 1979; Torke, 1982; Clottes et al., 1983; Straus, 1983b; Straus, 2018; Le Gall, 1984, 1992a-b, 1993, 1999, 2008; Wilkens, 1994; Van Neer, 1997; Cleyet-Merle, 1990; Muñoz and Casadevall, 1997; Célérier, 1998; Mussi et al., 2004; Albertini and Tagliacozzo, 2004; Van Neer and Wouters, 2007; Van Neer et al., 2007; Müller, 2008; Le Gall, 2008 Phoca-Cosmetatou, 2009; Russ, 2010b; Street and Turner, 2013; Müller, 2008; Guillaud et al., 2017b; **Supplementary Material**). Seasonality studies in several of these sites indicated that humans exploited fish mainly during the spring-summer (Guillaud et al., 2021).

Supporting the concept of how vital was fishing activities during the Upper Paleolithic, it is also possible to observe the presence of specific fishing artifacts such as fishhooks in the French sites of La Ferrassie, Laugerie-Basse, and Pont d’Ambon (Crawford-Burkitt, 1925; Johnstone, 1980; Chollet et al., 1980) and the German sites of Wustermark 22, Braunsbedra, and Klein Lieskow (Pasda, 2001; Gramsch et al., 2013). Additionally, harpoons made from animal bone, often bird bone, are frequently found in sites dating to the Upper Paleolithic in France (Cleyet-Merle, 1990) and Spain (Pokines and Krupa, 1997). Julien (1982) analyzed more than 1,000 harpoons from Magdalenian layers at French sites, such as Gourdan, La Madeleine, Laugerie-Basse, Mas d'Azil, and Lortet. These harpoons are often associated with abundant fish remains, suggesting fishing activities (Julien, 1982). More recently, several authors described harpoons during the Upper Paleolithic in Mediterranean area sites such as Cova de les Cendres, Foradada Cave, Tossal de la Roca, Nerja Cave, Hoyo de la Mina, and Victoria Cave (Román and Villaverde, 2012). In Central Europe, specifically in the Swabian Jura, Taller (2014) and Taller et al. (2012) also described several harpoons in Hohle Fels during the Magdalenian.

During the Upper Paleolithic, fish were also part of the imaginary and art (Dams, 1987; Cleyet-Merle, 1990; Le Gall, 2001; Guthrie, 2006). The fish images rendered in Paleolithic art are mainly of meaty-fatty species, like salmonids (Guthrie, 2006). Some examples of representations of fish range from carvings on bone and antlers to carvings and paintings on cave and rock shelter walls, such as salmonid fish in rock carvings from Niaux in France (Cleyet-Merle, 1990; Le Gall, 2001; Clottes, 2010), and the engraving of a fish identified as salmon from at Abri de Possion, also in France (White, 1986; Cleyet-Merle, 2016).

More French sites also present carvings and paintings such as Enléne, Les Eyzies, Trois Frères, Mas d'Azil, Lourdes, Montgaudier, Laugeri-Besse, Pech-Merle (Guthrie, 2006), Arcy-sur-Cure (Baffier et al., 2005), Cosquer (Clottes et al., 2005), and the Margot Cave (Berrouet et al., 2014). In Portugal, at the Magdalenian rock art sites of Côa and Fraga de Gato (Penascosa, Portugal), there are also representations of fish (Baptista et al., 1995; Zilhão, 1997; Reis, 2021). In the Iberian Peninsula, a fish carving is on the cave wall at El Pindal (Cantabrian Region). Sieveking (1991) interpreted this image with a large tail as a tunny. At the site of La Pileta Cave (southern Spain), researchers also described a Magdalenian fish paint (Barandiaran, 1964; Bicho et al., 2007).

However, fish is not only represented in non-portable art; several portable pieces of art show fish-shape images, for example, the fish-shaped scapula from El Pendo (Magdalenian) in the Iberian Peninsula (Sieveking, 1991) and the fish figures from the Magdalenian French sites of Espelugues, Isturitz Laugerie-Basse, La Madaleine and Lortet and Lourdes (Leroi-Gourhan, 1965). The Aurignacian record in Vogelherd (Swabian Jura) also offered a well studied piece of ivory that depict a fish resembling a salmonid, indicating the symbolic relevance of fish for modern humans (Conard et al., 2009). In general, most images are dominated by salmonid-type fish, although several authors have identified pike and eels, demonstrating that the makers of these images were familiar with different fish species (e.g. Cleyet-Merle, 1990; Le Gall, 2001).

Finally, archaeologists also recovered fish vertebrae in Upper Paleolithic burials as personal adornment. Some examples are several fish vertebrae discovered in Barma Grande Cave (Italy; Cleyet-Merle, 1990) with deer teeth and marine gastropods with a human skeleton. Archaeologists also recovered perforated fish vertebrae from Upper Paleolithic layers at Cave Rey (France; MacCurdy, 1924). Finally, Hahn (1988), Münzel (2001), and Münzel and Conard (2004) describe the presence of drilled and perforated fish bones from the Aurignacian layers at Geißenklösterle (Swabian Jura).

Therefore, based on the results of my study in Fuente del Salín Cave (Cantabrian Region), I observed the importance of fish exploitation in human populations during the Gravettian in this area, being in concordance with the optimality models since hunter-gatherers-fishermen exploited diverse prey (fish, molluscs, large game) and habitats (sea, rivers, open and rocky lands) in different seasons, following prey choice (Stephens and Krebs, 1986; Pianka, 2000) and patch (MacArthur and Pianka, 1969) models, probably due to several factors such as advancements in technology, regional growth of population, paleoenvironmental transformations, and changes in mobility patterns during the Upper Paleolithic in the Cantabrian Region.

These results coincide with previous observations since several authors documented the important role of fish and aquatic resources during the Upper Paleolithic in Europe through an apparent intensification in the exploitation joined land resources and the diversification of food procurement strategies, following optimality models (e.g. Payne, 1975; Stiner et al., 2000; Stiner, 2001, 2003, 2013; Munro, 2004; Speth, 2004; Hockett and Haws, 2009; Jones, 2009; Starkovich, 2011, 2014, 2018; Bicho and Esteves, 2022). In addition, researchers pointed out that during the Upper Paleolithic, and especially during the Magdalenian, the consumption of aquatic resources became a significant part of the human diet due to increased demographic pressure (e.g. Binford, 1968; Flannery, 1969).

## Chapter 4. Final remarks

This dissertation represents one of the few, if not the first, studies based on fish remains, summarizing several aspects, such as taxonomy, paleoecology, taphonomy, and fishing activities across the Paleolithic in Western and Central Europe. It considerably improved our knowledge of the role of fish during human evolution by studying assemblages from the Iberian Peninsula and southwestern German sites. Importantly, and based on my results, I can answer the research questions I mentioned in this manuscript.

**Research question 1**: Can aquatic ecosystems and paleoenvironments be reconstructed using fish remains in archaeological contexts? What is the relationship between the human communities and the environmental conditions they were facing?

Based on my results, a detailed taxonomical study of which fish species are present in one archaeological context, it is possible to reconstruct the aquatic ecosystems around the sites, differentiating between the freshwater and the marine resources. During the Lower Paleolithic, I observed a difference between south (Barranco León; endemic cyprinids, indicating warm and slow-running waters) and north (Gran Dolina; cold and running waters-related species) Iberia. In my studies based on Middle Paleolithic sites in Iberia (Gran Dolina and Navalmaíllo rock shelter) and Swabian Jura (Hohle Fels and Hohlenstein- Stadel), I observed no differences between both regions from the paleoecological point of view, characterized by cold-related fish species. Cold-related species, including coastal and marine fish, were also common during the Upper Paleolithic in the Cantabrian Region (Iberian Peninsula).

In terms of anthropogenic exploitation of fish, the similarity of aquatic ecosystems and fish associations in different Western-Central European regions probably point to other factors, such as a decrease of large game and high-ranked species or regional population pressure, and not paleoenvironmental changes, as the main elements what influence in the incorporation of fast small game, in this case, fish, as part of the human diet. Of course, we cannot exclude some affectation of the changes in the environment in archaeological contexts since, for example, my studies in Hohle Fels would indicate the coincidence of the increase of the Neanderthal presence at this site and the presence of cyprinids, which would indicate warmer conditions.

**Research question 2**: Researchers commonly recover fish remains from Paleolithic sites that are inland caves and rock shelters. It is crucial to clarify the origin of fish assemblages. Based on taphonomic studies, could we differentiate between non-human versus human agents as accumulators of fish remains?

I can summarize the parameters that help clarify this conflict based on my taphonomical studies. A wide range of sizes (primarily small animals), natural thanatocoenosis, spatial distribution like micromammals, and digestion marks characterize a non-anthropogenic accumulation of fish (in Gran Dolina and Navalmaíllo rock shelter). On the other hand, large-size individuals, similar distribution to other anthropogenic finds, the different seasons of death than in natural populations (spring-summer), and the absence of digestion and gnawing marks typify an anthropogenic accumulation (in Hohlenstein-Stadel) joined other anthropogenic signatures such as burning, high fragmentation and prey selection (in Fuente del Salín Cave).

**Research question 3:** What new evidence concerning subsistence activities during the Paleolithic in Western-Central Europe can I provide using detailed multi-spectrum studies (including spatial distribution, taphonomy, seasonality, and element representation) based on fish remains?

My detailed study indicates, for the first time in Germany, that in Hohlenstein-Stadel (Swabian Jura, Germany), Neanderthals exploited fish as sporadic food resources during the spring/summer and joined the large game contribution. This research emphasizes the importance of conducting further analyses in future excavations to comprehend Neanderthal fishing behavior better.

In addition, my results based on the fish assemblages of Fuente del Salín Cave highlight how vital this resource was as part of the human diet during the Upper Paleolithic in the Cantabrian Region (Iberian Peninsula), with the presence of a high diversity of preys (large game, molluscs, and fish), hunting areas (inland, coast, and see), and seasons, following prey choice and patch models from the optimal foraging theory.

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## Appendix 1

Agustí, J., Blain, H-A., Lozano-Fernández, I., Piñero, P., Oms, O., Furió, M., **Blanco-Lapaz, A**., López-García, J.M., Sala-Ramos, R. 2015. Chronological and environmental context of the first hominin dispersal into Western Europe: The case of Barranco León (Guadix-Baza Basin, SE Spain). Journal of Human Evolution. 87: 87-94. https://doi.org/10.1016/j.jhevol.2015.02.014

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# Chronological and environmental context of the first hominin dispersal into Western Europe: The case of Barranco León (Guadix-Baza Basin, SE Spain)

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## ABSTRACT

The early Pleistocene site of Barranco León (Guadix-Baza Basin, SE Spain), dated to 1.4 Ma (millions of years ago), records the oldest hominin occurrence in Western Europe, as evidenced by the discovery of one tooth and thousands of Mode 1 stone tools. In this paper a detailed analysis of the microvertebrate content of the D1 and D2 units from this site is presented. The early Pleistocene in the Guadix-Baza Basin is characterized by a sharp climatic deterioration, which possibly impeded the settlement of this region by the early hominin population from the southern Caucasus. Shortly afterwards, when the climatic conditions were again favorable, a hominin presence is suddenly evidenced at the units D1 and D2 of Barranco León. According to the microvertebrate analysis of these units, the mean annual temperature at the time of deposition was significantly higher than 13 °C, with prevalent humid conditions. However, although most of the species were inhabitants of water edges, an open landscape was present in the vicinity of the lake. The data reported here clearly support the idea that the early hominin occupation of Europe was strongly constrained by climatic and environmental conditions, rather than by physiography or cultural factors.

## Introduction

The early Pleistocene site of Barranco León (Guadix-Baza Basin, SE Spain) records the oldest hominin occurrence in Europe (Toro Moyano et al., 2013). This site has delivered a great number of stone tools of Mode 1 and one hominin tooth, associated with an abundant fauna of large and small vertebrates. Barranco León was first discovered in the summer of 1983, and originally reported as a purely paleontological site (Agustí et al., 1987a). Subsequent excavations in the nineties led to the discovery of a number of stone tools (Turq et al., 1996; Gibert et al., 1998). Re-excavation at the beginning of the twenty-first century considerably enlarged the stone tool assemblage (Toro Moyano et al., 2010) and led to the recovery of the hominin tooth (Toro Moyano et al., 2013).

The Guadix-Baza intramontane basin is located in the Betic Ranges (south of Iberian Peninsula; see Fig. 1a), in the contact area between the Mesozoic basement rocks (Internal Zones, to the South of the basin) and the cover Mesozoic rocks (External Zones, to the North). This basin was filled by marine deposits during part of the Miocene. The basin uplift that took place by 8 Ma (millions of years ago) (see Hüsing et al., 2010 and references therein) created a disconnection from the sea, and the basin became continental.

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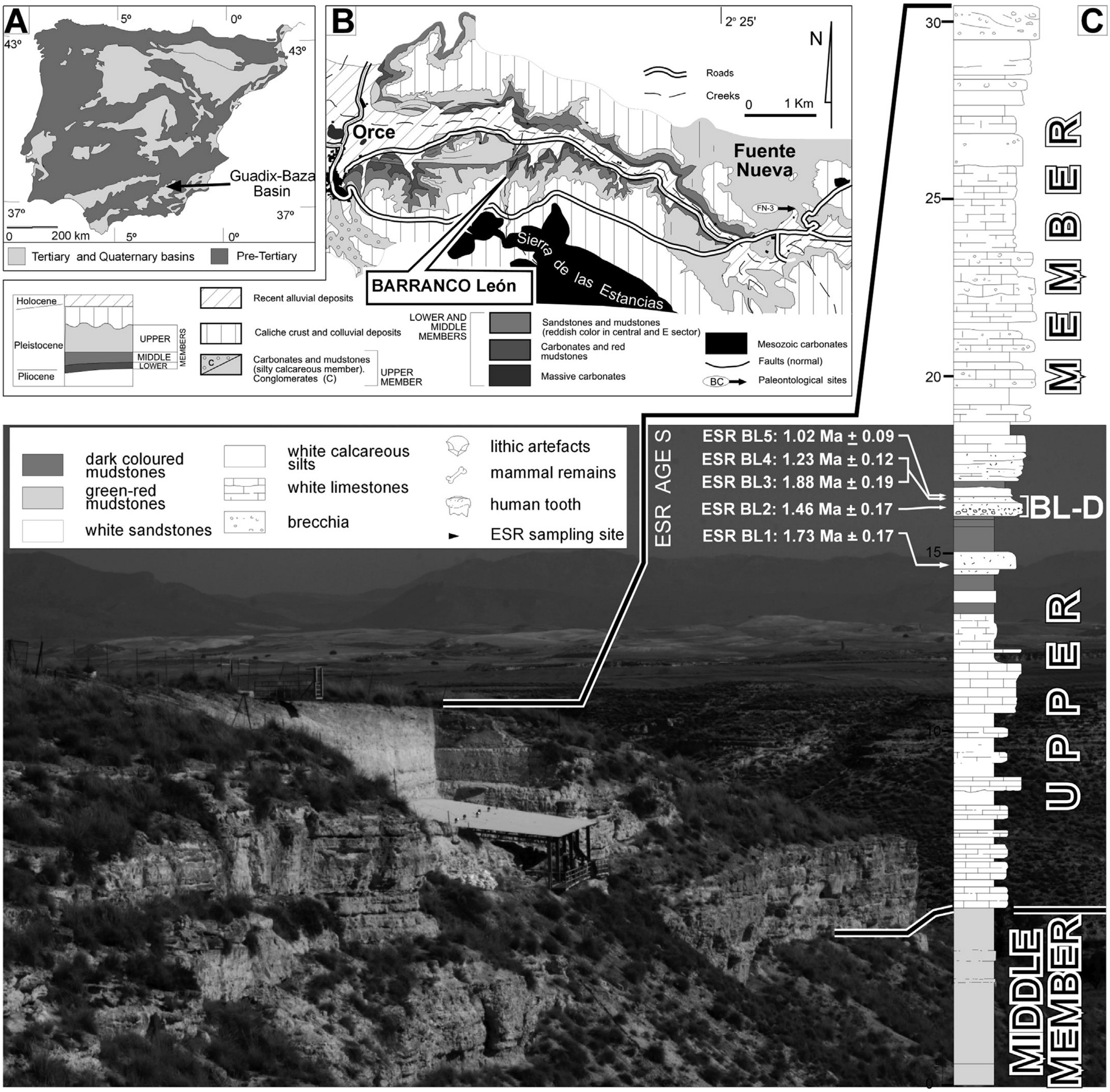

**Figure 1.** A: Location of the Guadix-Baza Basin in the context of the Cenozoic basins of the Iberian Peninsula. B: Geological units around Orce and location of Barranco León site. C: Barranco León section and site (right) and field view of the excavation area. Electron Spin Resonance (ESR) ages after Duval et al. (2012) and Toro Moyano et al. (2013). Unit D from this figure corresponds to units D1 and D2 from Figure 2.

Continental infill was active until the middle Pleistocene. Slightly before 280 ka (thousands of years ago), this basin began to erode due to the early development of the present day fluvial network (Díaz-Hernández and Julià, 2006), which drains the basin.

The Plio-Pleistocene basin infill is built up by the alluvial and fluvial Guadix Formation (see Viseras, 1991), while the lacustrine and palustrine formations are those of Baza, Gorafe-Huélago, and Solana (Vera, 1970). The Barranco León archaeological and paleontological sites studied here are located in the Orce area (see Fig. 1b), where the Plio-Pleistocene Baza Formation contains abundant paleontological sites and displays three distinct members (Vera et al., 1985; Oms et al., 2000a): the Lower, Middle, and Upper Members. The Lower Member contains shallow lacustrine and palustrine calcareous deposits. The Middle Member is built up by fluvial mudstones and sandstones. Finally, the Upper Member is also of lacustrine and palustrine origin and results from the accumulation of silty calcareous deposits as well as a coarser fraction. The Upper Member hosts the Barranco León section, located in the shallow lacustrine areas close to the basin margin. Fig. 1b shows the geological map around Barranco León with the location of the site in the context of the three members of the Baza Formation (see also Fig. 1c).

## Geological setting

The Barranco León section is roughly 25 m thick and hosts the archaeo-paleontological site of Barranco León 5 (Turq et al., 1996; Oms et al., 2000a). This section includes limestones, lutites, sandstones, conglomerates, and brecchias. This succession of lithologies records the paleoenvironmental changes of the lake margin conditions from saline to freshwater (Anadón and Gabàs, 2009). Geochemical studies of this succession (Anadón and Gabàs, 2009) detected hydrochemical variations due to changes in water source, solute composition, and water level. Thus, three water types interacted in the area: (1) those of the main Baza lake, which underwent large precipitation and evaporation, (2) dilute, meteoric surface waters and shallow groundwaters, and (3) saline groundwaters of meteoric origin that became saline after the dissolution of previously formed evaporates. Four main hydrochemical stages have been recorded in the Barranco León section (Anadón and Gabàs, 2009). Stage 4 (around meter 15 to 30 in Fig. 1c) contains the two levels studied here (D1 and D2). This stage is characterized by type 2 waters, belonging to a through-flowing open lacustrine system, which in the studied area was fed by both groundwater and streams.

Detailed sedimentological data for the two units analyzed here, D1 and D2, can be found in Anadón and Julià (2010), and microstratigraphic data can be found in Rodriguez Rivas (2009). Nomenclature for these units is shown in Fig. 2b, including nomenclature proposed by Turq et al. (1996). Unit D1 is composed of gravels with a sandy matrix and has a thickness from 65 to 0 cm. The base of this unit (see Fig. 2a, b) partially or completely erodes the previous unit, unit C (composed of beige calcisiltite to calcarenite). When the latter unit is completely eroded, D1 is directly in contact with unit B (black and dark green quartz-feldspatic sands). Figure 2.3 shows unpublished profiles from excavations held in 2010 that clearly illustrate these features. The sedimentology and lateral variations of this level have been studied in detail by Anadón et al. (2003; see also Oms et al., 2011). The cobbles and the pebbles of the gravels were studied by Anadón and Julià (2010), who show that they are dominated by palustrine intrabasinal limestones with scarce Mesozoic limestones from the adjacent External Zones. Unit D1 formed due to a sudden high energy current that transported gravels, matrix, bones, and archaeological remains. This high energy event is unique in the whole sequence at Barranco León. Gravels are broadly fining upwards and may display small-scale cross bedding. The single event nature of the deposition is also supported by the lack of lateral accretion surfaces or erosive features indicating recurrence of the process. Slightly reworked or in situ invertebrate fauna indicates fresh to oligosaline shallow lacustrine conditions.

Unit D2 is composed of greyish quartz-bioclastic sands capped by whitish limestones. Thickness is around 20 cm. Anadón and Julià (2010) report the occurrence of remains of fish teeth, *Valvata*, *Bithynia* opercules, and *Melanoides tuberculata*, the latter being particularly abundant. These sands and their faunal content are very similar to the matrix of unit D1 and here appear to have been formed in situ. The upper part of D2 is a level of whitish chalky limestone with abundant ostracods, mollusks, and charophyte remains.

## Material and methods

The small vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by water-screening during the 2010–2013 excavation campaigns at the Barranco León site. All of the sediment was water-screened using superimposed 5.0 and 0.5 mm mesh screens and bagged by square, layer, and excavation level. In subsequent years, the microfossils were processed, sorted, and classed in broad categories at the Institut Catalá de Paleoecologia Humana i Evolucio Social in Tarragona (IPHES, Spain). The sample includes more than 300 recognizable remains, representing 20 different species, including four fishes, four amphibians, five squamate reptiles, three insectivores, and four rodents (Table 1). The number of individuals for a particular species was determined by counting diagnostic elements.

In order to reconstruct the environment of the site, we used the method of habitat weightings (see Blain et al., 2008, 2011), distributing each taxon in the habitat(s) where it is possible to find them or their morphologically similar modern relatives at present in the Iberian Peninsula. The habitats were divided into five types: dry open land, wet meadows, woodland and woodland-margin areas, areas surrounding water, and rocky areas.

Each species was given a maximum possible score of 1.00, which was broken down according to the habitat preference of that species, so that if an animal occurred in more than one habitat type, its score was proportional to its habitat preference. Scores for higher-level taxonomic categories (providing no representatives have opposite ecological requirements) were calculated by counting the individual species scores of all the species contained within categories. Family-level groups or groups containing species with opposite ecological distributions (such as lacertids) were disregarded.

Because Spanish Pleistocene amphibians and reptiles are considered specifically identical to modern populations, the current species habitat distribution may be used for the habitat weightings. The distribution data are from Pleguezuelos and Martínez-Rica (1997), Salvador (1997), Carrascal and Salvador (2002–2006), García-París et al. (2004), and Pleguezuelos et al. (2004). In contrast with fishes, amphibians, and squamate reptiles, insectivores and rodents are represented by species that went extinct during the Pleistocene. However, some climatic inferences can be drawn on the basis of their generic assignment. The habitat distribution of the species represented in Barranco León is shown in Table 1.

## Results

### Unit D1

The unit D1 has yielded about 300 recognizable remains, including fish, amphibians, reptiles, insectivores, and rodents. The rodent association is dominated by the arvicolid species *Mimomys savini*. A second microtine species, *Allophaiomys* aff. *lavocati*, is much rarer. Finally, murids are represented by the species *Castillomys rivas* and *Apodemus mystacinus*. As direct ancestor of the middle Pleistocene *Arvicola mosbachensis*, the first recognized species of the water-rat lineage, it is assumed that *M. savini* had aquatic affinites. In contrast, both *Allophaiomys* aff. *lavocati* and *C. rivas* possibly indicate an open landscape. *Castillomys rivas* is an extinct rodent that is interpreted as a eurytopic species, i.e., it does not provide information about specific ecological conditions (Minwer-Barakat, 2005). Nevertheless, the development of wall-shaped ridges connecting the cusps of the crowns of the upper molars and a longitudinal ridge in the lower molars suggests a diet based on grains, so open meadows should be expected as a preferred habitat (Montoya et al., 1999). In addition to *C. rivas*, a second murid species, *A. mystacinus*, is present. Today, *A. mystacinus* and *Apodemus epimelas* (recorded as *A. mystacinus*) are found in areas with a relatively warm climate in the Balkan Peninsula and the Middle East. They are associated with dry forest and shrubland in rocky areas. Their presence can be related to the presence of rocky environments in the vicinity of the site (Agustí,

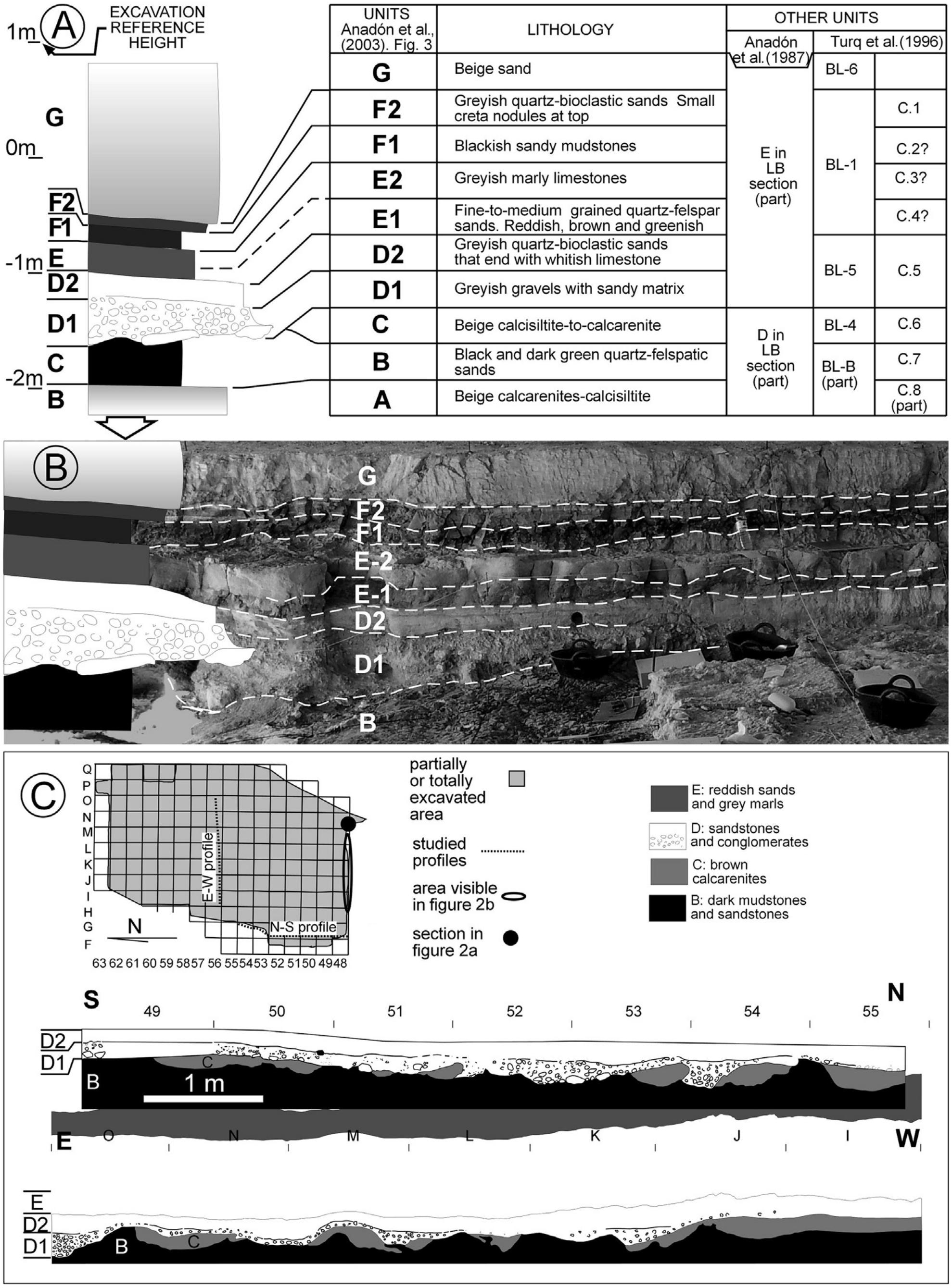

**Figure 2.** A: Barranco León section with the units by Anadón et al. (2003). Nomenclature by Turq et al. (1996) are also included. B: Section and view of the excavation profile (see below). C: Location of the section in Figure 2B and of the two sections at the bottom. Picture and sections from 2010 excavation.

1982; Mitchell-Jones et al., 1999; Storch, 2004; Minwer-Barakat, 2005). An equal proportion of the two murid species may indicate an ecological equilibrium between shrubland in rocky areas and open meadows.

Insectivores are represented by *Galemys* sp. and *Sorex minutus*. *Galemys* sp., the water mole, is an aquatic species, while the species of *Sorex* are usually associated with rather moist environments with abundant vegetation cover.

In addition to this small mammal association, unit D1 yielded the following amphibians and squamate reptiles species: *Discoglossus* sp., *Pelobates cultripes*, *Pelophylax* cf. *perezi*, cf. *Dopasia* sp., *Natrix maura*, *Coronella* cf. *girondica*, and *Rhinechis scalaris*. Taxa requiring presence of permanent aquatic environments (*Discoglossus*, *Pelophylax*, and *N. maura*) are well represented. Open environments are also represented with taxa of arid and stony areas like *P. cultripes* and *Rhinechis*. The genus *Dopasia* and *P. cultripes* may indicate the existence of warm wet Mediterranean woodland areas with soft soil. The presence of *Rh. scalaris* together with *C.* cf. *girondica* suggests warm climatic conditions.

Unit D1 has also yielded remains of three Cyprinid species, *Luciobarbus* aff. *sclateri*, *Squalius* aff. *cephalus*, and *Squalius* aff. *pyrenaicus*. *Luciobarbus sclateri* is a benthic species that has limnophilous habits. It usually occupies different sections of the river in the same range but usually disappears in cold and fast waters. In general, it is a typical inhabitant of the middle course of rivers, preferring rapid current and clear waters with rocky or gravelly

**Table 1**
Terrestrial small-vertebrates from the early Pleistocene of Barranco León in minimum number of individuals (MNI), with the distribution of each taxon in their potential habitats.

| | Level D2 | | Level D1 | | TOTAL | | Ecological requirements | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | MNI | % | MNI | % | MNI | % | Open dry | Open humid | Woodland | Rocky | Water edge |
| **Amphibians** | | | | | | | | | | | |
| *Discoglossus* sp. | 4 | 20.0% | 13 | 20.6% | 17 | 20.5% | | | | | 1 |
| *Pelobates cultripes* | | | 1 | 1.6% | 1 | 1.2% | 0.50 | | | 0.50 | |
| cf. *Bufo* sp. | 1 | 5.0% | | | 1 | 1.2% | | | | | |
| *Pelophylax* cf. *perezi* | 1 | 5.0% | 14 | 22.2% | 15 | 18.1% | | | | | 1 |
| **Squamates** | | | | | | | | | | | |
| cf. *Dopasia* sp. | | | 1 | 1.6% | 1 | 1.2% | | 0.25 | 0.75 | | |
| *Natrix maura* | 1 | 5.0% | 2 | 3.2% | 3 | 3.6% | | | | | 1 |
| *Coronella* cf. *girondica* | | | 1 | 1.6% | 1 | 1.2% | 0.25 | 0.25 | 0.25 | 0.25 | |
| *Rhinechis scalaris* | 1 | 5.0% | 1 | 1.6% | 2 | 2.4% | | 0.40 | 0.45 | 0.15 | |
| Colubrinae indet. | 1 | 5.0% | | | 1 | 1.2% | | | | | |
| **Insectivores** | | | | | | | | | | | |
| *Galemys* sp. | 1 | 5.0% | 1 | 1.6% | 2 | 2.4% | | | | | 1 |
| *Sorex minutus* | 1 | 5.0% | 1 | 1.6% | 2 | 2.4% | | 0.50 | 0.50 | | |
| *Erinaceus* sp. | 1 | 5.0% | | | 1 | 1.2% | 0.50 | 0.25 | 0.25 | | |
| **Rodents** | | | | | | | | | | | |
| *Apodemus* gr. *mystacinus-epimelas* | | | 1 | 1.6% | 1 | 1.2% | | | 0.50 | 0.50 | |
| *Castillomys rivas* | 1 | 5.0% | 1 | 1.6% | 2 | 2.4% | 0.50 | 0.50 | | | |
| *Mimomys savini* | 6 | 30.0% | 19 | 30.2% | 25 | 30.1% | | | | | 1 |
| *Allophaiomys* aff. *lavocati* | 1 | 5.0% | 7 | 11.1% | 8 | 9.6% | | | | | |
| **Total** | 20 | 100.0% | 63 | 100.0% | 83 | 100.0% | | | | | |

beds, especially during the breeding season. *Luciobarbus sclateri* can also be found in lakes and lagoons, including coastlines and standing water such as springs and ponds. It tolerates water with some organic contamination, with a wide range of thermal tolerance and oxygenation (Granado Lorencio, 2001). This species is endemic of the Iberian Peninsula, being present in most Spanish central and southern river basins as well as in Portugal. *Squalius cephalus* is an inhabitant of the water column and prefers clear waters and areas of pools and tables. Nowadays, this species lives in northern Spain, in Catalonia, Aragon, and Basque Country (Doadrio, 2002). *Squalius pyrenaicus* is a ubiquitous species that is able to survive in several environments. Although a generalist species, it usually prefers quiet and clean waters. It tolerates large temperature and dissolved oxygen differences (Doadrio and Casado, 1989). Currently, this species is found in the central and southern Iberian Peninsula, especially in the basins of the Tajo, Guadiana, Guadalquivir, Segura, Júcar rivers, and the Albufera of Valencia (Doadrio, 2002).

### *Unit D2*

Unit D2 has delivered more than 50 recognizable remains of small vertebrates, including fishes, amphibians, reptiles, insectivores, and rodents. Rodents form the most abundant group of small mammals, and again the water-rat *M. savini* is the most abundant species. The microtine *Allophaiomys* aff. *lavocati* is scarcely represented, while murids are less diversified than in unit D1, represented only by *C. rivas*.

The insectivore association includes *Galemys* sp., *S. minutus*, and *Erinaceus* sp. The hedgehog *Erinaceus* is generally indicative of rather dry conditions, or at least some species of this genus nowadays are adapted to environments in which water, rainfall, and/or vegetation cover are not abundant.

Among the herpetofauna, this unit has yielded fossil remains of *Discoglossus* sp., cf. *Bufo* sp., *Pelophylax* cf. *perezi*, *N. maura*, *Rh. scalaris*, and one indeterminate colubrine snake. With the exception of *Bufo* and *Rhinechis*, all of the taxa document the presence of sunny aquatic environments and their neighborhoods. The presence of the thermophilous snake *Rh. scalaris* suggests relatively warm climatic conditions with a mean annual temperature higher than 13 °C (Llorente et al., 1995).

This unit has also yielded the remains of Cyprinid fishes *Luciobarbus* aff. *bocagei* and *Squalius* aff. *pyrenaicus. Luciobarbus bocagei* tends to occupy regional sections of the river with less steep, farthest from the source and with large-sized basins. Adults occupy areas with lower rainfall and lower runoff and are also locally found in wider and deeper rivers (Salvador, 2012). *Luciobarbus bocagei* is endemic to the Iberian Peninsula and is currently present in central and western basins such as the Tajo, Duero, and Limia.

## Chronological context

The first indications of the age of the Barranco León section were provided by Oms et al. (2000b), who showed that the whole section had a reverse geomagnetic polarity. A combination of magnetostratigraphy and biostratigraphy indicates that Barranco León fits within the upper Matuyama chron, between the Olduvai and Jaramillo subchrons. Further refinements in the dating of the archaeological and paleontological levels of Barranco León were proposed by Duval et al. (2012) and Toro Moyano et al. (2013). Application of ESR dating to *Equus* teeth and quartz grains provided an overall age around 1.4 Ma (Duval et al., 2012).

Regarding the biochronology of the sites, the most valuable elements are the arvicolids *M. savini* and *Allophaiomys* aff. *lavocati. Mimomys savini*, the most abundant small mammal in all the levels of Barranco León, is characterized by its large size and rooted molars in adults. The molars are longer than those of several primitive populations of *M. savini* such as at Betfia 2 and Nogaisk (Maul, 2001), whose average length values are less than 3 mm. The mean length of the measured molars from units D1 and D2 of Barranco León are quite similar to the mean value from Monte Peglia (3.30 mm; Meulen, 1973). In turn, the samples from D1 and D2 show lower values than those of *M. savini* from the Gran Dolina section in Atapuerca (Spain). This is the case for Trinchera Dolina level (TD) 4 (3.43 mm), TD5b (3.46 mm), TD5a (3.49 mm), TD6–3 (3.43 mm), TD6–2 (3.59 mm), and TD6–1 (3.62 mm; Lozano-Fernández et al., 2013a, b).

The teeth of *Allophaiomys* aff. *lavocati* from Barranco León are clearly more derived than those of archaic populations of this genus, such as *Allophaiomys pliocaenicus* from Betfia 2 and Brielle (Meulen and Zagwijn, 1974) and *Allophaiomys ruffoi* from the Guadix-Baza Basin (Agustí et al., 1987b; Agustí, 1992), with less confluent triangles T4 and T5 and clearly distinct triangle T7 and lingual re-entrant angle LRA5 (sensu Meulen, 1973). The studied specimens are smaller than those of *A. burgondiae* from Monte Peglia (Meulen, 1973) and Valerots (Laplana et al., 2000).

The measurements of the small number of specimens of *Allophaiomys* from Barranco León fit the size ranges of the population of *Allophaiomys lavocati* from the Lower Red Unit of the Sima del Elefante (Laplana and Cuenca-Bescós, 2000). The average tooth length, width, and anteroconid complex length of *Allophaiomys* aff. *lavocati* from Barranco León are also very close to those of *A. lavocati* from Sima del Elefante. The sample from Barranco León, however, differs in its anterior lobe, which is not as narrow as in *A. lavocati* from this site. Therefore, the evidence provided by the shape and size of the molars from *M. savini* and *Allophaiomys* aff. *lavocati* points to the fact that the units of Barranco León are older than those of the base of Sima del Elefante in Atapuerca. Since these last levels have been dated to 1.22 ± 0.16 Ma (Carbonell et al., 2008), this result is consistent with the numerical age of 1.4 Ma provided by ESR (Duval et al., 2012).

## Environmental context

Today, the Guadix-Baza Basin is a quasi desert plateau located at an altitude of 1000 m above sea level with an extremely arid continental climate, though with Mediterranean characteristics. The mean annual temperature ranges between 11 °C and 15 °C, but with extreme seasonality (harsh winters and very warm summers) and mean annual precipitation ranges from between 300 and 400 mm, mainly occurring in March, April, and September with very irregular, torrential pattern rainfall (Espigares and Ros, 2003).

Previous paleoecological and paleoclimatical studies of Barranco León (unit D) suggested a warmer and more humid climate than actual conditions in the Guadix-Baza Basin (Blain et al., 2011). Mean annual temperatures were 4.9 °C higher and mean annual precipitation was 371 mm higher than today's values. In addition, there was a less pronounced difference between winter and summer temperatures: winters were warmer and summers were about the same as they are now or possibly slightly cooler. There were high levels of precipitation throughout the year, but the summer was slightly drier than today, in keeping with the characteristically Mediterranean climate (i.e., periods of drought during summer). The landscape was composed of a body of water exposed to the sun with rich lakeside vegetation and surrounded by loose, stony soil. The terrestrial landscape consisted of rich and diverse environments that alternated between dry meadows or shrublands alongside more humid areas favorable to the development of wetter woodlands and meadows.

The presence of wet woodlands around Barranco León is well supported in unit D1 by the occurrence of large cervids such as *Praemegaceros* cf. *verticornis* and *Metacervocerus rhenanus* (Abbazzi, 2010) and by palynological data, which indicate the existence of well-developed woodlands (50% of arboreal pollen) with predominantly Mediterranean taxa (Cupressaceae, *Quercus* sp. -evergreen oak-, *Olea*, *Phillyrea*), although some taxa (like *Betula*, *Corylus*, *Quercus* -deciduous oak-, *Cedrus*, and *Picea*) indicate more humid conditions (Jiménez Moreno, 2003). Large herbivores like *Mammuthus meridionalis* and *Stephanorhinus* cf. *hundsheimensis* as well as the prevalence of *Equus altidens* suggest wet, open meadows. The occurrence of *Hippopotamus antiquus*, which accounts for 27.1% of the large mammals at Barranco León, provides evidence supporting the presence of large bodies of water (Martínez-Navarro et al., 2003, 2010).

The results of the present study of the two fossiliferous levels of Barranco León enable a closer analysis of the paleoenvironmental and paleoclimatic conditions occurring when each of the units were deposited. The paleoherpetological and paleoichtyological data indicate that the temperature was higher than today, with the mean annual temperature higher than 13 °C. Moreover, the two units are dominated by vertebrates associated with areas bordering water (close to 90%; Fig. 3; Table 1). Unit D1 is characterized by the prevalence of woodland elements (35%), followed by open humid (27.1%), rocky (20%), and open dry elements (17.9%). However, the situation changes in unit D2, which is clearly dominated by open humid elements (more than 40%) and very few rocky small mammals (less than 4%; see Fig. 3). Therefore, although the microvertebrate evidence indicates the existence of a significant water column during the deposition of the two units, an open landscape was always present in the vicinity of the lake. The evolution of the microvertebrate associations suggests a trend towards more humid, less open conditions from D1 to D2 (see Fig. 4).

## Discussion

Thus far, Barranco León records the oldest evidence of hominin presence in Western Europe, both in terms of lithic industry and physical remains (Toro Moyano et al., 2013). However, there is a difference of about 0.5 Ma between the first hominin evidence out of Africa and the Iberian record: hominin presence in Georgia has been reported at the site of Dmanisi as early as 1.8 Ma (Vekua et al., 2002; Lordkipanidze et al., 2007; Ferring et al., 2011). How to explain this difference in age? In contrast with other Pleistocene successions in Western Europe, the Guadix-Baza Basin records an almost continuous stratigraphic and paleontological sequence. In this way, it has been possible to elaborate a very accurate biostratigraphic scale based on small mammals (Agustí et al., 2010). The levels biostratigraphically below Barranco León, such as Venta Micena, do not show any evidence of hominin presence, both in terms of lithic industries or hominin remains, in contrast with Barranco Léon, where the number of lithic tools so far reaches 1240 artefacts, including cores, flakes or fragments of flakes, and cobbles (Toro Moyano et al., 2013). However, Venta Micena has yielded more than 15,000 fossil remains, much more than Barranco León.

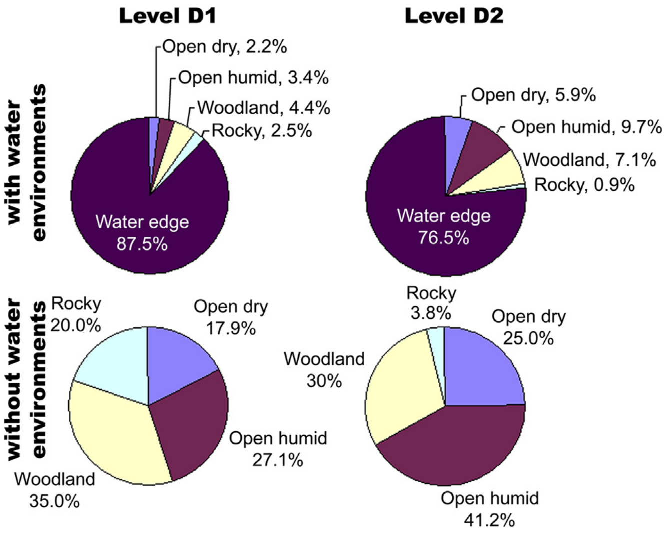

**Figure 3.** Distribution of relative abundances of small vertebrate habitat preferences and their MNI values. Top row: relative abundances of habitat preferences. Bottom row: relative abundances of habitat preferences without aquatic and water-edge habitats.

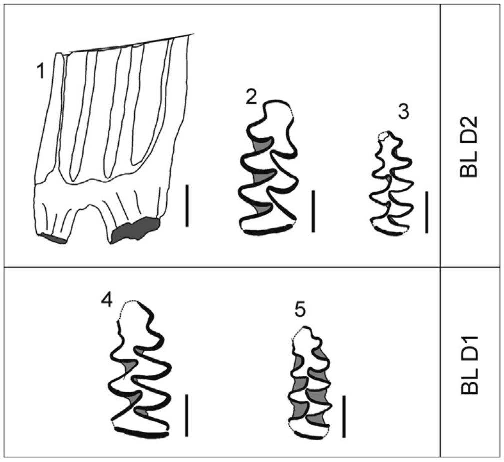

**Figure 4.** Occlusal view of lower first molars of the arvicolid species represented at D1 and D2. *Mimomys savini*: 1 (lateral view), 2, and 4. *Allophaiomys* aff. *lavocati*: 3 and 5.

Difference in age between the fossiliferous levels of Venta Micena and Barranco Léon can be estimated at about 200 ka (Agustí et al., 2010). Venta Micena and age-equivalent levels in Spain display evidence of drier and cooler conditions compared with the geologically younger desposits of Barranco León, (Agustí et al., 2009). Therefore, according to the Guadix-Baza record, it seems that hominin presence in the area was strongly influenced by climatic conditions, with the first hominin occurrence taking place only when mild, favorable conditions, both in terms of temperature and humidity, were present. The data reported here clearly support the idea that early human occupation of Europe was strongly constrained by climatic and environmental conditions, rather than by physiography or cultural factors.

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## Appendix 2

**(2) Blanco-Lapaz, A**., Martínez-Monzón, A., Blain, H-A., Cuenca-Bescós, G. 2021a. Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record. Palaeogeography, Palaeoclimatology, Palaeoecology, 574 (2): 11044. https://www.doi.org/10.1016/j.palaeo.2021.110444

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# Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record

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ABSTRACT

Fish bones are common in Pleistocene cave deposits in Europe. In this paper, we report on fish remains from the Gran Dolina cave (Trinchera del Ferrocarril) in the Sierra de Atapuerca in Spain, to increase what is known of the freshwater ecosystems close to the cave. The 19-m-thick section, divided into 11 stratigraphic levels, represents an Early to Middle Pleistocene time span as dated by biostratigraphy, ESR, U-series, and magnetostratigraphy. We focus on the Sondeo South site, excavated from 1993 to 1999, which has yielded 1087 fish bones comprising the following taxa: brown trout (*Salmo trutta*), the common European eel (*Anguilla anguilla*) and chub (*Squalius* sp.). Taphonomic studies suggest that the European eagle owl (*Bubo bubo*) was the most likely predator responsible for the accumulation. Changes observed in the body size of brown trout through the sequence cannot be attributed to climate change (contravening Bergmann's rule). Our study documents the presence of a pre-mountain river system characterized by permanent, oxygen-rich, relatively cold flowing waters around the Sierra de Atapuerca during Early-Middle Pleistocene times.

## 1. Introduction

Microvertebrate remains are commonly recovered from Pleistocene contexts in Europe. Over the course of the last few decades, abundant small-vertebrate remains from the Gran Dolina cave (Trinchera del Ferrocarril) in the Sierra de Atapuerca in Spain have been published: remains belonging to rodents and insectivores (Cuenca-Bescós et al., 2005, 2011, 2017; Cuenca-Bescós and García, 2007; Rofes and Cuenca-Bescós, 2009, 2011), bats (Galán et al., 2019), birds (Sánchez-Marco, 1999; Bennássar, 2010; Núñez-Lahuerta et al., 2019), and amphibians and reptiles (Blain, 2005, 2009; Blain et al., 2008, 2009, 2013). All these studies significantly expand our knowledge of the biochronology, depositional processes and paleoenvironmental conditions (see Rodríguez et al., 2011; Cuenca-Bescós et al., 2010, 2011, 2016).

Fish remains from the very first field campaigns (1987–1994) were mentioned by Doadrio (in Sanchíz, 1987) and published by Aguirre (1995), describing the presence of *Salmo trutta* and unidentified cyprinids. However, this was just a faunal list, and the references did not go any deeper into an interpretation of the remains. Other assemblages of fish remains belonging to neighboring sites have been cited as well. Cuenca-Bescós et al. (1997) mention the presence of *Salmo* sp. and *Leuciscus* sp. in the Middle Pleistocene site of Sima de los Huesos. Cuenca-Bescós et al. (2015) and Huguet et al. (2015) document the presence of the same taxa in the Early Pleistocene site of Sima del Elefante (TE), and the authors link the accumulation of fish and aquatic bird remains with the presence of the white-tailed sea eagle (*Haliaeetus albicilla*), recovered in level TE9c. Finally, Blanco-Lapaz and Vergès (2016) document the presence of *S. trutta* in the Neolithic site of El Mirador cave.

Previous archaeozoological studies and analyses, all of them based on Middle-Late Pleistocene sites, provide evidence of the exploitation of aquatic vertebrates by hominins in southwest and central Europe. Most of these pertain to marine coastal archaeological sites (e.g. Cleyet-Merle, 1990; Morales-Muñiz and Roselló-Izquierdo, 1988; Roselló-Izquierdo et al., 1995; Roselló-Izquierdo and Morales-Muñiz, 2005; Brown et al., 2011; Zilhão et al., 2020), and fewer studies are related to inland sites

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close to rivers and lakes (e.g. Morales, 1980; Russ and Jones, 2011; Conard et al., 2013; Rey-Rodríguez et al., 2018; Blanco-Lapaz, 2019; Guillaud et al., 2021). As regards the Iberian Peninsula, the previous studies based on Middle-Late Pleistocene sites indicate the presence of salmonids (*Salmo* sp., *S. trutta*) (Cueva Amalda, Cueva Millán, Cova dels Ermitons), the common eel (*Anguilla anguilla*) (Cueva Millán) and cyprinids (the *Pseudochondrostoma polylepis* group) (Cueva Millán) (Roselló-Izquierdo and Morales-Muñiz, 2005).

However, not all the fish assemblages recovered in Pleistocene archaeological sites were accumulated by humans. Other predators, such as small carnivores and birds of prey, have also been implicated (Nicholson, 1991, 2000; Le Gall, 1999; Russ, 2010b; Russ and Jones, 2011; Guillaud et al., 2017, Guillaud et al., 2018; Böhme, 2019).

From a paleoecological point of view, body size is one of the most significant biological traits in fishes, as it determines the life history and several physiological and biochemical processes (Bonner, 2011). Bergmann (1847) proposed the tendency of organisms to be smaller at high temperatures and low latitudes and larger at low temperatures and high latitudes. This global pattern, known as Bergmann's rule, has been relatively little studied in marine fishes (Alonso-Fernández et al., 2014; Fernández-Torres et al., 2018; Saunders and Tarling, 2018), freshwater fishes (Mousseau, 1997; Belk and Houston, 2002; Watt et al., 2010; Rypel, 2014; Adhikari, 2015), and particularly in Iberian freshwater fishes (Parra et al., 2009; Arranz-Urgell, 2017). In general, it has been proved that Bergmann's rule applies to freshwater fish, but the strength varies with size and trophic levels. Arranz-Urgell (2017), for example, proved that temperature affects the size metrics for perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernuus*), white bream (*Abramis brama*), and zander (*Sander luciperca*) in the Iberian Peninsula, showing that these species are relatively smaller as adults at higher water temperatures. On the other hand, Rypel (2014) evaluated the body size of various North American freshwater fish species in correlation with the mean annual temperature and the elevation. Bergmann's rule was observed for 11 (all of them cool- or cold-water species) out of 29 species, whereas the converse Bergmann rule was observed in 10 (all of them warm-water species) out of 29. Two non-native species, *S. trutta* (cold-water) and *Cyprinus carpio* (Cyprinidae) (warm-water), were also studied but in these cases, no correlation with Bergmann's rule was observed, proving that some freshwater fish species do not express this macroecological pattern, but the study suggests that a major and relatively unexplored link exists between the thermal requirements of species and the evolution of body size variation (Rypel, 2014).

Previous studies in Gran Dolina using natterjack toad (*Epidalea calamita*) remains analyzed the correlation between body size and climate, proving the validity of Bergmann's rule for this amphibian on the basis of the fossil record (Martínez-Monzón et al., 2018). The authors found the body size for this species to be negatively related to the mean annual temperature and the mean temperature of the coldest month (showing an increase in size in periods with cooler winters), and positively related to winter precipitation. In accordance with Bergmann's rule, we expected that the brown trout individuals in Gran Dolina might be bigger in colder periods and smaller in warmer periods.

Although some fish assemblages have previously been studied in the Sierra de Atapuerca (Aguirre, 1995; Cuenca-Bescós et al., 1997, 2015; Huguet et al., 2015), the present paper describes for the first time the fish remains from the Gran Dolina Sondeo South (TDS) excavations, exploring the origin and characteristics of this Early-Middle Pleistocene fish assemblage from a taxonomic, taphonomic and ecological point of view. This adds to our knowledge of the freshwater ecosystems of the Sierra de Atapuerca during the late Early and Middle Pleistocene.

## 2. Geological setting

The site of Gran Dolina (42°21′09″N 3°31′06″W; 900 m.a.s.l.) (in the railway Trench, labeled, TD) is a cave infilled by at least 25 m of Pleistocene sediments, located in the Sierra de Atapuerca (Burgos, Spain) (Fig. 1). The Gran Dolina sedimentary deposits reveal a rather common succession in karstic tiered caves that developed in relation to the progressive incision of the Arlanzón river. The stratigraphy of the cave comprises 11 layers, TD1 to TD11 from bottom to top. It reflects a broad evolution and includes cave interior deposits at the bottom (including silts, clays, and flowstones) below unit TD4, and an assemblage of diamictons and gravels, often showing channel cut-and-fill structures with abundant sand and silts, from TD4 to the top of the sequence (Campaña et al., 2017). Gran Dolina provides an unusual supply of archaeological remains and fossils of large and small vertebrates that have been used to document human activity and its relationship to the environment over the last one million years (Carbonell et al., 1995, 2008; Bermúdez de Castro et al., 1997, 2008; Rodríguez et al., 2011; Rodríguez-Gómez et al., 2013; Cuenca-Bescós et al., 2010, 2016; Saladié et al., 2021). The stratigraphic layers of the site have been extensively excavated, studied and dated using numerous methods, such as biostratigraphy, luminescence, electron spin resonance and paleomagnetism (Cuenca-Bescós et al., 1999, 2001, 2016; Falguéres et al., 1999; Parés and Pérez-González, 1999; Berger et al., 2008; Parés et al., 2013; Arnold et al., 2013). Gran Dolina contains one of the most complete Quaternary stratigraphic sequences in Spain, running from the Early to Middle Pleistocene and comprising some 700,000 years (1 Ma to 244 ka: see the latest updates on the chronology of Gran Dolina in Álvarez-Posada et al., 2018).

Regarding the current environment and climatic parameters of the study area, the province of Burgos is considered one of the coldest regions in the Iberian Peninsula (Font-Tullot, 2000); it has a continental Mediterranean climate with mean annual temperature values of 9.9 °C (meteorological station of Burgos Air Base, 891 m.a.s.l.). The Burgos region is characterized by its highly contrasting seasonality: winters are cold, including snowfalls and below-freezing temperatures that reach −15 °C, whereas summer mean temperatures are between 15 and 20 °C (Font-Tullot, 2000; Ninyerola et al., 2005). On the other hand, the region connects the Eurosiberian and Mediterranean bioclimatic regions of the Iberian Peninsula, which is reflected in the high biodiversity of the area.

## 3. Materials and methods

The fish remains from Gran Dolina layers TD4-TD8 (Early Pleistocene) and TD10 (Middle Pleistocene) were recovered during the 1991, 1993–1994 and 1996–1997 field campaigns, during the latter of which a test pit (TDS, around 9 $m^2$) was made. We here study the fossil assemblage, comprising 1087 fish remains (Table 1). The fish remains were collected by applying standard water-screening techniques (lowest mesh 0.5 mm) to the sediments excavated during the archaeological campaigns excavations.

The anatomy and taxonomy of each of the studied specimens were identified using material from the comparative collection housed in the Senckenberg Center for Human Evolution (University of Tübingen). Traces of human activities such as butchery or burning, animal modifications such as gnawing, pits and digestion marks, as well as environmental alterations, were also checked during this study.

All the elements were classified, and the bone surface was observed using a binocular microscope (OPTIKA SZM-2); pictures were taken using a Zeiss Stemi 305 EDU microscope. Bone surface damage was allocated to three categories of digestion mark: null-light (0), moderate (1) and moderate-heavy (1_2) (modified from Andrews, 1990; Fernández-Jalvo et al., 2016; Guillaud et al., 2015, 2018) (Table 3, Figs. 2 and 4B). For each level, the number of identified specimens (NISP) was determined.

Several fish studies have determined the season of death (seasonality) using sclerochronological methods (Van Neer et al., 1999; Le Gall, 2003; Guillaud et al., 2017) based on scales and vertebrae. Here, however, the high degree of mineralization observed on the vertebrae together with the absence of fossil scales prevent any study using such a

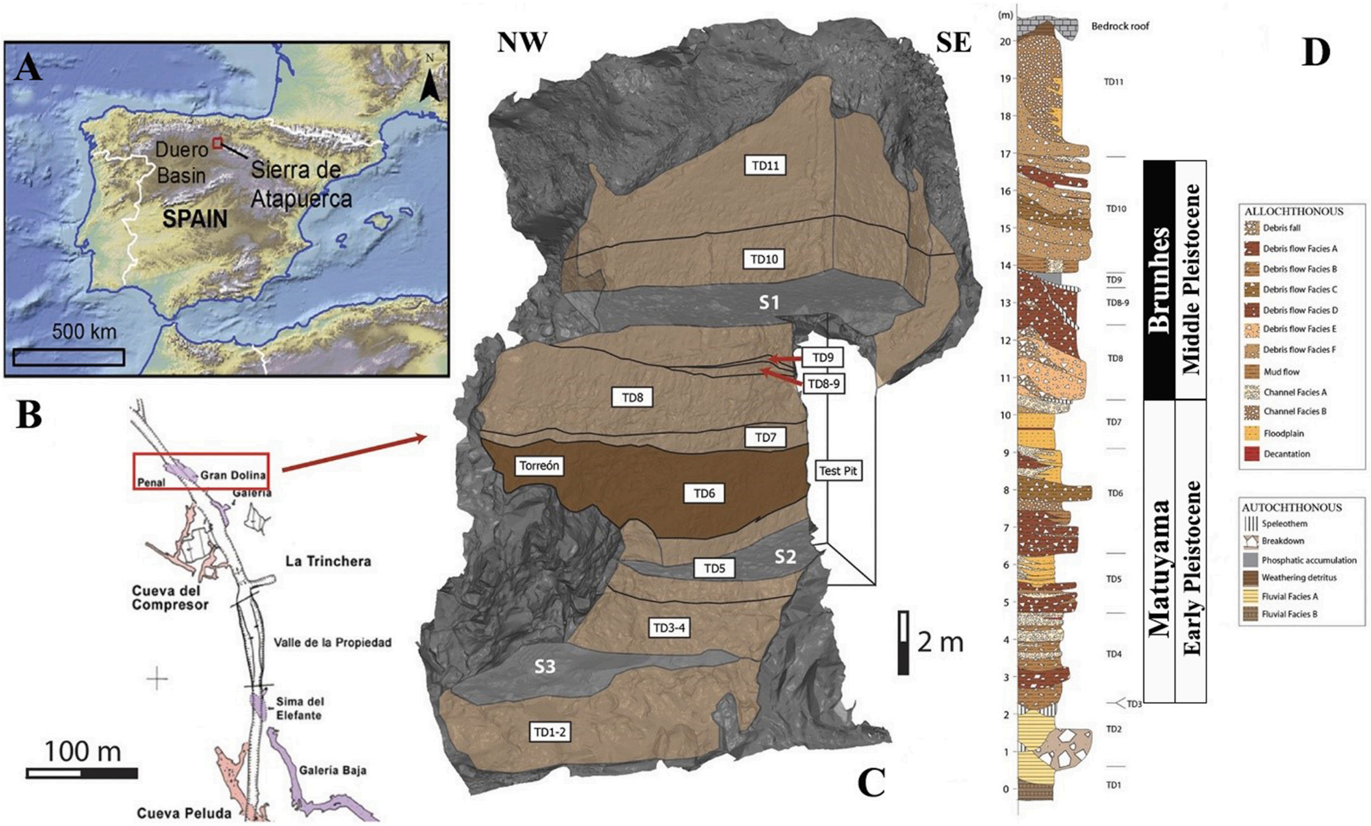

**Fig. 1.** (**A**) Location of the Sierra de Atapuerca. (**B**) Location of the Gran Dolina site situated in a railway trench ("Trinchera"). (**C**) General 3D model of the Gran Dolina site in 2012. Brown areas indicate stratigraphic units. Grey areas are the wall and roof of the cave. (**D**) Stratigraphic units (TD1 to TD11) and sedimentary facies of the Gran Dolina site. 1A map created by ArcGis 10.1 using the elevation data of the free access dataset SRTM90 (http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1). 3D model of 1C created by 3DReshaper 8.1 software (http://www.3dreshaper.com/en/) (modified from Campaña et al., 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Fish taxa identified in the Early and Middle Pleistocene layers of Gran Dolina (Sierra de Atapuerca, Spain). NISP: number of identified specimens; % Percentage of the assemblage.

| Levels | Salmonidae | | | | Anguillidae | | Cyprinidae | | | | Unidentified | | NISP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *S. trutta* | | Unidentified | | *A. anguilla* | | *Squalius* sp. | | Unidentified | | | | |
| | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | |
| TD10-1 | 6 | 85.7 | | | | | | | 1 | 14.3 | | | 7 |
| TD10-2 | 8 | 61.5 | | | | | | | 5 | 38.5 | | | 13 |
| TD10-3 | 33 | 76.7 | | | 5 | 11.6 | | | 5 | 11.6 | | | 43 |
| TD10-4 | 63 | 63.0 | 1 | 1.0 | 6 | 6.0 | 4 | 4.0 | 26 | 26.0 | | | 100 |
| TD8a | 13 | 54.2 | | | | | | | 11 | 45.8 | | | 24 |
| TD8b | | | | | | | | | | | | | 0 |
| TD7 | | | | | 2 | 100.0 | | | | | | | 2 |
| TD6-1 | 216 | 89.6 | 1 | 0.4 | 1 | 0.4 | | | 23 | 9.5 | | | 241 |
| TD6-2 | | | | | | | | | | | | | 0 |
| TD6-3 | 349 | 95.9 | 2 | 0.5 | | | | | 11 | 3.0 | 2 | 0.5 | 364 |
| TD5a | 131 | 99.2 | | | 1 | 0.8 | | | | | | | 132 |
| TD5b | 109 | 89.3 | | | 1 | 0.8 | 1 | 0.8 | 11 | 9.0 | | | 122 |
| TD5c | | | | | | | | | 1 | 100.0 | | | 1 |
| TD5d | 1 | 100.0 | | | | | | | | | | | 1 |
| TD4 | 37 | 100.0 | | | | | | | | | | | 37 |
| NISP | 966 | | 4 | | 16 | | 5 | | 94 | | 2 | | 1087 |
| % | 88.9 | | 0.4 | | 1.5 | | 0.5 | | 8.6 | | 0.2 | | |

methodology.

In accordance with Martínez-Monzón et al. (2018), the climatic values of the mean annual temperature (MAT), the mean temperature of the coldest month (MTC) and the mean temperature of the warmest month (MTW) were obtained from the paleoclimate reconstructions conducted by Blain et al. (2009, 2012, 2013) using herpetofaunal assemblages as climate proxies (Table 4).

Due to the abundance of *Salmo trutta*, this species was selected to infer the average total body length from well-preserved vertebrae based on published regressive statistics using the total length of the vertebrae (BL) (Prenda et al., 2002; Blanco-Lapaz and Vergès, 2016) (Table 2, Figs. 3A, B and 4C).

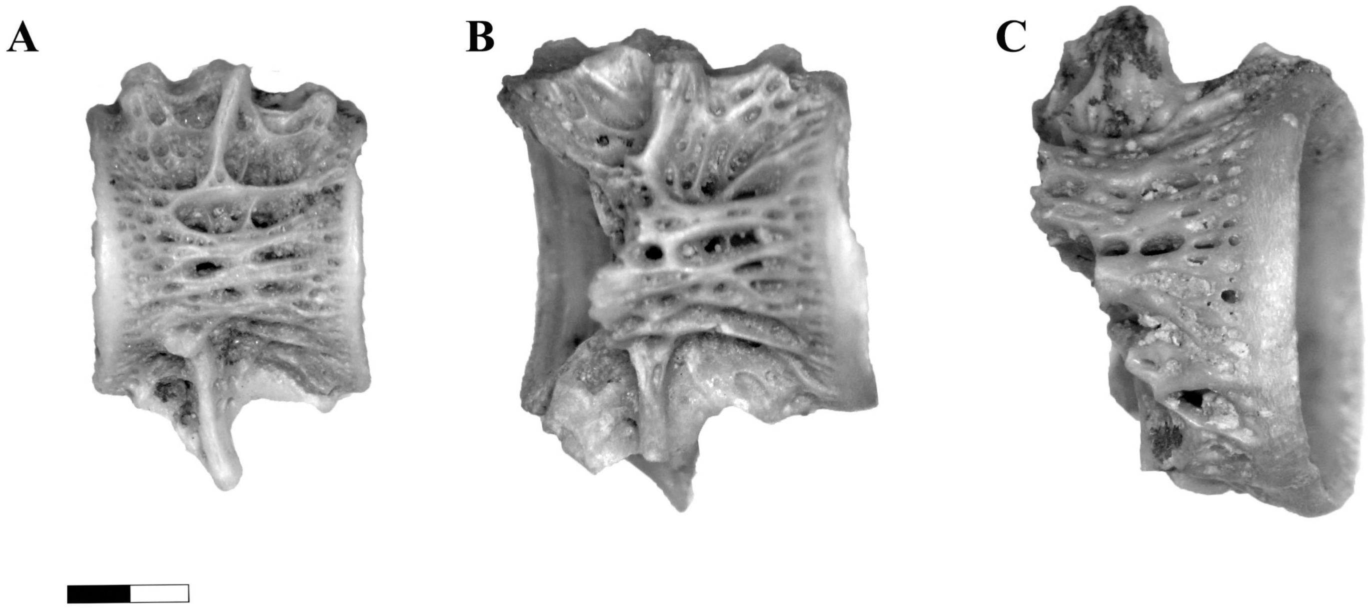

**Fig. 2.** Categories of digestion marks on *S. trutta* caudal vertebrae in lateral view (TD6-3). (**A**) null-light digestion (category 0). (**B**) almost complete vertebra showing moderate digestion (category 1). (**C**) vertebra showing damage in more than 50% of the bone, moderate-heavy (category 1_2). Scale 5 mm.

**Table 2**
Body size estimations for *Salmo trutta* individuals from the Early-Middle Pleistocene of Gran Dolina (Sierra de Atapuerca, Spain).

| Levels | <10 cm | | 10–20 cm | | 20–30 cm | | 30–40 cm | | 40–50 cm | | 50–60 cm | | + 60 cm | | Total NISP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | |
| TD10-1 | | | 3 | 100.0 | | | | | | | | | | | 3 |
| TD10-2 | | | 1 | 25.0 | | | 1 | 25.0 | | | 2 | 50.0 | | | 4 |
| TD10-3 | | | 8 | 36.4 | 6 | 27.3 | 3 | 13.6 | 3 | 13.6 | 1 | 4.5 | 1 | 4.5 | 22 |
| TD10-4 | | | 8 | 17.8 | 11 | 24.4 | 13 | 28.9 | 8 | 17.8 | 3 | 6.7 | 2 | 4.4 | 45 |
| TD8a | | | 4 | 33.3 | 5 | 41.7 | 1 | 8.3 | 2 | 16.7 | | | | | 12 |
| TD7 | | | | | | | | | | | | | | | 0 |
| TD6-1 | 8 | 4.1 | 187 | 95.9 | | 0.0 | | 0.0 | | | | | | | 195 |
| TD6-3 | | | 4 | 1.4 | 149 | 51.4 | 76 | 26.2 | 43 | 14.8 | 16 | 5.5 | 2 | 0.7 | 290 |
| TD5a | | | 7 | 5.9 | 13 | 10.9 | 47 | 39.5 | 46 | 38.7 | 6 | 5.0 | | | 119 |
| TD5b | 2 | 2.2 | 27 | 29.0 | 30 | 32.3 | 16 | 17.2 | 14 | 15.1 | 4 | 4.3 | | | 93 |
| TD5c | | | | | | | | | | | | | | | 0 |
| TD5d | | | | | | | | | | | | | | | 0 |
| TD4 | | | 3 | 8.8 | 29 | 85.3 | 2 | 5.9 | | | | | | | 34 |
| Total NISP | 10 | | 252 | | 243 | | 159 | | 116 | | 32 | | 5 | | 817 |
| % | 1.2 | | 30.8 | | 29.7 | | 19.5 | | 14.20 | | 3.92 | | 0.61 | | |

In order to understand the relationships between body size and temperature, we performed simple least square (OLS) regression models conducted with R (R core team) taking on a significance level of $\alpha = 0.05$.

## 4. Results

A total of 1087 fish remains were identified in the Early to Middle Pleistocene layers of the Gran Dolina TDS sequence. All the levels yielded some evidence of fish, with the exception of levels TD6-2 and TD8b. The levels with the highest number of remains were TD6-3 and TD6-1, followed by TD5a, TD5b and TD10-4.

### *4.1. Taxonomic composition*

The whole fish assemblage comprises three different families: Salmonidae, Cyprinidae and Anguillidae (Table 1, Fig. 4A). The predominant fish family is Salmonidae (90.3%), and most of the remains belong to the brown trout (*S. trutta*) (Fig. 3A–B) (88.9%). This species is represented almost exclusively by vertebrae and teeth. Less frequent are remains of Cyprinidae (carp family) (9.1%), The genus *Squalius* was identified in levels TD10-4 and TD5b based on two pharyngeal arches characteristic of this taxon (Fig. 3C–E). The rest of the cyprinid remains correspond to vertebrae that are not possible to identify to genus or species level due to the similar vertebral morphology in this family (Prenda and Granado-Lorencio, 1992; Russ, 2010a). The assemblage also shows the presence in levels TD5a, TD5b, TD6-1, TD7, TD10-3 and TD10-4 of the common European eel (*Anguilla anguilla*) (1.5%), only represented by vertebrae (Fig. 3F) and constituting the first record of this species in the Early-Middle Pleistocene sites of Atapuerca.

#### *4.1.1. Salmonidae*

As mentioned above, Salmonidae and particularly the species *S. trutta* is the most represented taxon in the whole assemblage. Of the 37 fish remains recovered in TD4, only the brown trout (*S. trutta*) was identified. The sub-levels of TD5 are dominated by the same species (94.1%) although no item was recovered in level TD5c, only one vertebra in TD5d (100% of the sample), and the rest of the brown trout remains are distributed between TD5b (NISP = 109; 89.3%) and TD5a (NISP = 131; 99.2%). In TD6, salmonids are also the most represented taxon in both sub-levels, TD6-3 (96.4%) and TD6-1 (90.0%). *S. trutta* is again the predominant species (TD6-3, NISP = 216; TD6-1, NISP = 349),

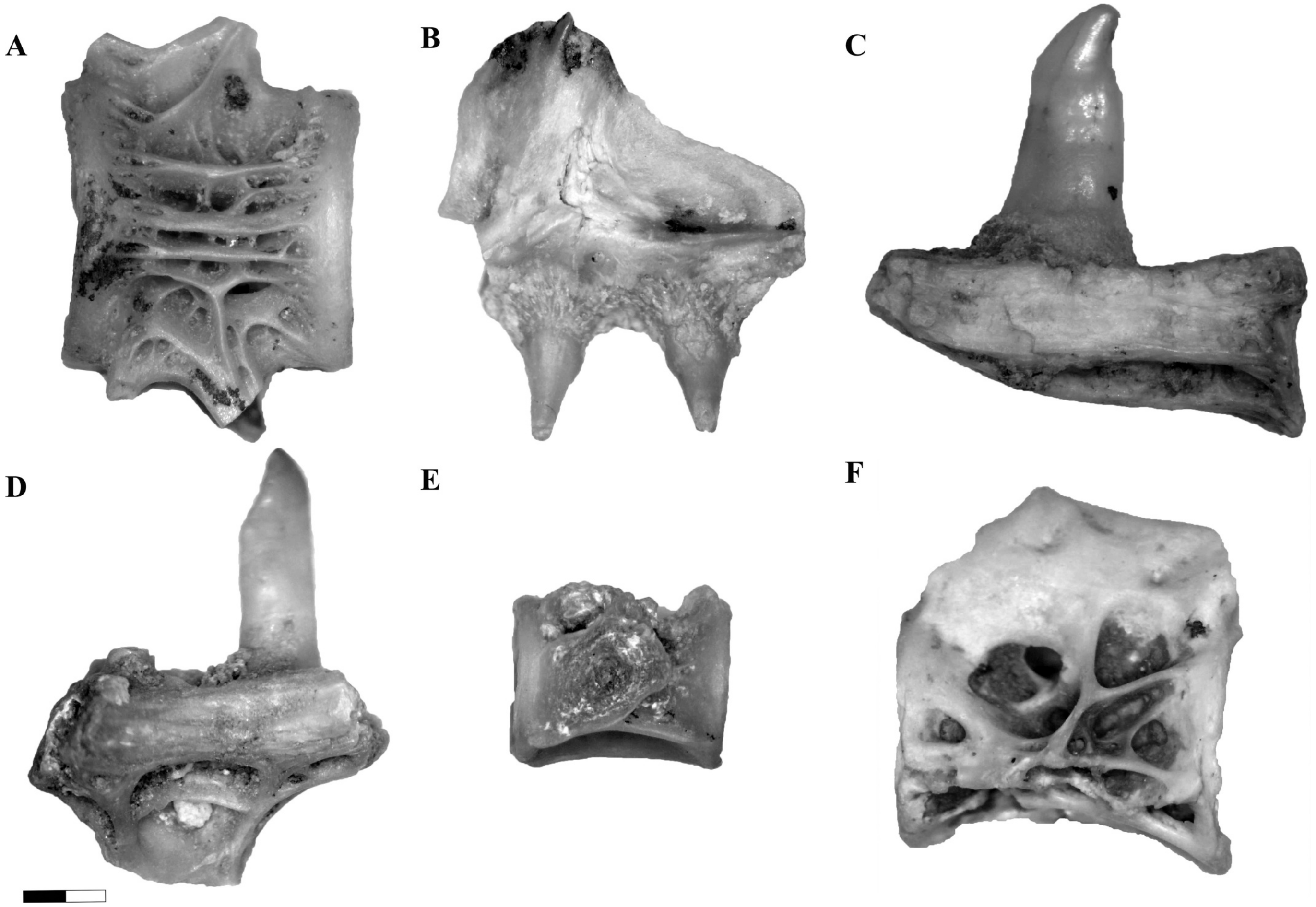

**Fig. 3.** Fish taxa from the Early and Middle Pleistocene of Gran Dolina (Spain). (**A**) Caudal vertebra of *S. trutta* in lateral view (TD6-1). (**B**) Premaxillary fragment of *S. trutta* in medial view, showing two teeth on the top (TD5b). (**C**) Branchial arch fragment of *Squalius* sp. in ventral-external view (TD10-4). (**D**) Pharyngeal arch fragment of *Squalius* sp. in dorsal-internal view (TD10-4). (**E**) Thoracic vertebra of unidentified cyprinid in lateral view (TD6-1) and (**F**) Thoracic vertebra of *A. anguilla* in lateral view (TD10-3). Scale 5 mm.

although unidentified salmonid remains were recovered in both sub-levels (TD6-3, NISP = 1; TD6-1, NISP = 2). TD7 does not include any salmonid remains. The TD8a assemblage is also dominated by the brown trout (NISP = 13, 54.2%). In all the TD10 sub-levels, Salmonidae is the most represented family, and its highest peak is reached in TD10-1, where only *S. trutta* is present (NISP = 6, 85.7%), although a decrease in the number of remains is observed from TD10-4 (NISP = 63) to TD10-1 (NISP = 6) (Fig. 4A).

### 4.1.2. Cyprinidae

Cyprinids do not occur in the assemblage until sub-level TD5c, where they are the only represented taxon (NISP = 1). Cyprinid remains correspond to 9.8% of the sample in TD5b (NISP = 12), where only two remains are identified at genus level as *Squalius* sp. Thereafter cyprinids appear again and represent 3% of the sample in TD6-3 (NISP = 11). The percentage and number of cyprinid remains increase in TD6-1, where 9.5% of the sample corresponds to this family (NISP = 23). Then the percentage further increases from TD8a to TD10-1 with some variations. TD8a has the highest representation for the family in the whole TDS assemblage, reaching 45.8% (NISP = 11), and in TD10 the percentages fluctuate from one sub-level to another, with TD10-4 (30%), TD10-3 (11.6%), TD10-2 (38.5%) and TD10-1 (14.3%). The percentage of cyprinid remains increases in the TD10 sub-levels in comparison with other levels, where cyprinids are less represented in the sample (less than 10%) (Fig. 4A).

### 4.1.3. Anguillidae

The family Anguillidae, only represented here by one species, *A. anguilla*, is present in TD5b and TD5a, representing 0.8% of the sample in both cases (NISP = 1). *A. anguilla* is the only species in TD7, with two remains. This species appears again in TD10-4, representing 6% of the sample (NISP = 6) and in TD10-3, with 11.6% (NISP = 5). The species is missing in TD10-2 and TD10-1.

## 4.2. Fish bone representation and taphonomy

The TDS samples are characterized by mainly postcranial elements in all levels. Vertebrae are the only postcranial remains recovered (total NISP = 1067; 98.2%), whereas cranial bones (NISP = 20; 1.8%) are clearly underrepresented and are absent in levels TD10-1/2, TD8a, TD7, TD5c-d and TD4 (Fig. 4D). The cranial bones recovered correspond to teeth in the case of *S. trutta* and to pharyngeal arches in the case of cyprinids. No scales, spines or ribs were recovered in this assemblage.

Bone modification analysis indicates no damage in the form of deformation, rounding or polishing. The absence of bite marks or crushed bones means that chewing action by carnivores or humans can be ruled out (Nicholson, 1993). No evidence of human activities such as butchery or burning was documented in any item either. Only digestion marks are observed in our assemblage. As outlined above, three categories of digestion marks were distinguished depending on the intensity of digestion (modified from Andrews, 1990 and Guillaud et al., 2015, 2018): null-light (category 0) (Fig. 2A), where the elements show no

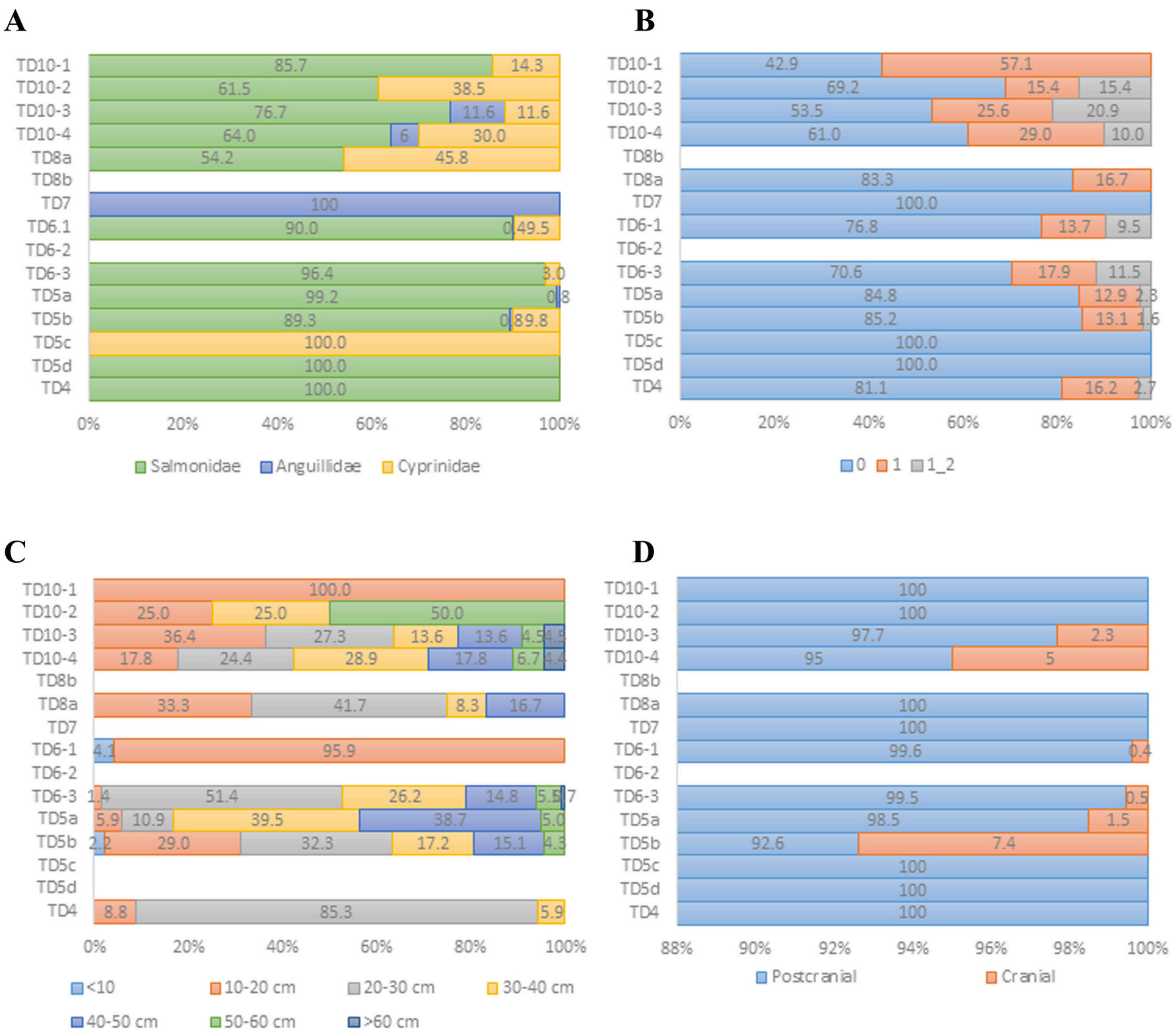

**Fig. 4.** Evolution through the Early and Middle Pleistocene sequence of Gran Dolina (Atapuerca, Spain) in %. (**A**) % for each taxon (based on Table 1). (**B**) categories of digestion marks (based on Table 3. (**C**) *S. trutta* size categories (based on Table 2 and (**D**) fish bone representation (postcranial and cranial).

alteration or only minimal alteration on their surface and only 25% or less is damaged, the shape of the bone remaining unchanged; moderate (category 1) (Fig. 2B), showing a loss of part of the bone although affecting less than 50% of the bone's surface area; moderate-heavy (category 1_2) (Fig. 2C), characterized by a major loss of bone (more than 50%) or compressed bones. The taphonomic alteration of bones is quite similar from one level to another, and no relevant differences are observable between the Middle and Early Pleistocene layers in Gran Dolina. In the Early Pleistocene levels (TD4-TD8), the most represented category is 0, which ranges between 70.6% and 100% of the samples, whereas category 1 ranges between 0% and 17.9%. The third category, 1_2, is underrepresented, and the maximum percentage is 11.5%, which is present in TD6-3. The proportion in the Middle Pleistocene levels (TD10-1/TD10-4) is similar: although the percentage of category 1 increases and ranges between 15.4% and 57.1%, the most common category is 0, which ranges between 42.9% and 69.2%. Category 1_2 is also relatively more represented, its values ranging between 10% and 20.9%, although in TD10-1 it is missing (Table 3, Fig. 4B). As a whole, the Gran Dolina sequence shows the most represented category to be 0 (NISP = 808, 74.3%), followed by category 1 (NISP = 187, 17.2%) and category 1_2 (NISP = 92, 8.5%).

### 4.2.1. *Salmonidae*

Category 0 is the one most represented among the Salmonidae remains, amounting to 71.4% (NISP = 623) of the total; 18.5% (NISP = 161) correspond to category 1, and 10.1% to category 1_2 (NISP = 88) (Table 3).

### 4.2.2. *Cyprinidae*

All the remains belonging to *Squalius* sp. from TD5b (NISP = 1) and TD10-4 (NISP = 4) show category 1. For the unidentified cyprinid remains, category 0 represents 85.1% (NISP = 80) of the sample; category 1 represents 12.7% (NISP = 12); and category 1_2 is present only in 2.2% (NISP = 2) of the total (Table 3).

### 4.2.3. *Anguillidae*

The common European eel remains are slightly different in that more samples are characterized as category 1 (56.3%, NISP = 9) than category 0 (43.7%, NISP = 7). No eel vertebra shows category 1_2 (Table 3).

**Table 3**
Identified digestion mark categories: 0 (null-light), 1 (moderate) and 1_2 (moderate-heavy) in the Early and Middle Pleistocene layers of Gran Dolina (Sierra de Atapuerca, Spain).

| Levels | Categories | Salmonidae | | | | Anguillidae | | Cyprinidae | | | | Pisces indet. | | Total NISP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Salmo trutta* | | Unidentified | | *A. anguilla* | | *Squalius* sp. | | Unidentified | | | | |
| | | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | NISP | % | |
| TD10-1 | 0 | 2 | 66.7 | | | | | | | 1 | 33.3 | | | 3 |
| | 1 | 4 | 100.0 | | | | | | | | | | | 4 |
| | 1_2 | | | | | | | | | | | | | 0 |
| TD10-2 | 0 | 5 | 55.6 | | | | | | | 4 | 44.4 | | | 9 |
| | 1 | 1 | 50.0 | | | | | | | 1 | 50.0 | | | 2 |
| | 1_2 | 2 | 100.0 | | | | | | | | | | | 2 |
| TD10-3 | 0 | 16 | 69.6 | | | 3 | 13.0 | | | 4 | 17.4 | | | 23 |
| | 1 | 8 | 72.7 | | | 2 | 18.2 | | | 1 | 9.1 | | | 11 |
| | 1_2 | 9 | 100.0 | | | | | | | | | | | 9 |
| TD10-4 | 0 | 38 | 62.3 | | | 2 | 3.3 | | | 21 | 34.4 | | | 61 |
| | 1 | 18 | 62.1 | | | 4 | 13.8 | 4 | 13.7 | 3 | 10.3 | | | 29 |
| | 1_2 | 7 | 70.0 | 1 | 10.0 | | | | | 2 | 20.0 | | | 10 |
| TD8a | 0 | 10 | 50.0 | | | | | | | 10 | 50.0 | | | 20 |
| | 1 | 3 | 75.0 | | | | | | | 1 | 25.0 | | | 4 |
| | 1_2 | | | | | | | | | | | | | 0 |
| TD7 | 0 | | | | | 2 | 100 | | | | | | | 2 |
| | 1 | | | | | | | | | | | | | 0 |
| | 1_2 | | | | | | | | | | | | | 0 |
| TD6-1 | 0 | 166 | 89.7 | | | | | | | 19 | 10.3 | | | 185 |
| | 1 | 28 | 84.8 | | | 1 | 3.0 | | | 4 | 12.1 | | | 33 |
| | 1_2 | 22 | 95.7 | 1 | 4.3 | | | | | | | | | 23 |
| TD6-3 | 0 | 243 | 94.6 | 2 | 0.8 | | | | | 10 | 3.9 | 2 | 0.8 | 257 |
| | 1 | 64 | 98.5 | | | | | | | 1 | 1.5 | | | 65 |
| | 1_2 | 42 | 100.0 | | | | | | | | | | | 42 |
| TD5a | 0 | 112 | 100.0 | | | | | | | | | | | 112 |
| | 1 | 16 | 94.1 | | | 1 | 5.9 | | | | | | | 17 |
| | 1_2 | 3 | 100.0 | | | | | | | | | | | 3 |
| TD5b | 0 | 94 | 90.4 | | | | | | | 10 | 9.6 | | | 104 |
| | 1 | 13 | 81.3 | | | 1 | 6.3 | 1 | 6.3 | 1 | 6.3 | | | 16 |
| | 1_2 | 2 | 100.0 | | | | | | | | | | | 2 |
| TD5c | 0 | | | | | | | | | 1 | 100.0 | | | 1 |
| | 1 | | | | | | | | | | | | | 0 |
| | 1_2 | | | | | | | | | | | | | 0 |
| TD5d | 0 | 1 | 100.0 | | | | | | | | | | | 1 |
| | 1 | | | | | | | | | | | | | 0 |
| | 1_2 | | | | | | | | | | | | | 0 |
| TD4 | 0 | 30 | 100.0 | | | | | | | | | | | 30 |
| | 1 | 6 | 100.0 | | | | | | | | | | | 6 |
| | 1_2 | 1 | 100.0 | | | | | | | | | | | 1 |
| Total NISP | | 966 | | 4 | | 16 | | 5 | | 94 | | 2 | | 1087 |
| % | | 88.9 | | 0.4 | | 1.5 | | 0.5 | | 8.6 | | 0.2 | | 100.0 |

### 4.3. *Body size evolution of S. trutta through the sequence and its relationship with temperature*

In general terms, significant body size variability is observed for *S. trutta* throughout the TDS sequence. This differs from the brown trout assemblage described in the Neolithic site of El Mirador cave, also in Atapuerca, where the probable accumulating agent was humans (Blanco-Lapaz and Vergès, 2016). This conclusion was based on the fact that only *S. trutta* was recovered in the assemblage, on the absence of any digestion marks, and on a body size range between 10 and 40 cm, indicating a more bounded body size (Blanco-Lapaz and Vergès, 2016). El Mirador corresponds to a typical anthropic fish accumulation as described by Russ (2010b) and Russ and Jones (2011).

The least represented body size corresponds to individuals smaller than 10 cm and is only present here in TD5b and TD6-1. Individuals with an estimated length between 10 and 20 cm are present in all levels, but their percentage varies between 1.4% in TD6-3 and 95.9% in TD6-1. In TD8a, it decreases again to 33.3%, remaining more or less stable during the first Middle Pleistocene layers (TD10-1, 17.8%; TD10-2, 36.4%; TD10-3, 25%) and reaching 100% in TD10-4 although in this case it is probably not significant since only three vertebrae were analyzed. Over the course of the sequence, two periods show greater variability in body size: the first period corresponds to the Early Pleistocene layers TD5b-TD6-3, whereas the second period corresponds to the Middle Pleistocene layers (TD10-4-TD10-2). For both periods, the variability in body size is substantial, and all sizes between 10 and 60 cm are represented, indeed even sizes greater than 60 cm in TD6-3, TD10-4, and TD10-3 (Fig. 4C).

The results of the regression models between the different measurements of temperature (MAT, MTC and MTW) and body size show no significant relationship (*p*-value >0.05).

## 5. Discussion

### 5.1. *Freshwater ecosystems around the Sierra de Atapuerca*

The fish assemblages described here permit a better description of the freshwater ecosystems around the Sierra de Atapuerca. The common brown trout, *S. trutta,* requires oxygen-rich water and a specific temperature for hatching and growing. Nowadays, *S. trutta* is the only native salmonid species in the Iberian Peninsula (Elvira, 1995; Elvira and Almodóvar, 2001) and is usually found in cold running water with temperatures ranging from 0 to 20 °C (Jonsson and Jonsson, 2009; Elliott and Elliott, 2010).

Cyprinids are more typical of temperate waters and live in water temperatures between 10 and 25 °C (Doadrio, 2002; Tissot and Souchon, 2010). Accordingly, cyprinids such as the genus *Squalius* can be found in salmonid zones, as they also thrive in running water. However, cyprinids in general are present in multiple environments, showing enormous diversity in their diet, which includes arthropods and other fishes (Doadrio, 2002).

The third taxon represented in our assemblage is the common European eel (*A. anguilla*), a catadromous fish present in all watersheds but strongly limited by dams today (Mota et al., 2016). The development of the eel occurs in rivers up to the beginning of sexual maturity; then they leave the continent for the Bermuda area, where they reproduce. After reproduction, they return to the Iberian Peninsula to lay their eggs. In the archaeological record, therefore, we could find remains belonging to both periods of their life. In the Iberian Peninsula, the eel has disappeared today from most of the Ebro, Tajo, Duero and Guadiana catchment areas (Doadrio, 2002). In present-day terms, all three main groups of fishes, *Salmo trutta*, Cyprinidae and *Anguilla* are present in pre-mountain river sections in western Europe and the Iberian Peninsula (Fig. 3D).

Understanding the role of these fish as part of the faunal assemblage is important in adding to our knowledge of the freshwater ecosystem in Gran Dolina (TD), corroborating the image of a typical river forest with the presence of limestones (Allué et al., 2015). The Sierra de Atapuerca sites are known to have been very close to river systems such as the Duero and Ebro basins, with the Arlanzón river as a main feature. Geomorphology too suggests that the Arlanzón was closer to the cave than today (Ortega et al., 2014).

Other small-vertebrate groups studied in the TDS also indicate a faunal association characteristic of Mediterranean wetland and associated freshwater ecosystems. Amphibian and reptile assemblages suggest that aquatic environments were quite well developed throughout the TDS sequence, with the presence of the viperine snake (*Natrix maura*) in all the levels of TD10, TD8a and TD4 and the rarer occurrence of the water frog (genus *Pelophylax*) in levels TD10-4, TD10-3, TD8a, TD6-3 and TD5a. Additionally, water-edge taxa (*Triturus* sp., *Pelodytes punctatus* and *Natrix natrix/astreptophora*) are well represented throughout the whole sequence (Blain et al., 2008, 2009, 2012). The viperine snake (*N. maura*) is a snake of aquatic habits, which appears in all types of continental water bodies. It has been observed in natural environments such as rivers, lagoons, ponds, and marshes. In the former, it occupies all stretches from the lower to the upper part, although it avoids the points of greatest current (Santos et al., 2002). *Pelophylax perezi* is today the most widespread water frog in the Iberian Peninsula. It is a strictly aquatic species with low ecological requirements (Llorente et al., 2002). It rarely moves more than 5 m from the water-edge (Lizana et al., 1989). It occupies all types of aquatic environments (Malkmus, 1982, 1997; Meijide et al., 1994; Lizana et al., 1995), both temporary and permanent, although it cannot be considered a species characteristic of temporary environments. It avoids water bodies with cold water, mountain streams with excessive slopes, and water courses with closed vegetation (Malkmus, 1979, 1982, 1997). Its presence has been recorded in both lotic environments (rivers, streams, irrigation ditches), where it selects areas with little current, and lentic environments (ponds, agricultural ponds, marshes, ditches, reservoirs) (Gracia and Pleguezuelos, 1990; Pollo et al., 1998).

The larval stages of *P. perezi* are typical bottom dwellers of water bodies (Díaz-Paniagua, 1985). Given the late reproductive period of the species, they occupy water bodies with summer characteristics: smaller dimensions, less vegetation cover, higher temperature, and lower oxygen concentrations (Díaz-Paniagua, 1983; Díaz-Paniagua, 1988). They almost always occupy relatively deep and permanent waters (García-París, 1989). In the latter bodies of water, the larvae of this species show a clear preference for occupying areas densely covered by submerged aquatic vegetation (thus showing a certain depth), avoiding deeper areas where aquatic vegetation is non-existent (Díaz-Paniagua, 1987).

Sánchez-Marco (1999) analyzed the bird remains from TD6. The only aquatic bird classified to species level was *Anas crecca*, although Núñez-Lahuerta et al. (2019) confirmed the presence of many anseriforms using eggshells remains, also in TD6.

The Eurasian green-winged teal (*Anas crecca*) is a common and widespread duck that breeds in temperate Eurosiberia and migrates south in winter. It is a highly gregarious duck outside the breeding season and can form large flocks. It is commonly found in sheltered wetlands and feeds on seeds and aquatic invertebrates. It nests on the ground, near water and under cover. In the breeding season, it is a common inhabitant of sheltered freshwater wetlands with some tall vegetation, such as taiga bogs or small lakes and ponds with extensive reedbeds. In winter, it is often seen in brackish waters and even in sheltered inlets and lagoons along the seashore (Carboneras, 1992).

Piscivorous birds of prey such as the European eagle owl, *Bubo* (Russ, 2010b; Guillaud et al., 2018), or the white–tailed sea eagle, *Haliaeetus albicilla*, have also been found in the Sierra de Atapuerca. Most of the fish diet of the European eagle owl corresponds to salmonids and cyprinids (Russ, 2010a, 2010b), although other authors have described the presence of clupeids and anguillids in their diet (Guillaud et al., 2018). The fish diet of *H. albicilla* is mainly constituted by cyprinids, pike (*Esox lucius*) and perch (*Perca fluviatilis*) (Mlíkovský, 2009; Van Rijn et al., 2010).

Finally, some small-mammal associations recovered in Gran Dolina are also related to aquatic ecosystems. These include *Arvicola* aff. *sapidus* (in TD10), *Mimomys savini* (in TD4 to TD7), *Castor fiber* (in T4 to TD10), and the eulipotyphlans *Neomys* sp. and *Dolinasorex glyphodon* (in TD4 to TD6), indicating the presence of a water edge, above all during the transition TD5-TD6 and in particular during the aquatic habitat maximum in TD10, accompanied by a slight decrease in the open dry habitatsand a minor increase in open humid and woodland ones (Rofes and Cuenca-Bescós, 2009, 2011; Moya-Costa et al., 2019). Water-foraging bats such as *Myotis capaccinii* and *Myotis nattereri* are recovered from these levels (TD5-TD6), also indicating water resources (Galán et al., 2019).

In conclusion, though concordant with other paleoenvironmental proxies, the fish remains from TDS studied here make it possible for the first time to offer a more detailed description of some of the freshwater ecosystems around Gran Dolina during the Early-Middle Pleistocene, in particular the presence of a pre-mountain river system characterized by permanent, oxygen-rich, relatively cold running waters.

### 5.2. *The accumulator of the fish remains*

To understand whether the fossil assemblage is a reflection of the natural communities around the sites, it is important, in Pleistocene caves and rock shelter sites, to identify the accumulator of the small vertebrates (Russ, 2010b) and in this case the fishes. Previous studies indicate that the amphibians and reptiles in Gran Dolina are of mixed provenance. Some of them may certainly have been accumulated inside the cave by a predator, as in the case of small mammals, but for others, such as the natterjack toad *Epidalea calamita*, a more probable origin is in situ mortality within the cave during wintering (Blain et al., 2008; Martínez-Monzón et al., 2018). For small-mammal assemblages, taphonomic observations corroborate the hypothesis that large accumulations of rodents and insectivores stem mostly from fossil pellets that enter the cave with sediment and are allochthonous in origin (Fernández-Jalvo and Andrews, 1992). Given the type of digestion and the breaks in the fossils, these are mostly due to nocturnal birds of prey such as the barn owl (*Tyto alba*) and the eagle owl (*B. bubo*), opportunists that hunt a broad range of prey (Bennássar, 2010). The role of birds of prey and above all the eagle owl has been studied in various European regions, such as France (Bayle, 1994; Cochard, 2008), as well as in the Iberian Peninsula (Cramp, 1985; Lloveras et al., 2009). According to our results on the different taphonomic categories, all percentages (Fig. 4B) are similar to those obtained by Guillaud et al. (2018) in their study of *Bubo* pellets, indicating that this bird of prey was probably the main accumulator of fish remains, capturing the fish from spring to autumn.

The European eagle owl is a nocturnal, opportunistic predator that shows a generalist and very varied diet (including medium-sized mammals such as hedgehogs and lagomorphs but also small rodents, birds, and amphibians); the resultant deposits of partially digested skeletal remains are present in the vicinity of the nest area (Andrews, 1990). The diversity of species represented in the assemblage would thus also be a typical characteristic for this accumulator of fish remains (Russ and Jones, 2009; Russ, 2010b; Guillaud et al., 2018).

Fish consumption by *B. bubo* has also been studied in the Grotte du Bourrouilla (France) by Le Gall (1999), indicating that the fish eaten by this species measure from a few centimeters up to 40 cm, although the majority in our *S. trutta* samples are between 10 and 30–40 cm in size (Table 3, Fig. 4C). The fact that we describe the presence of different body size classes among our *S. trutta* indicates non-selectivity of prey among the brown trout community. Many other studies have indicated the Eurasian eagle owl (*B. bubo*) as a possible accumulating agent at European archaeological sites. These include Andrews (1990), Sanchís-Serra (2000), Laroulandie (2002), De Cupere et al. (2009) and Russ (2010b).

Other predators documented in Gran Dolina can be ruled out, such as hominins and carnivores (canids, felids, mustelids, bears and hyenas), as well as other birds of prey such as other Strigiformes and diurnal raptors (Accipitriformes). Several fish-feeding experiments and studies involving carnivores (*Canis familiaris*) (Jones, 1984, 1986) and humans (*Homo sapiens*) (Jones, 1984, 1986; Nicholson, 1993) identified various characteristics for recognizing digested material. However, these signals have proved not to be species-specific and can only establish whether the remains were digested or not. As there are no chewed or crushed fish bones in the TDS fossil assemblage, we can rule out humans and carnivores as possible accumulator candidates, as these are known to produce such types of modification. Hyenas, for example, produce substantial and characteristic damage on the bone surface and the total destruction of bones.Experimental research by Russ and Jones (2011) on four female brown bears (*Ursus arctos*) showed that bears focus on large salmonids (longer than 30 cm in total length). The bears selected head elements, but whole fish were also consumed, and digested fish remains were only present in feces deposited in the wider environment but never within the caves (Russ and Jones, 2009, 2011). Other mammalian carnivores such as the otter (*Lutra lutra*) (not described in Gran Dolina but comparable with other small-medium-sized carnivores) and wolf (*Canis lupus*) (Russ and Jones, 2009) produce greater damage on fish bones (Guillaud et al., 2015). Previous studies of the feces of small-medium-sized felids show that the digestion processes of these animals generally produce extremely broken bones with high levels of rounding and polishing (Andrews and Evans, 1983; Andrews, 1990; Matthews, 2002).

The other birds of prey (mainly Strigiformes) represented as fossils in Gran Dolina, such as *Tyto alba*, are too small compared with *Bubo* to have been able to catch the larger specimens of *S. trutta* documented in some of the layers (Broughton et al., 2006; Russ, 2010a, 2010b). Although most of the diet of *H. albicilla* is constituted by aquatic birds, fish are also part of their food acquisition (Mlíkovský, 2009; Van Rijn et al., 2010). Taphonomic studies of accipitriform pellets confirm severe and extreme digestion on the bone surface (Lloveras et al., 2008; Fernández-Jalvo et al., 2016). Such modification is not reported on any of the fish remains from TDS. In conclusion, the great diversity of fish species, the fish bone representation and the less destructive digestion suggest the European eagle owl (*Bubo bubo*) as the potential fish bone accumulator in Gran Dolina, also proving the presence of a river system close to the cave, since the vital domain of these nocturnal birds of prey is an area of around 2.3 km$^2$ during incubation (around 500 m away) and parental care (around 250 m away) (Penteriani and Delgado, 2008, Penteriani et al., 2015).

### 5.3. Fish body size and climate

Two differentiated peaks can be observed among our fish assemblages, indicating maximum average body size values of *S. trutta* in the timespan between the sub-levels TD5b and TD6-3 and from sub-levels TD10-4 to TD10-3 respectively (Table 4, Fig. 5A). Both peaks also represent the group of sub-levels with the highest body size variability in the assemblage, encompassing lengths from less than 10 cm to more than 60 cm. In accordance with Bergmann's rule, the brown trout individuals in Gran Dolina would be expected to be bigger under colder temperatures and smaller under warmer temperatures. At first sight, this seems not to be the case here, because the two observed peaks of higher sizes (TD5b/TD6-3 and TD10-4/TD10-3) correspond to different estimated MATs (11.4 °C and 12.6 °C respectively (Table 4, Fig. 5D)). In addition, no statistical relationship between the body size of *S. trutta* and temperature is found. This indicates that, in this concrete case, the species in question does not follow Bergmann's rule (either standard or converse). Moreover, no relevant relationship is evidenced between body size and MTW and MTC (Fig. 5 C–D).

Even though there is no statistical relationship between temperature and body size, it is noteworthy that the maximum mean body size of *S. trutta* is reached in the coldest period of the entire sequence (TD5b/TD6-3), which falls within the Early Pleistocene. In addition, during the levels corresponding to this period (TD5a to TD6-1), the variation in body size of *S. trutta* follows Bergmann's rule, whereas in the upper levels of the sequence corresponding to the Middle Pleistocene (TD8a to TD10-1), it does not show any recognizable pattern. Furthermore, the Middle Pleistocene levels are those with the lowest numbers of remains, and although the sample size for these layers is considered enough to provide adequate and representative statistical results, this difference in the number of remains analyzed per level may generate some bias in our results. On the other hand, the level with the lowest sample size (TD8a) is almost in accordance with the trend exhibited during the Early Pleistocene, which may constitute an indication of the suitability of the present sample sizes for this kind of analysis. The most likely explanation for this divergence affecting the Middle Pleistocene is that other ecological factors such as competition, resources or predation are influencing the changes in body size of *S. trutta* to a greater extent than climate during this period.

In any case, both Bergmann's rule and the converse Bergmann rule have been found in freshwater fishes (Rypel, 2014). Likewise, it has also been widely reported that these organisms may not show any pattern relating climate and body size (Rypel, 2014; Belk and Houston, 2002). Specifically for *S. trutta*, some studies have obtained no clear results on its adhesion to Bergmann's rule (Rypel, 2014), whereas the converse Bergmann rule has been found in others (Parra et al., 2009).

It seems that studies of macroecological patterns such as Bergmann's rule in poikilothermic organisms and particularly in freshwater fish such as *S. trutta* have not yet reached a clear consensus, so further investigation is required. Even though this study has not yielded conclusive results about body size patterns, investigators should keep on considering the fossil record as a valuable source of new data for paleoecological studies. The unique characteristics of the fossil record (for example, the absence of overexploitation of larger individuals, or the huge timespans it provides for study) make it an excellent source of data that will contribute to the resolution of current macroecological questions.

On the other hand, one of the problems in paleoarchaeological investigation is that fish remains will often be identified and interpreted separately from other faunal remains. In order to identify the potential predator, the ecosystem and the paleoenvironment, however, we must consider the faunal register as a whole, especially when fish are mixed with other small vertebrates. Hopefully, the results of this paper will encourage further fish studies in European Pleistocene sites to increase our knowledge of freshwater ecosystems, using fish remains as part of paleoenvironmental and paleoecological reconstructions to interpret their role during this period and in human evolution.

**Table 4**
*Salmo trutta* body size estimations in Gran Dolina (Sierra de Atapuerca, Spain), organized according to the climate units established by Martínez Monzón et al. (2018) and averaged values for mean annual temperature (MAT), mean temperature of coldest month (MTC) and mean temperature of warmest month (MTW) (from Blain et al., 2009, 2012, 2013).

| Level | Body size *Salmo trutta* (mm) | | | | | | | Average | Total NISP | Temperature (°C) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | <100 | 100–200 | 200–300 | 300–400 | 400–500 | 500–600 | >600 | | | MTW | MTC | MAT |
| TD5b | 2 | 25 | 24 | 14 | 12 | 3 | | 273.3 | 80 | 19.5 | 3.3 | 11.8 |
| TD5b/TD6-3 | | 10 | 118 | 127 | 91 | 23 | 2 | 352.3 | 371 | 19.5 | 3.3 | 11.4 |
| TD6-3/TD6-1 | 8 | 191 | 51 | | | | | 165.1 | 250 | 20 | 3.6 | 12.3 |
| TD8a | | 4 | 5 | 1 | 2 | | | 172.9 | 12 | 20.2 | 3.7 | 12.6 |
| TD10-4/TD10-3 | | 8 | 12 | 14 | 10 | 3 | 2 | 348.7 | 49 | 20.2 | 3.7 | 12.6 |
| TD10-3/TD10-1 | | 9 | 6 | 3 | 1 | 3 | 1 | 295.6 | 23 | 19.8 | 3.8 | 11.7 |

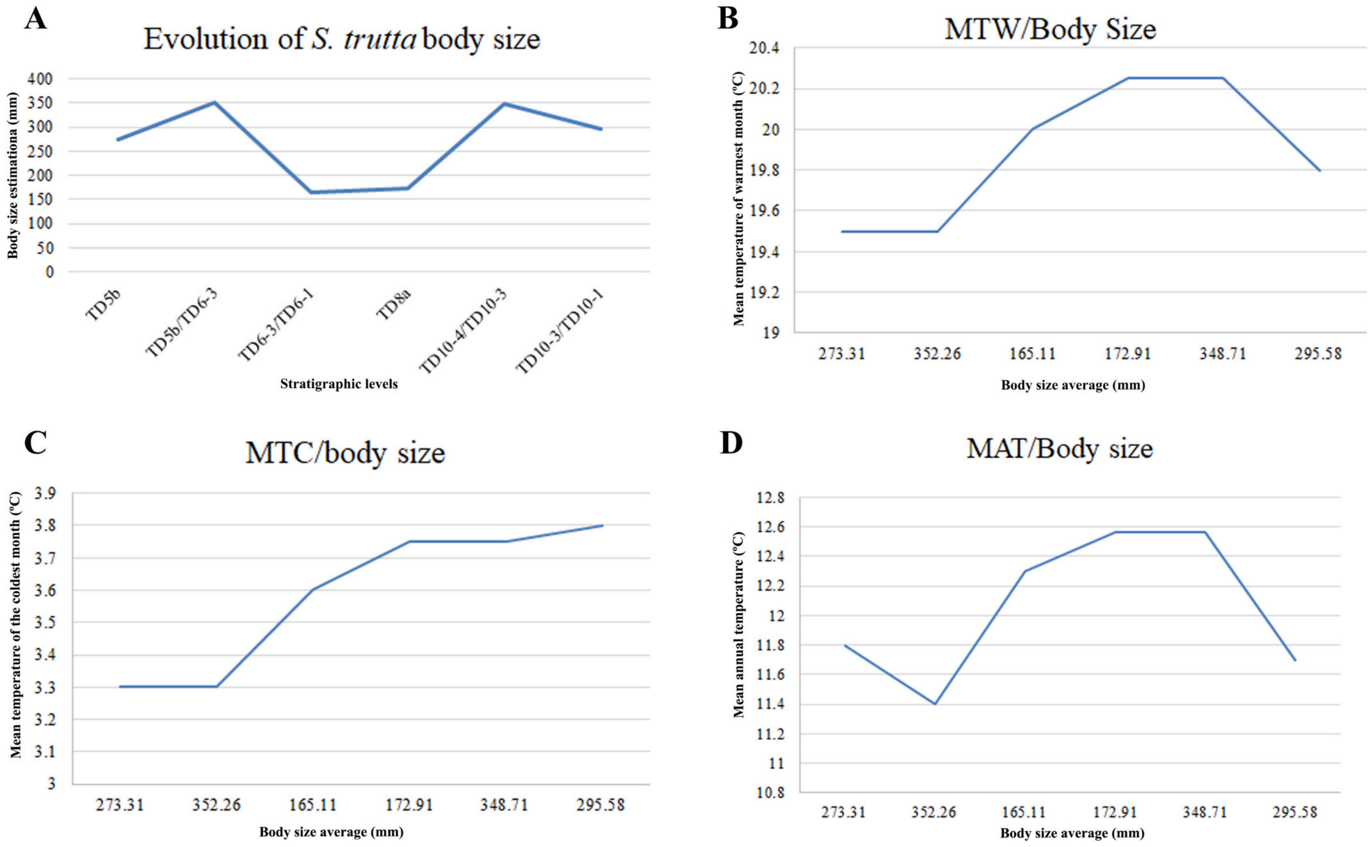

**Fig. 5.** Body size/climate correlation for *S. trutta* in the Early and Middle Pleistocene of Gran Dolina (Sierra de Atapuerca, Spain). **(A)** Evolution of the average body size through stratigraphic levels, **(B)** Correlation of the average body size and the averaged values for mean temperature of warmest month (MTW), **(C)** Correlation of the average body size and the averaged values for mean temperature of coldest month (MTC), **(D)** Correlation of the average body size and the averaged values for mean annual temperature (MAT).

## 6. Conclusions

The fish taxa identified in this paper permit us to enlarge the faunal list of the Gran Dolina site (northern Iberia), adding to other small-vertebrate taxa such as amphibians, reptiles, small mammals, and birds and providing a valuable overview of the freshwater ecosystems around the Sierra de Atapuerca during the Early-Middle Pleistocene. In addition to *Salmo trutta* (brown trout), which is the most represented taxon, this study provides the first record in Sierra de Atapuerca for *Squalius* sp. (chub) and *Anguilla anguilla* (common European eel).

The origin of the fish assemblage is also clarified, in that the presence of digestion marks on the bone surface categorized from null to medium-high in intensity point to *Bubo bubo* (European eagle owl) as a potential predator. This accumulating agent has been identified in other sites in the Sierra de Atapuerca such as Sima del Elefante, as well as at other Pleistocene sites in Spain, France, Belgium, and Germany and for other taxa such as micromammals and herpetofauna. This thus suggests that human activity in Gran Dolina was not the potential accumulator of the fish remains. Other criteria, such as bone representation, the body size of the fishes, and species representation, also need to be taken into account to investigate the potential fish bone accumulator in archaeological cave sites. For the first time in an Iberian Pleistocene site, this research also reveals that the body size of *Salmo trutta* does not follow Bergman's rule, unlike other taxa such as amphibians or lacustrine fish species.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix 3

Blain, H-A., Sánchez-Bandera, C., Fagoaga, A., **Blanco-Lapaz, A**., Martínez-Monzón, A., Bisbal-Chinesta, J.F., Moclán, A., Huguet, R., Laplana, C., Márquez, B., Sevilla, P., Arsuaga, J.L., Pérez-González, A., Baquedano, E. 2022**.** A warm and humid paleoecological context for the Neanderthal mountain settlement at the Navalmaíllo rock shelter (Iberian Central System, Madrid)**.** Quaternary Science Reviews. 293: 107727. https://doi.org/10.1016/j.quascirev.2022.107727

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# A warm and humid paleoecological context for the Neanderthal mountain settlement at the Navalmaíllo rockshelter (Iberian Central System, Madrid)

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## ABSTRACT

Neanderthals have been claimed to have had a selective adaptation to rugged, wooded landscapes that would have partially compensate their high basal metabolic rate and locomotor energetic costs through reducing search time and increasing diet breadth. The archaeological site of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid), located in a mountain environment in central Iberian Peninsula, has been interpreted as a repeated short-term occupation hunting camp by Neanderthal groups, mainly focused on primary access to large bovids and cervids. Navalmaíllo rockshelter has also furnished fish, toads, frogs, tortoises, lizards and snakes remains. This association of amphibians and reptiles suggests a much warmer climate (+2.8 °C) for layer F than at present, with similar temperatures during the summer but higher temperatures throughout the remaining months. Rainfall was slightly more abundant (+180.6 mm) than today, with a more contrasted regime during the year, with rainier winters and drier summers. A two-month period of aridity is observed during summer, representing a similar duration to present-day climatic conditions. Reconstructed landscapes are mainly constituted by open areas with dry grassland and rocky or stony areas, evolving laterally to humid meadows, probably close to the aquatic and peri-aquatic areas, such as rivers or ponds with riverside vegetation. Woodland environments are

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also well represented around the site, with medium scrublands to forest formations. Fish complete this reconstruction by documenting the presence of a pre-mountain well-developed river system characterized by relatively cold, permanent, oxygen-rich, and running waters. Such reconstruction is in disagreement with previous pollen interpretation for Layer F that suggested a very open and cold environment. Our new interpretation suggests that the Neanderthal occupation of the Navalmaíllo rockshelter occurred during a somewhat temperate and humid period, probably within the later part of the Marine Isotope Stage 5, effectively favouring the presence of a high biodiversity around the site.

## 1. Introduction

Neanderthals have been claimed to have had a selective adaptation to rugged, wooded landscapes that would have both influenced their distribution across Eurasia and their terminal presence restricted largely to mountainous refugia (Finlayson, 2004; Stewart, 2005; Dusseldorp, 2009; Henry et al., 2017; López-García et al., 2019, 2022). By situating residential camps in settings of high biodiversity and compact, vertically ordered environmental zonation, Neanderthals would have been able to partially compensate for their high basal metabolic rate and locomotor energetic costs through reducing search time and increasing diet breadth. According to Henry et al. (2017), an irregular landscape not only tends to produce greater biodiversity and concomitant increased diet breadth, it also organizes environmental zones into elevational belts that are more tightly packed than those associated with more regular terrain. Moreover, subsistence resources in such vertically zoned environments tend to peak at different times, often staggered over several seasons, thus reducing the need for Neanderthal groups to have repositioned their residential camps as often. Within the context of the rugged landscape of the rich and diverse Mediterranean woodland environment, Neanderthal placement of residential camps may have offered several adaptive benefits that would have acted to off-set the disadvantages associated with their relatively small site exploitation territory areas (e.g. Henry et al., 2017; Nabais and Zilhão, 2019; Spagnolo et al., 2019; Spikins et al., 2019; Stewart et al., 2019). From another perspective, Neanderthal leg morphology, while being relatively disadvantageous in regular landscapes, may actually have conferred locomotive advantages in more rugged landscapes (Higgins and Ruff, 2011). Additionally, the short, compact stature of Neanderthals, traditionally linked to adaptation to cold climatic conditions, also may have been beneficial to maneuvering within and exploiting more closed environments such as those found in the Mediterranean woodlands (Bro-Jørgensen, 2008).

Recently, Moclán et al. (2021) proposed a complete zooarchaeological and taphonomic analysis of the large and medium-sized vertebrates recovered from layers F and D at the Navalmaíllo rockshelter. According to these authors, these assemblages constitute, at the moment, one of the largest set of studied faunal remains for the Iberian inland (>13,000 faunal remains), and suggested the site to serves as a reference for understanding the varied subsistence strategies of Neanderthal groups in the region. Moclán et al. (2021) interprets the functionality of layers F and D at the Navalmaíllo rockshelter to have been a hunting camp used by Neanderthal groups during some short-term episodes of use of the site, mainly focused on primary access to large bovids and cervids and less frequently on horses, rhinoceroses and small sized animals. These preys were captured locally, transported to the camp, and following their processing, parts of them would have been transported elsewhere.

Previous paleoenvironmental reconstruction at Navalmaíllo rockshelter has been based on pollen (Ruiz Zapata et al., 2015), suggesting very open landscapes (Layers F and α-β), interpreted as indicative of cool and dry conditions, inhibiting the development of a complex floristic cortege. In contrast with such reconstruction, the predominance of large bovids (*Bos*/*Bison*) and medium-sized cervids (*Cervus elaphus*, *Dama* and, *Capreolus*), against horses (*Equus ferus, Equus hydruntinus*) and rhinoceroses (*Stephanorhinus hemitoechus*) rather suggest that forest extension may have been better represented than previously interpreted during this period. Such apparent discrepancy between the pollen and faunal reconstructions probably have a taphonomic reason.

In this line of characterizing Neanderthal activities and their probably ecologically-constrained occupation of the territory in Mediterranean Europe, this study aims to describe for the first time the fish, amphibian and reptile assemblages from the Navalmaíllo rockshelter (layers FL, F and D), and to present paleoenvironmental and paleoclimatic considerations of the environment around the site, when Neanderthals once thrived in the Lozoya Valley. Comparison with other sites from the Calvero de la Higuera Archaeological Park and from the lower altitude sites from the south-eastern part of the Madrid Region are also drawn in order to understand their spatial and altitudinal occupation of the territory during interglacial periods.

## 2. Navalmaíllo rockshelter

The Navalmaíllo rockshelter was discovered in 2002 and has been excavated without interruption since then. It is part of the Calvero de la Higuera Archaeological Park near Pinilla del Valle (altitude 1114 m. a.s.l.) in the upper reaches of the Lozoya River valley in the Sierra de Guadarrama (in the Central System mountain range) (Fig. 1) some 55 km north of Madrid (Arsuaga et al., 2010, 2012; Baquedano et al., 2012, 2015, 2016, 2021; Huguet et al., 2010; Laplana et al., 2015; Márquez et al., 2013; Pérez-González et al., 2010). The Calvero de la Higuera sites - caves and rockshelters - are associated with the cavities that developed in Upper Cretaceous carbonate rock; these were occupied by Neanderthals during isotopic stages 5, 4 and 3 (Pérez-González et al., 2010). Navalmaíllo is a rockshelter with a surface area of some 250 m2 that was formed by the Valmaíllo Stream (Análisis y Gestión del Subsuelo S.L. [AGS], 2006; Pérez-González et al., 2010). The excavation area is divided in two: Navalmaíllo North and Navalmaíllo South.

The stratigraphic sequence at Navalmaíllo North (Arriaza et al., 2017; Pérez-González et al., 2010), from bottom to top, starts with at least 2 m of allochthonous fluvial deposits (FL) - sands and siliceous gravel - deposited by the Valmaíllo Stream. Directly above this unit lies level F, a 0.85 m thick clay-sand deposit (color 10 YR 4/3) with dolostone clasts. Two thermoluminescence dates are available, one of 71.685 ± 5.082 ka, the other 77.230 ± 6.016 ka, placing this level at the end of MIS5a or the beginning of MIS4. Palynological data for level F suggest an open environment (Ruiz Zapata et al., 2015). This level contains abundant archaeological remains along with hearths (Baquedano et al., 2012). About ~50 m2 have been excavated to a depth of ~20 cm. Large blocks of dolomite

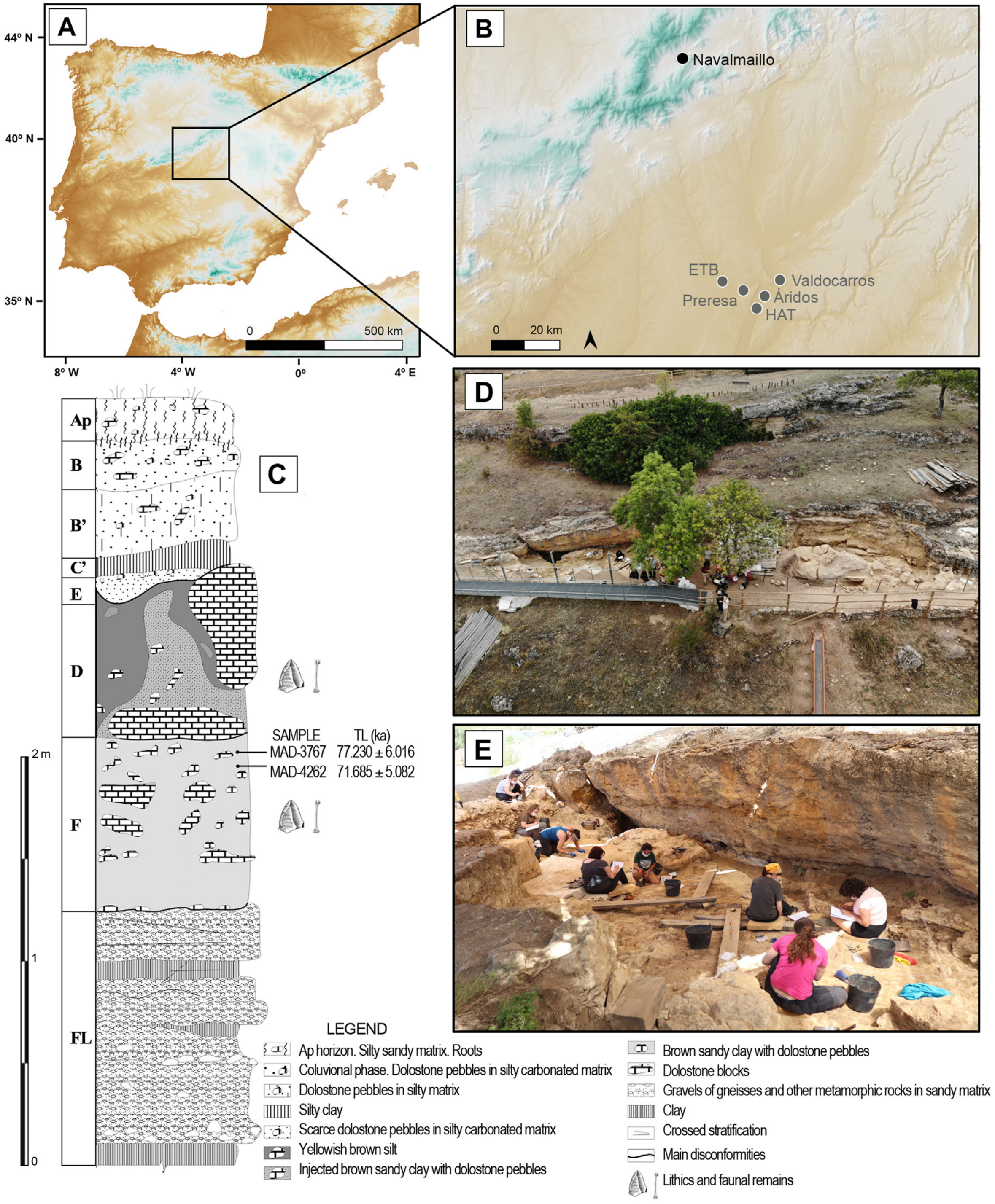

**Fig. 1.** Geographic and geological context of the Navalmaíllo rockshelter (Madrid, Spain). A, B. Geographic location of Navalmaíllo rockshelter and of the other localities from the South-East of Madrid Region mentioned in the text. C. Synthetic stratigraphic column (modified from Arriaza et al., 2017). D. Aerial view taken with a drone, showing the entire surface of the site, with the northern sector on the left of the picture and the southern sector on the right (J. Trueba, Madrid Scientific Films). E. Detail view of the excavation in the northern sector (T. Sanz).

are found at the top of level F, some with their longest axis exceeding 1 m in length. These blocks originated from the ceiling of the rockshelter, which caved in. These dolostone blocks, alongside hydroplastically injected level F sediment and percolated sediment from overlying units form level D. A clayey deposit, level C', is locally found overlying level D. Two conglomerate levels (α and β), up to 1 m thick, with dolostone clasts and a silt-sand matrix (7.5 YR 6/3) show signs of anthropic activity (still under study), and contain lithic and faunal remains, and hearths (Baquedano et al., 2012). The stratigraphic sequence at Navalmaíllo North ends with a 0.20–0.40 m thick Ap horizon (10 YR 5/2).

The stratigraphic sequence at Navalmaíllo South, from bottom to top, starts with levels F and D, as in Navalmaíllo North. Level B, up to 1.4 m thick, is a dolostone conglomerate with a silt-sand matrix which overlies level D throughout the majority of the excavation area. A local (1 m in diameter) and dense fossiliferous breccia, level C, is found towards the base of level B, also overlying level D, with a silt-sand matrix. An Ap horizon (10 YR 5/2), 0.20–0.40 m thick, ends the stratigraphic sequence at Navalmaíllo South.

Analysis of the archaeological remains of level F show over 60% of the total to have a lithic industry origin (Márquez et al., 2016b). Most of the lithic remains (~78%) are made from quartz collected in the surrounding area (Márquez et al., 2013); indeed, some 97% of all the lithic remains represent locally collected material (Abrunhosa et al., 2014, 2019, 2020). A tendency towards apparently intentional microlithization has been noticed, at least for tools made from quartz (Márquez et al., 2013). The presence of hammerstones, anvils and bipolar products indicates that the bipolar percussion technique was used in the production of small quartz tools. The simple flake is the most common technological category represented, although different types of retouched elements have been recovered (Márquez et al., 2013). Use-wear studies have revealed the versatile use of tools at the site, for example in butchering and wood working, etc. (Márquez et al., 2016a; b, 2017).

The hearths discovered show little vertical development (shallow hearths), although with some structural organisation in some cases (Baquedano et al., 2012).

Preliminary studies of the faunal remains have shown the most common taxa to be large and medium-sized animals; evidence of anthropic action is clear (e.g. there are two bovine metapodials identified as bone retouchers) (Huguet et al., 2010; Moclán et al., 2018, 2020, 2021). Lynxes appear to have been responsible for the accumulated remains of rabbits (Arriaza et al., 2017); little other carnivore action is apparent. Finally, Moclán et al. (2021), interprets the functionality of levels F and D at the Navalmaíllo rockshelter from a zooarchaeological and taphonomic standpoint. According to these authors, the site appears to have been used repeatedly by Neanderthal groups as a short-term hunting camp. Human use of animal resources at the site reflects a focus on primary access to large bovids and cervids. Access to horses, rhinoceroses and small sized animals was much less frequent. Animals were captured locally, transported to the camp, and following their processing, parts of them would have been transported elsewhere. All phases of butchery were identified, along with the extraction of marrow from long bones, revealing a clear interest in obtaining this nutritious food. Competition with carnivores was low-level, but lynxes were responsible for accumulating lagomorph remains, and hyenas appear to have fed on carrion left over by the camp's occasional Neanderthal users (Arriaza et al., 2017). Other carnivores may have done so too from time to time.

## 3. Material and methods

### 3.1. Systematic paleontology

The fish, amphibian and most of reptile fossil remains used for this study (Table 1) consist of disarticulated elements collected by water-screening of the sediments obtained during the archaeological excavations from 2004 to 2019 at the site of Navalmaíllo rockshelter. Sediments were water-screened using superimposed 10, 2.5 and 0.5 mm mesh screens and bagged by square, layer and excavation levels. In subsequent years, the microfossils were processed, sorted and classed in broad categories at the Museo Arqueológico Regional de la Comunidad de Madrid (Alcalá de Henares, Spain), where the material is curently housed. Additionally, some larger coordinated elements, as tortoise shell elements, were found during the excavation process and thus have been coordinated in the field.

We identified the fish remains recovered at Navalmaíllo rockshelter mainly by using the modern reference collection at the University of Tübingen and osteological atlases (Lepiksaar, 1994; Watt et al., 1997). The taxonomic nomenclature follows Cannon (1987). To determinate the body size based on fish vertebrae, we visually estimated the fish size through direct comparisons with specimens of known length data from the reference collection when osteometric models were not available, for example, in cyprinid remains. In addition, we used published regression equations (Prenda et al., 2002) to estimate the fish size of brown trout (*Salmo trutta*) based on the total length of the vertebrae.

The amphibian and squamate specific attributions were mainly based on the best available diagnostic elements: ilia, scapulae and sacra for anurans, frontal, quadrate and jaws for lizards, vertebrae for blanids, and trunk vertebrae for snakes. The taxonomic classification of the current species follows Speybroeck et al. (2020). Taxonomic identification of chelonians is based on the overall morphology of the shell elements and on the pattern resulting from the impression of the epidermal shields, according to the criteria given by Gmira (1995) and Hervet (2000, 2004). Comparisons were made using the dry skeleton collections of the Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain) and the osteological collections hosted at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES, Tarragona, Spain).

The different assemblages have been quantified in Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI). As usual in archaeozoology, the MNE corresponds to the number of anatomical elements taking into account the refitting of some broken elements. The Minimum Number of Individuals has been done by counting the most represented element divided by the number of present elements in a living specimen (i.e. taking into account laterality when possible). In the case of anurans, sex has also been used for humeri. In the case of tortoises, size of the plates has been taken into account and morphological particularity in addition to anatomical feature previously mentioned.

### 3.2. Taphonomy

A full taphonomic study was out of purpose of the present study. Nevertheless basic analyses have been done during the study of the remains, in order to insure that there were not important taphonomic bias in our assemblages that may alter our paleoenvironmental and paleoclimatic reconstructions. The complete taxonomical and anatomical analyses done in this work would permit to detect any abnormal skeletal representation. Traces of human activities such as butchery or burning, animal modifications such as gnawing, pits and digestion marks, as well as environmental alterations, were also checked during this study. Bone surface damage was allocated to three categories of digestion mark: null-light, moderate and moderate-heavy (modified from Andrews, 1990; Pinto-Llona and Andrews, 1999; Fernández-Jalvo et al., 2016; Guillaud et al., 2015, 2018; Bisbal-Chinesta et al., 2020).

### 3.3. Paleoenvironmental reconstruction

The Habitat Weighting method (adapted by Blain et al., 2008 for herpetofauna) has been used for the paleoenvironmental reconstruction. This method is based on distributing each amphibian and reptile taxon in the habitat(s) in which they can be found today on the Iberian Peninsula, and estimating the representation of these different habitats around the site in the past based on the MNI per taxon (Table 2).

The five habitat categories included are: *Open Dry*: environments with little vegetation or vegetation of low height and subject to seasonal changes in humidity, especially during the summer drought; *Open Humid*: wet areas with low perennial and dense

**Table 1**
Stratigraphical distribution of the fish, amphibians and reptiles represented in the Late Pleistocene site of Navalmaíllo rockshelter (Madrid, Spain), by Minimum Number of Elements (MNE) and by Minimum Number of Individuals (MNI).

| | North Sector | | | | | | | | South Sector | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Layer FL | | Layer F | | Layer D | | Layer ß | | Layer C | | Layer B | | TOTAL | |
| | MNE | MNI | MNE | MNI | MNE | MNI | MNE | MNI | MNE | MNI | MNE | MNI | MNE | MNI |
| *Salmo trutta* | | | 10 | 1 | | | | | | | | | **10** | **1** |
| Cyprinidae indet. | | | 4 | 1 | | | | | | | | | **4** | **1** |
| *Bufo spinosus* | 4 | 2 | 13 | 2 | 1 | 1 | | | | | | | **18** | **5** |
| *Epidalea calamita* | 13 | 2 | 116 | 12 | 4 | 1 | 3 | 1 | 2 | 1 | 6 | 1 | **147** | **18** |
| Bufonidae indet. | | | 20 | | 2 | | | | | | 1 | | **23** | **0** |
| *Rana* cf. *R. iberica* | | | 1 | 1 | | | | | | | 1 | 1 | **2** | **2** |
| Anura indet. | | | 8 | | | | | | | | | | **8** | **0** |
| *Testudo hermanni* | 1 | 1 | 197 | 5 | 19 | 1 | | | 7 | 2 | | | **224** | **9** |
| Lacertidae indet. (large-sized) | | | 31 | 6 | 4 | 1 | 1 | 1 | | | | | **37** | **8** |
| Lacertidae indet. (small-sized) | 2 | 1 | 16 | 3 | | | | | | | | | **18** | **4** |
| *Chalcides* cf. *Ch. striatus* | | | 2 | 1 | | | | | | | | | **2** | **1** |
| *Blanus* sp. | | | 1 | 1 | | | | | | | | | **1** | **1** |
| Lacertilia indet. | | | 1 | | | | | | | | | | **1** | **0** |
| *Malpolon monspessulanus* | | | 8 | 2 | | | | | | | | | **8** | **2** |
| *Natrix* cf. *N. astreptophora* | | | 2 | 1 | 1 | 1 | | | | | | | **3** | **2** |
| *Coronella* cf. *C. girondica* | | | 18 | 1 | | | | | | | | | **18** | **1** |
| *Coronella* sp. | 1 | 1 | | | 1 | 1 | | | | | 1 | 1 | **3** | **3** |
| *Zamenis scalaris* | | | 9 | 2 | | | | | | | | | **9** | **2** |
| Colubridae/Psammophiidae indet. | | | 6 | | | | | | | | | | **6** | **0** |
| *Vipera* cf. *V. latastei* | | | 16 | 1 | 1 | 1 | | | | | | | **17** | **2** |
| Ophidia indet. | | | 52 | | 2 | | | | | | | | **54** | **0** |
| **TOTAL** | **21** | **7** | **531** | **40** | **35** | **7** | **4** | **2** | **9** | **3** | **9** | **3** | **612** | **61** |

**Table 2**
Distribution by habitats of the amphibians and reptiles represented in the Late Pleistocene site of Navalmaíllo rockshelter (Madrid, Spain).

| | open-dry | open-humid | woodland | rocky | water-edge |
|---|---|---|---|---|---|
| *Bufo spinosus* | 0.1 | 0.3 | 0.4 | | 0.2 |
| *Epidalea calamita* | 0.45 | | 0.2 | 0.25 | 0.1 |
| *Rana iberica* | | 0.4 | 0.4 | | 0.2 |
| *Testudo hermanni* | 0.25 | | 0.5 | 0.25 | |
| *Chalcides striatus* | 0.3 | 0.3 | 0.2 | 0.2 | |
| *Blanus rufus* | 0.45 | 0.1 | 0.45 | | |
| *Malpolon monspessulanus* | 0.35 | 0.15 | 0.25 | 0.25 | |
| *Natrix astreptophora* | | 0.5 | 0.25 | | 0.25 |
| *Coronella girondica* | 0.25 | 0.25 | 0.25 | 0.25 | |
| *Zamenis scalaris* | 0.35 | 0.15 | 0.3 | 0.2 | |
| *Vipera latastei* | 0.4 | | 0.2 | 0.4 | |

vegetation that remains wet throughout the year; *Woodland*: environments with greater plant cover reaching comparatively greater heights, from medium shrublands to closed forests, including the margins of these areas; *Rocky*: open environments with low or scarce vegetation, poor substrate and an abundance of emerged rock and stones; *Water Edge*: aquatic and peri-aquatic environments, permanent or temporary bodies of water and their immediate surrounding areas, with hydrophilic and hygrophilous vegetation.

The percentage data for each species are provided in Blain et al. (2008, 2010, 2011a, 2011b, 2013a) and López-García et al. (2011) for herpetofauna, revised and adapted regionally for Madrid region and central Spain in Blain et al. (2019).

### 3.4. Paleoclimatic reconstruction

In order to obtain the paleoclimatic estimates for Navalmaíllo rockshelter, the Mutual Ecogeographic Range Method (MER) with the Uncertain Distribution Area-Occupied Distribution Area (UDA-ODA) discrimination technique was applied to the herpetofaunal assemblage identified at the site. MER method consists of identifying a modern geographical region exhibiting the same species assemblage as the fossil one and extrapolating the mean of the climatic parameters of that region to the past (Blain et al., 2016). This method uses determined climatic variables of potential ecophysiological significance (Dahl, 1998), such as mean annual temperature or maximum temperature of the warmest month, among others. It assumes that the species ecological niche is preserved, i.e. fossil representatives of the extant species have the same climatic tolerances and preferences as their living counterparts (Jackson and Overpeck, 2000; Jackson and Williams, 2004). MER method suggests avoiding species whose distribution is strongly affected by perturbing parameters as human pressure. Thereby, *Testudo hermanni* has been removed from this study because it has suffered range contraction and many subpopulations are small and fragmented (Bertolero, 2015; Morales Pérez and Sanchis Serra, 2009). However, the climatic requirements of existing populations can be compared with the quantitative results.

For the current spatial distributions, we used the data from Loureiro et al. (2008) for Portugal and from SIARE (AHE, 2021) for Spain, both represented in a geographic system (datum WGS 84) with a 10 × 10 km square grid. In those cases in which species level identification has not been achieved (i.e., *Blanus* sp. and *Coronella* sp.), all the extant species belonging to the genus have been contemplated. Because of these premises, when searching for analogous assemblage, careful attention is paid to ensure that the real current distribution corresponds to the potential ecological/climatic distribution and has not been strongly affected by other limiting or perturbing parameters, such as urbanism, landscape anthropization, predation, competition with another species, etc.

The UDA-ODA discrimination technique is based in the implementation of Geographic Information Systems (GIS) in the MER method. The objective is the reproducibility of the results, the management of huge quantities of information and the sharpening of species distribution creating more accurate distributions (ODA's) to be used in the overlapping process, instead of the coarse-grained distributions given by many atlases. The sharpening factor used consists of the upper elevation limit where all the species could coincide (1800 m. a.s.l.), which also refers to upper elevation limit of *Blanus cinereus* and *Chalcides striatus* (Table 3; Pleguezuelos et al., 2002).

From these more precise regions, we extracted the current mean values of the following climatic parameters from WorldClim 2.1 (Fick and Hijmans, 2017) with 30 arcseconds resolution grid: annual climatic parameters (MAT, mean annual temperature; MAP, mean annual precipitation) and monthly climatic parameters (mean monthly temperature; mean monthly precipitation). The same climatic parameters were calculated for the valley where the site is located (1970–2000), ranging from the deepest areas to 1600 m. a.s.l. Data sets were processed using the ArcGIS 10.3 application (ESRI, 2014). The mean and standard deviation were calculated using the statistical software IBM SPSS Statistics 22 (IBM Corp. Released, 2013).

To measure aridity, we used the Gaussen, Lautensach-Meyer, Dantin-Revenga and De Martonne indices. The Gaussen index ($P < 2 \times T$) considers a dry month when its pluviometric level (P), measured in mm, is less than twice the value of the average temperature in °C for that month (T). The Dantin-Revenga index is calculated as $100 \times \mathrm{MAT}/\mathrm{MAP}$, and the De Martonne aridity index as $\mathrm{MAP}/(\mathrm{MAT} + 10)$.

## 4. Results

### 4.1. Systematic paleontology

Class Teleostei Müller, 1845 *sensu* Arratia, 1999

A total of 14 fish vertebrae have been recovered from the 2005–2007 excavation campaigns at the Navalmaíllo rockshelter. These remains mainly come from layer F.

Order Salmoniformes Bleeker, 1859
Family Salmonidae Cuvier, 1816
Genus *Salmo* Linnaeus, 1758

*Salmo trutta* Linnaeus, 1758 – Brown trout.

Material: layer F (4 precaudal and 6 caudal vertebrae)

Description: Fossil vertebrae have the typical honeycomb structure of genus *Salmo* (Fig. 2A and B). The centra are circular and taller than long, and exhibit a lateral surface with an irregular network of indefinite lamellae. Foramina are circular (broadly ovate), often large, few in number and cover the complete lateral surface of the vertebra. The largest foramina occur at midlenght of the centrum and may extend nearly half of its length; small foramina are situated along the anterior and posterior margins of the lateral surface. In general, the centrum has a clear fluffy appearance. The presence of a neural foramen is observed on caudal vertebrae. The first precaudal vertebra which shows pointed and dorsoventrally flattened transverse processes that do not protrude as ears, appears to be wider and taller than long (Prenda et al., 1997). According to Feltham and Marquiss (1989) and Turrero et al. (2013) these characters permit to distinguish between *Salmo salar* and *Salmo trutta*, the latter being unique native species of the Iberian Peninsula (Elvira, 1995; Elvira and Almodóvar, 2001).

Remarks: *S. trutta* remains document a small-sized individual. Most of the brown trout vertebrae recovered at Navalmaíllo rockshelter suggest a body-size range between 17.4 and 17.9 cm.

Order Cypriniformes Bleeker, 1859
Family Cyprinidae Linnaeus, 1758
Cyprinidae indet.

Material: Layer F (2 precaudal and 2 caudal vertebrae).

Description: Precaudal vertebrae attributed to cyprinids show a characteristic cubic body with a medial fossa occupying most of the vertebral body (Fig. 2C). Some of the fish caudal vertebrae recovered at the Navalmaíllo rockshelter possess a narrow centrum on their middle portion, a smooth surface and a single, very well defined lamella (Fig. 2D). These features are those found in the cyprinidae, whereas in salmonids, the foramina are found all over the surface of the caudal vertebrae. Among cyprinids a specific attribution based on vertebrae only is not possible (e.g. Prenda et al., 1997; Russ, 2010; Guillaud et al., 2021), consequently this material cannot be assigned further than to a family level.

Remarks: As in the case of *S. trutta*, the cyprinid remains document a small-sized individual, with a body-size range no longer than 15 cm.

**Table 3**
Distribution of amphibian and reptile remains from Navalmaíllo rockshelter in terms of presence/absence plus the upper elevation limit in meters (m) of their living counterparts (IUCN, 2021). * = absence of lower elevation limit.

| Taxa | Loureiro et al. (2008) | SIARE | Upper elevation limit | Lower elevation limit |
|---|---|---|---|---|
| *Bufo spinosus* | *Bufo* | *Bufo spinosus* | 3000 | * |
| *Epidalea calamita* | *Bufo calamita* | *Epidalea calamita* | 2540 | * |
| *Rana* cf. *R. iberica* | *Rana iberica* | *Rana iberica* | 2425 | * |
| *Testudo hermanni* | Absent | *Testudo hermanni* | | |
| *Chalcides* cf. *Ch. striatus* | *Chalcides striatus* | *Chalcides striatus* | 1800 | * |
| *Blanus* sp. | Blanus cinereus | *Blanus cinereus* | 1800 | * |
| | | *Blanus mariae* | ? | ? |
| *Malpolon monspessulanus* | *Malpolon monspessulanus* | *Malpolon monspessulanus* | 2160 | * |
| *Natrix* cf. *N. astreptophora* | *Natrix* | *Natrix astreptophora* | 3060 | * |
| *Coronella* cf. *C. girondica* | *Coronella girondica* | *Coronella girondica* | 2900 | * |
| *Coronella* sp. | *Coronella austriaca* | *Coronella austriaca* | 2750 | * |
| | *Coronella girondica* | *Coronella girondica* | 2900 | * |
| *Zamenis scalaris* | *Zamenis scalaris* | *Zamenis scalaris* | 2200 | * |
| *Vipera* cf. *V. latastei* | *Vipera latastei* | *Vipera latastei* | 3000 | * |

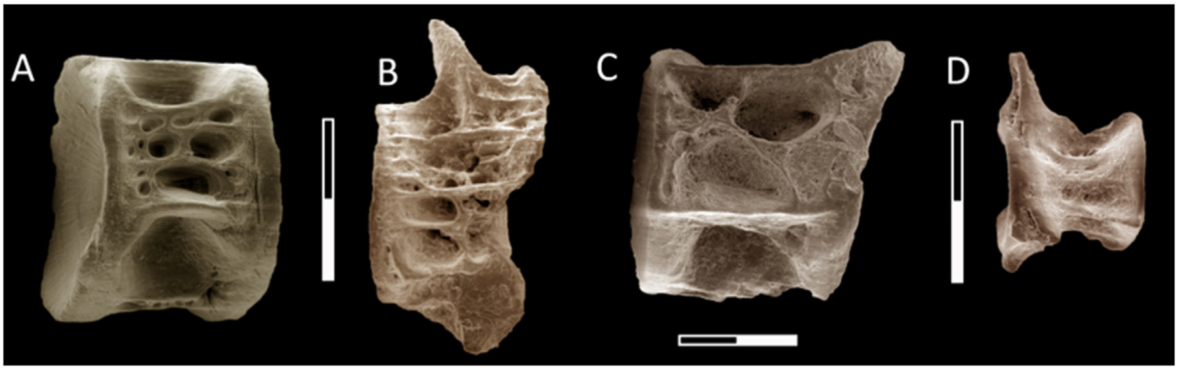

**Fig. 2.** Fossil fish from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A-B. *Salmo trutta*. A. precaudal vertebra (NV′09 A23 FL 420–430) in ventral view; B. caudal vertebra showing moderate digestion marks (NV′05 HI1819 FL 480–500) in lateral view. C-D. Cyprinidae indet. C. precaudal vertebra (NV′07 D18 FL550-560) in lateral view; D. caudal vertebra (NV′09 A23 F420–430C) in lateral view. Scales = 1 mm.

Class Amphibia Linnaeus, 1758
Order Anura Duméril, 1805

Toads and frogs are represented in Navalmaíllo rockshelter by 198 elements, documenting 25 individuals belonging to three species. Eight fragmentary elements (an angular, a vertebra, a right humerus, and five phalanges) have been left at order level in level F (Table 1).

Family Bufonidae Gray, 1825

Twenty elements, mainly fragmentary bones or bones with low diagnostic value preventing a more precise attribution, were attributed at family level, belonging to either *Bufo* or *Epidalea*.

*Bufo* Garsault, 1764
*Bufo spinosus* Daudin, 1803 – Spiny Toad.

Material: Layer FL (1 left scapula, 1 right humerus of female, 1 right humerus of male, and 1 radioulna); Layer F (1 vertebra, 3 radioulnae, 2 tibiofibulae, and 7 phalanges); Layer D (1 sacrum).

Description: The left fossil scapula (Fig. 3A) is robust, higher than wide, and bears a robust, detached glenoid process (*processus glenoidalis*) that is clearly visible in dorsal view. Besides the size and general robustness of this fossil, the attribution to *B. spinosus* is supported by the lack of supraglenoid fossa on the base of the glenoid process, unlike in *Epidalea calamita* where this fossa is small, but always present.

Two large humeri of *B. spinosus* have been recovered in the Navalmaíllo rockshelter. They correspond to a right humerus of female (Fig. 3B) and a right humerus of male (Fig. 3C). Both humeri are robust and show a straight diaphysis in ventral view. Their condyles, weakly ossified, are displaced on the radial side in comparison with the diaphysis main axis. The male's humerus display a rather long and well-developed medial crest.

The other elements attributed to *B. spinosus* are mainly characterized by their large size. The single reported vertebra only preserves the centrum. It is procoelous and its cotyle is slightly dorsoventrally flattened. The sacrum also has only the centrum. This element is broken in two pieces (probably recently). Its size is quite large and presents an anterior cotyle and two well individualized posterior condyles. Finally, the radioulnae (Fig. 3D), tibiofibula and phalanges have the robust and short morphology typical of bufonid bones. The fossil radioulnae consists only of its distal part. The neck (*collum antibrachii*) is relatively wide in comparison with the head of the bone (*capitulum*). The tibiofibula is also broken and consists of the fragment of its central region at the level of the *foramen nutritium*. Nevertheless, it clearly corresponds to a large sized and robust element that can be attributed with certainty to a large bufonid toad. The three phalanges are robust and short and, by association, can be referred to *B. spinosus*.

Remarks: These fossil elements clearly suggest the occurrence of a common toad (*Bufo* sensu lato) in the Navalmaíllo rockshelter. According to genetic and external characters (Arntzen et al., 2013), common toads were represented in the past by a single ancestral species (*Bufo* s.l.) that split into two different descendants, *Bufo* sensu stricto (found in most of Europe and the western part of North Asia) and *Bufo spinosus* (typical of the Iberian Peninsula, the south-western France, following a geographic limit between the distribution of the two species from Normandy to Franche-Comté Regions, and North-Africa). Spanish populations of this toad (formerly subspecies *spinosus*) were said to be much larger than their conspecific populations of continental Europe. Size has been sometimes used as an osteological criterion to propose attribution to subspecies level in the past (Bailon, 1991; Sanchiz in Montoya et al., 1999; 2001), but no formal measurements have been proposed in order to separate *Bufo spinosus* from *Bufo*, which otherwise show no skeletal differences. In conclusion, the attribution of our fossils to *Bufo spinosus* is based more on biogeographical criteria than on osteological arguments.

*Epidalea* Cope, 1864
*Epidalea calamita* (Laurenti, 1768) – Natterjack Toad.

Material: Layer FL (2 vertebrae, 1 urostyle, 1 left ilium, 1 right ilium, 1 left scapula, 1 right scapula, 1 coracoid, 2 left humeri of male, 1 radioulna, 1 tibiofibula, and 1 phalange); Layer F (1 sphenethmoid, 1 pterigoid, 10 vertebrae, 1 sacrum, 8 urostyles, 7 left ilia, 12 right ilia, 1 left scapula, 2 right scapulae, 1 coracoid, 2 clavicles, 8 left humeri of female, 2 right humeri of female, 3 left humeri of male, 3 right humeri of male, 12 radioulnae, 2 femora, 9 tibiofibulae, 2 tarsa, and 29 phalanges); Layer D (2 vertebrae, 1 right ilium, and 1 right humerus of female); Layer ß (1 sacrum, 1 radioulna, and 1 femur); Layer C (1 right humerus of female, and 1 radioulna); Layer B (2 vertebrae, 1 left ilium, 1 right scapula, 1 coracoid, 1 right humerus of male, and 1 radioulna).

Description: The only sphenethmoid (Fig. 3E), is as long as it is wide in dorsal view, with short lateral processes. The roof of the

**Fig. 3.** Fossil anurans from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A-D. *Bufo spinosus*. A. left scapula (NV′07 Sector 4 E18 FL 550–560) in dorsal (A1) and lateral (A2) views; B. right humerus of female (NV′07 Sector 4 E18 FL 550–560) in ventral view; C. right humerus of male (NV′07 Sector 4 E18 FL 550–560) in ventral view; D. radioulna (NV′07 D18 F + F1 Perfilado Sección) in lateral view. E-J. *Epidalea calamita*. E. sphenethmoid (NV′09 B22 F 430–440) in dorsal (E1) and anterior (E2) views; F. left ilium (NV′07 D18 F 550–560) in lateral view; G. right ilium (NV′07 D18 F 540–550) in lateral view; H. right scapula (NV′07 E18 Sector II F1 550–560) in ventral (H1) and lateral (H2) views; I. right humerus of male (NV′07 D18 F 550–560) in ventral view; J: femur (NV′09 B22 F 430–440) in dorsal (J1) and medial (J2) views. K. tibiofibula (NV′09 B22 F 430–440) in dorsal view. L-M. cf. *Rana* sp. L. right premaxilla (NV′06 D19 1 F 490–500) in anterior (L1) and posterior (L2) views; M. coracoid (NV′10 AK30 B 220–230) in dorsal view. Scale = 2 mm.

anterior alveoli (*antrum olfactorium*) is slightly indented. In anterior view, it shows a small thickening (*sella amplificans*) on the floor of the anterior alveoli, generally absent in *B. spinosus*.

The fossil urostyles present a similar morphology. They are devoid of any transverse apophyses (*processus transversus*) or a horizontal blade (*lamina horizontalis*). On the anterior view, the articulation with the sacrum occurs thanks to two cotyles (*fossa condyloidea*). These two cotyles are slightly dorso-ventrally flattened and partially fused medially. The neural crest (*crista dorsalis*) is moderately high and the neural arch of the *canalis coccygeus* has an ogival shape.

The ilia (Fig. 3F and G) do not bear any ilial blade (*crista dorsalis*). The upper tuberosity (*tuber superior*) is low, with a single-lobed pointed dorsal edge as in *E. calamita*, and contrary to *B. spinosus*, where it is rounded. The ilial shaft shows a more or less developed lateral-ventral excrescence (*lamina calamita*) on the anterior branch.

The fossil scapulae are more or less fragmentary. The best preserved one (Fig. 3H) is higher than it is wide and bears a robust, detached glenoid process that is clearly visible on dorsal view. All scapulae present the small supraglenoid fossa, characteristic of *E. calamita*, and as already said, absent in *B. spinosus*.

The fossil humeri (Fig. 3I) document both female and male individuals. As it is common in bufonids, the condyle, generally weakly ossified, is displaced on the radial side in comparison with the diaphysis main axis. Their diaphyses are slightly more curved than in *B. spinosus*. As mentioned previously, the male humeri display a rather long and well-developed medial crest, whereas in females this crest is usually absent.

Three femora (Fig. 3J) are represented in our material. They are relatively long, robust and sigmoid. They both bear a sharp-edged femoral crest that does not divide, whereas in *B. spinosus*, this crest divides and forms a triangular surface.

The remaining elements (vertebrae, coracoid, clavicle, radio-ulnae, tibiofibulae, tarsa, and one phalange) are incomplete, nonetheless showing the general robust morphology of bufonid toads. The specific attribution of these skeletal elements is most commonly done according to their size, as already explained, *E. calamita* being generally smaller than *B. spinosus*. However, although the sacrum is only represented by the centrum, it presents an anterior cotyle and two more or less fused posterior condyles, features that are more typical of *E. calamita*.

Family Ranidae Batsch, 1796
*Rana* Linnaeus, 1758
cf. *Rana* sp.

Material: Layer F (1 right premaxilla), Layer B (1 coracoid).

Description: One right premaxilla (Fig. 3L) is reported to a brown frog in layer F. The premaxilla is paired, dentate (around 11–14 tooth loci) and characterized by the presence of a somewhat narrow *pars dentalis*. The development of the palatine process is not perceptible on the fossil. The *pars facialis* (= frontal process in Bailon, 1999) is incomplete, but seems to have been rather long and moderately wide.

The coracoid (Fig. 3M), recovered from layer B, is also incomplete, with a thick distal end (= *pars epicoracoidalis*) and a flat and wide proximal one (= *pars glenoidalis*). The anterior margin is strongly concave, connected to the larger anterior extension of the *pars glenoidalis* (even if incompleted on our fossil) and *pars epicoracoidalis*.

Remarks: These fossil elements may suggest the occurrence of a small-sized brown frog (genus *Rana*) in Navalmaíllo rockshelter. Within the overall inter- and intraspecific morphological variability observed among Iberian brown frogs, the morphology of the *pars dentalis* of the premaxilla seems to be closer to that in *Rana temporaria* and *Rana iberica* (much more robust and straighter), whereas in *Rana pyrenaica* and *Rana dalmatina*, the *pars dentalis* is relatively thinner and medially depressed (Blain and Arribas, 2017). Concerning the coracoid, attribution to the genus *Rana* is supported by the relative robustness of the medial part of the bone, whereas in the genus *Pelophylax*, this medial part is usually thinner (see Bailon, 1999). The well-developed concavity of the anterior margin is reminiscent of *R. temporaria* and *R. iberica*, whereas in *R. pyrenaica* and *R. dalmatina* it is usually much less concave (Blain and Arribas, 2017). Today, only the Iberian stream frog (*Rana iberica*) is present in the vicinity of the site (AHE, 2021).

Class Reptilia Laurenti, 1768
Order Testudines Linnaeus, 1758 or Chelonii Brongniart, 1800

The chelonian presence at Navalmaíllo rockshelter is altogether low in the assemblage. Several layers have provided chelonian remains (Table 1), although they are by far more abundant at layer F. Most of the fossils may be classified as pertaining to a tortoise (cf. *Testudo* sp.), but only a few elements enabled to reach species level, identified as Hermann's tortoise (*Testudo hermanni*). Nevertheless, as there is no evidence of any turtle shell, all the fragmentary remains have been attributed to tortoise and have been referred to the single species represented with certainty in the site, *T. hermanni*.

Family Testudinidae Batsch, 1788
*Testudo* Linnaeus, 1758
*Testudo hermanni* Gmelin, 1789 – Hermann's Tortoise.

Material: Layer FL [1 neural]; Layer F [9 neurals (3 sulcus-crossed, 1 not sulcus-crossed, and 5 indeterminate fragments), 1 pygal, 36 pleurals (10 pair, 11 unpair, and 15 indeterminate), 21 peripherals (1 left tenth?, 1 right eleventh, and 19 indeterminate), and 82 indeterminate fragments of the carapace, 3 left epiplastrons, 1 entoplastron, 1 right hyoplastron, 2 right hypoplastrons, 1 right xiphiplastron, 21 indeterminate fragments of plastron, and 20 indeterminate shell fragments]; Layer D [7 pleurals (5 pair, 1 unpair, and 1 indeterminate), 6 peripherals, and 6 indeterminate plates (4 from the carapace, 1 from the plastron, and 1 indeterminate)]; Layer C [2 nuchals, 3 peripherals, and 2 indeterminate fragments (1 from the carapace and 1 from the plastron)].

Description: The shell bones (with a few exceptions) are characterized by their relative thickness and the presence of well-developed growth-striae on the external side. This set of characteristics allows us to relate the fossils to the terrestrial tortoises (Testudinidae) and to distinguish them from the pond turtles group present in Europe (Emydidae and Geoemydidae). Attribution to *T. hermanni* principally relies on the morphology of the nuchal, eleventh peripheral, epiplastron, and hyoplastron.

Two relatively large nuchals have been recovered from layer C (Fig. 4A and B). They are hexagonal with wide lateral sides. The posterior end is broken on the two specimens, but their total width can be estimated to have been much longer than its total length. On the best preserved specimen, the length of the cervical scale corresponds approximately to one third of the estimated nuchal total length. The posterior edge of the cervical scale is more or less straight, as seen in *Emys* and *Testudo*, whereas in *Mauremys* the posterior end of the cervical spine is truncated by the pointed insertion of the vertebral scale V1 (Holman, 1995; Hervet, 2000). Sulci Cervical (Cer)/V1, Cer/Marginal 1 (M1), M1/V1 and short V1/Costal 1 (C1) and M1/Cer are visible on both fossil specimens. The marginal ventral bulge (= "bourrelet" in Hervet, 2000) of the nuchal is overhanging, well-marked, continuous and regular. The extent of the ventral edge of the scales is long over its entire width, whereas in *Emys* and *Mauremys* it is usually shorter at the level of the cervical scale and becomes progressively wider towards the M1 (Hervet, 2000). The distance between the ventral edge of the scales and the edge of the overhanging bulge is short, whereas it is usually longer in *Emys* and *Mauremys* (Hervet, 2000).

A total of ten neurals have been recovered from layers F and FL (Fig. 4C and D). Most of them are very fragmentary and do not preserve their external outline. Nevertheless, two are particularly well preserved. The first one, even if incomplete anteriorly, has a rectangular outline (Fig. 4C). It is crossed by a sulcus probably in its posterior half. The missing anterior part is decisive to establish if it may correspond either to a first neural (if longer than wide), a third neural (if as long than wide), or a fifth neural (if anteriorly wider than posteriorly). The second one (Fig. 4D) shows a hexagonal outline. It is longer than wide and is crossed by a sulcus (V4/V5?). It may correspond to an eighth neural.

A very thick pygal comes from layer F (Fig. 4E). It is trapezoid-shaped, quite as long as wide, but, as the outer surface is very

**Fig. 4.** Fossil tortoises from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A-P. *Testudo hermanni*. A. Nuchal (NV′12 AN30 C 304. n° 132) in dorsal (A1) and ventral (A2) views; B. Nuchal (NV′12 AN30 C 303. n°48 and 49) in dorsal (B1) and ventral (B2) views; C. Neural (NV′13 H19 FL-24C 664. n°105) in dorsal (C1) and ventral (C2) views; D. Eight neural (NV′07 E18 F 530–540) in dorsal (D1) and ventral (D2) views; E. Pygal (NV′15 A24 F 434. n°100) in dorsal (E1). ventral (E2) and lateral (E3) views; F. Pair pleural (NV′08 F16 F 494. n°98) in dorsal view; G. Sixth peripheral (NV′07 D18 F 500–510) in lateral (G1) and medial (G2) views; H. Left tenth? peripheral (NV′17 B23 F 457. n°316) in lateral (H1) and anterior (H2) views; I. Right eleventh peripheral (NV′14 B21 F 452. n°86) in lateral (I1) and medial (I2) views; J. Left epiplastron (NV′07 D18 F 520–530) in dorsal (J1). ventral (J2). and medial (J3) views; K. Left epiplastron (NV′11 B22 F 445. n°108) in dorsal (K1) and ventral (K2) views; L. Entoplastron (NV′08 C19 F 481. n°348) in ventral view; M. Right hyoplastron (NV′14 C22 F 468. n°112) in dorsal (M1) and ventral (M2) views; N. Right hypoplastron (NV′06 E18 F 508. n°367) in ventral view; O. Right hypoplastron (NV′04 E18 F 500. n°382) in ventral view; P. Right xiphiplastron (NV′07 D18 F 520–530) in dorsal (P1) and ventral (P2) views. Scales = 5 mm.

badly preserved, the dorsomedial sulcus typical of *T. hermanni* is not visible. This sulcus does not seem to be present (or at least is not well marked) on the inner surface (Fig. 4E2). According to Hervet (2000), this character seems to be highly variable, and the trapezoid shape of the fossil is more characteristic of *T. hermanni* than *T. graeca* (Cheylan, 1981) and above all, when thickness is also taken into account, than *Emys* and *Mauremys*. Hervet (2000) also suggests that the pygal is more curved longitudinally in males than in females. According to this character, our fossil seems to be more in accordance with a female than a male.

Pleurals are usually highly incomplete and precise attribution to a particular plate is difficult. Their distal end is characterized by a poorly developed free extension of the ribs that ends in an indentation for the suture with the peripheral plates. The difference between the width of pair and unpair plates is marked. Pair plates (Pl2, Pl4, and Pl6 Fig. 4F) are crossed longitudinally by the sulcus C/V and the intercostals transversally at two third of their total length. Unpair plates (Pl3 and Pl5) contain only the C/V sulci on their proximal end.

Peripherals (Fig. 4G–I) are wider than long dorsally, and with a roughly rectangular shape.

In profile, they are much higher above the ventral margin in *Testudo* than in *Emys* and *Mauremys* (Hervet, 2000). A unique Per11 has been recovered in layer F (Fig. 4I). It presents a characteristic anteroposterior elongation of the inferior free edge and, jointly, a very closed angle between this free edge and the side in contact with the pygal plate. Moreover, a drop-out (“décrochement” in Hervet, 2000) is well marked: the anterior end of the sutural margin with the pygal does not join the pleural/peripheral suture line as in *T. graeca*. This character, when associated with the anteroposterior elongation of the inferior free edge is characteristic of *T. hermanni* (Cheylan, 1981; Hervet, 2000). According to Hervet (2000), this elongation also presents a sexual dimorphism, being longer in males than females. We lack a consistent reference collection to infer reliable conclusions about this fact, but it seems that the fossil Per11 from Navalmaíllo rockshelter may be more consistent with a female.

Three left epiplastrons are represented in Layer F (Fig. 4J and K). They are differently preserved. One of them, the largest, is more or less complete (Fig. 4J), whereas the other two are much more fragmentary (Fig. 4K). The anterior plastral lobe is trapezoidal and relatively flat. The medial area of the dorsal epiplastral lip is slightly concave. The posterior overhanging of the dorsal epiplastral lip remains anterior to the entoplastron. A gular pocket seems to be lacking on the smallest specimens, whereas in the largest it is more pronounced. The gular notch seems to have been wide and slightly concave. Considering their overall morphology, these epiplastrons are similar to *T. hermanni* and differ from those in *T. graeca*, where the medial area of the dorsal epiplastral lip is usually flat or convex, the posterior overhanging of the dorsal epiplastral lip reaches the level of the entoplastron, and the gular notch is usually much less concave (Hervet, 2000).

The only entoplastron (Fig. 4L) is very incomplete and preserves only the anteriormost part of this element. However, it is characterized by having a deep and narrow impression of the gular/humeral and gular/gular sulci, resulting in a very sharp angle, like in *T. hermanni*, whereas in *T. graeca* this angle is usually more open (see Hervet, 2000).

The right hyoplastron (Fig. 4M) corresponds to a lateral portion of the bone. It is rather flat and crossed posteriorly by the sulcus between the pectoral and abdominal scales. It does not present a hinge between the hyoplastron and the hypoplastron, as in *Testudo* and *Mauremys*, whereas in *Emys* a hinge is present extending along the whole of its posterior width (Hervet, 2000).

The two preserved fragments of right hypoplastrons are rather fragmentary (Fig. 2N–O). Together they document the antero-medial part (Fig. 4N) and the postero-medial part (Fig. 2O). Their ventral surfaces present well-developed growth-striae. The angle formed by the medial part of the abdomino-femoral sulcus with the posterior margin of the hypoplastron is quite open, suggesting that the abdomino-femoral sulcus may reach a point much more anteriorly located on the ventral surface (Fig. 4O). This character is only present in *T. hermanni*, whereas in *T. graeca* this angle is smaller. In *Mauremys* and *Emys,* this sulcus is parallel to the posterior margin and located at half way of the length of this element in *Mauremys*, and at the last third of the length in *Emys* (Cheylan, 1981; Hervet, 2000).

Finally, a small lateral fragment of a xiphiplastron is preserved in layer F (Fig. 4P). Due to its incompleteness, it is rather difficult to know exactly to which part of the bone it may correspond. Nevertheless, it presents a subrounded lateral margin of the posterior plastral lobe, typical of terrestrial chelonians.

Remarks: Several characters observed in the material analyzed here are exclusive to terrestrial forms or constitute an exclusive combination of characters for most of the Neogene members of this group (Bailón, 2010; Gmira, 1995; Hervet, 2000, 2004; Pérez-García and Vlachos, 2014; Pérez-García et al., 2011, 2015): well-developed growth rings; granular outer surface; relatively thick plates; deep sulci between the scutes; very thick nuchal plate; alternation of rectangular and octagonal/hexagonal neurals; well-developed alternating pattern of costals consisting of medially alternating long and short plates versus laterally short and long ones; reduced proximal region of the ribs; coincidence of the pleuro-marginal sulci with the costo-peripheral sutures; eleventh pair of marginals next to, or in contact with the antero-lateral margins of the pygal plate; presence of a medially thickened epiplastral lip; slight overlapping of the gular scutes on the entoplastron. Each of these character stages allow us to exclude the assignment of this taxon to the Western European freshwater turtles *Emys orbicularis* and *Mauremys leprosa*. As already mentioned before, various osteological characters suggest an attribution of the fossils recovered in Navalmaíllo rockshelter to the extant *T. hermanni* (relative width of nuchals, morphology of the pygal and eleventh peripheral, general morphology of epiplastrons and the anteriorly located and outline of the abdomino-femoral sulcus on the hyoplastron).

Concerning the MNI, a careful observation of the whole assemblages has been done by levels. In layer C, with only 7 recovered shell elements, the presence of two nuchals of slightly different size suggest that at least two adult individuals were represented. Although it has not been possible to refit the fossil elements from layer D, the general morphology and size from the 19 remains seems to fit with a unique adult individual (even if some plates present a different coloration, probably due to post-depositional processes). Layer F is by far the richest concerning the presence of chelonians, with some 197 elements. At least 5 individuals have been identified: a very juvenile individual (estimated carapace length around 7–10 cm), a subadult/thin plates (estimated carapace length about 15 cm), two adults (estimated carapace length about 20 cm, and one of them may be a female), and a very thick adult (female?) individual (estimated carapace length maybe about 25–30 cm). For the not-thick adult category, the repetition of anatomical elements (left epiplastrons and right hypoplastrons) suggests the occurrence of two individuals. The very juvenile individual from layer F is represented by a neural and 7 indeterminate fragments. The subadult individual is represented by one neural, 5 pleurals (2 pair, 1 unpair, 2 indeterminate), 1 peripheral, and 18 indeterminate fragments. The thicker individual would be represented at least by a pygal, a peripheral (10th), and a left epiplastron. All the remaining elements may be ascribed to the adult category. Finally, the only element (neural) from Layer FL documents an adult individual.

### Order Squamata Oppel, 1811

Among squamate remains, some 58 remains have been attributed to higher rank category. These are one fragment of maxilla or dentary of a lizard (Lacertilia indet.) whose teeth do not preserve their apexes, a fragment of left maxilla and 5 indeterminate vertebrae of a colubrid/psammophiid in Layer F and some 50 snake vertebrae (mainly cervical and caudal vertebrae and some fragmentary trunk vertebrae), and 4 ribs of an unidentified snake (Ophidia indet.) in Layers F and D.

### Family Lacertidae Batsch, 1788

The material attributed to lizards in the Navalmaíllo rockshelter is fragmented and/or represented by non-diagnostical elements that preclude any attribution to species, and even genus level in the current state of our osteological knowledge of Iberian lacertids. However, according to their relative size, this material can be separated into two categories. The first one (Lacertidae indet, large-sized) refers to medium and large-sized lacertids as it is the case today in the vicinity of the site for *Timon lepidus* and *Lacerta schreiberi*. The second category (Lacertidae indet, small-sized) refers to the current species *Iberolacerta cyreni*, *Podarcis muralis*, *Podarcis guadarramae*, *Psammodromus hispanicus*, *Psammodromus algirus*, and *Acanthodactylus erythrurus*.

### Lacertidae indet (large-sized)

Material: Layer F (6 left maxillae, 1 right maxilla, 5 left dentaries, 1 fragment of dentary, 8 fragments of maxilla or dentary, 1 splenial, 7 vertebrae, 1 scapulo-coracoid, and 1 femur); Layer D (1 fragment

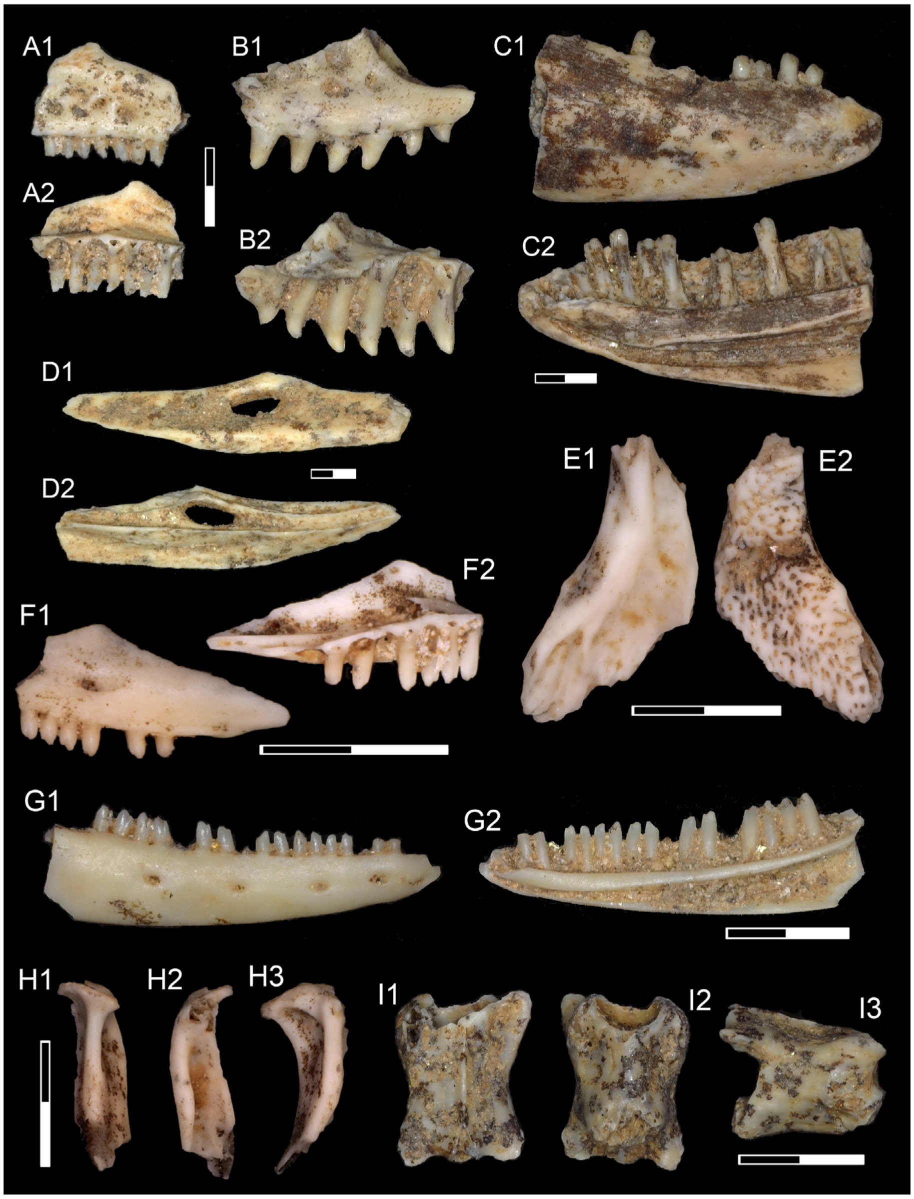

**Fig. 5.** Fossil lacertids from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A-D. Lacertidae indet. (large-sized). A. right maxilla (NV′04 E18 F 500–510) in lateral (A1) and medial (A2) views; B. left maxilla (NV′06 D19 F 490–500) in lateral (B1) and medial (B2) views; C. left dentary (NV′07 E18 F sector III 520–530) in lateral (C1) and medial (C2) views; D. splenial (NV′06 D19 F 490–500) in lateral (D1) and medial (D2) views. E-I. Lacertidae indet. (small-sized). E. frontal (NV′09 A23 F 420–430) in ventral (E1) and dorsal (E2) views; F: left maxilla (NV′06 D19 F 580–590) in lateral (F1) and medial (F2) views; G: right dentary (NV′06 D19 F 480–490) in lateral (G1) and medial (G2) views; H: quadrate (NV′09 A23 F 420–430) in anterodorsal (H1), posteroventral (H2), and medial (H3) views; I. vertebra (NV′07 E18 FL sector IV 550–560) in dorsal (I1), ventral (I2) and right lateral (I3) views. Scales = 2 mm.

of maxilla or dentary, 2 vertebrae, and 1 sacral vertebra); Layer ß (1 hemipelvis).

Description: As said above, most of the fossils are very incomplete. It is the case for the maxilla and dentary. Their pertaining to the family Lacertidae is mainly based on the teeth morphology and their pleurodont insertion on the bone. The teeth are isodont, cylindrical and mono-, or bicuspid and on the dentaries the Meckelian canal is wide open.

Six fragments of left maxillae have been recovered. Three of them correspond to the ventro-central part of this element (Fig. 5A). Preserved teeth are mainly bicuspid and do not project more than one third of their total length beyond the dental crest (*crista dentalis*), which, according to Barahona Quintana (1996) and Barahona and Barbadillo (1997), agrees with the extant species *T. lepidus*, *L. schreiberi* and *L. bilineata*. In medial view, the superior alveolar foramina is visible, and the supradental shelf is rather thick and straight. In lateral view, the surface presents no ornament and two small labial foramina are present. The other three fragments correspond to the anterior part of this element, at the level of the insertion of the anterior process, with some preserved monocuspid and slightly hooked teeth. Again, teeth do not project more than one third of their total length beyond the dental crest. In lateral view, small labial foramina are present. The right maxilla (Fig. 5B) corresponds to the anteriormost part of this element and preserves the 6 anterior teeth. As is usual in anterior teeth, they are robust, knife-shaped and monocuspid. In lateral view, the lappet is present but broken on the anterior process, and three small labial foramina are visible on the surface of the bone.

The best preserved dentary (Fig. 5C) is quite large and robust. It corresponds to the anterior part of the element and presents 15 tooth positions but only 6 preserved teeth. Those teeth are mainly bicuspid and project poorly (less than one third of their total length) beyond the dental crest. In medial view, the Meckelian canal is open and the subdental shelf is robust and thick. In lateral view, the surface is smooth and bears 6 mental foramina. Most of the remaining dentaries do not preserve any teeth or are very fragmented preventing the observation of relevant features.

A complete splenial (Fig. 4D) has been identified among the material. It is the largest element of the assemblage, with a maximum length about 16.8 mm. It is triangular in shape. The medial surface is slightly concave, with the posterior alveolar foramen being visible towards the middle of its length, while the smaller anterior alveolar foramen must probably be covered by a calcareous concretion. The lateral surface has two longitudinal ridges, a dorsal ridge and a medial ridge. In its anterior section, the medial ridge occupies a position on the ventral margin of the bone, while in its posterior section it is located in the medial zone. According to Barahona Quintana (1996) and Barahona and Barbadillo (1997), the anterior edge of the splenial is frequently bifurcated in adult specimens of *L. bilineata*, *L. schreiberi* and *T. lepidus*, as it seems to be the case on our fossil specimen.

Other elements, such as fragments of vertebrae, scapulacoracoid, hemipelvis and femur display a morphology that is common to all the family, and only their relative larger size permits to include them in this category.

Remarks: Today only *T. lepidus* and *L. schreiberi* are represented in the area, whereas *L. bilineata* is found in more northern regions of the Iberian peninsula. None of the fossil elements recovered at the Navalmaíllo rockshelter permit to distinguish between these two species. The very large size usually observed in the adults of *T. lepidus* hasn't been found in any of them, so that these fossil elements are either juvenile or subadult specimens of *T. lepidus*, or subadults of *L. schreiberi*.

Lacertidae indet. (small-sized)

Material: Layer FL (1 right dentary, and 1 vertebra); Layer F (1 right frontal, 1 left maxilla, 3 right dentaries, 1 dentary with undetermined laterality, 4 fragments of maxilla or dentary, 1 quadrate, 4 vertebrae, and 1 femur).

Description: A small-sized right frontal (Fig. 5E) has been recovered in layer F from Navalmaíllo rockshelter. It is incomplete and corresponds to the posterior part of the bone. The medial margin is broken, and it is therefore difficult to say whether it was fused or not with its opposite bone. On the dorsal surface, it shows a relatively dense dermic ornamentation. Morphologically, this frontal differs strongly from what is seen in the genus *Acanthodactylus* by the presence of a denser dermic ornamentation, and a less medially constricted central part. It is more similar with the frontal in the genera *Psammodromus* and *Podarcis*. In *Psammodromus*, the fusion of the frontals seems to be quite common (Barahona Quintana, 1996; Barahona and Barbadillo, 1997; Blain et al., 2007), whereas in *Podarcis* the frontals are separated (Arnold, 1973) and more rarely fused (Barahona and Barbadillo, 1997). In both genera, the impression of the postfrontal (or postorbitofrontal) is well marked (Barahona Quintana, 1996; Blain et al., 2007), as it is in the fossil, where this impression is visible in lateral view. According to these two characteristics, the fossil may be referred either to *Psammodromus* or to *Podarcis*.

A small-sized left maxilla (Fig. 5F) has been identified in the site. It corresponds to the posterior part of the bone, which shows the posterior process and the infraorbital foramen, and from its 8 tooth loci, only 6 teeth have been preserved. These teeth are mainly bicuspid and project half of their total length beyond the dental crest. In medial view, the supradental shelf seems to have been rather thin. In lateral view, the surface presents no ornamentation and a relatively large and shallow labial foramina is present anteriorly to the posterior process. The fossil does not show a particularly developed lateral step on the posterior process as is usually the case in adult specimens of *Podarcis* (Barahona Quintana, 1996; Barahona and Barbadillo, 1997), thus hinting towards an attribution to *Psammodromus*. However, this character documented by a single fossil cannot be taken as decisive.

Five small-sized dentaries have been identified among the fossil material. The most complete one comes from layer F (Fig. 5G). Its total preserved length is around 6.8 mm and the length of the dental shelf is around 6.0 mm. This element is quite complete but lacks the posterior projections, which are broken. It is relatively elongate and gracile. It bears 19 tooth positions in which only 14 teeth remain in place. All of them are bicuspidate and project a little bit less than half of their total length beyond the dental crest. In medial view, the Meckelian canal is open on its whole length and the subdental shelf is rather thick anteriorly. In lateral view, the surface is smooth, bears 5 mental foramina and present an impression of the coronoid on the posterodorsal limit of the bone. The length of the dental shelf, around 6.0 mm, is concordant in size with the adults of the extant smallest-sized Iberian species as *Podarcis muralis*, *Podarcis guadarramae*, and Psammodromus hispanicus. The projection of the teeth beyond the dental crest, together with the slender aspect of the teeth, would be consistent with a representative of the genus *Podarcis* (Blain et al., 2007). However such an interpretation has to be made carefully, as lacertids usually present a large inter and intra-specific variability. The other dentaries from layer F have a quite similar morphology to the description above. Only one of these fragments seems to be slightly larger compared to the most complete dentary. The dentary from layer FL, is highly incomplete and only documents the centro-posterior part of this element. It also seems to be relatively elongate and gracile. Its total preserved length is around 5.0 mm and bears 9 tooth positions in which only 4 teeth are preserved. All the apices are rather worn, but still seem to have been bicuspidate. These teeth also project beyond the dental crest slightly further than a third of their total length.

The quadrate (Fig. 5H) is strongly incomplete and only preserves the central part of the element in the region where the posterior crest is found. Its total height is around 2.0 mm. The wing extension of the mandibular condyle is not preserved, and thus preventsany comparison.

Finally, six small-sized procoelous vertebrae (Fig. 5I) and one femur have also been referred to small lacertids. Vertebrae centrum lengths are between 2 and 3 mm. Some vertebrae are rather worn and/or digested, but their overall morphologies are consistent with an attribution to either *Psammodromus* or *Podarcis*.

Remarks: From the potential small lacertid taxa represented today in central Iberian Peninsula, the morphology and estimated size of the fossils recovered at Navalmaíllo Rockshelter seems to be concordant with the extant species *Podarcis muralis*, *Podarcis guadarramae*, and Psammodromus hispanicus. The fragmentation of the fossils and the relatively reduced size of the sample prevents a more precise attribution.

Family Scincidae Oppel, 1811

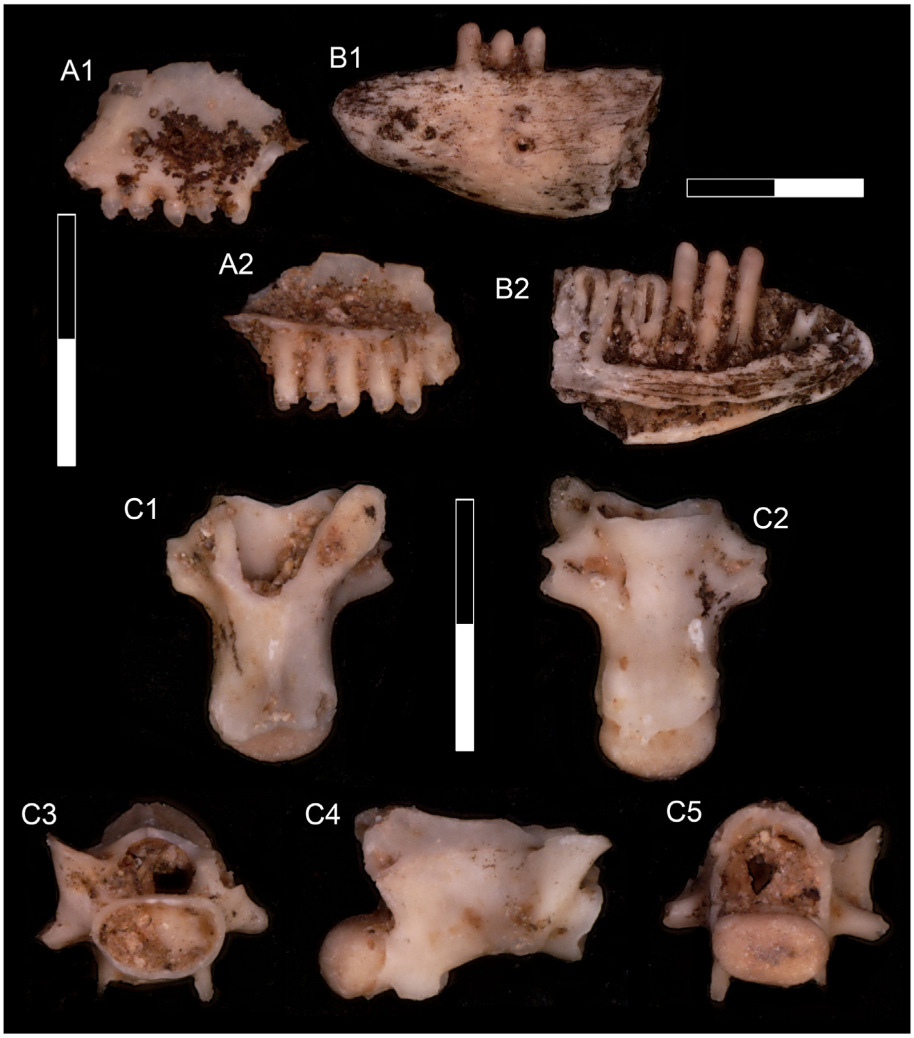

**Fig. 6.** Fossil skinks and amphisbaenids from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A-B. *Chalcides* sp. A. left maxilla (NV'06 E18 F 510–520) in lateral (A1) and medial (A2) views; B. left dentary (NV'06 E18 1 F 500–520) in lateral (B1) and medial (B2) views. C. *Blanus* sp. caudal vertebra (NV'09 A23 F 420–430) in dorsal (C1), ventral (C2), right lateral (C3), anterior (C4), and posterior (C5) views. Scales = 2 mm.

*Chalcides* Laurenti, 1768
*Chalcides striatus* (Cuvier, 1829) – Iberian Three-toed Skink.
*Chalcides* cf. *Ch. striatus*.

Material: Layer F (1 left maxilla, and 1 left dentary)

Description: The fossil maxilla and dentary bear the typical dentition of scincid lizards with pleurodont, isodont, cylindrical and monocuspid teeth with a blunt apex. In lingual view, every tooth apex shows more or less visible ornamentation, with delicate vertical striation limited ventrally by a transverse groove.

The maxilla (Fig. 6A) is very fragmentary and documents the central part of the element. Its maximum length is 1.97 mm. It documents 6 tooth positions from which 5 preserve teeth, with a morphology similar to the one described previously. The supradental shelf seems to have been rather thin.

The dentary (Fig. 6B) corresponds to the anterior part of the element with 10 preserved tooth positions. The Meckel canal is probably open on all its length. The anterior three preserved teeth are rather thin and elongate and show a width/height ratio equal to 0.18±0.01. Such ratio is closer to that of the extant species *Ch. striatus*, which is characterized by slender teeth with a tooth width/height ratio equal to 0.22±0.03, whereas *Chalcides bedriagai* has slightly more robust teeth (width/height ratio equal to 0.3) (Barbadillo, 1989; Blain, 2005, 2009; Blain et al., 2007). Two labial foramina are visible in lateral view. The lateral surface of the bone, as well as the subdental shelf, shows some strong taphonomical alteration, suggesting weathering or cracking/fissuration.

Family Blanidae Kearney, 2003
*Blanus* Wagler, 1830
*Blanus* sp. –Worm Lizard.

Material: Layer F (1 caudal vertebra)

Description: A unique amphisbaenid caudal vertebra has been recovered at Navalmaíllo rockshelter. This vertebra is small (centrum length = 2.2 mm), procoelous, and with a dorsoventrally flattened cotyle and a condyle (Fig. 6C). The neural arch is also strongly dorsoventrally flattened, with a concave posterior end. The neural spine is reduced. The ventral surface of the centrum is flat, with slightly convex margins. Two robust haemapophyses are present even if incomplete, indicating a caudal position for this

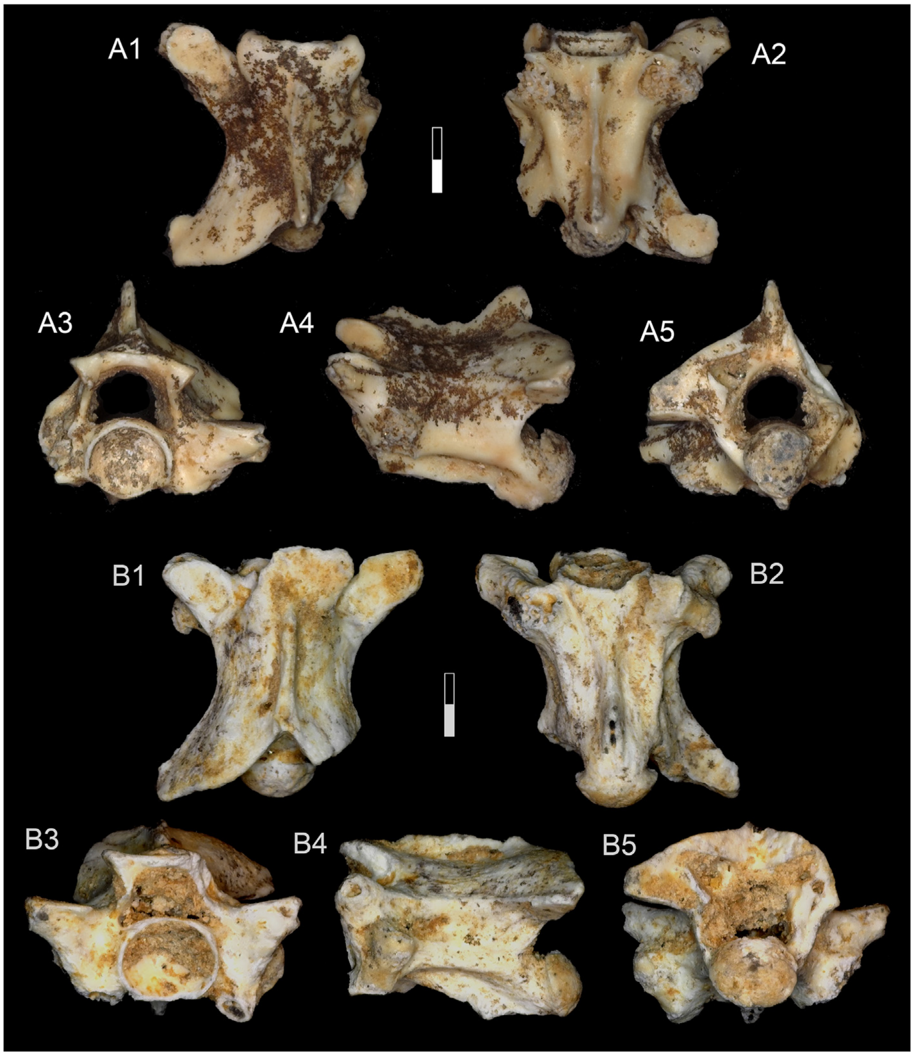

**Fig. 7.** Fossil snakes (Psammophiidae and Natricidae) from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A. *Malpolon monspessulanus*, trunk vertebra (NV′08 E16 F 480–490) in dorsal (A1), ventral (A2), anterior (A3), left lateral (A4) and posterior (A5) views; B. *Natrix* cf. *N. astreptophora*, trunk vertebra (NV′07 H18 F0 560–570) in dorsal (B1), ventral (B2), anterior (B3), left lateral (B4) and posterior (B5) views. Scales = 2 mm.

vertebra. Pleurapophyses are large and robust, and directed laterally. The only preserved prezygapophysis is well-developed and inclined upward. The overall morphology of this vertebra does not differ from those of *Blanus rufus* and *Blanus cinereus*, the only current representatives of the family in Western Europe.

Family Psammophiidae Boie, 1827
*Malpolon* Fitzinger, 1826
*Malpolon monspessulanus* (Hermann, 1804) – Western Montpellier Snake.

Material: Layer F (8 trunk vertebrae, from which 3 can be considered as from an adult and 5 as from ajuvenile specimen).

Description: *M. monspessulanus* is represented in the Navalmaíllo rockshelter mainly by medium-sized vertebrae (Fig. 7A). The mean of the center length is 4.5 mm (n = 8), with vertebrae ranging from 3.4 to 5.3 mm. These trunk vertebrae are quite elongated, particularly in comparison with those of *Zamenis scalaris* and to a lesser extent with those of genera *Coronella* and *Hemorrhois*. In ventral view, the centum is narrow, with slightly divergent lateral margins towards the front and has a long and narrow haemal keel over its entire length with well-defined lateral margins. The articular surfaces of the prezygapophyses are sub-oval and more anteriorly directed than in *C. girondica* and *Rh. scalaris* where they are larger and round or sub-rectangular (Blain, 2005, 2009). In posterior view, the posterior edges of the neural arch are more or less straight and forming an angle close to 90°.

Family Natricidae Bonaparte, 1840
*Natrix* Laurenti, 1768
*Natrix astreptophora* (Seoane, 1884) – Iberian Grass Snake.
*Natrix* cf. *N. astreptophora*.

Material: Layer F (2 trunk vertebrae); Layer D (1 trunk vertebra).

Description: Three trunk vertebrae pertaining to a grass snake (i.e. *Natrix* group + *Natrix helvetica* + *Natrix astreptophora*) have been recovered among the paleoherpetological remains from the Navalmaíllo rockshelter. The first one (NV′17 AA24 F 420–430) has a centrum length (CL) measuring 6.1 mm, the second one (NV′07 H18 F0 560–570; Fig. 7B) 6.9 mm, and the third one (NV′09 I18 1D 520–530) is somewhat smaller, with 4.6 mm. These vertebrae have a well-developed hypapophysis and, in posterior view, the neural

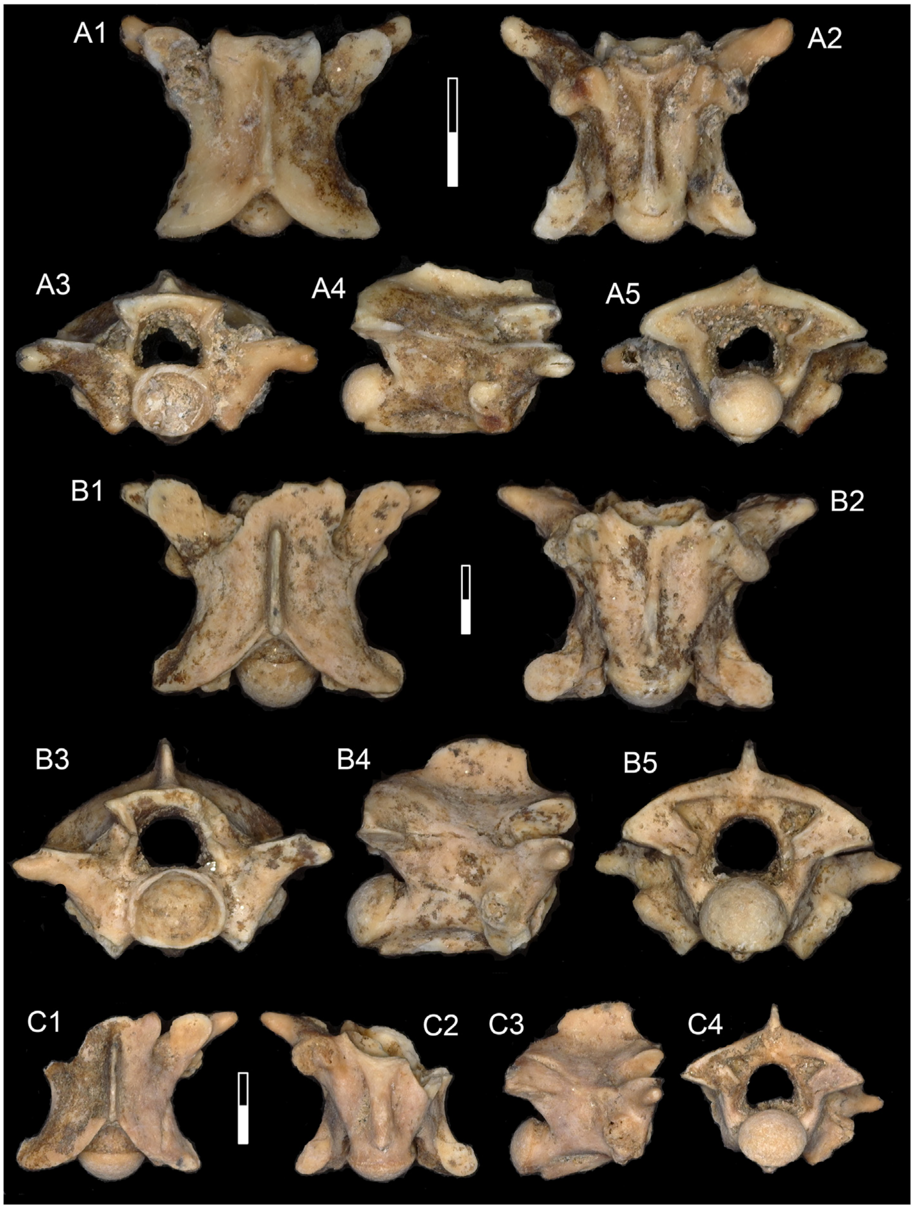

**Fig. 8.** Fossil snakes (Colubridae) from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A. *Coronella* cf. *C. girondica*, trunk vertebra (NV′05 C19 F 460–470) in dorsal (A1), ventral (A2), anterior (A3), right lateral (A4) and posterior (A5) views; B–C. *Zamenis scalaris*. B. trunk vertebra of an adult (NV′07 Sector III E18 F 530–540) in dorsal (B1), ventral (B2), anterior (B3), right lateral (B4) and posterior (B5) views; C. trunk vertebra of a juvenile (NV′07 D18 F 540–550) in dorsal (C1), ventral (C2), right lateral (C3) and posterior (C4) views. Scales = 2 mm.

arch is convex. The condyle and cotyle are small and circular. These vertebrae can be attributed to a grass snake mainly based on the morphology of the centrum, which is flat and with well-marked lateral margins, whereas in *Natrix maura* the centrum is slightly convex and with more or less diffuse lateral margins (Szyndlar, 1984). The morphology of the extremity of the hypapophysis and the parapophyseal processes, not preserved on the two largest vertebrae (Fig. 7B), but preserved on the smaller vertebra, is robust and obtuse like in grass snake, whereas it is slenderer and with a pointed tip in *N. maura* (Szyndlar, 1984).

Remark: These fossil elements clearly suggest the occurrence of a grass snake in the Navalmaíllo rockshelter. Grass snakes have been separated recently to three species genetically and osteologically, but of these *N. astreptophora* based on a very few specimens (Pokrant et al., 2016; Kindler et al., 2017). *N. astreptophora* is living today in the Iberian Peninsula and north-western Africa, whereas *Natrix helvetica* lives in western Europe (from Britain to France and Italy) and the *Natrix* group in remaining Eurasia. Osteological differentiation between the three newly erected species is still confused and our attribution to *N. astreptophora* here is only based on biogeographical arguments.

Family Colubridae Oppel, 1811
*Coronella* Laurenti, 1768
*Coronella girondica* (Daudin, 1803) – Southern Smooth Snake.
*Coronella* cf. *C. girondica*.

Material: Layer F (7 anterior trunk vertebrae and 10 trunk vertebrae).

*Coronella* sp. – Smooth Snake.

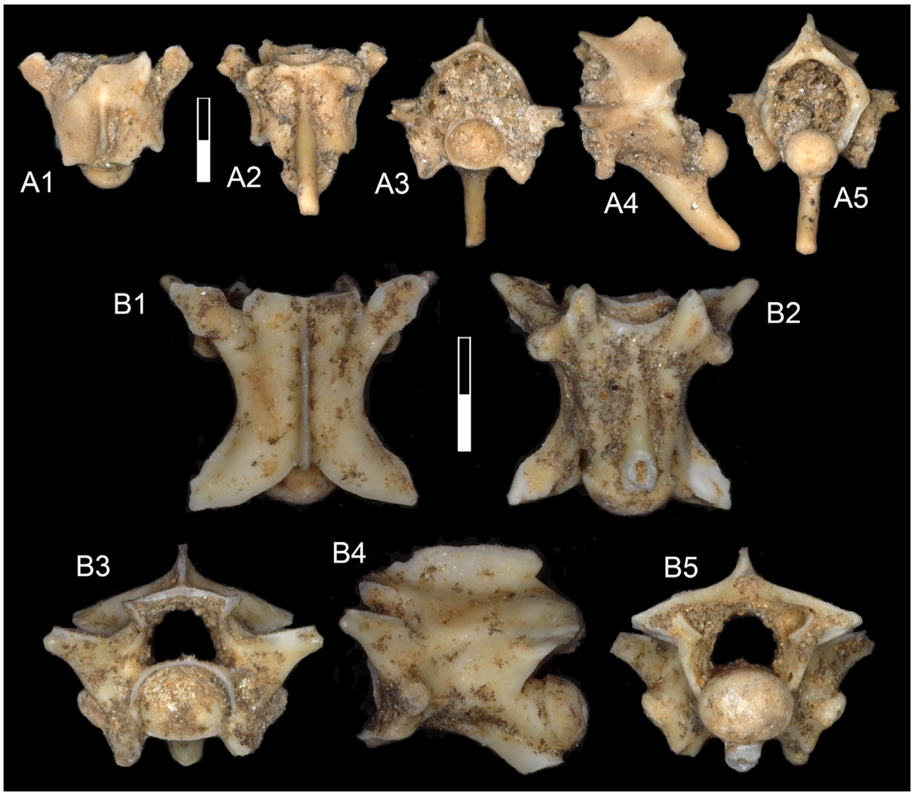

**Fig. 9.** Fossil snakes (Viperidae) from the Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid). A-B. *Vipera* cf. *V. latastei*. A. anterior trunk vertebra (NV′11 D18 Sector IV F 550–560) in dorsal (A1), ventral (A2), anterior (A3), left lateral (A4) and posterior (A5) views; B. trunk vertebra (NV′07 Sector I E18 F 530–540) in dorsal (B1), ventral (B2), anterior (B3), left lateral (B4) and posterior (B5) views. Scales = 2 mm.

Material: Layer FL (2 trunk vertebrae); Layer D (1 anterior trunk vertebra); Layer B (1 trunk vertebra).

Description: Smooth snakes are only documented by vertebrae in the Navalmaíllo rockshelter. These vertebrae are small, with a centrum length always shorter than 5 mm and, in posterior view, the neural arch is very flattened dorsoventrally (Fig. 8A). The ventral surface of the centrum does not bear any hypapophysis on the trunk vertebrae and the haemal keel is smooth, rather well defined and, its posterior end is slightly spatulated. The trunk vertebrae of adult individuals of *C. girondica* are differentiated from the vertebrae of juvenile or sub-adult individuals of other Iberian species essentially by a more marked pre-condylar constriction (Blain, 2005, 2009). Morphologically, these trunk vertebrae differ from *Coronella austriaca* by their prezygapophyseal processes, which are narrower at the base and longer, as well as by the size of the parapophyses in relation to the diapophyses, which are shorter in *C. girondica* than in *C. austriaca* (Szyndlar, 1984; Bailon, 1991). The anterior trunk (cervical) vertebrae possess a similar morphology than trunk vertebrae, but are characterized by the presence of a hypapophysis. Finally, due to the incompleteness, the fossil vertebrae recovered in layers FL, D and B are attributed to the genus level only.

*Zamenis* Wagler, 1830
*Zamenis scalaris* (Schinz, 1822) – Ladder Snake.

Material: Layer F (9 trunk vertebrae, from which 5 can be considered as from an adult and 4 as from a juvenile specimen)

Description: A total of nine trunk vertebrae have been attributed to the Ladder snake in the Navalmaíllo rockshelter. Difference in size (centrum length) among these fossil vertebrae suggests on one hand the presence of an adult specimen with five vertebrae presenting a CL longer than 4.5 mm (i.e. NV′07 Sector III E18 F 530–540 = 5.3 mm, Fig. 6B; NV′05 G17 F 480–490 = 8.4 mm; NV′07 Sector I D18 F 510–520 = 5.7 mm; NV′08 F16 F 480–490 = 4.7 mm; and NV′13 F16 F 500–510 = 5.0 mm, respectively) and, on the other hand, a probably younger specimen represented by four vertebrae with a CL comprised between 3.2 and 3.9 mm (3.2 mm, Fig. 8C; 3.25 mm; 3.5 mm; and 3.9 mm). In addition to the features already mentioned for the other species, the trunk vertebrae of *Z. scalaris* differ from those of *Hemorrhois hippocrepis* being more robust and shorter. Morphologically, the articular surfaces of the prezygapophyses are larger and round or sub-rectangular like in *C. girondica,* whereas in *H. hippocrepis* and especially *M. monspessulanus* they are oval and more anteriorly directed. In ventral view, the haemal keel is generally wider with diffuse lateral edges, and sometimes slightly spatulate in *Z. scalaris*. Finally, the trunk vertebrae have slenderer prezygapophyseal processes in *Z. scalaris* than in *Zanemis longissimus* (Szyndlar, 1984).

Family Viperidae Oppel, 1811
*Vipera* Garsault, 1764
*Vipera latastei* (Boscá, 1878) – Lataste's Viper.
*Vipera* cf. *V. latastei*.

Material: Layer F (3 cervical vertebrae, and 13 trunk vertebrae); Layer D (1 trunk vertebra).

Description: The fossil trunk vertebrae referred to Viperidae in the Navalmaíllo rockshelter show the typical features of the genus *Vipera*: presence of a more or less straight hypapophysis, a dorsoventrally flattened and convex neural arch in posterior view, a convex centrum in cross-section and with diffuse lateral margins, a developed condyle and acetabulum, and a dorsally inclined zygapophysis articular surface. One of the cervical vertebra preserves a hypapophysis somewhat longer than the centrum and seems to have had a relatively high neural spine (Fig. 9A). This is typically a character of *V. latastei*, whereas in other Iberian viperids, the hypapophysis is shorter than the centrum and the neural spine is generally lower than long (Szyndlar, 1984, 1987; Szyndlar and Rage, 1999). Trunk vertebrae are rather long with a centrum length between 2.8 and 5.6 mm (CL = 4.09 ± 0.85 mm; n = 12). Attribution of trunk vertebrae (Fig. 9B) at species level is more difficult and the distinction among species can be partly based on the development of the neural spine: *V. latastei* and *V. aspis* are distinguished from those of the *Vipera berus* group by a stronger development of the neural spine (Szyndlar, 1984). However, these traits are subtle and specific attribution should be made with extreme caution.

### 4.2. *Taphonomic considerations*

According to the different degrees of digestion (mostly light, except on two trout vertebrae from layer F showing a moderate digestion), the predator responsible for the fish accumulation is interpreted as a category 3 predator such as the Eurasian eagle owl (*Bubo*), ruling out any possible human activity as accumulation agent. Several authors (e.g. Sanchís-Serra, 2000; De cupere et al., 2009; Russ, 2010; Guillaud et al., 2021; Blanco-Lapaz et al., 2021) also argued the Eurasian eagle owl as the agent responsible of fish assemblage accumulation in archaeological contexts. This species is sedentary and currently present in the area, having opportunistic hunting habits nearby rivers (some 2.3 km around its nest according to Penteriani and Delgado, 2008; 2015). Additionally, the reduced fish assemblage from the Navalmaíllo rockshelter and the only representation of small fishes (less than 20 cm), would be a supplementary argument to support the fish accumulation by a non-human predator. A similar fish assemblage has been described by Guillaud et al. (2021) in the Late Pleistocene of Caverne Marie-Jeanne (Belgium).

Concerning amphibians and reptiles, only tortoises from Layers F and D have been fully studied from a taphonomic point of view (Moclán et al., 2021). From the 37 burnt remains identified at Layers F and D (over a total of >13.000 studied remains), 14 belongs to *T. hermanni* (Moclán et al., 2021). Although the presence of burn remains of tortoises in Neanderthal contexts had sometimes been related with the anthropic modification of these animals (Speth and Tchernov, 2002; Nabais and Zilhão, 2019), Moclán et al. (2021) discarded the consumption of tortoises at Navalmaíllo rockshelter. In this site, the use of fire during different moments of the Neanderthal occupation may have produced the accidental burning of a high part of the burnt faunal assemblage (Moclán et al., 2021). Furthermore, other possible anthropic activity (cut marks, percussion, etc.) have not been detected on the tortoise remains. The absence of tooth marks on the tortoise remains also precludes to know if carnivores have been implicated in their accumulation. Different types of post-depositional alterations were detected, including manganese oxidation, and biochemical alterations (Moclán et al., 2021).

The high percentage of broken elements for amphibians and squamate reptiles may indicate an accumulation by a predator, very probably small to medium-sized carnivores. The main agent of lagomorph accumulation in the Navalmaíllo rockshelter has been identified as a small carnivore, probably an Iberian lynx (Arriaza et al., 2017). The Iberian lynx is know to predate mainly on rabbits the whole year, but secondary prey appear mostly in autumn and winter, when the availability of rabbits throughout the annual cycle tends to be minimal (Fedriani et al., 1999; Palomares et al., 2001). In this case, beyond some large- and medium-sized preys, the diet can be completed by several species of micromammals, small birds and, very rarely, reptiles (Delibes, 1980; Aymerich, 1982; Calzada, 2000). The Iberian lynx can not be ruled out, but based on its modern diet, it is very probably not the main accumulator agent of the herpetofauna in Navalmaíllo rockshelter. Other accumulation agents can also have been involved in the site, as other unidentified little carnivores (Arriaza et al., 2017; Moclán et al., 2021), and the eagle-owl (*Bubo*), already mentioned in the case of the fish accumulation. The eagle-owl is a generalist and opportunistic predator, which, on the Iberian Peninsula, hunts a wide range of herpetofauna species, as *Bufo spinosus*, *Pelophylax perezi*, *Pelobates cultripes*, *Mauremys leprosa*, *Podarcis hispanica* sensu lato, *Psammodromus algirus*, *Timon lepidus*, and Colubridae snakes (Hiraldo et al., 1975; Pérez-Mellado, 1978; Vericad et al., 1976; Serrano, 1998; Penteriani and Delgado, 2016). Besides predators, the ratio of NISP to the MNI, which is indicative of a high number of preserved skeletal elements per carcass, is high for *Testudo hermanni* (39.4:1), fish (10:1) and snakes (*Coronella* 18:1 and, *Vipera* 16:1). For the laters (fish and snakes), this may be an artefact of the NMI estimate for these groups. However, this rate is similarly high for *E. calamita* (9.6:1), which may suggest that some of the carcasses at the site were largely complete, probably linked with an in situ mortality during wintering. No burning marks, cut marks, and tooth marks have been detected on the amphibians and squamate reptiles. Moderate manganese oxidation and biochemical alterations are also frequently observed on those bones.

As a summary, several accumulator agents, as well as in situ mortality, seem to have produced the small-vertebrate assemblages from the Navalmaíllo rockshelter. No important bias is thus to be declared that would hamper any quantitative or qualitative paleoenvironmental and paleoclimatic reconstructions.

### 4.3. *Paleoenvironmental reconstructions*

The reconstructed landscape around the Navalmaíllo rockshelter is consistent with the predominance of Mediterranean and xero-thermophilic species (*E. calamita* and to a lesser extent by *T. hermanni*) over the comparatively more hydro-hygrophilous (such as *Rana* cf. *R. iberica* and *Natrix* cf. *N. astreptophora*). Only layers FL, F and D have a sufficient number of individuals (MNI) for proposing a consistent palaeoenvironmental reconstruction. However, it is worth mentioning that materials found in level D come either injected from level F or percolated from overlying levels.

The Habitat Weighting method for these layers suggests a major presence around the cave of open environments, primarily made up of open dry habitats (24.2–33.3%) and to a lesser extent rocky (16.7–20.7%) and open humid habitats (9.5–17.5%). The presence of

**Table 4**
Palaeoenvironmental reconstructions based on the Habitat Weighting method for the layers of Navalmaíllo rockshelter (Madrid, Spain). The values are in percentages (%).

| | Open Dry | Open Humid | Woodland | Rocky | Water edge |
|---|---|---|---|---|---|
| Layer FL | 26.7 | 14.1 | 32.5 | 16.7 | 10.0 |
| Layer F | 33.3 | 9.5 | 29.5 | 20.7 | 7.0 |
| Layer D | 24.2 | 17.5 | 30.0 | 19.2 | 9.2 |
| Layer ß | 45.0 | – | 20.0 | 25.0 | 10.0 |
| Layer C | 31.7 | – | 40.0 | 25.0 | 3.3 |
| Layer B | 23.3 | 21.7 | 28.3 | 16.7 | 10.0 |

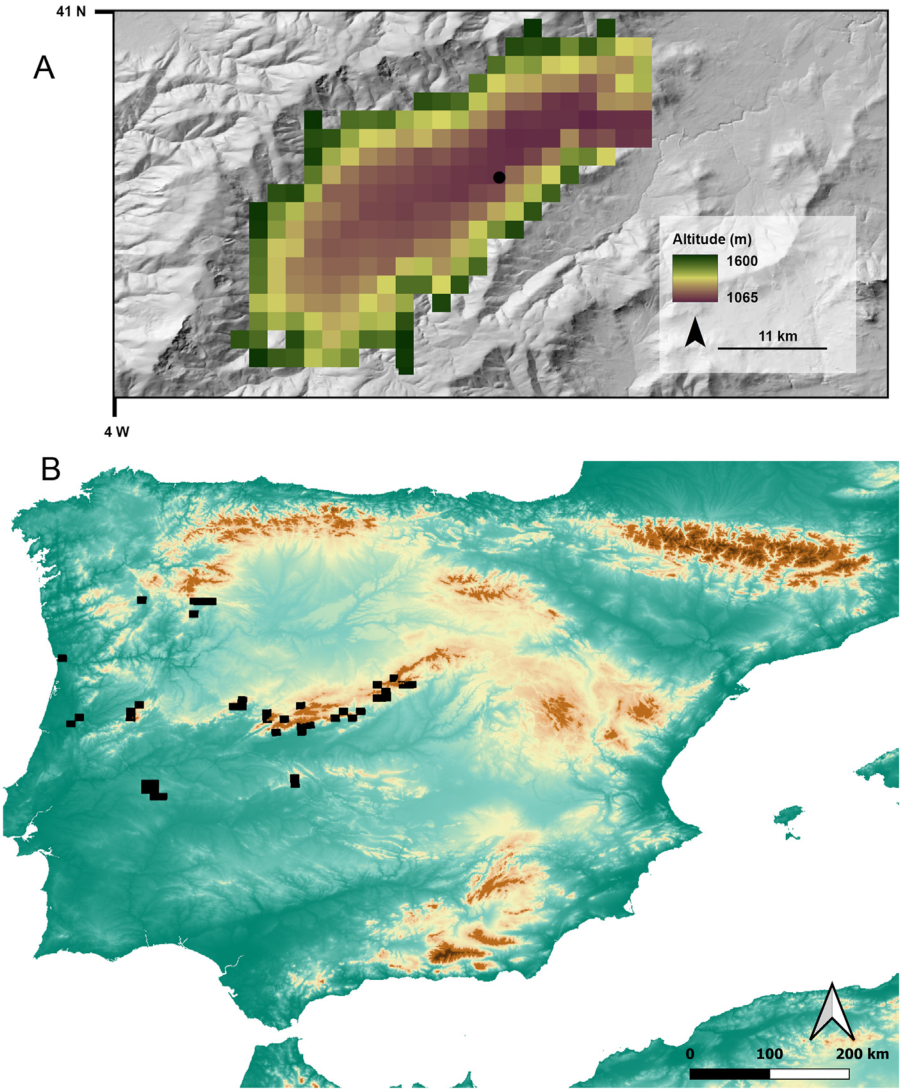

**Fig. 10.** A. Selected altitude and area for the current climate calculation in the Lozoya Valley. The black dot represents the location of the Navalmaíllo rockshelter; B. Overlap of the current distribution for the amphibians and squamate reptiles from the layer F of the Navalmaíllo rockshelter. Black squares correspond to the 10 × 10 species distribution squares from SIARE and Loureiro et al. (2008) after removing the areas higher than the upper elevation where all the species could potentially coincide (1800 m. a.s.l.).

woodland environments was also detected, which include medium scrublands to forest formations (29.5–32.5%), together with aquatic and peri-aquatic areas (7.0–10.0%), such as rivers or ponds with riverside vegetation (Table 4). The comparison between the three layers shows that layer F is the one with the highest tendency towards drier environments (open dry and rocky), to the detriment of wetter ones (open humid and water edge).

Additionally, the presence of fish is interesting in the site, as amphibians and reptiles do not document any typical taxa closely related to water (as would have been *Pelophylax perezi*, *Natrix maura* or turtles). Fish thus permit to complete the description of aquatic environments.

The common brown trout (*S. trutta*) requires clean oxygen-rich water and a specific temperature for hatching and growing. In the Iberian Peninsula, *S. trutta* is usually present in running waters with temperatures ranging from 0 to 20 °C although is most common in cold waters (less than 15 °C) (Jonsson and Jonsson, 2009; Elliott and Elliott, 2010). Cyprinids are usually more typical of temperate (between 10 and 25 °C) waters (Doadrio et al., 2011; Tissot and Souchon, 2010). Among cyprinids, genera such as *Squalius* (chub) and *Chondrostoma* (nase) can be found in the same water zone as salmonids, as they also thrive in running water but cyprinids, in general, are present in a higher diversity of environments showing an enormous diet diversity, including arthropods or other fish (Doadrio et al., 2011).

Even though today, the course of the Loyoza river is blocked by several artificial reservoirs (Rubio, 2015), the oxygen levels in the Lozoya river system range from 7.91 to 9.73 mg/L $O_2$ (Rubio, 2015), and the average temperature from 7.68 °C to 10.01 °C indicating well-oxygenated and cold waters (García-Rodríguez et al., 2009; Rubio, 2015). Such similar well-developed and permanent river system seem to have existed during the Late Pleistocene (MIS 5) close to the Navalmaíllo rockshelter, characterized by clean, well-oxygenated, and running cold waters.

### 4.4. Paleoclimatic reconstructions

The application of the MER method and UDA-ODA discrimination technique to layer F of the Navalmaíllo rockshelter paleoherpetofaunal assemblage results in a common overlapping area of

**Table 5**
Climatic values from Lozoya Valley nowadays (1970–2000; data from WorldClim 2.1 data, Fick and Hijmans, 2017) and climatic parameters of layer F from the Navalmaíllo rockshelter calculated (in °C for temperature and mm for precipitation) by the Mutual Ecogeographic Range method with the fundament of UDA-ODA discrimination technique. MAT = mean annual temperature, MAP = mean annual precipitation, Area = surface of the overlapping area (in km$^2$), SD = standard deviation, MIN = minimum, MAX = maximum.

| | Temperature (°C) | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAT | J | F | M | A | M | J | J | A | S | O | N | D |
| **Layer F** | Area (km2) = 3951 | | | | | | | | | | | | |
| MEAN | 12.1 | 4.8 | 5.9 | 8.1 | 9.6 | 13.0 | 17.5 | 21.0 | 20.8 | 17.8 | 12.7 | 8.3 | 5.8 |
| SD | 2.2 | 2.5 | 2.6 | 2.6 | 2.5 | 2.2 | 2.0 | 1.9 | 1.8 | 2.1 | 2.4 | 2.5 | 2.5 |
| MIN | 6.7 | −0.7 | −0.2 | 1.9 | 3.1 | 7.0 | 12.2 | 16.1 | 16.2 | 12.7 | 7.1 | 3.0 | 0.5 |
| MAX | 16.1 | 10.2 | 11.3 | 13.2 | 14.7 | 17.0 | 21.7 | 24.9 | 24.7 | 21.9 | 17.3 | 13.7 | 11.2 |
| **Lozoya Valley (1970–2000)** | Area (km2) = 154.84 | | | | | | | | | | | | |
| MEAN | 9.3 | 1.4 | 2.4 | 4.8 | 6.9 | 10.5 | 15.3 | 19.1 | 19.1 | 15.3 | 9.8 | 5.1 | 2.5 |
| SD | 0.1 | 0.7 | 0.9 | 1.0 | 1.2 | 1.1 | 1.0 | 0.8 | 0.9 | 0.8 | 0.9 | 0.8 | 0.7 |
| **Δ** | | | | | | | | | | | | | |
| MEAN | 2.8 | 3.4 | 3.6 | 3.3 | 2.7 | 2.5 | 2.3 | 1.8 | 1.7 | 2.5 | 2.9 | 3.2 | 3.4 |
| | **Precipitation (mm)** | | | | | | | | | | | | |
| | MAP | J | F | M | A | M | J | J | A | S | O | N | D |
| **Layer F** | Area (km2) = 3951 | | | | | | | | | | | | |
| MEAN | 802 | 101 | 85.1 | 60.1 | 71.5 | 72.6 | 43.6 | 16 | 15.5 | 40.7 | 86.6 | 97.6 | 111.7 |
| SD | 345.2 | 55.5 | 47.2 | 28.6 | 26.7 | 24.5 | 12.8 | 6.8 | 6.1 | 15.2 | 36.5 | 43.7 | 56.8 |
| MIN | 327 | 27.0 | 24.0 | 19.0 | 32.0 | 34.0 | 24.0 | 5.0 | 6.0 | 23.0 | 34.0 | 35.0 | 37.0 |
| MAX | 2055 | 296 | 230 | 145 | 160 | 162 | 83 | 37 | 41 | 124 | 208 | 257 | 320 |
| **Lozoya Valley (1970–2000)** | Area (km2) = 154.84 | | | | | | | | | | | | |
| MEAN | 621.4 | 59.3 | 47.4 | 40.8 | 62.8 | 74.6 | 45.4 | 22.0 | 21.1 | 37.5 | 65.5 | 74.3 | 70.7 |
| SD | 7.7 | 15.1 | 10.4 | 8.2 | 12.0 | 12.4 | 5.8 | 2.5 | 1.4 | 4.5 | 12.6 | 17.8 | 16.7 |
| **Δ** | | | | | | | | | | | | | |
| MEAN | 180.6 | 41.7 | 37.7 | 19.3 | 8.8 | −2.0 | −1.9 | −6.0 | −5.5 | 3.1 | 21.0 | 23.3 | 40.9 |

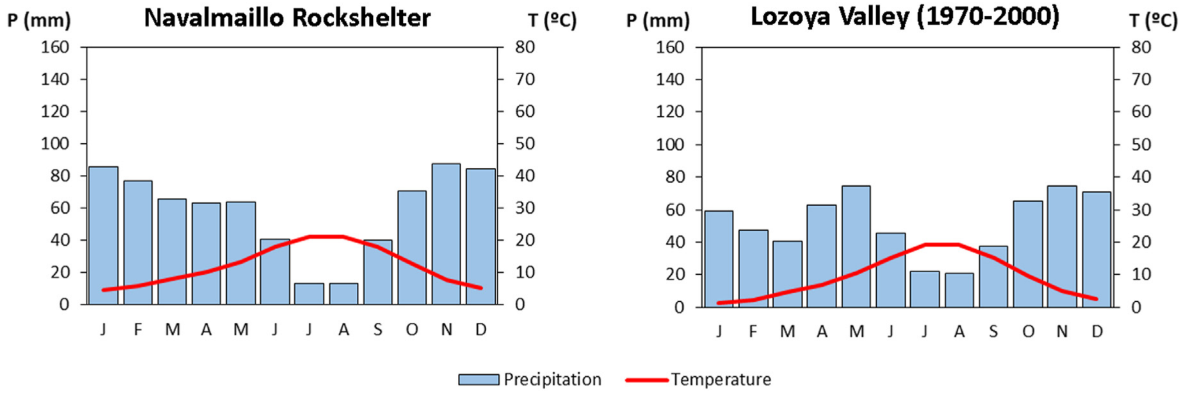

**Fig. 11.** Climatograms corresponding to the quantitative climate reconstructions of the layer F from the Navalmaíllo rockshelter plus the modern climate values of the Pinilla del Valle area (1970–2000; calculated from WorldClim 2.1 data, Fick and Hijmans, 2017), applying the scale P = 2 × T, where P = precipitation, T = temperature.

**Table 6**
Climatic interpretation of the climatograms obtained for the layer F of the Navalmaíllo rockshelter. Abreviations: MTC, mean temperature of the coldest month.

| | Layer F - ODA | | Lozoya Valley (1970–2000) | |
|---|---|---|---|---|
| Mean annual temperature | 12.0 °C | cold | 9.3 °C | low |
| Atmospheric temperature range | 16.2 °C | high | 17.7 °C | high |
| Summer temperature | no months>22 °C | warm-temperate | no months>22 °C | warm-temperate |
| Winter temperature | MTC = 4.8 °C | cold | MTC = 1.4 °C | cold |
| Mean annual precipitation | 802 mm | low | 621 mm | low |
| Distribution of rainfall | fairly regular | winter | fairly regular | winter |
| Type of precipitation | rain | rain | | |
| Gaussen Index | 2 | Continental | 2 | Continental |
| Lautensach-Mayer Index | 2 | semi-humid | 2 | semi-humid |
| Dantin-Revenga Index | 1.5 | humid | 1.5 | humid |
| De Martonne Index | 36.3 | humid | 32.1 | humid |

3951 km$^2$. These areas are located on the north-western part of the Iberian Peninsula, mainly around the Central System mountain range (Fig. 10). The estimated MAT is 12.1 ± 2.2 °C and the MAP is 802 ± 101 mm (Table 5). Climatograms were made to better visualize the monthly evolution of temperature and precipitation, applying the scale P = 2 × T in order to evaluate directly the

Gaussen aridity index (Fig. 11). The climatic interpretation is synthetized in Table 6. The climate inferred is cold with a strong continental pattern. The summer is warm-temperate and the winter is cold. Rainfall is low and with a fairly irregular pattern, occurring mainly during the winter and spring. The aridity indexes suggest a semi-humid (or humid according to the De Martonne index), continental Mediterranean climate with two dry months in July and August (Fig. 11; Table 6).

In comparison with current climatic data (1970–2000) from the Lozoya Valley selected area (Fig. 11; Table 5), the paleoclimatic reconstruction indicates somewhat higher MAT than today (+2.8 °C), with similar temperatures during summer but higher throughout the other months of the year. The total amount of rainfall is somewhat higher (+180.6 mm) than the current level in the Lozoya Valley. Precipitation values increase for the colder months, but decrease for the warmer ones, pointing to a more marked contrast in the rainfall regime along the year (Fig. 11; Table 6). The aridity index values suggest similar values, in both cases indicating semi-humid to humid conditions.

## 5. Discussion

Paleoenvironmental and paleoclimatic reconstructions for Layer F of the Navalmaíllo rockshelter suggest the presence of well represented open-dry environments under warmer than present, semi-humid, continental Mediterranean climate with two dry months during the summer. Probably thanks to the altitudinal gradient, woodland environments were rather extended, including medium scrublands to forest formations. More humid patches may have been found mainly close to the aquatic areas such as rivers or ponds with riverside vegetation.

### 5.1. Comparison with other proxies at Navalmaillo rockshelter

Up to date, the only paleoenvironmental reconstruction at Navalmaíllo rockshelter has been based on pollen (Ruiz Zapata et al., 2015). A total of 26 taxa have been identified, of which 10 are arboreal, 3 shrubs and 13 herbaceous, together with 3 aquatic elements, monoecious spores and triletes. *Pinus* is the dominant element of the arboreal group, accompanied by evergreen and deciduous *Quercus* and Oleaceae and the presence of *Juniperus*, *Fraxinus*, *Populus*, *Ulmus* and *Betula*, defining the existence of Mediterranean type conditions. The presence of Cyperaceae, Juncaceae, *Typha* and taxa associated with humid conditions define fluctuations in the humidity rate along the stratigraphical sequence. In its evolution, after the development of a not very varied arboreal landscape (NVP-13, 15 and, 18 in Ruiz Zapata et al., 2015), a dominance of the forest mass (Layer FL, named NVP-H in Ruiz Zapata et al., 2015) can be perceived, which evolves towards very open landscapes (Layers F and α-β).

From a paleoclimatic point of view, Layer FL, shows a forested landscape, with a high representation of pine trees and the initial expansion of deciduous *Quercus*, which has been interpreted to correspond to MIS 5, coinciding with the European records, in which the expansion of deciduous taxa occurs at this time (Tzedakis et al., 2003; Binká et al., 2011). The subsequent development of the Mediterranean component (evergreen *Quercus* and Oleaceae), is coincident with that of other southern European sequences (Fernández et al., 2007; Carrión et al., 2007, 2019; Arsuaga et al., 2012; Ochando et al., 2019, 2022). During Layer F, the data show a significant decrease in the arboreal group. The low pollen conservation at this level of the sequence could be related to a dry period, during which wind erosion would be accentuated, causing pollen hiatuses. Layers α-β may correspond to MIS 3, when, together with *Pinus* and *Juniperus*, there is a strong expansion of Chenopodiaceae and Asteraceae, as in the neighboring site of the Buena Pinta cave (Ruiz Zapata et al., 2007), where, once again, the development of a predominantly herbaceous plant landscape is evident, indicative of cool and dry conditions, capable of inhibiting the development of a complex floristic cortege.

This reconstruction for Layer F clashes with the data presented here. The Layer FL does not appear to be less forested than Layer F according to the herpetofaunal assemblage (Table 4), however it is true that the number of remains/taxa in other layers than Layer F is rather low to ensure a quantitative paleoenvironmental interpretation. Pollen and herpetofauna however concur in the Mediterranean character of the climate, with existence of a rather well extended herbaceous area. The discrepancy among proxies may come from a worse conservation of pollen in Layer F. Predominance of large bovids (*Bos*/*Bison*) and medium-sized cervids (*Cervus elaphus*, *Dama* and, *Capreolus*), against horses (*Equus ferus, Equus hydruntinus*) and rhinoceroses (*Stephanorhinus hemitoechus*) suggest that forest extension may have been subsequent during this period, although this may represent human hunting preferences rather than purely climatic conditions. The occurrence of *Rupicapra pyrenaica* in the faunal list also supports the presence of rocky areas around the site, whereas *Castor fiber* suggest well developed water environments.

### 5.2. Comparison with Camino cave (Pinilla del Valle)

The Cueva del Camino (Camino cave) site is another locality of the Pinilla del Valle complex, located at around 40 m north from the Navalmaíllo rockshelter and that has proved to be a highly relevant location for studying the ecological changes linked to the climatic fluctuations at the end of MIS 5 and the beginning of MIS 4 (Laplana et al., 2013; Blain et al., 2014a). Environmental reconstructions using amphibians and reptiles suggested a rather open, patchy landscape throughout the succession, with abundant evidence of dry meadows, scrublands and rocky habitats. The climate has been considered as generally warm, reaching mean annual temperatures of up to 13.8 °C (i.e. higher than today's by up to 2.9 °C). Nevertheless, three cooler events have been identified throughout the succession as reflected by the presence of *Rana iberica*, *Anguis fragilis* and *Coronella austriaca*. The first of these events has been cautiously correlated with MIS 5b; the second, recorded in the Central sector, may correlate with the Stadial I pollen event occurring at the end of MIS 5a; and the third event, corresponding to the coldest MAT of the entire succession, with MATs 0.9 °C lower than today's, may correspond to the transition from MIS 5a to MIS 4 (Blain et al., 2014a).

Direct comparisons between the quantitative reconstructions obtained for Camino cave have to be taken cautiously, as the climatic database and the baseline for modern comparison are different between this study and Blain et al. (2014a). Nevertheless, a rough comparison suggests that Layer F from Navalmaíllo is concordant climatically with the anomaly values obtained for the Northern Sector (MIS 5c?) and the lower part of the Central Sector sequence (MIS 5a?).

From a paleoenvironmental point of view, landscape quantification, using the habitat weighting method shows similar reconstructions to those obtained for the Northern and Central Sectors of Camino cave (Blain et al., 2014a), with abundant evidence of dry meadows, scrublands and rocky habitats for the Layers F and ß. On the other hand, Layer B seems to be somewhat closer to the landscape reconstructed for the Southern Sector (MIS 4) of Camino cave, with a higher percentage of open-humid and water areas (due to the higher representation in the assemblage of the Iberian stream frog).

To further compare the different herpetofaunal assemblages

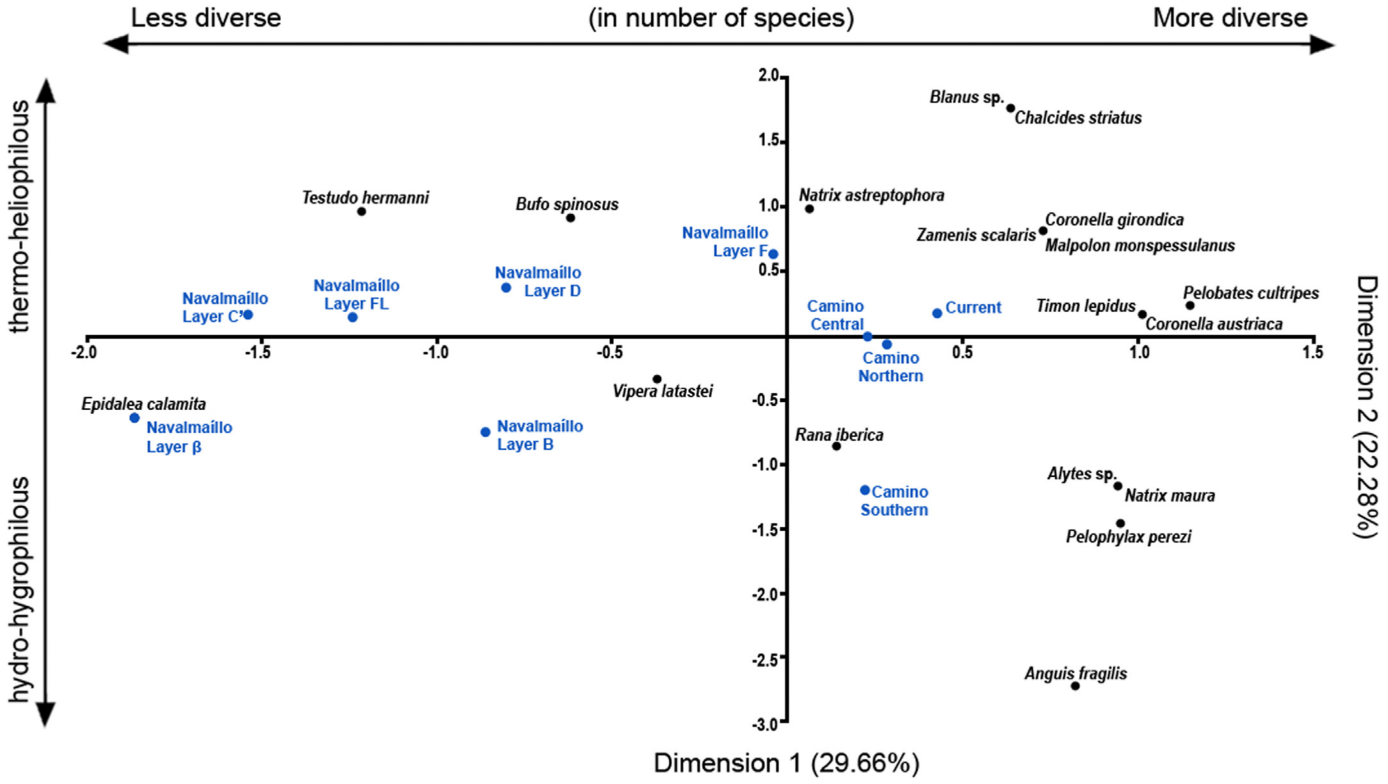

**Fig. 12.** Correspondence analysis of the herpetofaunal assemblages (in blue) and taxa (in black) from Pinilla del Valle sites (Navalmaíllo rockshelter and the Camino cave's sectors) and modern herpetofaunal assemblage from the Lozoya Valley. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

from the Navalmaíllo rockshelter with those of the different sectors from the Camino cave (Laplana et al., 2013; Blain et al., 2014a) and to infer possible trends through composition changes in the local sequence, a data matrix based on presence/absence has been created. The current herpetofauna of Pinilla del Valle and the surrounding Lozoya Valley (UTM squares 10 × 10 km 30 T-VL22, 30 T-VL23, 30 T-VL32 and 30 T-VL33) has also been added to the data matrix, this information having been extracted from the SIARE distribution maps of the Spanish herpetofauna (AHE, 2021). The different herpetofaunal assemblages are shown in the columns, and the taxa are shown in the rows along with their presence (1) or absence (0). In addition, some normalizations have been applied so as to reduce dispersion and facilitate interpretation. Taxa that do not reach species level have not been included for the concurrences of the Camino sectors and the Navalmaíllo layers, except for *Alytes* sp. (*Alytes obstetricans* sensu lato) and *Blanus* sp. For the current concurrence, only taxa with documented records in the Pinilla del Valle sites have been included. A correspondence analysis (CA) was applied on the data matrix (Greenacre, 2010), by using the Paleontological Statistics program (PAST4) for all statistical analyses (Hammer et al., 2001).

For the herpetofaunal sequence of Pinilla del Valle sites, excluding the current concurrence, the most represented species are *Epidalea calamita* (present in all the assemblages), *Vipera latastei*/*Vipera* cf. *Vipera latastei* (6 assemblages, 60% of the assemblages), both *Bufo* gr. *Bufo* bufo (*Bufo spinosus*) and *Testudo hermanni* (5 assemblages, 50%). The remaining taxa show lower values of concurrence (between 4 and 1 assemblages). The least representative taxa are *Blanus* sp. and *Chalcides* cf. *Chalcides striatus* (1 assemblage, 10%). All but two taxa in the sequence are currently present in the central Iberian Peninsula, with representation in Pinilla del Valle or in its closest surrounding area. The exceptions are *A. fragilis* (present in the region but not in the Loyoza Valley) and *T. hermanni*, which during the Late Pleistocene presented a continuous record in the Iberian inland from the previous interglacial (MIS 5e) until the period before the Last Glacial Maximum (MIS 2) (Morales Pérez and Sanchis Serra, 2009; Bisbal-Chinesta and Blain, 2018). The current distribution in Iberia of this tortoise is restricted to coastal areas with a Mediterranean climate in the northern half of the Iberian Mediterranean coast, although at the east of its distribution in Italy and the Balkans it also appears in sub-Mediterranean temperate climates (Bertolero, 2010).

The CA of the herpetofaunal sequences from Pinilla del Valle sites, including the modern concurrence, shows an interrelationship between species composition in the concurrences and changes of aridity-humidity in the environment. In the graphic representation of the CA, the horizontal axis is interpreted in a left-right direction from lower to higher number of concurring species in the assemblages of the layers, while the vertical axis shows differences in a top-bottom direction from lower to higher moisture (Fig. 12).

The CA additionally permits to distinguish three groups among the represented herpetofaunal taxa (Fig. 12). The first group is formed by the dominant species, *E. calamita*, *B. spinosus*, *T. hermanni* and *V. latastei*, and are displayed in the left half of the graph. These are Mediterranean/generalist species that tolerate continental Mediterranean conditions, typical of central Iberia. The second group is composed of thermo-heliophilous taxa, which appear in the upper right sector of the graph, which mostly, but not exclusively (*N. astreptophora* and *C. austriaca*), prefer open dry land (*P. cultripes*, *Blanus* sp., *C. striatus*, *T. lepidus*, *M. monspessulanus*, *C. girondica* and *Z. scalaris*). The third group is formed by hydro-hygrophilous taxa, in the lower right sector, and are associated with aquatic (*P. perezi*, *R. iberica*, and *N. maura*) or high humidity environments (*Alytes* sp. and *Anguis fragilis*).

The CA of the assemblages shows a similar pattern (Fig. 12). The dominant role of *E. calamita, B. spinosus, T. hermanni* and *V. latastei* in the Pinilla del Valle record and the low number of taxa in concurrence have generated a grouping of assemblages from Navalmaíllo layers in the left side following the horizontal axis of the CA graph. The assemblages of the Camino sectors are placed around the current herpetofaunal concurrence on the right side of the graph, following a vertical ordination axis according to their herpetofaunal composition. Layer F is located in an intermediate position on the horizontal axis, but close to the Camino assemblages in which thermo-heliophilous species predominate.

### *5.3. Comparison with sites from the Jarama and Manzanares Valleys (south-east of Madrid)*

The valleys of the Jarama and Manzanares rivers are located in the Tagus basin, within the South Sub-Meseta of the Iberian Peninsula, at approximately 100 km from the archaeological sites of Pinilla del Valle and at a lower altitude of 500 m (Fig. 1). These valleys are characterized by the development of a great number of fluvial terraces related to Quaternary climatic oscillations, and both rivers are responsible for the terraces' configuration, tectonics, isostatic rising and block adjustment, as well as lithological structural controls (Pérez-González, 1994). The successive fossil amphibian and reptile assemblages from the Middle to Late Pleistocene sites from the Manzanares and Jarama River Valleys permitted the reconstruction of part of the climate instability with high-amplitude and rapid shifts of the last 450 ka and their associated landscapes: Áridos-1 (MIS11b), Valdocarros II (MIS8a/MIS7e), Estanque de Tormentas de Butarque H-02 (MIS7d or MIS6), PRERESA (MIS7/6 or MIS5a) and HAT (MIS5a) (Blain et al., 2012a, b, 2013b, 2014b, 2015, 2017, 2018, 2019).

The configuration and temporal evolution of the reconstructed habitats by the herpetofaunal assemblages suggest the existence, in the lower valleys of the Jarama and Manzanares Rivers, of a landscape with gallery forests along watercourses. Parallel to these forested areas would be the presence of wet meadows in the flood plain. Then, according to the distance from the river, they would give way, on the surrounding plateau, to shrubby and finally dry grasslands and steppe zones, with scattered rocky exposures. The changes observed over the sequence could be related to the retractions of the wettest environments and the increase of dry habitats in accordance with the fluctuations of the river water regime and rainfalls. Such a situation is in accordance with the overall climate comparison performed between the studied sites that suggest two different climatic patterns (+ a transitional one): an interglacial "warm" pattern and a glacial "cold" one. During relatively "warm" periods (MIS 11b, MIS 7, MIS 5a and today) the climate is clearly Mediterranean, with mild winters and a long period of dryness in summer and an early autumn, and by contrast during "cold" periods (MIS 8 and MIS 6) the climate is more continental (Mediterranean), although preserving some dryness during the summer. The environment is particularly open during dry periods (independently of being cold or warm) with a percentage of open-dry environment about 40%. The main difference between an interglacial and a glacial period is the opposite representation of woodlands vs. moist environments (water-edge + open-humid): the latter being better represented during cold periods than during warm periods.

Considering this paleoecological context, there are two open-air sites of interest which are chronologically close from the Navalmaíllo rockshelter: HAT and PRERESA. HAT (MIS 5a) corresponds to two test pits excavated in 2001, involving a total area of 6 $m^2$ and a total volume of 8.55 $m^3$ (Panera et al., 2005). A numerical date of 74 + 16/-12.1 ka was obtained by thermoluminescence (TL) in the upper part of the section, suggesting that this site was formed during the second half of MIS 5. In addition to the small vertebrates, the excavations yielded a horse molar (*Equus caballus*) and about 60 pieces of lithic industries. Flint is the dominant raw material (corresponding to over 66% of the total), followed by quartzite and quartz. All the elements of the working chain have been found in the site, even if quantitatively they do not correspond to a complete sample (Panera et al., 2005). The macro-tooling is represented only by a worked pebble, which was initially used as a hammerstone. The small surface area excavated only allows us to indicate that this is a place where hominids brought the raw materials to produce tools for cutting animal carcasses in situ (Panera et al., 2005). Although less chronologically well-constrained, PRERESA (MIS 5a or MIS 7/6) seems also to have been formed during interglacial conditions (Blain et al., 2013b, 2019). An area of approximately 255 $m^2$ was systematically excavated between 2003 and 2005 (Yravedra et al., 2012). This excavation yielded 754 lithic industry artifacts, as well as remains of mollusks, small vertebrates and large herbivores (*Bos primigenius*, *Dama* sp, *Cervus elaphus*, *Capreolus*, *Equus* sp, and *Palaeoloxodon/Mamuthus*) and carnivores (*Vulpes*, *Lynx pardinus*, *Meles* and *Canis lupus*) (Yravedra et al., 2012). The taphonomic and zooarchaeological analysis of the remains of large mammals shows that the preservation conditions are excellent. Carnivore action is relatively low and there is ample evidence of human activity on the large bones, particularly on the proboscidean bones (Yravedra et al., 2012). A nearly complete *Bos primigenius* skeleton with some anatomically connected elements was recovered from an area of about 120 $m^2$. The lithic industry of PRERESA is rich in debris and simple flakes. The assemblage consists of 748 flint and 6 quartz pieces. The operative chain of the flint industries is complete. The cores are not very elaborated. The absence of macrotools and the low representation of retouched tools can be noted. Of these, the most common are retouched flakes, followed by denticulated and composite tools. A scraper and a chisel were also recovered. The dispersion and distribution of faunal remains, as well as the characteristics and distribution of the lithic industry, and the cut and impact marks found on a number of bones, suggest that some of the carcasses were butchered by hominids. It is likely that the unretouched flakes were shaped and used in situ (Yravedra et al., 2012).

The herpetofaunal assemblages of HAT (MIS 5a) and PRERESA (MIS 5a or MIS 7/6), both with interglacial climatic conditions, show a general scenario of dominance of open dry habitats, although with significant differences. In HAT the prevalence of open dry environments is accentuated (56.2%), to the detriment of open wet areas (2.5%), vegetation cover of woods and/or scrublands (16.4%) and rocky zones (9.6%). In PRERESA the open dry habitats are also predominant (42.5%), but with a better representation of the remaining habitats compared to HAT (open-humid: 6.7%; woodland: 24.2%; and rocky: 16.4%). When compared with the results obtained for the Layers F, FL and D from the Navalmaíllo rockshelter, the ecological conditions seem to have been much harsher (concerning aridity) at lower altitudes (Jarama and Manzanares valleys) than in the mountain areas of the Lozoya valley. So, if, as said in the introduction, Neanderthals were strongly related with woodlands (or diversity-rich emplacements), both interglacial and glacial (but not transition) periods at lower altitudes would not have been particularly favorable for their hunting activities, with the exception of environments in the proximity of major watercourses.

### 5.4. Implication for Neanderthal paleoecology and territory occupation

Evidence from stable isotope studies of Neanderthal remains indicate that they were top-level carnivores, receiving most of their protein from large mammals (Richards and Trinkaus, 2009), and even at times from extremely large mammals such as rhinoceros and mammoths (Bocherens et al., 2005; Bocherens, 2011). Several zooarchaeological studies confirmed the systematic exploitation of large mammals during the Middle Palaeolithic, and it is accepted that they were regularly hunted (e.g. Gaudzinski, 1996; Gaudzinski and Roebroeks, 2000). Neanderthals are also supposed to have had a higher daily energetic cost of foraging (Frohehle and Churchill, 2009; Snodgrass and Leonard, 2009) and this is why their residential camps were usually located in settings of high biodiversity and compact, vertically ordered environmental zonation (Henry et al., 2017).

According to López-García et al. (2019), the hominins that inhabited the western Mediterranean region in the late Middle Pleistocene and Late Pleistocene were closely associated with Mediterranean forested areas (between 31.9 and 49.7% of the landscape). However, such inferences have recently been pondered by similar analyses done on the herpetofaunal assemblages that suggest a broadening of their earlier ecological niche clearly observed at around 426 ka, towards the occupation of more open arid areas (Blain et al., 2021). After this threshold, it seems that hominins are present for the first time in very open environments in central Iberian Peninsula, as it would be the case in Áridos-1 and Ambrona (level AS4/3), sites where the extension of woodland area has been estimated to be comprised between 10% and 20%. Other Spanish sites such as Cuesta de la Bajada, Trinchera Elefante level TE19, Valdocarros 2 (level 2), and Estanque de Tormentas de Butarque (H02) also suggested that late Middle Pleistocene hominins were able to cope with more contrasted and more open conditions than previous hominins and could thus settle in the inner part of the Central Meseta, even though most of these sites are mainly located in fluvial contexts. Such arid conditions are supposed to be a priori less beneficial for Neanderthal populations (Henry et al., 2017). The consecutive hypothetical enlargement of their distribution inside the Iberian Peninsula raised the question about their altitudinal distribution and/or the durability of their settlements far from the river valleys.

Riverside ecosystems form authentic ecological corridors that connect different ecosystems and facilitate the movement of a number of vertebrate species (Forman, 1995; Cohen et al., 2012). Such riverside ecosystems are generally associated with a highly varied biodiversity, both of animals and plants. This biodiversity could be one of the reasons why the Manzanares and Jarama Valleys were regularly visited by hominins throughout the Pleistocene, as tens of Palaeolithical sites recorded throughout the river terraces have revealed (Panera and Rubio-Jara, 2002; Rubio-Jara, 2011). Moreover, the evidence of proboscidean exploitation occurring between MIS 6 and MIS 5 in this area, suggests that there was no substantial change of subsistence strategies between the Lower and Middle Palaeolithic (Panera et al., 2014). A large number of Acheulean sites containing lithic industry together with proboscidean remains dating to the final Middle Pleistocene and early Late Pleistocene have been recorded in the Manzanares Valley (e.g. Meléndez and Aguirre, 1958; Santonja et al., 1980; Sesé and Soto, 2002; Baena Preysler et al., 2010). Cut and percussion marks and green-bone fractures (Rus and Vega Toscano, 1984; Manzano et al., 2010; Yravedra et al., 2012) show that these mega-herbivores were constantly exploited as a resource during the Middle Palaeolithic. The geographical location of this area, the Mediterranean climate characteristics identified during this period (Sesé et al., 2011; Blain et al., 2019) as well as its surrounding ecosystems, could have favored the presence of large mammals along the riverbanks of the final reach of the river, especially during the summer drought period, establishing a special case of the concentrate resources model (Haggett et al., 1977; Butzer, 1982). This does not seem to have any relation with changes in the availability of animal or plant resources, which would propitiate a greater interest on proboscideans, but with the advantages they offered to groups of hunter-gatherers (Panera et al., 2014).

However as seen before, the lowland in central Iberian Peninsula during interglacial periods appears to have been much arid (and consequently leading to lesser woodland coverage: only 16.4% in HAT and 24.2% in PRERESA) than mountain areas (Navalmaíllo). Consequently, as rugged terrain was not a problem for Neanderthals, the Lozoya valley was certainly a good place for them during drier periods (interglacials or summer), providing them with settings of high biodiversity and compact, vertically ordered environmental zonation, where they focused more preferentially on cervids and equids (Moclán et al., 2021). One exception could be the site of Camino cave, interpreted as a hyena den (Díez Fernández-Lomana, 1992; Huguet et al., 2010; Arsuaga et al., 2010, 2012), where the extension of woodland was reconstructed to be comprised between 23.8 and 10.8% for the Northern and Central Sectors. Additionally, analyses of spears and lithic armatures, Levallois points, suggest that Neanderthal hunting weapons consisted mainly of robust spears that would have been used for thrusting or throwing over relatively short distances, again consistent with notions of intercept over pursuit hunting practices (Shea, 1998; Schmitt et al., 2003). Thus, the more forested areas from higher elevation areas in central Iberian Peninsula would have also been favorable to such activities, particularly during periods when low altitude plains were more arid.

## 6. Conclusions

Fish, amphibians and reptiles from the early Late Pleistocene of the Navalmaíllo rockshelter (Pinilla del Valle, Madrid) have been studied for the first time. Conclusions are as follow:

1. The faunal list is constituted by: *Salmo trutta* (Salmonidae) and undetermined cyprinidae, *Bufo spinosus* and *Epidalea calamita* (Bufonidae), *Rana* cf. *R. iberica* (Ranidae), *Testudo hermanni* (Testudinidae), Lacertidae indet. (large- and small-sized), *Chalcides* cf. *Ch. striatus* (Scincidae), *Blanus* sp. (Blanidae), *Malpolon monspessulanus* (Psammophiidae), *Natrix* cf. *N. astreptophora* (Natricidae), *Coronella* cf. *C. girondica* and *Zamenis scalaris* (Colubridae), and *Vipera* cf. *V. latastei* (Viperidae).
2. All these taxa are currently present in central Iberian Peninsula, with the only exception of the tortoise *T. hermanni.*
3. Mutual Ecogeographic Range applied to the association of amphibians and reptiles from Layer F suggests a much warmer climate (+2.8 °C) than at present, with similar temperatures during summer but warmer temperatures throughout the other months.
4. Rainfall reconstruction indicates slightly higher values (+180.6 mm) than at present, with a more contrasted regime during the year, of more humid winters and drier summers (with a two-month period of aridity).
5. Habitat Weighting suggests a landscape mainly constituted by open areas with dry grassland (24.2–33.3%) and rocky or stony areas (16.7–20.7%), evolving laterally to humid meadows (9.5–17.5%), probably those close to the aquatic and peri-aquatic areas (7.1–12.0%), such as rivers or ponds with riverside vegetation. Woodland environments are also well represented around the site, with medium scrublands to forest formations

(29.5–32.5%). Fish complete this reconstruction by documenting the presence of a pre-mountain well-developed river system characterized by relatively cold, permanent, oxygen-rich, and running waters.

6. Such reconstruction disagrees with previous pollen-based interpretation for Layer F, that suggests a very open and cold environment.
7. The new interpretation suggests that the Neanderthal occupation of the Navalmaíllo rockshelter occurred during a somewhat warm-temperate and humid period within probably the later part of the MIS 5, favouring the presence of a high biodiversity around the site.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

No data was used for the research described in the article.

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## Appendix 4

**Blanco-Lapaz, A**., Kitagawa, K., Kind, C-K. 2021b. Aquatic resource exploitation during the Paleolithic in the Swabian Jura based on fish remains from Hohlenstein-Stadel Cave. Quartär, 68: 1-14. https://doi.org/10.7485/qu.2021.68.94293

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# Aquatic resources exploitation during the Palaeolithic in the Swabian Jura based on fish remains from Hohlenstein-Stadel Cave

## *Die Nutzung aquatischer Ressourcen während des Paläolithikums auf der Schwäbischen Alb: Fischreste aus der Stadel-Höhle im Hohlenstein*

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**Abstract -** Large game has generally biased our interpretations about Palaeolithic subsistence practices. Studies based on small game and birds point to their exploitation by archaic and modern humans in Central Europe, but studies of aquatic resources and, more specifically, of fish remains are still scarce. Hohlenstein-Stadel in the Swabian Jura represents a well-documented Palaeolithic cave for studying diverse food resources that were available and potentially exploited by humans. The site is also notable for its early Upper Palaeolithic mobiliary art, a prominent example being the Lion Man ivory figurine.

Our study focuses on the fish remains that were collected by water-screening during 2009-2013 excavations and sheds light on aspects such as taxonomy, taphonomy and paleoecology. These remains were found in the Middle Palaeolithic layers, with an age between 45 ka calBP and 42 ka calBP, and the Aurignacian layers, with an age between 35 and 40 ka calBP. The taxonomic study of the fish remains help us characterize the freshwater palaeoenvironment in this region as well as the relationship, including fishing strategies, between humans and fish. The identified species belong to European grayling (*Thymallus thymallus*), burbot (*Lota lota*), and European bullhead (*Cottus gobio*), which are all common species that inhabit cold waters. Only one cyprinid is recovered in the assemblage, corresponding to the chub (*Squalius* cf. *cephalus*). The remains also demonstrate diversified subsistence strategies with a significant contribution of small game during the Middle Palaeolithic and Aurignacian in Europe.

***Zusammenfassung -*** *Großwild hat im Allgemeinen unsere Interpretationen zu paläolithischen Subsistenzpraktiken bestimmt. Studien zu Kleinwild und Vögeln weisen auf ihre Ausbeutung durch den archaischen und modernen Menschen in Mitteleuropa hin, Studien zu aquatischen Ressourcen und insbesondere zu Fischresten sind jedoch noch selten. Der Hohlenstein-Stadel auf der Schwäbischen Alb stellt eine gut dokumentierte altsteinzeitliche Höhle zur Erforschung verschiedener verfügbarer und potenziell nutzbarer Nahrungsressourcen dar. Die Stätte ist auch für ihre frühe jungpaläolithische mobile Kunst bekannt, ein prominentes Beispiel ist die Elfenbeinfigur des Löwenmenschen. Unsere Studie konzentriert sich auf die Fischreste, die während der Ausgrabungen 2009-2013 durch Schlämmen gesammelt wurden, und beleuchtet Aspekte wie Taxonomie, Taphonomie und Paläoökologie. Diese Überreste wurden in den mittelpaläolithischen Schichten mit einem Alter zwischen 45 ka calBP und 42 ka calBP und in den Aurignacian-Schichten mit einem Alter zwischen 35 und 40 ka calBP gefunden. Die taxonomische Untersuchung der Fischreste hilft uns, die Süßwasser-Paläoumgebung in dieser Region sowie die Beziehung zwischen Mensch und Fisch, einschließlich der Fangstrategien, zu charakterisieren. Die identifizierten Arten gehören zur Europäischen Äsche (Thymallus thymallus), zur Quappe (Lota lota) und zur Europäischen Groppe (Cottus gobio), alles Arten, die kalte Gewässer bewohnen. Nur ein Cyprinide wurde in den Proben gefunden, der dem Döbel entspricht (Squalius cf. cephalus). Die Überreste zeigen auch diversifizierte Subsistenzstrategien mit einem signifikanten Beitrag von Kleintieren während des Mittelpaläolithikums und Aurignacian in Europa.*

**Keywords - Hohlenstein-Stadel, Middle Palaeolithic, Aurignacian, freshwater fish, Seasonality, Swabian Jura**
***Hohlenstein-Stadel, Mittelpaläolithikum, Aurignacien, Süßwasserfisch, Saisonalität, Schwäbischen Alb***

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## Introduction

The Swabian Jura in southwestern Germany plays a special role in our understanding of Neanderthal and modern human occupations during the Palaeolithic in Central Europe. Although multiple sites with amazing finds have been discovered, four cave sites are especially important due to their find richness: Geißenklösterle (Conard et al. 2019; Hahn 1988) and Hohle Fels (Conard 2009), in the Ach Valley; and Vogelherd (Niven 2006; Riek 1934) and Hohlenstein-Stadel (Wetzel 1961; Kind 2019) (Fig. 1: A), in the Lone Valley. All four caves are also listed as UNESCO World Heritage Sites (Heidenreich & Meister 2019).

The Hohlenstein site complex (48°32′57″N 10°10′21″E) (Fig. 1: A) is a large rocky massif located at the southern rim of the Lonetal (Lone Valley) in the Swabian Jura (Baden-Württemberg, Germany), about 25 km northeast of the city of Ulm. This massif has yielded at least three Palaeolithic cave sites. Bärenhöhle, in the western part of the massif, has mostly yielded Middle and Upper Palaeolithic finds. Kleine Scheuer, to the east of Bärenhöhle, is a rockshelter where Late Upper Palaeolithic artefacts were discovered. Hohlenstein-Stadel, the focus of this study, is located in the eastern part of the massif and is beyond doubt the most important of the three sites (Kind et al. 2014). Hohlenstein-Stadel shows an impressive Late Pleistocene stratigraphy with layers dating from the Middle Palaeolithic to the Magdalenian (Wetzel 1961). Excavations took place from 1935 to 1939 and from 1956 to 1961, under the direction of Robert Wetzel, as well as between 2008 and 2013, by the State Office for Cultural Heritage Baden-Württemberg (Kind 2019).

Our analysis consists of fish remains that were recovered from a small sondage (11 m$^2$) 25-30 m from the cave entrance during the 2009-2013 excavations, which were conducted by the State Office for Cultural Heritage Baden-Württemberg. Kind (2019) described 17 layers in total and an excavation area with 11 quadrants. The basal layer, Layer M, is archaeologically sterile but the subsequent twelve layers (K-M to C) belong to the Middle Palaeolithic.

Barbieri and Miller (2019), in their geoarchaeological studies, note that the lowest layer, K-M, is characterized by a rich presence of bone, tooth and coprolite material signifying the use of the cave by various animals. In this layer, a few charcoal fragments and lithic artefacts represent the evidence of human activity. Layer K appears to contain more fragments of burnt bones than Layer K-M, a fact that could be

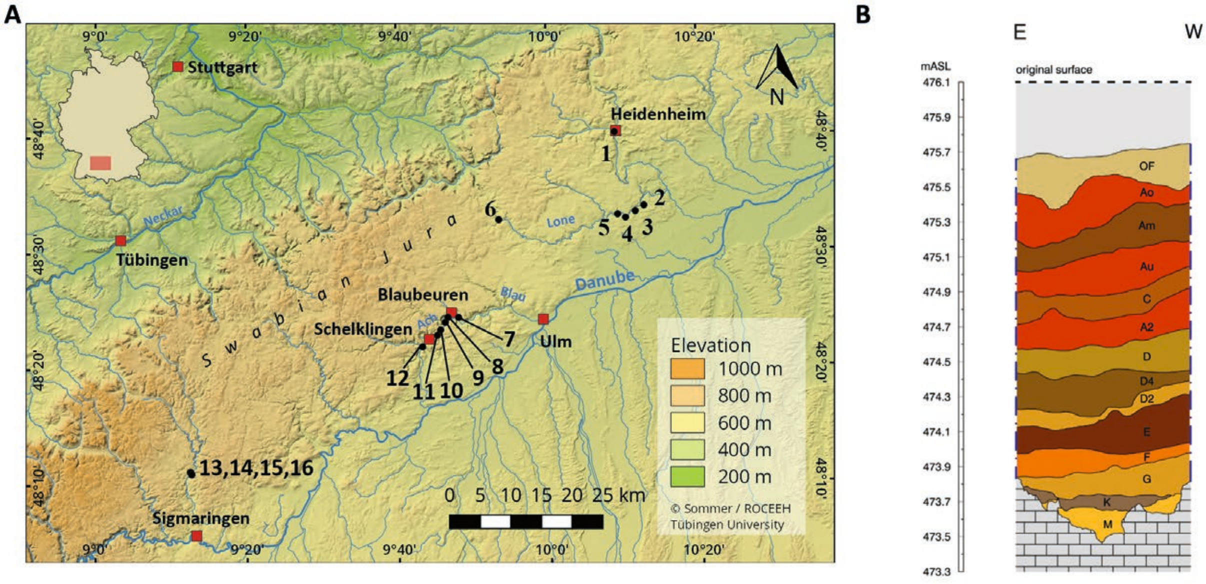

**Fig. 1. A**: General location of the Hohlenstein-Stadel Complex and the Swabian Jura sites: 1. Heidenschmiede, 2. Langmahdhalde, 3. Vogelherd, 4. Hohlensteinl site complex: Stadel, Bärenhöhle and Kleine Scheuer, 5. Bockstein, 6. Haldenstein, 7. Große Grotte, 8. Brillenhöhle, 9. Geißenklösterle, 10. Sirgenstein, 11. Hohle Fels, 12. Kogelstein, 13. Annakapelienhöhle, 14. Göpfelsteinhöhle, 15. Schafstallhöhle, 16. Nikolaushöhle. Modified from © Sommer/ROCEEH Universität Tübingen. **B**: Hohlenstein-Stadel Cave. Idealized stratigraphic sequence of the new excavations from 2009-2013. The layers K-M (not pictured in the figure, Layer K-M existed in addition to those in this idealized profile) to C belong to the Middle Palaeolithic, the layers Au, Am, and Ao to the Aurignacian. Layer M is archaeologically sterile, layer OF is a surface with sediment mixing. © State Office for Cultural Heritage Baden-Württemberg. Modified from Kind et al. 2014.

***Abb. 1. A**: Lage des Hohlenstein-Stadel Komplex und verschiedener Fundstellen auf der Schwäbischen Alb: 1. Heidenschmiede, 2. Langmahdhalde, 3. Vogelherd, 4. Hohlenstein: Stadel, Bärenhöhle und Kleine Scheuer, 5. Bockstein, 6. Haldenstein, 7. Große Grotte, 8. Brillenhöhle, 9. Geißenklösterle, 10. Sirgenstein, 11. Hohle Fels, 12. Kogelstein, 13. Annakapelienhöhle, 14. Göpfelsteinhöhle, 15. Schafstallhöhle, 16. Nikolaushöhle. Geändert nach © Sommer/ROCEEH Universität Tübingen. **B**: Hohlenstein-Stadel-Höhle. Idealisierte stratigraphische Abfolge der neuen Ausgrabungen von 2009-2013. Die Schichten K-M (in dieser Abb. nicht dargestellt) bis C gehören zum Mittelpaläolithikum, die Schichten Au, Am und Ao zum Aurignacian. Schicht M ist archäologisch steril, Schicht OF stellt eine Sedimentmischung an der Oberfläche dar. © Landesamt für Denkmalpflege Baden-Württemberg. Modifiziert nach Kind et al. 2014.*

associated with increased human presence. Few intense erosional events were present in Layer G, and Layer F is characterized by a higher frequency of coprolite fragments and phosphate loess. No further changes were observed throughout layers D2 and D4 where the pieces of bone are particularly well preserved. Layer D lacks phosphate minerals, bones, and charcoal, which suggests that humans and animals were not present in the cave during the accumulation of these sediments. Layer A2, which also contains numerous coprolites, bone and tooth fragments, shows no significant changes when compared to the other Middle Palaeolithic layers of the sequence. Layer C shows a slight but significant decrease in the proportion of coprolites, phosphate crusts, weathered bones, and splinters of teeth. In conclusion, Barbieri and Miller (2019) demonstrate the continuous presence of large carnivore activity (except for layer D), such as hyenas, during the Middle Palaeolithic as well as occasional human activities, which is indicated by the fragments of burnt bone.

Kind (2019) studied the lithic artefacts (N = 631) proving that the lithic raw materials from this site as others in the Swabian Jura are dominated by local Jurassic cherts ca. 3 km of the sites (Conard et al. 2012; Çep, 2013). Although all levels except layer M testify to human occupation in Hohlenstein-Stadel, the majority of the lithic material is recovered from Layer A2 (N = 96), D (N = 210) and K-M (N = 113) and only partial reduction sequences can be reconstructed within the assemblage, characterized by the low presence of blades, cores and tools (Tab. 1). The low frequency of lithic artifacts, appear to reveal characteristics typical of many layers from caves in southwestern Germany during the same period (Conard et al. 2012; Kind 2019). Previous research has demonstrated that the Middle Palaeolithic assemblages resulted from short and sparse Neanderthal occupations (Beck 1999; Kitagawa 2014; Kind 2019), which has been documented at other sites in the Swabian Jura (e.g., Conard et al. 2012; Böttcher et al. 2001). Hohlenstein-Stadel has also yielded a Neanderthal remain, which corresponds to a right femur shaft from a male individual (Kunter & Wahl 1992) and has been analyzed for paleogenetics (Posth et al. 2017).

On the top of the stratigraphic sequence of the recent excavations, three Aurignacian layers (35,361-40,421 calBP) (Au-Ao) (Tab. 2) were characterized by an extremely low density of lithic artefacts (N = 18) (Tab. 1). Animal remains were, however, common in these layers. Geoarchaeological studies show that, in comparison to the Middle Palaeolithic sequence, the phosphatic proportions in the Aurignacian layercs are lower and there is evidence of a change in the sedimentation which favored the preservation of calcite. This change could indicate several scenarios such as lower availability of water from the karst landscape or lower acidity, which resulted from fewer animals in the cave (Barbieri & Miller 2019). Organic tools, such as projectile points, awls and retouchers, made from bone, antler and ivory, were recovered from these Aurignacian layers in both the recent excavations and the earlier excavations of Wetzel (Wetzel 1961; Hahn 1989). Similar artefacts were also recovered from the Aurignacian horizons in Hohle Fels and Geißenklösterle (Wolf 2015; Kitagawa & Conard 2020). In addition, the new excavations in Hohlenstein-Stadel revealed perforated personal ornaments including fox canines/incisors, wolf incisors, reindeer canine as well as an ivory pendant, adding to the handful of personal ornaments which were found in the earlier excavations of Wetzel (Beutelspacher et al. 2011; Hahn 1988; Kind et al. 2014; Kind 2019). Two human teeth (an unerupted lower left third premolar and an unerupted

| Layers | Flakes | Blades | Chunks | Cores | Chips | Tools | Total |
|---|---|---|---|---|---|---|---|
| Ao | - | - | - | - | 1 | - | 1 |
| Am | 3 | 3 | - | - | 2 | - | 8 |
| Au | 1 | - | - | - | 8 | - | 9 |
| C | 3 | - | - | 1 | 8 | - | 12 |
| A2 | 21 | 1 | 1 | 2 | 71 | - | 96 |
| D | 43 | - | 11 | 1 | 151 | 4 | 210 |
| D4 | 4 | - | 1 | - | 9 | - | 14 |
| D2 | 1 | - | 2 | - | 4 | - | 7 |
| E | - | - | 2 | - | 13 | 1 | 16 |
| F | 7 | - | 2 | - | 24 | - | 33 |
| G | 4 | - | - | - | 15 | - | 19 |
| J-L | 23 | 2 | 7 | 2 | 89 | 1 | 124 |
| K-M | 17 | - | 6 | - | 58 | 1 | 82 |
| Total | 127 | 6 | 32 | 6 | 453 | 7 | 633 |

**Tab. 1.** Hohlenstein-Stadel Cave. Frequencies of lithic artefacts. Modified from Kind 2019.

***Tab. 1.*** *Hohlenstein-Stadel Höhle. Häufigkeiten lithischer Artefakte. Modifiziert nach Kind 2019.*

| Lab-No. | GH | AH | Technocomplex | $^{14}$C BP | δ$^{13}$C (%o) | calBP (Calpal) | calBP (Oxcal) |
|---|---|---|---|---:|---:|---:|---:|
| ETH-41231 | Ao | 1o | Aurignacian | 31,950 ± 210 | - 18.5 ± 1.1 | 36,000 ± 363 | 35,361-36,310 |
| ETH-41232 | Am | 1m | Aurignacian | 33,390 ± 245 | - 21.1 ± 1.1 | 37,985 ± 740 | 36,836-38,440 |
| ETH-38797 | Au | 1u | Aurignacian | 35,185 ± 270 | - 23.0 ± 1.1 | 40,165 ± 860 | 39,046-40,421 |
| ETH-38798 | C | 3 | Middle Palaeolithic | 39,805 ± 420 | - 22.4 ± 1.1 | 43,640 ± 607 | 42,811-44,316 |
| ETH-38799 | A2 | 4 | Middle Palaeolithic | 41,920 ± 545 | - 23.2 ± 1.1 | 45,364 ± 835 | 44,361-46,327 |
| ETH-38800 | D | 5 | Middle Palaeolithic | 40,560 ± 480 | - 22.3 ± 1.1 | 44,137 ± 771 | 43,248-45,038 |
| ETH-41234 | E | 6 | Middle Palaeolithic | 46,440 ± 1,050 | - 21.4.± 1.1 | 49,904 ± 2,202 | out of range |

**Tab. 2.** Hohlenstein-Stadel. Radiocarbon-dates. Calibration with CalPal (U. Danzeglocke/O. Jöris/B. Weninger, CalPal-2007online: http://www.calpal-online.de) and Oxcal (IntCal13: Reimer et al. 2009; oxcal v 4.2. Bronk Ramsey 2009). The calibrated data were calculated before 1950. All samples from bone. GH = Geological Horizon, AH = Archaeological Horizon.

***Tab. 2.*** *Hohlenstein-Stadel. Radiokarbon-Daten. Kalibrierung mit CalPal (U. Danzeglocke/O. Jöris/B. Weninger, CalPal-2007online: http://www.calpal-online.de) und Oxcal (IntCal13: Reimer et al. 2009; oxcal v 4.2. Bronk Ramsey 2009). Die kalibrierten Daten wurden vor 1950 berechnet. Alle Proben wurden aus Knochen gewonnen. GH = Geologischer Horizont, AH = Archäologischer Horizont.*

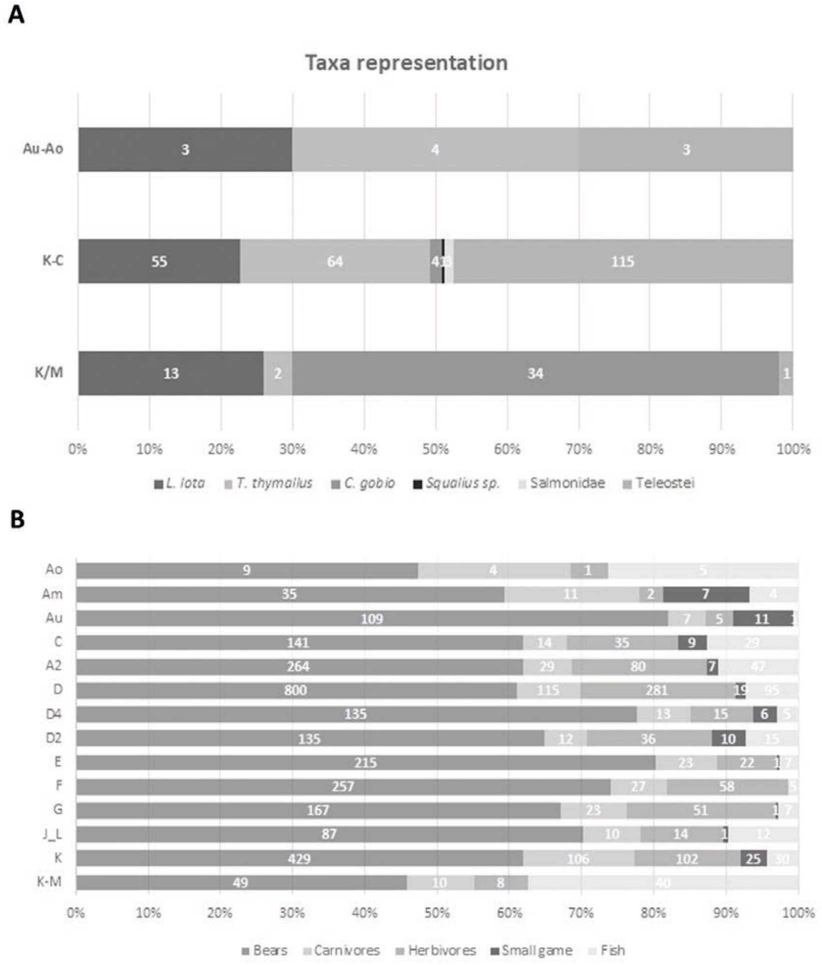

**Fig. 2. A**: Representation of percentage by groups of layers and taxa from Hohlenstein-Stadel. K-M, K to C are Middle Palaeolithic layers (large number of remains belong to Teleostei corresponds to spine and scale fragments); Au-Ao, layers belonging to the Aurignacian. **B**: Faunal representation of percentage in the Middle Palaeolithic Layers K to C, including bear, carnivorous, herbivorous, small game [modified from Kitagawa (2019)] and fish.

***Abb. 2. A****: Prozentuale Darstellung nach Schichtengruppen und Taxa aus Hohlenstein-Stadel. K-M, K bis C sind Mittelpaläolithische Schichten (eine große Anzahl von Überresten gehört zu Teleostei, entspricht Wirbelsäulen- und Schuppenfragmenten); Au-Ao, Schichten, die zum Aurignacian gehören.* ***B****: Faunistische Darstellung des Prozentsatzes in den mittelpaläolithischen Schichten K bis C, einschließlich Bären, Carnivoren, Pflanzenfresser, kleine Tiere [modifiziert von Kitagawa (2019)] und Fisch.*

lower left deciduous canine) were also found in the Aurignacian layers during the most recent excavations (2009-2013). Based on their morphology, as well as metric analyses, both teeth can be safely attributed to modern human individuals (El Zaatari & Harvati 2019). The stratigraphy of the recent excavation ends with a surface level revealing mixed finds with Middle and Upper Palaeolithic lithics as well as Holocene material, including ceramics (OF) (Fig. 1: B).

The middle to large-sized mammals, which were studied by Kitagawa (2014, 2019) show that both hominins and non-human predators visited the site. During the Middle Palaeolithic, the cave served as a den for hyenas and a short-term Neanderthal occupation site, which is documented by the presence of burnt bones and lithic artefacts. Cave bears dominate the Hohlenstein-Stadel faunal assemblage, that is also observed in other Swabian Jura sites such as Geißenklösterle or Hohle Fels. Kitagawa et al. (2012) concluded that the cave bears often occupied these caves during the winter season, showing accumulated remains by natural causes and predation by hyenas and other large carnivores. During the Middle Paleolithic in Hohlestein-Stadel, carnivores are less represented in comparison with herbivores and cave bear (Fig. 2: B), but the assemblage represents one of the richest spectra of large and middle sized carnivores in the Swabian Jura in comparison to Geißenklösterle or Hohle Fels, representing a palimpsest of hominin, cave bear and carnivore activities (Kitagawa et al. 2012; Kitagawa 2014).

In Hohlenstein-Stadel, the proportion of the specimens with anthropogenic modifications (excluding organic artifacts) such as cutmarks, impact fractures or burning is relatively low throughout the sequence, observing a greater number of specimens with impact fractures than those with cutmarks (Kitagawa et al. 2012; Kitagawa 2014, 2019). The majority of the cutmarks are present on herbivore remains but also are present on cave bear remains (Kitagawa 2014). The occasional exploitation of cave bears is also documented in other sites in the Swabian Jura such as Hohle Fels or Geißenklösterle, proving that the Neanderthals often used the same caves that cave bears used (Münzel & Conard 2004a; Conard et al. 2012).

The common prey animals during the Middle Palaeolithic at this site include horses, wholly rhinoceros, reindeer and mammoths as well as aurochs/bison and red deer. Reindeer and horse remains point to summer-fall as the season of the death and presumably the season of Neanderthal occupations (Kitagawa 2014).

The Aurignacian is characterized by relatively few indicators of anthropogenic subsistence activities but, the symbolic activity of the Aurignacian is demonstrated by the Lion Man figurine and the accompanying personal ornaments. While the abundance of carnivores decreases compared to the Middle Palaeolithic, cave bears remain dominant and there is evidence of their opportunistic exploitation by humans (Kitagawa 2014).

The previous studies of micromammals from the Middle Palaeolithic and Aurignacian layers indicated a spectrum which is dominated (more than 40 %) by tundra species, such as arctic and Norway lemming (*Dicrostonyx torquatus* and *Lemmus lemmus*) and narrow-headed voles (*Microtus gregalis*), although steppe species, such as steppe pikas (*Ochotona pusilla*), grey dwarf hamster (*Cricetulus migratorius*), ground squirrel (*Spermophilus superciliosus*), and southern birch mouse (*Sicista subtilis*), were also present in the assemblages (Ziegler 2019). From layer K-M to G, *M. gregalis* is more frequent than *D. torquatus*. From layer E to the Aurignacian layers, the tundra species dominate (more than 40-60 %). Only in layer F is there a decrease in tundra species and an increase in generalist species, which is possibly indicative of interstadial conditions. In conclusion, Ziegler (2019) argued that the upper layers (E to Ao) as well as the lower layers (K-M to F) are characterized by a fluctuation between cooler stadial and more temperate interstadial periods. The birds are represented by ptarmigans (*Lagopus* sp.), geese (*Anser* sp.), grouse (*Tetrao/Lyrurus* sp.) and ducks (*Anas* sp.) in the Middle Palaeolithic layers and grouse and ptarmigans in the Aurignacian layers (Krönneck & Kind 2019). The presence of ducks and geese is indicative of water sources near the site (Krönneck et al. 2004; Krönneck 2012).

Previous studies on the Hohlenstein-Stadel fish assemblage are scarce and focus on the taxonomical aspect of the analysis, describing the presence of mainly grayling (*Thymallus thymallus*) and burbot (*Lota lota*) (Blanco-Lapaz 2019).

The nearest aquatic source today is the seasonal Lone River, which is located about 50 m in front of the cave. In the past, the Lone River was one of the major rivers feeding into the Danube River in the Swabian Jura (Strasser et al. 2009). The four taxa recovered in Hohlenstein-Stadel for this study are still present in the rivers and streams of the Swabian Jura today (Leuner & Klein 2000) and, therefore, were likely captured locally.

Other studies on fish from the nearby sites, such as of Geißenklösterle and Hohle Fels, indicate the presence of similar species, such as European bullhead (*Cottus gobio*), common minnow (*Phoxinus phoxinus*), burbot (*Lota lota*) and grayling (*Thymallus thymallus*) (Torke 1981). Böhme (2019) described the accumulation of fish, amphibian, and reptile remains in late Pleistocene deposits of Geißenklösterle from pellets that the birds of prey left in the cave. The fish remains recovered in the Middle Palaeolithic deposits of this site correspond to grayling, burbot and European bullhead. In the Aurignacian layers, the same species are present in the sample in addition to the common minnow. The author also described the presence of the common frog (*Rana temporaria*), which is the only species that occurs in glacial climate phases that correspond to the Middle Palaeolithic and Aurignacian in Geißenklösterle.

In addition to these studies, Conard et al. (2013) also mentioned the presence of burbot, grayling and cyprinids in the Middle Palaeolithic and Aurignacian layers of Hohle Fels. The authors also described a gradual increase in the exploitation of small game and fish during the Aurignacian. During the Middle Palaeolithic, a marginal fish exploitation was observed; however, the sample size was scarce, with only 19 recovered fish remains. An ivory figurine depicting a fish that resembles a salmonid from Vogelherd also attests to modern humans interaction with, and exploitation of fish in the Upper Palaeolithic (Conard 2009).

## Method and Materials

### Taxonomy

A total of 302 fish remains were collected, by screening, from the archaeological layers of Hohlenstein-Stadel during the 2009-2013 campaigns. Of these, 193 were identified to the species level, 7 to the family level, and 102 as unidentified fish remains. When grouped, 53 remains were recovered from Layer K-M, 239 from Middle Palaeolithic layers K to C, and 10 from the Aurignacian layers Au to Ao (Fig. 2).

During the analysis of this material, a binocular EXACTA OPTECH model LFZ s/n 201030 20W was used. Anatomical and taxonomical classifications were conducted using the modern reference collection at the University of Tübingen and several osteological atlases (Lepiksaar 1994; Watt et al. 1997; Conroy et al. 2005). The taxonomic nomenclature from Cannon (1987) and Wheeler and Jones (2009) was employed and this study refers to the number of identified specimens (NISP) as a standard measure of abundance (Grayson 1984), but indeterminate fragments were also considered in the taphonomic studies. Many fragments were indeterminate due to poor preservation. For this paper, when osteometric models to estimate the fish size were not available, it was visually estimated through direct comparison (Guillaud et al. 2017b; Guillaud et al. 2021) with specimens of known length data from the modern comparative collection (University of Tübingen).

### Taphonomy, element representation and accumulation agents

It is important that fish remains are reliably attributed to human activities before making inferences about human behavior such as seasonality and subsistence strategies (Butler 1990; Russ 2010, 2011; Hardy & Moncel 2011; Guillaud et al. 2018, 2021; Blanco-Lapaz et al. 2021). Several accumulating agents can create assemblages of fish remains at archaeological sites. Humans are not the only agents, and various animals have been investigated as possible agents of accumulation. Potential non-human accumulators include otters (Nicholson 2000; Guillaud et al. 2017b), bears (Russ & Jones 2011), wolves (Butler & Schroeder 1998) and birds (Russ 2010; Guillaud et al. 2018, 2019; Blanco-Lapaz et al. 2021).

To determine the main agent responsible for the accumulation of the fish remains, it is necessary to consider different aspects of the fish assemblage, such as the biology (ecology, species diversity and fish size), diversity, taphonomy (element representation, element fragmentation, bone surface modification such digestion marks and spatial distribution) and species seasonality.

Bone modification, such as digestion marks, compression, mechanical deformation, bite marks, or burning, was analyzed. Previous studies have distinguished several categories of digestion marks depending on the intensity of digestion (Andrews 1990; Guillaud et al. 2018; Blanco-Lapaz et al. 2021; Frontini et al. 2021). This analysis has identified three different categories of digestion marks: null-light (0), moderate (1), and moderate-heavy (1-2) (Blanco-Lapaz et al. 2021) (modified from Andrews 1990; Guillaud et al. 2015). The presence of bite marks or crushed bones can give us insights into the gnawing activities carried out by terrestrial carnivores such as foxes or wolves (Nicholson 1993) while digestive marks are indicative of other carnivorous birds (Andrews 1990).

### Seasonality

Previous studies indicate that fish remains can serve as an important tool to explore the seasonal occupation of sites or the seasonal exploitation of aquatic resources (e.g., Casteel 1976; Mellars & Wilkinson 1980; Mouini et al. 2010; Guezi & Kara 2015). Several elements such as otoliths, vertebrae, and scales, are commonly used for seasonality studies. In this study, scales were used due to their good preservation. We conducted a sclerochronological analysis on the well-preserved grayling (*T. thymallus*) scales.

This method is based on the study of growth marks (or annuli) which are present on scales. These growth increments were measured from the focus (or center) to the distal margin of the scale, based on the distance between the edge and the last growth ring, as well as the edge and the second to last growth ring (Beamish & McFarlane 1983; Guillaud et al. 2017a). Using published data on the periodicity of the increment formation from modern fish individuals from France, Finland, Switzerland and Sweden (Guillaud et al. 2017a), we can estimate the death of the animal and infer the seasonality of fish exploitation. In Guillaud et al. (2017a), the analysis of marginal increment in growth rings indicates an active period of growth from March to June. The average distance between the last growth ring and the scale edge increases during the growth season.

To estimate the periodicity of the increment formation, marginal increment analysis (MIA, Beamish

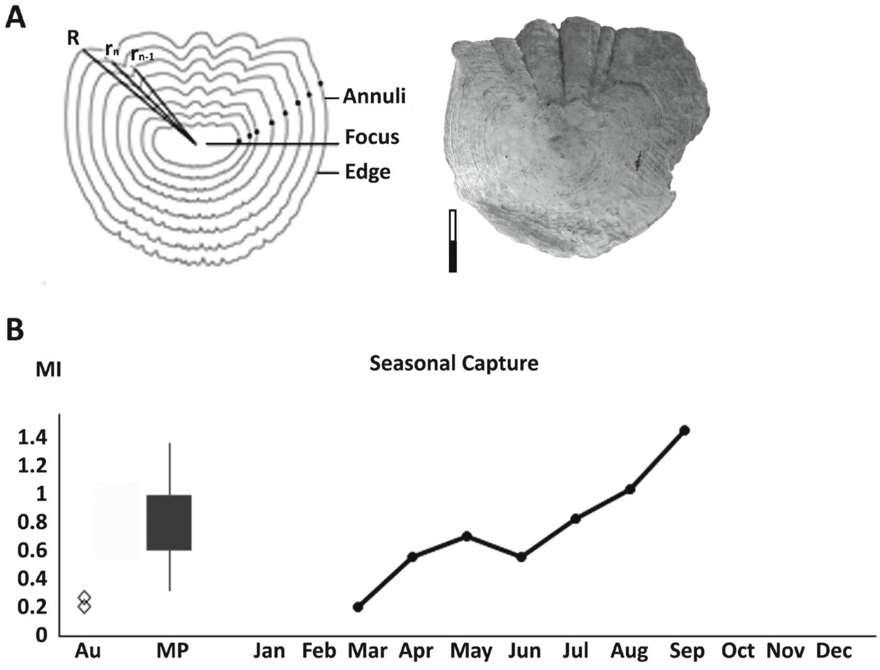

**Fig. 3. A**: Schematic description of a typical grayling (*T. thymallus*) scale (left) with the localization of the focus, the edge, the annuli (or growth rings) and the scale radii ($r_n$ and $r_n$-1) (modified from Guillaud et al. 2017a). Example of archaeological grayling scale from Middle Palaeolithic of Hohlenstein-Stadel (ST13_D2_193/172_1073) (right). Size 2 mm. **B**: Monthly Marginal increment (MI) performed on all modern specimens (modified from Guillaud et al. 2017a) (left) in comparison with the archaeological fish remains: Au, Aurignacian fish remains from Hohlenstein-Stadel; MP, Middle Palaeolithic fish remains from Hohlenstein-Stadel (right).

***Abb. 3. A**: Schematische Beschreibung einer typischen Äschenschuppe (T. thymallus) (links) mit der Lokalisation des Fokus, des Randes, der Ringe (oder Jahresringe) und der Schuppenradien ($r_n$ und $r_n$-1) (modifiziert nach Guillaud et al. 2017a). Beispiel einer archäologischen Äschenschuppe aus dem Mittelpaläolithikum Hohlenstein-Stadel (ST13_D2_193/172_1073) (rechts). Durchmesser 2 mm. **B**: Monthly Marginal Increment (MI) durchgeführt an allen modernen Exemplaren (modifiziert nach Guillaud et al. 2017a) (links) im Vergleich zu den archäologischen Fischresten: Au, Aurignacien Fischreste aus dem Hohlenstein-Stadel; MP, Mittelpaläolithische Fischreste aus dem Hohlenstein-Stadel (rechts).*

| Layers | *T. thymallus* (Grayling) | | | | *L. lota* (Burbot) | | | | *C. gobio* (Bullhead) | | | | *S. cf. cephalus* (Chub) | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ce | Cv | Tv | Sc | Ce | Cv | Tv | Sc | Ce | Cv | Tv | Sc | Ce | Cv | Tv | Sc | |
| Ao | - | - | - | 3 | - | - | 1 | - | - | - | - | - | - | - | - | - | 4 |
| Am | - | - | - | - | - | - | 2 | - | - | - | - | - | - | - | - | - | 2 |
| Au | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 |
| C | - | 2 | 9 | 5 | - | - | 2 | - | - | - | - | - | - | - | - | - | 18 |
| A2 | - | - | - | 6 | - | - | 3 | - | - | - | - | - | - | - | - | - | 9 |
| D | - | 27 | 6 | 14 | - | 5 | 11 | - | - | - | 4 | - | - | - | - | - | 67 |
| D4 | - | 2 | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 4 |
| D2 | - | - | - | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 1 |
| E | - | - | 1 | - | - | 2 | - | - | - | - | - | - | - | 1 | - | - | 4 |
| F | - | - | 1 | - | - | - | - | - | - | - | - | - | 1 | - | - | - | 2 |
| G | - | 1 | - | 2 | - | 1 | - | - | - | - | - | - | - | - | - | - | 4 |
| J_L | - | - | - | 1 | 1 | 4 | 1 | - | - | - | - | - | - | - | - | - | 7 |
| K | - | 3 | 1 | - | - | 12 | 10 | - | - | - | - | - | - | - | - | - | 26 |
| K-M | - | - | 2 | - | - | 6 | 10 | - | - | 34 | - | - | - | - | - | - | 52 |

**Tab. 3.** NISP of each anatomical element and identified remain to species level recovered in Hohlenstein-Stadel Cave. Ce, Cranial element; Cv, Caudal vertebra; Tv, Thoracic vertebra; Sc, Scale.

***Tab. 3.** NISP von jedem anatomischen Element (auf Artebene), das in der Hohlenstein-Stadel-Höhle gefunden wurde. Ce, Schädelelement; Cv, Schwanzwirbel; Tv, Brustwirbel; Sc, Schuppen.*

& McFarlane 1983) was carried out on our archaeological scales by calculating the monthly marginal increment (MI) according to the following formula: $MI = (R - r_n) / r_n - r_n\text{-}1)$ where R is the scale radius, $r_n$ is the distance between the edge and the last growth ring and $r_n\text{-}1$ is the distance between the edge and the second last growth ring (Fig. 3: A). In our assemblage, 130 scales were recovered. Of these, 34 scales, securely identified as grayling, were considered because the rest were very fragmentary and impossible to classify. The majority of the identified scales (NISP = 22) come from two squares (193/172 and 194/172) located in the center of the excavation area. However, after the removal of incomplete, fragmented and regenerated scales, only 14 Middle Palaeolithic grayling scales and two Aurignacian grayling scales were considered suitable for the MIA (Fig. 3: B).

## Results and Discussion

### Taxonomy and Ecology

This paper provides the first comprehensive presentation of the freshwater fish assemblage of Hohlenstein-Stadel. It gives insight into the freshwater ecosystem around this site, which was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich and cold running waters. The presence of some micromammals, such as the eulipotyphlan water shrew (*Neomys* sp.) (Ziegler 2019), and birds (ducks and geese) (Krönneck & Kind 2019) also indicates the presence of well-developed local water sources and rivers.

The fish assemblage from the archaeological layers comprises four different taxonomic families: Salmonidae, Lotidae, Cyprinidae and Cottidae (Fig. 2 & Tab. 3). The predominant family recovered in Layer K-M is Cottidae, represented by only one species, the bullhead (*C. gobio*). This species was not recovered in the Aurignacian layers (Fig. 2: A). In layers K-M to C (Middle Palaeolithic), the most common family is Salmonidae (represented by the grayling, *T. thymallus*), followed by Lotidae (represented by the burbot, *L. lota*). In the Aurignacian layers (Au to Ao), the broad pattern remains and *T. thymallus* and *L. lota* are the most represented species in the assemblage (Fig. 2: A).

As mentioned above, the salmonids are represented by the European grayling (*T. thymallus*). The grayling is native to the northern parts of the Palearctic and Nearctic ecozones, ranging across Eurasia from the United Kingdom to northern Europe and Siberia. These fish require cool, well-oxygenated water, preferably with swift currents; they are found in large, sandy- or gravel-bottomed rivers and lakes, but may also occasionally be found in brackish conditions. Generally omnivorous, they feed primarily on crustaceans, insects and zooplanktons. As they are highly sensitive to changes in water quality, graylings may be considered as an indicator species. This species can reach a maximum weight of 1.5 kg and a maximum size of 50 cm (Füllner et al. 2016). The majority of the grayling specimens recovered from Hohlenstein-Stadel are ca. 30 cm.

Only one species of Lotidae, the burbot (*L. lota*), is represented in the assemblage of Hohlenstein-Stadel. Burbot is the only gadiform (cod-like) freshwater fish. This species has a circumpolar distribution above 40 °N. Populations are continuous from the British Isles across Europe and Asia to the Bering Strait and Canada. Burbots live in large, cold rivers, lakes, and reservoirs. They primarily prefer freshwater habitats but can thrive in brackish environments for spawning. During summer, they are typically found in colder water below the thermocline. In Lake Superior (Canada), burbots can live at depths below 300 m. As benthic fish, they tolerate an array of substrate types, including mud, sand, rubble, boulder, silt and gravel. Adults construct extensive burrows in the substrate for shelter during the day. Burbot populations are fluvial during the winter months and they migrate to near-shore reefs and shoals to spawn in grounds of sand or gravel. As adults, they are, active crepuscular hunters and their diet is primarily piscivorian, preying on lamprey, whitefish, young northern pike, suckers, bullheads and stickleback. This species can reach a maximum weight of 4 kg and a maximum size of 80 cm (Füllner et al. 2016) although for the Hohlenstein-Stadel specimens range between 20-30 cm.

The European bullhead (*C. gobio*) is the only species recovered in the assemblage from the Cottidae family. The European bullhead is a small demersal fish characteristic of cold, clear, fast-flowing small streams and middle-sized rivers. It also occurs near the gravelly shores of cold lakes. The diet of this species is typically based on insects, crustaceans and other invertebrates, and it breeds in the spring. Some individuals can measure up to 15 cm although they are usually about 6 cm. This species is also common prey for the burbot and other carnivorous fish (Füllner et al. 2016). Their body, length ranges mostly between 6 and 12 cm in the Hohlenstein-Stadel assemblage.

In the assemblage, only two remains were identified to genus level and correspond to branchial arch fragments of a chub (*S.* cf. *cephalus*). We attribute the remain to *Squalius* because it presents traits that are characteristic of this genus, such as the presence of a second tooth row. Although the only species of this genus present in Germany is *S. cephalus*, we classify this specimen as *S.* cf. *cephalus* because it was in a fragmentary state. Cyprinids are more typical of temperate waters and live in water temperatures between 10-25 °C (Doadrio et al. 2011; Tissot & Souchon 2010). Accordingly, cyprinids such as the genus *Squalius* can be found in salmonid zones as they also thrive in running water. However, cyprinids in general are present in multiple environments, showing enormous diversity in their diet, which includes arthropods and other fish (Doadrio et al. 2011). The individuals of *S. cephalus* can be measured up to

60 cm and it can weigh 2-4 kgwhen they reach the ages of 15-16 years (Füllner et al. 2016). All the individuals recovered in Hohlenstein-Stadel are smaller than 10 cm. Cyprinids are present exclusively in layers F and E, which points to a more temperate environment (Fig. 2: A). Ziegler (2019) also indicated a relative decrease in the tundra environment in layer F, based on the recovered micromammal species. Although the author noted its small sample size (N = 35), micromammals and cyprinids both point to a likely interstadial condition in the F and E layers.

Three of the four identified fish taxa from Hohlenstein-Stadel (European grayling, burbot and European bullhead) are good indicators of low water temperatures (with average temperature that ranges between 10-12 °C) (Mallet et al. 2011). Only the chub is associated with a habitat with more temperate water but it can also live in cold water (Doadrio et al. 2011). All these fish species have also been recovered in Hohle Fels (Conard et al. 2013), Geißenklösterle (Torke 1981; Böhme 2019), Kogelstein (Böttcher et al. 2000) and Brillenhöhle (Lepiksaar 1973). This corresponds to the spectrum of tundra and steppe mammalian fauna from the region (Weinstock 1999; Münzel & Conard 2004a, b; Niven 2006; Krönneck 2012; Kitagawa 2012, 2014).

In other Middle Palaeolithic and Aurignacian sites from Central Europe, the presence of grayling (*T. thymallus*), burbot (*L. lota*), bullhead (*C. gobio*), and chub or cyprinids has also been documented. Böhme (2011) described a characteristic salmonid region in association with the Höhlenruine Hunas site in Bavaria with the presence of bullhead, grayling, burbot, common minnow, and brown trout (*S. trutta*) while Böttcher (2014) identified greater fish diversity in Sesselfelsgrotte, with sturgeons (*Acipenser* sp.), pike (*Esox lucius*), Danube salmon (*Hucho hucho*), cisco (*Coregonus* sp.), grayling (*T. thymallus*), burbot (*L. lota*), zingel (*Zingel zingel*), bullhead (*C. gobio*) and the cyprinids: barbel (*Barbus barbus*), nase (*Chondrostoma nasus*), common dace (*Leuciscus leuciscus*), vimba bream (*Vimba vimba*) and stone loach (*Barbatula barbatula*). The high diversity and small size of the Sesselfelsgrotte assemblage, as well as the taphonomy, could indicate the non-anthropogenic origin of the fish accumulation (Böttcher 2014).

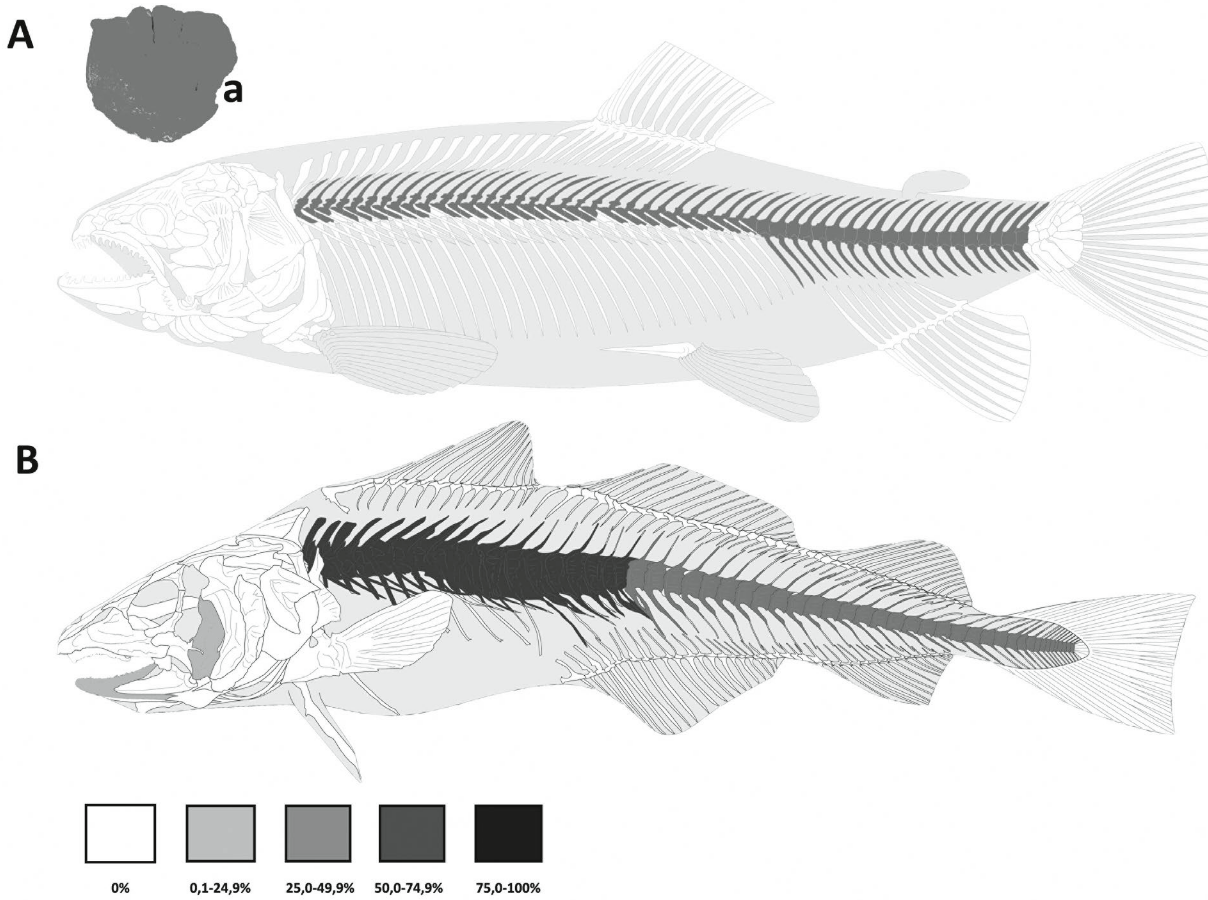

**Fig. 4.** Percentage of skeletal element present in Hohlenstein-Stadel Cave. **A**: Salmonid skeleton representing the grayling (*T. thymallus*) including their scale representation on the top left (**a**). **B**: Gadid skeleton representing the burbot (*L. lota*). Modified from Michel Coutureau & Philippe Béarez (collab.), 2017/ArcheoZoo.org (License CC BY NC SA 4.0 International).

***Abb. 4.** Prozentsatz der Skeletelemente aus dem Hohlenstein-Stadel-Höhle. **A**: Salmonidenskelett einer Äsche (T. thymallus), einschließlich ihrer Schuppendarstellung oben links (**a**). **B**: Gadid-Skelett einer Quappe (L. lota). Modifiziert von Michel Coutureau & Philippe Béarez (zusammen), 2017/ ArcheoZoo.org (Lizenz CC BY NC SA 4.0 International).*

Guillaud et al. (2021) analyzed two Belgian Palaeolithic caves, Walou and Marie-Jeanne, both with the presence of bullhead, burbot and grayling. The same authors also analyzed several sites in France (Vaufrey Cave, Baume Moula-Guercy, Barasses II Cave and Abri des Pêcheurs). In all cases, grayling and burbot are the dominant species, representing more tha 50 % of the recovered fish remains (Guillaud et al. 2021). In Borsuka Cave (Southern Poland), burbot and cyprinids remains were also recovered, representing more than 71 % of the fish sample (Wilczyński et al. 2012).

We can observe that in all the studied sites from Western-Central Europe, the dominant fish correspond to burbot, grayling and cyprinids, to Hohlenstein-Stadel.

### *Taphonomy, fish bone representation, and accumulation agents*

Hohlenstein-Stadel samples are characterized by postcranial elements, namely vertebrae and scales (total NISP = 299; 99 %). Cranial bones (NISP = 2; 1 %) are clearly underrepresented. They are only recovered from the Middle Palaeolithic layers and absent in the Aurignacian layers (Tab. 3 & Fig. 4). The cranial bones correspond to a fragment pharyngeal arch corresponding to *S.* cf. *cephalus* and a quadrate and a dentary fragment of *L. lota* (Fig. 4: B).

In Hohlenstein-Stadel, the herbivore remains present several carnivore modifications such as gnawing, scoring, pits and punctures, which could correspond to scavenging and predation activities. On the contrary, Fish remains with no carnivore modification are likely an indication that carnivores which visited the cave such as red/arctic foxes, wolves, cave/brown bears and hyenas were not the primary agents of the fish accumulation (Russ 2010; Russ et al. 2011).

Taphonomic analysis indicates no damages such as mechanical deformation, rounding or polishing due to the compression during the digestion process (Blanco-Lapaz et al. 2021; Frontini et al. 2021), which means that birds of prey can also be ruled out as an accumulation agent of fish (Nicholson 1993). Some authors (Andrews 1990; Bennasar-Serra 2010) also that micromammal accumulations produced by birds of prey are located, generally, close to their nests and commonly in adjacent areas to the wall of the caves. In Hohlenstein-Stadel, the fish remains were recovered mainly in the center of the excavation area, excluding birds of prey as the main fish accumulators.

Burning is the most common form of anthropogenic modification across the sequencefor mammalian bones, which are often fragmented and charred (Kitagawa 2012; Kitagawa et al. 2014). Although there is no direct evidence of clear anthropogenic modifications on the fish remains, the lack of carnivore and birds of prey modifications makes humans the most likely accumulating agent for the fish assemblage in Hohlenstein-Stadel.

The abundance of scales (NISP = 130; 43 %) possibly indicates the processing of fish by humans through the removal of scales for consumption. Although there is no direct evidence of fishing artefacts, such as hooks or harpoons, humans likely used composite tools or fishing traps made of wood or plant fibers, which do not preserve in the wet, humid conditions of the cave. Further analyses would need to be conducted to demonstrate the hunting and processing method of fish at Hohlenstein-Stadel.

### **Season of capture and fishing pattern differences**

The MIA study of the Middle Palaeolithic and Aurignacian scales from Hohlenstein-Stadel shows a relatively large growth zone at the edge, which is observed in the majority of the archaeological scales. In the Middle Palaeolithic layers, the MIA analysis indicates that the majority of the scales derive from fish that died during summer or fall (Fig. 3: B & Tab. 4). In layer Au, we observed a fish captured during the first half of the year, possibly in spring, although, the results are not conclusive with two samples (Fig. 3: B & Tab. 4). In both cases, no scales showed capture during winter, the most common season for natural death due to decreased food availability (Barret 1997; Roselló-Izquierdo & Morales-Muñiz 2005; Doadrio et al. 2011).

Studies of seasonality based on fish remains in Western and Central Europe are relevant for understanding the human occupation and subsistence practices during the Middle Palaeolithic and Aurignacian (Le Gall 2000; Roselló-Izquierdo & Morales-Muñiz

| Layer | ID | Age (year) | MI (mm) | Season |
|---|---|---|---|---|
| Ao | ST13_919_ | 7 | 0.47 | April/June |
| Ao | ST13_920_ | 6 | 0.39 | April/June |
| C | ST13 194/172 167.1 | 4 | 1.08 | September |
| C | ST13 194/172 151 | 5 | 1.29 | September |
| C | ST13 194/172 167 | 3 | 0.75 | July/August |
| C | ST13 194/172 151 | 5 | 0.72 | July/August |
| A2 | ST13 195/172 144 | 8 | 1.20 | September |
| D | ST13 194/172 951 | 5 | 1.24 | September |
| D | ST13 194/172 1031 | 4 | 0.91 | August/ September |
| D | ST13 195/172 367 | 5 | 0.61 | May/June |
| D | ST13 195/172 544 | 4 | 0.35 | March/April |
| D | ST13 194/172 1136 | 5 | 0.95 | August/ September |
| D | ST13 194/172 506 | 4 | 0.81 | July/August |
| D2 | ST13 193/172 1057 | 3 | 0.44 | April/June |
| D2 | ST13 193/172 997 | 4 | 0.63 | May/June |
| D2 | ST13 193/172 1073 | 5 | 0.42 | April/June |

**Tab. 4.** Seasonal data from Hohlenstein-Stadel, indicating for each studied grayling scale, the level, the ID number, the MI value and the season of capture/death.

***Tab. 4.*** *Saisondaten aus dem Hohlenstein-Stadel, die für jede untersuchte Äschenschuppe Schicht, ID Nummer, den MI-Wert und die Fang-/Todessaison angeben.*

2005; Guillaud et al. 2017a, 2021) and are particularly important due to the scarce data on aquatic resources (Morales & Roselló 1989). Furthermore, exploring how common fishing was – if it was a casual, opportunistic or systematic activity – can have great implications for understanding what role fishing played in the diets of hunter-gatherers in Western and Central Europe.

Only a few changes have been observed in the subsistence practices of the Middle Palaeolithic and the Aurignacian at Hohlenstein-Stadel (Kitagawa 2014, 2019). Although large game dominated during the Middle Palaeolithic, including horse and reindeer, fish may have complemented the Neanderthal diet during summer and fall. During the Aurignacian, reindeer exploitation increased considerably (Kitagawa 2014, 2019). Again, fish could have been an extra food resource in the diet of modern humans. The exploitation of small game and marine mollusks in several Middle Palaeolithic sites indicates that the Neanderthal diet was diversified, depending on the available resources (Starkovich 2011; Guillaud et al. 2021; Moncel et al. 2021). Seasonal data are extremely rare but point to a preferential capture. In the future, similar studies in other Swabian Jura sites with rich Aurignacian occupations, such as Geißenklösterle or Hohle Fels, will help us consider broader patterns of fishing practices in the region and test whether this seasonal signal is robust.

## Conclusions

Generally, studies of the use and exploitation of aquatic resources during the Middle Palaeolithic and Aurignacian remain rare in Central and Western Europe, making it hard to reconstruct fishing activities by archaic and modern humans (Guillaud et al. 2021; Moncel et al. 2021). In the Swabian Jura, the fish assemblages from some sites have been analyzed (Torke 1981; Böttcher et al. 2001; Conard et al. 2013; Böhme 2019).

Analyses of taphonomy, taxonomy, paleoecology, and seasonality on fish remains from Hohlenstein-Stadel showed that during the Middle Palaeolithic and Aurignacian, Neanderthals and modern humans mostly exploited two species of fish, European grayling (*T. thymallus*) and burbot (*L. lota*). The majority of the 302 (NISP) fish remains are postcranial remains, including vertebrae and scales. All recovered taxa (European grayling, burbot, European bullhead, and common chub) have been documented in other Palaeolithic sites from Southwestern Germany (Torke 1981; Conard et al. 2013; Böhme 2019).

No important ecological changes were observed during the Middle Palaeolithic and Aurignacian in Hohlenstein-Stadel. The grayling and the burbot are present throughout the sequence. The bullhead, which decreased during the Middle Palaeolithic are absent in the Aurignacian layers. Cyprinids, which are only present in layers F and E, could indicate a more temperate environment. This observation is supported by the previous studies on micromammals (Ziegler 2019) and could be interpreted as an indication for interstadial condition with decreased tundra elements from the landscape during certain phases of the Middle Palaeolithic.

Despite the low density of lithic artefacts and herbivore remains with anthropogenic marks recovered at the site, they are more frequent in layers A2, D and K/K-M. (Kitagawa 2014; Kind 2019). The fish assemblage follows the same and most of the remains are present in those layers as well, which possibly points to sporadic and opportunistic fishing. The cave is narrow and lacks regular exposure to sunlight that likely made this cave unfavorable for long-term occupations (Kitagawa 2014). In general, several arguments support the hypothesis of short-term Neanderthal occupations in Hohlenstein-Stadel such as low density of lithic artefacts and the preference of local raw materials by expedient reduction sequences (Conard et al. 2012; Picin et al. 2020; Moncel et al. 2021), few anthropogenic marks on bones, the narrowness of the cave and the seasonality studies based on the reindeer and horse remains (Kitagawa 2014, 2019). The present seasonality studies based on fish remains complement the previous work based on large game, indicating presumably in both cases, summer-fall as the season of Neanderthal occupations.

Our results indicate that fishing exploitation during the Middle Palaeolithic and Aurignacian in Central Europe was limited but were observed throughout the region and future studies on fish remains are necessary to better understand the local freshwater ecosystems, the taphonomic history of fish accumulation, and the subsistence practices of Palaeolithic hunter-gatherers. Currently, further studies from other Swabian Palaeolithic sites are underway. They could broaden our knowledge and put greater focus on non-mammalian fauna from Palaeolithic sites. Exploring more fish assemblages from Middle Palaeolithic sites could also help to reconsider the assumption that the Neanderthals were unable to use fish as a resource in continental waters. Future studies may also provide evidence that fishing, although limited, was part of Neanderthal subsistence activities and suggest that their dietary patterns were more diverse than commonly assumed.

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**Contribution Roles:** A. Blanco-Lapaz analyzed the fish assemblage. K. Kitagawa provided zooarchaeological data. C-J. Kind provided archaeological and geological context. The manuscript was written by A. Blanco-Lapaz. All authors contributed to sections of the manuscript. All authors reviewed and approved the manuscript before submission.

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Luzi, E., **Blanco-Lapaz, A**., Rhodes, S.E., Conard, N.J. 2022. Paleoclimatic and paleoenvironmental reconstructions based on the small vertebrates from the Middle Paleolithic of Hohle Fels Cave, SW Germany. Archaeological and Anthropological Sciences 14(6): 107. https://www.doi.org/10.1007/s12520-022-01568-5

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ORIGINAL PAPER

# Paleoclimatic and paleoenvironmental reconstructions based on the small vertebrates from the Middle Paleolithic of Hohle Fels Cave, SW Germany

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## Abstract

In this paper, we analyse the fish and small mammal assemblages from the Middle Paleolithic horizons of Hohle Fels Cave to reconstruct the paleoclimatic and paleoenvironmental conditions faced by the Neanderthal groups who occupied the site. The fish assemblage indicates that the freshwater ecosystem around this site was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters. The results of the Habitat Weighting Method and the Bioclimatic Model applied to the small mammal assemblage, coupled with the new dates obtained for the Archaeological Horizon (AH) IX, allow us to identify two different climatic phases. One phase (AH X-XII) is more temperate possibly corresponding to the end of Marine Isotope Stage (MIS) 5; the other (AH VI-IX) is colder and more arid corresponding to the end of MIS 4 through the beginning of MIS 3. Open environments with a relatively stable forest component dominated the landscape during this part of the Middle Paleolithic. These two climatic phases appear to correspond to different levels of occupational intensity by Neanderthals, with higher occupational intensity during mild climatic periods and lower intensity during cold, arid periods. Our climatic reconstruction and recent absolute dating, together with the recovery of a complete leaf point near the top of AH X, have important implications for the cultural stratigraphy and cultural chronology of the region. Archaeologist have traditionally viewed leaf points as key artefacts of the *Blattspitzengruppe*, a cultural complex attributed to the end of Middle Paleolithic; however, this stratigraphic, climatic, and chronological context indicates the need to revise this interpretation.

**Keywords** Small mammals · Fish · Habitat Weighting · Bioclimatic Model · Late Pleistocene · Swabian Jura

## Introduction

The Swabian Jura (South-western Germany) is a key region for Paleolithic studies, in particular of the transition between the Middle and Upper Paleolithic and the evolution of the Upper Paleolithic industries (Aurignacian, Gravettian, Magdalenian). The caves in this region (Fig. 1) have been the subject of intensive research for the last 150 years and produced an astonishing archaeological record that helped develop and improve our understanding of past lifeways, subsistence strategies, and technologies of both Neanderthal and modern human groups. The Ach and the Lone Valleys are located along two tributaries of the Danube in the Swabian Jura. The caves and shelters that can be found along these valleys, such as in Hohle Fels, Geißenklösterle, Vogelherd, and Hohlenstein-Stadel (Conard et al. 2009; Conard and Kind 2017), are renowned for the musical instruments and the ivory figurines that have been recovered there. The

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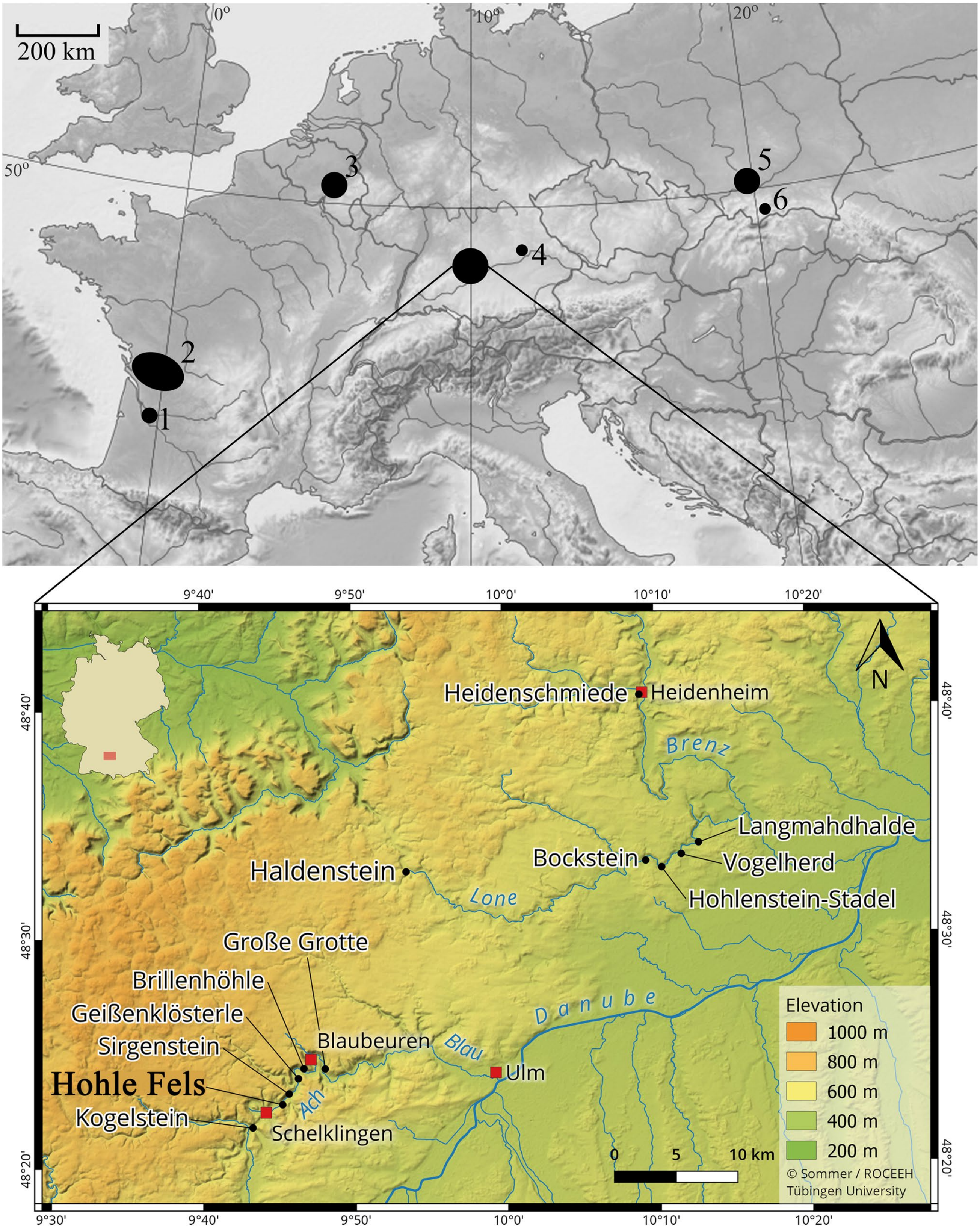


**Fig. 1** Location of Hohle Fels Cave and other sites mentioned in the discussion. 1, Gironde; 2, Charente-Maritimes and Charente; 3, Scladina and Marie-Jeanne Caves; 4, Sesselfelsgrotte; 5, Biśnik and Koziarnia Caves; 6, Obłazowa Cave. Detailed map of the Swabian Jura modified after Sommer 2019

study of subsistence strategies during the Middle and Upper Paleolithic provides useful insights into the behaviour of human groups (Barth et al. 2009; Conard et al. 2013; Kitagawa 2014; Wong et al. 2020b; Bertacchi et al. 2021, among others) and recently the potential of small vertebrate studies for the reconstruction of the climatic and environmental conditions faced by those groups was highlighted by the publications of the small mammal assemblage at Hohle Fels (Rhodes et al. 2019), Geißenklösterle (Rhodes et al. 2018), and Langmahdhalde (Wong et al. 2020a).

In this paper, we propose a new climatic and environmental reconstruction of the conditions faced by Neanderthal groups during their occupations of Hohle Fels Cave and try to understand how these conditions might have influenced their strategies and occupation patterns.

## The site

Hohle Fels Cave (48° 22′ 45″ N; E9° 45′14″ E) is located in the Ach River valley (Fig. 1), at 564 m a.s.l. and ca. 7 m above the current floor of the valley. The first scientific investigation of the cave led by Fraas and Hartmann started in 1870–1871 and yielded faunal remains (mostly cave bears), lithic tools, and bone and antler artifacts (Hahn 1978). After that, Schmidt (1912) published the results of his research conducted in 1906 in the book *Die Diluviale Vorzeit Deutschland*. Between 1958 and 1960, further excavations were carried out by Matschak and Riek, and between 1977 and 1979 by Hahn (Hahn 1978, 1979). This last effort provided proof of a well-preserved stratigraphy an abundance of artifacts (Hahn 1979). Systematic investigation of Hohle Fels started in 1988 under the direction of Hahn (until his death in 1997) and has continued every year from 1997 until the present under the direction of Conard. The excavations exposed a ca 5.5 m-thick sequence, spanning from the Middle Paleolithic to the Magdalenian (Fig. 2). In the past 25 years of researches, the site yielded abundant lithic and faunal remains, but it is especially renowned for the symbolic artifacts including ivory animal and human figurines, personal ornaments, and musical instruments recovered in the Aurignacian levels (Conard 2009; Conard et al. 2009; Wolf and Conard. 2015; Velliky et al. 2021, among others). The material analysed in this study is derived from the horizons assigned to Middle Paleolithic, i.e., Archeological Horizons (AH) VI to XII, which correspond to Geological Horizons (GH) 9–15, excavated between 2014 and 2021 (Fig. 2). The description of the GHs follows Miller (2015) and the field notes from the excavation campaigns.

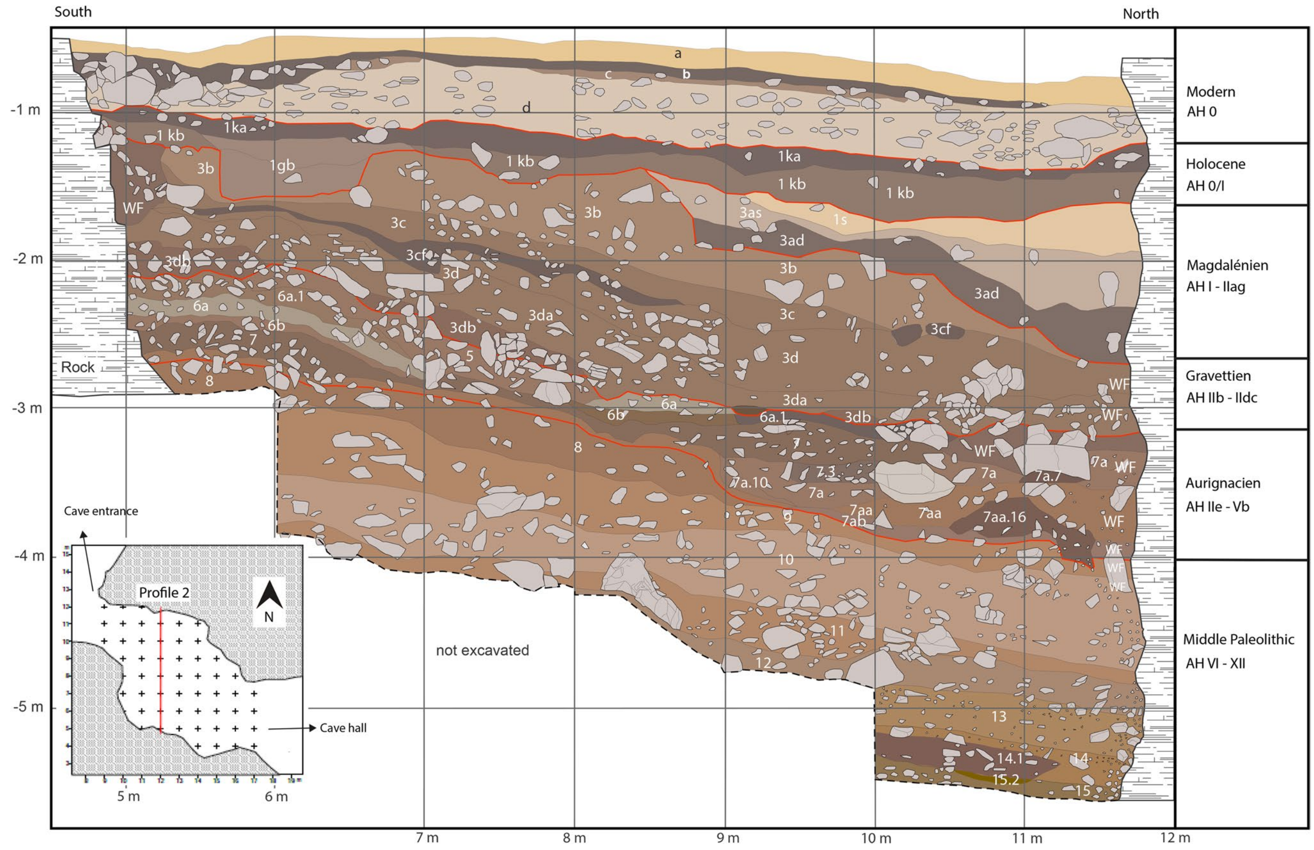


**Fig. 2** Profile 2 of Hohle Fels cave, modified after Conard and Janas 2021. Graphic by A. Janas

- GH 9: ca. 30 cm thick. The sediment is brown (7.5 YR 5/6) with yellowish-brown layers alternating with reddish-brown layers. It is composed of silt, with little clay and some lime sand. Limestone blocks make up 20–30% of the units, are sub-rounded, and range in size between 8 and 25 cm. The transition to GH 10 appears gradually over 4 cm.
- GH 10: ca. 30 cm thick. The sediment is brown (7.5 YR 6/4–5/4), has a relatively high proportion of calcite sand and is composed mostly of silt. Limestone blocks are less present than in GH 9 and are angular to slightly rounded. The passage to GH 11 is clear in the east part, over 2 cm, and more gradual in the west part, over 4 cm.
- GH 11: ca. 10–20 cm. The sediment is yellowish-brown (7.5 YR 6/4–5/6) and composed of silty clay. Limestone blocks are smaller, 2–15 cm in size. Gradual transition to GH 12.
- GH 12: the sediment is greenish-brown (10 YR 5/4), composed of clayey silt with a high proportion of coarse limestone sand. Limestone blocks are small, 2–8 cm in size.
- GH 13: the sediment is yellow–brown, darker, and almost reddish in the lower part (10 YR 5/8 upper, 10 YR 4/6 lower). It is composed of silty clay with a relatively high proportion of coarse and fine lime sand. Irregular limestone rubbles up to 20 cm. Transition to GH 14 is gradual but visible.
- GH 14: The sediment is yellow–brown, almost reddish (10 YR 4/6). It is composed of silty clay with a lot of coarse and fine limestone sand. In its lower portion, the sediment is yellowish-brown (10YR 5/6) and composed of clayey silt. Limestone blocks up to 30 cm. GH 14.1 is a feature characterized by grey-brown sediment (10YR 5/4) and unusually high find density. Transition to GH 15 is very clear, sometimes over a few millimetres.
- GH 15: the sediment is yellowish-brown (10 YR 5/4), lighter colour in the northern Sect. (10 YR 5/6). It is composed of clayey silt with a high proportion of limestone sand. High amount of limestone clasts, 50–80%. GH 15.2 is a feature at the contact with GH 14.1 that presents lighter colour (10 YR 5/6) and a high density of bones and small mammal bones.

GH 9 to 11 are dated between 35 and 40 ka years BP, corresponding to ~ 39–44 ka cal BP (OxCal 4.4, IntCal 20, Bronk Ramsey 2009) and clearly represent minimum ages (Conard and Bolus 2008; Conard 2009; Higham et al. 2012), while new ESR dates for GH 12 put it at 62 ± 4 ka (Conard et al. 2021).

One previous study explored the presence of fish remains in Hohle Fels from the Middle Paleolithic layers and indicated the presence of burbot (*Lota lota*), grayling (*Thymallus thymallus*), and unidentifiable cyprinids, all of which correspond to species of fish commonly found in the Danube and its tributaries such as the Ach River (Conard et al. 2013). In this study, the authors reported the common presence of fish bones and scales in the Aurignacian and Gravettian deposits but suggested this presence to be only sporadic in the Middle Paleolithic layers. In the present paper, the sample was enlarged to more than 3400 remains in contrast to the original study that included only 19 specimens from the upper portion of the Middle Paleolithic deposits. Additionally, we present a detailed paleoenvironmental study based on the fish species recovered from the site.

Recent studies (Rhodes et al. 2019; Rhodes and Conard 2021) analysed the small mammal assemblages from the Middle Paleolithic GHs available at the time (GH 9–12) and compared them to the early Upper Paleolithic (i.e. Aurignacian) in order to explore the climatic and environmental changes during the Middle to Upper Paleolithic transition. The paleoclimatic reconstruction based on the rodent assemblage describes GH 12 as the less cold and arid layer in the Middle Paleolithic sequence and indicates a decrease in temperature and precipitation in GH 9–11 (Rhodes and Conard 2021). The landscape surrounding the site was a mosaic of arctic tundra and boreal and deciduous forests, with a steppe component always present but fluctuating through time (Rhodes 2019; Rhodes et al. 2019). In this study, we increased the samples for the Middle Paleolithic GHs already published and add samples from the new Middle Paleolithic GHs 13, 14, and 15 excavated in 2020 and 2021.

## Material and methods

Small vertebrate material was recovered through water screening using 0.5-mm sieves. The material analysed comes from one square meter excavation units 11, 25, 26, 27, and 28. These are the squares that currently present the whole Middle Paleolithic sequence, going from GH 9 to 15 (Fig. 2). For each GH, we present the number of identified specimens (NISP) and the minimum number of individuals (MNI).

### Fishes

We analysed this assemblage using a Zeiss Stemi 305 stereomicroscope and photographed the material using a Dino-Lite Edge Digital Microscope. Anatomical and taxonomical classifications were done by comparison method of external characteristics of those remains using the reference collection hosted in Senckenberg Centre for Human Evolution and Palaeoenvironment (University of Tübingen) and several osteological atlases (Lepiksaar 1994; Watt et al. 1997; Conroy et al. 2005). The taxonomic nomenclature used has been extracted from Cannon (1987) and Wheeler and Jones (2009).

## Small mammals

The identification of the small mammal was based on the best diagnostic elements available: for lagomorphs and rodents, mandibles, maxilla, and isolated teeth; for shrews, mandibles, and maxilla; for moles and bats, mandibles, maxilla, isolated teeth, and postcranial bones were analysed. The criteria for the identification of the material, the nomenclature for morphological descriptions, and the measurements taken follow Niethammer and Krapp (1978; 1982), Nadachowski (1982), and Borodin and Markova (2015) for Rodentia; Laplana et al. (2015) for Lagomorpha; and Niethammer and Krapp (1990) for Eulipothyphla; Sevilla García (1988) for Chiroptera. Comparison of the fossil specimens to the osteological collection of the University of Tübingen was also crucial for the identification. Taxonomic nomenclature follows Wilson and Reeder (2005), except for *Clethrionomys glareolus* (see Tesakov et al., 2010; Kryštufek et al., 2019), *Alexandromys oeconomus* (Lissovsky et al. 2018, among others), and *Lasiopodomys anglicus* (see Petrova et al., 2015; Baca et al., 2019). Photos of the material have been taken using a Zeiss Stereo Discovery V8.

Morphometric analysis has been conducted on complete first lower molars of adult specimens of *Arvicola amphibius*. The Schmelzband-Differenzierung-Quotient or SDQ index (Heinrich 1978) quantifies the difference in enamel thickness between the anterior and the posterior wall of each triangle of the tooth (Fig. 3).

$$\mathrm{SDQ_T} = \frac{\mathrm{ssp}}{\mathrm{ssa}} * 100$$

To calculate the SDQ value of a population, it is necessary to obtain the mean SDQ for each m1 (comprehending all the triangles (T1 to T5) and the two sides of PL)

$$\mathrm{SDQ_{m1}} = \frac{\Sigma \mathrm{SDQ_T}}{7}$$

and then the mean of the SDQ of all ($n$) m1 taken into account

$$\mathrm{SDQ_{pop}} = \frac{\Sigma \mathrm{SDQ_{m1}}}{n}.$$

Photos of the specimens have been taken using a Leica EZ4HD microscope. Measurements have been taken on the photos using ImageJ software. Data have been analysed using PAST software (Hammer et al. 2001).

## Paleoenvironmental reconstruction

The habitat weighting method (Evans et al. 1981; Andrews 2006) based on small mammals has been applied in order to obtain a reconstruction of the landscape and environment surrounding the site. Each mammal species has been assigned to the habitat(s) where it can be currently found. We decided to use two different sets of values, one based on ecological preferences (Suppl. Material 1), and one based on habitat suitability (Suppl. Material 2).

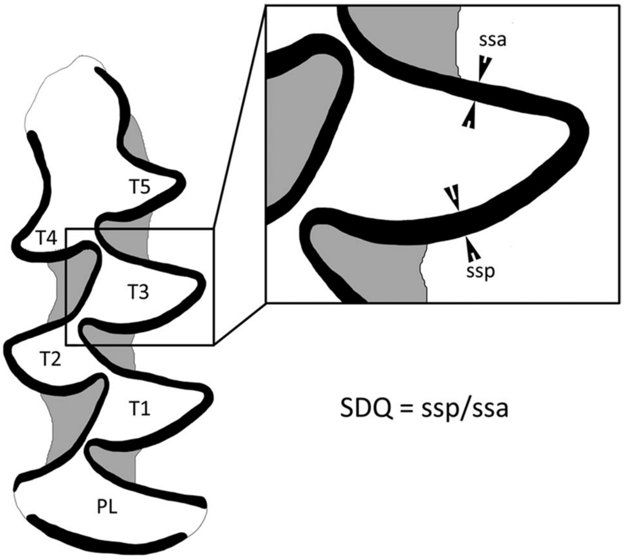


**Fig. 3** Scheme for the measurement of the Schmelzband-Differenzierung-Quotient (SDQ) index in first lower molar of *Arvicola amphibius*

For ecological preferences, six categories have been identified (following López-García et al. 2014, 2017a, 2017b): open dry grassland and steppe (OD), open humid evergreen meadows (OH), open woodland with moderate ground cover, woodland margins, and forest patches (OW), woodland, or mature forest (Wo), rocky environment (R), and water-related environments (Wa).

For habitat suitability, we follow the attributions of the IUNC Red List (IUCN 2021): "forest" including forested and wooded areas, and forest margins; "shrubland" intended as shrubs, bushland and thickets; "grassland," characterized by grasses and broadleaf herbaceous plants with sparsely distributed or absent woody plants; "wetland"; and "desert." Since most of the species are no longer present in Southern Germany, we use the attribution(s) given in the global distribution for each species.

We use *Spermophilus citellus* as current reference for *S. superciliosus* and *Cricetulus migratorius* as current reference for *Allocricetus* vel *Cricetulus* sp.

## Paleoclimatic reconstruction

Paleoclimatic data have been calculated for each GH based on the insectivore and rodent assemblage, using the Bioclimatic model described in Hernández Fernández (2001,

2005) and recently updated by Royer et al. (2020). The insectivores and rodents' assemblages have been analysed using the Climatic Restriction Index ($CRI_i = 1/n$, where "$n$" is the number of climatic zones where the species are represented and "$i$" is the climatic zone where the species appears). Starting from the CRI, the Bioclimatic Component has been calculated (BC; representation by the level of each of the available climatic zones): $BC_i = (\Sigma CRI_i)$ X 100/S (where S is the number of species per GH). From the BC, it was possible to estimate climatic parameters by means of multiple linear regression method (Hernández Fernández and Peláez-Campomanes 2005; Royer et al. 2020), using the R script file published by Royer et al. (2020). For this study, the mean annual temperature (MAT expressed in °C) and mean annual precipitations (P expressed in mm) are calculated. Current data for the town of Schelklingen (Fig. 1) show a MAT of 8.3°C and P of 1059 mm (climate-data.org). *Talpa* sp. has been considered as *T. europaea*, being the only species for this genus present at Hohle Fels. *Sorex* sp., *Neomys* sp., and *Sicista* sp. have not been included in the calculation. As for the environmental reconstructions, we use *Spermophilus citellus* as current reference for *S. superciliosus* and *Cricetulus migratorius* as current reference for *Allocricetus* vel *Cricetulus* sp.

## Results and discussion

### Taphonomic analysis: preliminary results

#### Fishes

Anthropogenic marks such as burned bones or cut marks and non-anthropogenic damage indicators on the bone surface of the fish that remain such as digestion marks, compression, uniaxial mechanical deformation, or bite marks were analysed. Previous studies have distinguished several categories of digestion marks, depending on the intensity of digestion (Andrews 1990; Guillaud et al. 2018; Frontini et al. 2021; Blanco-Lapaz et al. 2021). The presence of bite marks or crushed bones can give us insight into the gnawing activities carried out by terrestrial carnivores such as foxes or wolves (Nicholson 1993) while digestive marks are indicative of other carnivorous birds (Andrews 1990).

Taphonomic analysis of the fish assemblage from the Middle Paleolithic horizons of Hohle Fels indicates no damages such as mechanical deformation, rounding, or polishing due to compression during the digestion process (Frontini et al. 2021; Blanco-Lapaz et al. 2021). Bite marks, crush marks, or digestive marks were absent from all the fish remains, which means that carnivores and birds can be ruled out as accumulating agents (Nicholson 1993). No direct anthropogenic marks that indicate burning or butchery activities were documented.

The lack of carnivore modifications on fish bones likely indicates that carnivores, which visited the cave, including red/arctic foxes, wolf, cave/brown bears, hyenas, and birds of prey (Conard et al. 2013; Rhodes et al. 2019; Baumann et al. 2020; Beattie et al. 2021), were not the primary agents of accumulation for the fish remains, leaving humans as most probable accumulation agents. On the other hand, we cannot yet definitively prove that the fish remains were accumulated by humans since there is no direct evidence of anthropogenic modifications such as cut marks or burned bones on the assemblage. Further, more detailed taphonomic studies (ongoing) might provide more data and help identify the main agent of the fish accumulation during the Middle Paleolithic at Hohle Fels.

#### Small mammals

A comprehensive taphonomic analysis of small mammals from GH 9 to 12 has been published by Rhodes et al. 2019) and suggests that the small mammal material was most likely accumulated by the snowy owl *Bubo scandiacus*, the Eurasian eagle-owl *Bubo bubo*, and/or the great grey owl *Strix nebulosa*, with a limited contribution by foxes. As these predators are mostly generalist hunters, the composition of the assemblages should accurately reflect the diversity of the small mammal community on the landscape at the time of the accumulation.

In this study, a total of 2093 first lower molars of Arvicolids from GH 13 to 15 have been analysed according to the criteria described in Fernández-Jalvo et al. (2016), observing the degree and frequency of digestion signs, in order to determine the principal agents of the small mammal accumulation (Table 1). Due to the high percentage of teeth with absent to moderate modifications, this preliminary study indicates that predators of category 1 or 2 are most likely responsible for the accumulation. Nocturnal birds of prey, such as *Tyto alba*, *Asio flammeus*, and *Asio otus* (cat. 1) or *Bubo scandiacus* and *Strix nebulosa* (cat.2) are listed as possible accumulators (Fernández-Jalvo et al. 2016). Nevertheless, the low percentage of teeth with heavy or extreme digestion signs might indicate that small carnivores (e.g., *Mustela* spp. or *Vulpes* spp.) or diurnal birds of prey (such as *Falco* spp.) also played a role in the formation of the small mammal assemblages. An ongoing study regarding the bird assemblage of Hohle Fels already identified four species of birds of prey from GH 13: *Falco tinnunculus*, *Corvus corax*, *Asio flammeus*, and *Bubo bubo* (Beattie et al. 2021). These preliminary results confirm that opportunistic hunters (Andrews 1990) are the principal responsible for the small mammal accumulation that should therefore accurately reflect the composition of the small mammal community on the landscape surrounding the site.

**Table 1** First lower molars of arvicolids with signs of digestion for the geological horizons (GH) excavated during 2020–2021 campaigns

| | | *Alexandromys oeconomus* | *Arvicola amphibius* | *Chionomys nivalis* | *Dicrostonyx torquatus* | *Lasiopodomys anglicus* | *Lemmus lemmus* | *Microtus arvalis* | Arvicolidae indet | % |
|---|---|---|---|---|---|---|---|---|---|---|
| GH 13 | Absent | 55 | 17 | 18 | 6 | 361 | 33 | 82 | 13 | 93.75 |
| | Light | 1 | 0 | 0 | 0 | 5 | 1 | 1 | 0 | 1.28 |
| | Moderate | 3 | 0 | 1 | 1 | 9 | 0 | 0 | 2 | 2.56 |
| | Heavy | 2 | 0 | 0 | 1 | 1 | 0 | 3 | 4 | 1.76 |
| | Extreme | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0.64 |
| GH 14 | Absent | 47 | 15 | 9 | 5 | 276 | 7 | 54 | 22 | 91.39 |
| | Light | 3 | 0 | 0 | 0 | 13 | 0 | 2 | 0 | 3.78 |
| | Moderate | 2 | 0 | 1 | 1 | 8 | 0 | 0 | 1 | 2.73 |
| | Heavy | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 4 | 1.47 |
| | Extreme | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0.63 |
| GH 15 | Absent | 84 | 17 | 12 | 52 | 653 | 60 | 59 | 25 | 96.40 |
| | Light | 2 | 0 | 0 | 1 | 8 | 0 | 3 | 0 | 1.40 |
| | Moderate | 1 | 0 | 0 | 1 | 11 | 0 | 0 | 5 | 1.80 |
| | Heavy | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0.40 |
| | Extreme | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.00 |

## Paleoclimatic and paleoenvironmental reconstructions for Neanderthal occupations at Hohle Fels Cave

### Fishes

A total of 3482 fish remains, belonging to 8 species, were analysed (Table 2, Fig. 4). The Middle Paleolithic fish assemblage from Hohle Fels comprises five families: Salmonidae, Lotidae, Cyprinidae, Cottidae, and Esocidae. The predominant family recovered is Salmonidae, represented by three species, the European grayling (*Thymallus thymallus*, NISP = 1381, MNI = 15), the brown trout (*Salmo trutta*, NISP = 3, MNI = 2), and the Danubian trout (*Hucho hucho*, NISP = 2, MNI = 1). Lotidae, represented by the burbot (*Lota lota*, NISP = 1112, MNI = 11), is the second most common family in the assemblage. The third most represented family is Cottidae, with one species, the bullhead (*Cottus gobio*, NISP = 73, MNI = 10). Two species belonging to the carp family, Cyprinidae, have been identified: the common chub (*Leuciscus cephalus*, NISP = 6, NMI = 5) and the common nase (*Chondrostoma nasus*, NISP = 2, NMI = 1). Esocidae is the least represented family classified in the assemblage with one specimen identified as the northern pike (*Esox lucius*, NISP = 1, MNI = 1).

As mentioned above, the Salmonidae family is represented by three different species. The European grayling (*T. thymallus*), which is present throughout the sequence, is native to

**Table 2** Identified taxa of Fish from the Middle Paleolithic Geological Horizons (GH) in Hohle Fels. NISP: number of identified specimens; MNI: minimum number of individuals. 1, Salmonidae; 2, Lotidae; 3, Cottidae; 4, Cyprinidae; 5, Esocidae; 6, Teleostei

| | | GH 9 | | GH 10 | | GH 11 | | GH 12 | | GH 13 | | GH 14 | | GH 15 | | Total NISP | Total MNI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | | |
| 1 | *T. thymallus* | 34 | 1 | 13 | 1 | 92 | 1 | 727 | 4 | 119 | 3 | 148 | 2 | 248 | 3 | 1381 | 15 |
| | *S. trutta* | 1 | 1 | | | | | 2 | 1 | | | | | | | 3 | 2 |
| | *H. hucho* | | | 1 | 1 | | | | | | | 1 | 1 | | | 2 | 2 |
| | Unident | 1 | 1 | | | 3 | 1 | 15 | 1 | 1 | 1 | 1 | 1 | 11 | 1 | 32 | 6 |
| 2 | *L. lota* | 29 | 1 | 12 | 1 | 91 | 1 | 539 | 4 | 156 | 1 | 155 | 1 | 130 | 2 | 1112 | 11 |
| 3 | *C. gobio* | | | | | | | 9 | 1 | 14 | 3 | 39 | 4 | 11 | 2 | 73 | 10 |
| 4 | *L. cephalus* | | | | | | | 2 | 2 | 2 | 1 | 2 | 2 | | | 6 | 5 |
| | *C. nassus* | | | | | | | | | | | 2 | 1 | | | 2 | 1 |
| | Unident | 1 | 1 | | | 2 | 1 | 8 | 1 | 34 | 1 | 48 | 1 | 1 | 1 | 94 | 6 |
| 5 | *E. lucius* | | | | | | | | | | | | | 1 | 1 | 1 | 1 |
| 6 | Unident | 20 | | 18 | | 51 | | 281 | | 145 | | 163 | | 98 | | 776 | - |
| Total | | 86 | 5 | 44 | 3 | 239 | 4 | 1583 | 14 | 471 | 10 | 559 | 13 | 500 | 10 | 3482 | 59 |

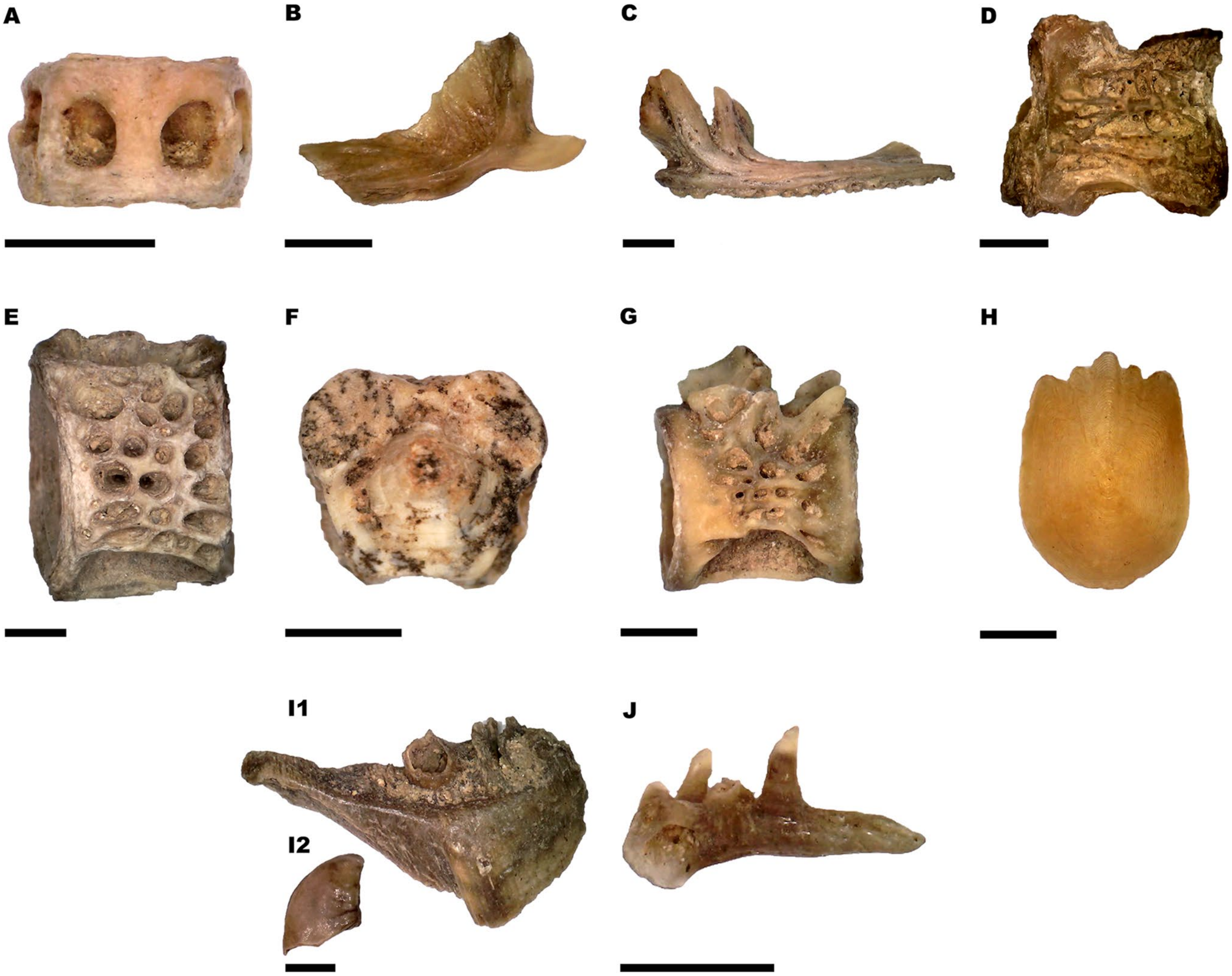


**Fig. 4** **A** Precaudal vertebra. Pike (*Esox lucius*), HF21 25 3727 15 XII; **B** Left praeoeperculum fragment. Bullhead (*Cottus gobio*), HF21 25 3786.1 15 XII; **C** Left praemaxilar. Burbot (*Lota lota*), HF21 25 3786.2 15 XII; **D** Caudal vertebra. Burbot (*Lota lota*), HF21 25 3786.3 15 XII; **E** Precaudal vertebra. Danuvian trout (*Hucho hucho*), HF21 25 3551 14 XI; F. Precaudal vertebra. Brown trout (*Salmo trutta*), HF17 26 1633 12 IX; **G** Precaudal vertebra. Grayling (*Thymallus thymallus*), HF21 25 3785.1 15 XII; **H** Scale. Grayling (*Thymallus thymallus*), HF21 25 3785.2 15 XII; **I1** Left pharyngeal arch fragment. Common nase (*Chondrostoma nasus*), HF21 25 3316.1 14 XI; **I2** pharyngeal tooth fragment. Common nase (*Chondrostoma nasus*), HF21 25 3316.2 14 XI; **J** Left pharyngeal arch fragment. Common chub (*Leuciscus cephalus*), HF21 11 2411 14 XI. Scale 2 mm

the northern parts of the Palearctic and Nearctic ecozones, ranging from the UK and northern Europe across Eurasia to Siberia. These fishes require cool, well-oxygenated water, preferably with a swift current; they are found in large, sandy- or gravel-bottomed rivers and lakes, but *T. thymallus* may occasionally be found in brackish conditions. Generally omnivorous, they feed primarily on crustaceans, insects, and zooplankton. As they are highly sensitive to changes in water quality, *Thymallus* fishes may be considered indicator species. This species can reach a maximum weight of 1.5 kg and a maximum size of 50 cm (Füllner et al. 2016). The brown trout (*S. trutta*), which has only been found in layers GH 9 and 12, requires oxygen-rich water and a specific temperature for hatching and growing. Nowadays, *S. trutta* is usually found in cold running water with temperatures ranging from 0 to 20ºC (Jonsson and Jonsson 2009; Elliott and Elliott 2010). The Danubian trout (*H. hucho*), only present in GH 10 and 14, is endemic to the Danube basin in Europe and reaches about 1.5 m in length and more than 50 kg in weight, although the average length is between 60 to 120 cm. This permanent cold-water salmonid spawns in April, when water reaches a temperature of 6 to 9 °C (Füllner et al. 2016).

The burbot (*Lota lota*), the only gadiform (cod-like) freshwater species, is present in the Hohle Fels assemblage throughout the sequence. This species has a circumpolar distribution above 40°N. Populations are continuous from the

British Isles across Europe and Asia to the Bering Strait. Burbots live in large, cold rivers, lakes, and reservoirs, primarily preferring freshwater habitats, but can thrive in brackish environments for spawning. During the summer, they are typically found in the colder water below the thermocline. As benthic fish, they tolerate an array of substrate types, including mud, sand, rubble, boulder, silt, and gravel for feeding. Burbot populations are fluvial during the winter months, and they migrate to near-shore reefs and shoals to spawn on the grounds of sand or gravel. As adults, they are primarily piscivores, preying on lamprey, whitefish, young northern pike, suckers, bullhead, and stickleback. This species can reach a maximum weight of 4 kg and a maximum size of 80 cm (Füllner et al., 2016).

The European bullhead (*C. gobio*) is found in Hohle Fels from GH 12 to 15 and is missing in the rest of the layers (GH 9–11). The European bullhead is a small demersal fish and prefers cold, clear, fast-flowing small streams and middle-sized rivers. It occurs on gravelly shores of cold lakes as well. The diet of this species is typically based on insects, crustaceans, and other invertebrates and it breeds in the spring. Some individuals can measure up to 15 cm although they are usually about 6 cm in length. This species is also a common prey of the burbot and other carnivorous fishes (Füllner et al., 2016).

The two species of cyprinids recovered from Hohle Fels are more typical of temperate waters and live in waters with temperatures between 10 and 25 °C (Doadrio 2002; Tissot and Souchon 2010). In Hohle Fels, the common chub (*L. cephalus*) is present in GH 12–14. This species is distributed throughout most of northern Eurasia, can reach lengths up to 60 cm, can weigh between 2 and 4 kg, and reach ages of 15–16 years (Füllner et al., 2016). The common nase (*C. nasus*) is only present in GH 14 and the individuals of this species are naturally found in drainages of the Black Sea (e.g. Danube), the southern Baltic Sea, and the southern North Sea. They range from 25 to 40 cm in length and weigh about 1 kg (Füllner et al., 2016). Accordingly, cyprinids such as the genus *Leuciscus* or *Chondrostoma* can be found in salmonid zones, as they also thrive in running water. However, cyprinids in general are present in multiple environments and show enormous diversity in their diet, which includes arthropods and other fishes (Doadrio, 2002).

The least represented species classified at Hohle Fels corresponds to the northern pike (*E. lucius*), represented in the assemblage by one caudal vertebra in GH 15. This species is carnivorous and typical of the fresh waters of the Northern Hemisphere. The northern pike has an average length of 50 cm but it can measure up to 150 cm and weigh 25 kg (Füllner et al., 2016).

No relevant environment changes are observed during the Hohle Fels sequence based on the fish remains since the majority of the identified species, such as the European grayling, the brown trout, the Danubian trout, the burbot, the bullhead, and the pike are common cold-water species (Füllner et al., 2016). The presence of these species characterizes the fish assemblages as belonging to a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters. Only the common chub and nase are associated with habitat with temperate water but can also live in cold waters (Doadrio, 2002).

## Small mammals

A total of 6538 small mammal remains, corresponding to a MNI of 2310, were identified. Six insectivores, one bat (only identifiable at genus level as *Myotis* sp.), one small lagomorph (*Ochotona pusilla*), and 14 rodents are represented at Hohle Fels (Table 3, Fig. 5). A few taxonomical remarks: the red-toothed shrews, with intermediate size between *Sorex* ex gr. *araneus* and *S. minutus*, a slightly posterior position of the mandibular foramen and a somewhat slender condylar articulation (Fig. 5B) has been assigned to *S. tundrensis*, following van Kolfschoten (2014); *Neomys fodiens* and *N. anomalus* (Fig. 5D and 5E) have been separated following the metric criteria in Popov and Zidarova (2008); *Sicista* cf. *subtilis* and *S.* cf. *betulina* (Fig. 5T and 5U) have been separated following the morphological and metric criteria of Niethammer and Krapp (1982); the small size hamsters (Fig. 5S) have been assigned to *Allocricetus* vel *Cricetulus* sp. due to the low number of specimens which does not allow the morphological and morphometric population study necessary to discriminate between the two genera (Hir 1993; Cuenca Bescós 2003).

To reconstruct the environment and landscape in the surrounding of the site, we decided to apply the Habitat Weighting Method with two different sets of values, one indicating the ecological preferences of each species, to obtain a general view of the changes in the environment while the other is based on habitat suitability, which allows us to recognize oscillation in the sequence by including different categories and dividing them further into sub-habitats.

We also decided to give particular weight to the changes in the relative frequency of the two lemming species present at Hohle Fels, *Lemmus lemmus* and *Dicrostonyx torquatus*. These two species are in fact strongly linked to subarctic and tundra environments (Wilson et al. 2017; IUCN 2021). They are easily identifiable so that they cannot be confused with other arvicolines in the sequence (Nadachowski 1982) and are therefore good indicators of cooling periods. A summary of the results of the environmental analysis is given in Fig. 6.

Based on the percentage of lemmings (Table 3, Fig. 6), GH 14 seems to represent a more temperate period than GH 15. Conditions got slightly cooler and then colder respectively in GH 13 and 12. During GH 11 and 10 it is possible to observe an amelioration but at GH 9 there seems to be a recrudescence of the colder climate. The results of Habitat Weighting based on ecological preferences describe four

**Table 3** Identified taxa of small mammals from the Middle Paleolithic Geological Horizons (GH) in Hohle Fels. NISP: number of identified specimens; MNI: minimum number of individuals

| | GH 9 | | | GH 10 | | | GH 11 | | | GH 12 | | | GH 13 | | | GH 14 | | | GH 15 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NISP | MNI | % MNI | NISP | MNI | % MNI | NISP | MNI | % MNI | NISP | MNI | % MNI | NISP | MNI | % MNI | NISP | MNI | % MNI | NISP | MNI | % MNI |
| *Talpa europaea* | | | | 1 | 1 | 0.61 | | | | 2 | 1 | 0.22 | 5 | 1 | 0.28 | 2 | 1 | 0.37 | 10 | 3 | 0.55 |
| *Talpa* sp. | | | | 2 | | | 1 | | | 2 | | | | | | 7 | | | 7 | | |
| *Sorex* ex gr. *araneus* | 11 | 4 | 1.72 | 12 | 9 | 5.49 | 18 | 12 | 4.14 | 22 | 9 | 2.00 | 50 | 30 | 8.29 | 18 | 9 | 3.35 | 17 | 12 | 2.21 |
| *Sorex minutus* | | | | 1 | 1 | 0.61 | 1 | 1 | 0.34 | | | | 4 | 2 | 0.55 | 3 | 3 | 1.12 | 1 | 1 | 0.18 |
| *Sorex tundrensis* | 1 | 1 | 0.43 | 2 | 2 | 1.22 | 1 | 1 | 0.34 | 7 | 4 | 0.89 | 7 | 4 | 1.10 | 4 | 3 | 1.12 | 19 | 12 | 2.21 |
| *Sorex* sp. | 3 | | | 5 | | | 6 | | | 20 | | | 42 | | | 35 | | | 41 | | |
| *Neomys* cf. *anomalus* | | | | | | | | | | 2 | 2 | 0.45 | 1 | 1 | 0.28 | 2 | 1 | 0.37 | 4 | 2 | 0.37 |
| *Neomys* cf. *fodiens* | 1 | 1 | 0.43 | | | | | | | 3 | 3 | 0.67 | 1 | 1 | 0.28 | | | | 5 | 3 | 0.55 |
| *Neomys* sp. | | | | 1 | | | | | | 4 | | | 7 | | | 3 | | | 12 | | |
| Soricidae indet | 5 | | | 11 | | | 9 | | | 18 | | | 112 | | | 95 | | | 54 | | |
| *Myotis* sp. | | | | | | | | | | 1 | | | | | | | | | | | |
| *Ochotona pusilla* | | | | | | | | | | | | | 1 | 1 | 0.28 | 4 | 1 | 0.37 | 15 | 2 | 0.37 |
| *Alexandromys oeconomus* | 28 | 15 | 6.47 | 32 | 16 | 9.76 | 30 | 16 | 5.52 | 41 | 22 | 4.90 | 61 | 36 | 9.94 | 53 | 29 | 10.78 | 87 | 46 | 8.46 |
| *Arvicola amphibius* | 15 | 3 | 1.29 | 16 | 3 | 1.83 | 45 | 6 | 2.07 | 27 | 6 | 1.34 | 36 | 9 | 2.49 | 26 | 10 | 3.72 | 65 | 11 | 2.02 |
| *Chionomys nivalis* | 4 | 3 | 1.29 | 9 | 6 | 3.66 | 10 | 7 | 2.41 | 10 | 7 | 1.56 | 19 | 11 | 3.04 | 10 | 6 | 2.23 | 12 | 6 | 1.10 |
| *Clethrionomys glareolus* | 1 | 1 | 0.43 | | | | | | | | | | | | | | | | | | |
| *Dicrostonyx torquatus* | 55 | 9 | 3.88 | 32 | 3 | 1.83 | 64 | 12 | 4.14 | 64 | 11 | 2.45 | 46 | 5 | 1.38 | 19 | 4 | 1.49 | 194 | 31 | 5.70 |
| *Lasiopodomys anglicus* | 244 | 132 | 56.90 | 166 | 91 | 55.49 | 236 | 130 | 44.83 | 367 | 200 | 44.54 | 377 | 194 | 53.59 | 299 | 161 | 59.85 | 672 | 337 | 61.95 |
| *Lemmus lemmus* | 198 | 24 | 10.34 | 92 | 8 | 4.88 | 284 | 32 | 11.03 | 335 | 67 | 14.92 | 186 | 19 | 5.25 | 51 | 5 | 1.86 | 254 | 34 | 6.25 |
| *Microtus arvalis* | 74 | 38 | 16.38 | 36 | 23 | 14.02 | 182 | 71 | 24.48 | 226 | 114 | 25.39 | 86 | 45 | 12.43 | 56 | 29 | 10.78 | 62 | 38 | 6.99 |
| Arvicolidae indet | 3 | | | 5 | | | 16 | | | 27 | | | 23 | | | 29 | | | 32 | | |
| *Allocricetus* vel *Cricetulus* sp. | | | | | | | | | | | | | | | | 2 | 1 | 0.37 | 7 | 3 | 0.55 |
| *Apodemus* cf. *sylvaticus* | | | | | | | | | | | | | | | | 1 | 1 | 0.37 | | | |
| *Allactaga* cf. *major* | | | | | | | | | | | | | 1 | 1 | 0.28 | 1 | 1 | 0.37 | | | |
| *Sicista* cf. *betulina* | | | | | | | | | | | | | 1 | 1 | 0.28 | 1 | 1 | 0.37 | | | |
| *Sicista* cf. *subtilis* | | | | | | | | | | 1 | 1 | 0.22 | | | | 4 | 2 | 0.74 | 1 | 1 | 0.18 |
| *Sicista* sp. | | | | | | | | | | 1 | | | | | | 1 | | | 2 | | |
| *Spermophilus superciliosus* | 1 | 1 | 0.43 | 3 | 1 | 0.61 | 3 | 2 | 0.69 | 5 | 2 | 0.45 | 3 | 1 | 0.28 | 1 | 1 | 0.37 | 7 | 2 | 0.37 |
| Total | 644 | 232 | | 426 | 164 | | 906 | 290 | | 1185 | 449 | | 1069 | 362 | | 727 | 269 | | 1580 | 544 | |

different phases (Table 4). GH 15 to 13 represent a humid phase, with dominating open humid meadows (OH) and water-related environments (Wa). GH 12 and 11 represent a more arid phase, with an increase in open dry grassland (OD) and open woodland (OW) and a decrease in Wa and OH. Elements of mature forest (Wo) slightly decrease in this phase. In these two GHs, the relative percentage of *Microtus arvalis* reached its maximum, alongside a decrease in the proportion of *Lasiopodomys anglicus*, which however remains dominant (Table 3). This indicates a moment in the Late Pleistocene that can be considered relatively less cold than the following GHs, but still colder than the preceding phase when subarctic and tundra elements are less represented. GH 10 represents another relatively humid phase, while GH 9 presents again as cold and relatively dry (Fig. 6).

The Habitat Weighting based on habitat suitability offers a different perspective and allows us to understand better the changes in the landscape and environmental conditions (Table 5). It is interesting to notice that the forest component seems to be relatively stable thought the sequence, except for GH 15 and GH 9 that present the lowest percentages. This stability might be linked to the constant presence of water in the Ach River system, as testified by the fish assemblage, that might have been able to support a riparian forest. The relative percentage of wetlands also does not vary much, although it is possible to divide the sequence into two phases: GH 15 to 13 with wetlands at > 9%, and GH 12 to 9 with < 9%. An interesting result is an increase in shrublands with a general decrease of all the other habitats, i.e. grassland, forest, wetlands, rocky, and desert, in GH 12 and partially in GH 11. This might indicate a process of degradation of the grasslands, possibly brought by the loss of ground-water resources, as indicated by the % of Wa and Wetland. It might also point to a stronger seasonality in precipitations that could generate generally drier conditions and facilitate woody plant encroachment (Archer et al. 2017).

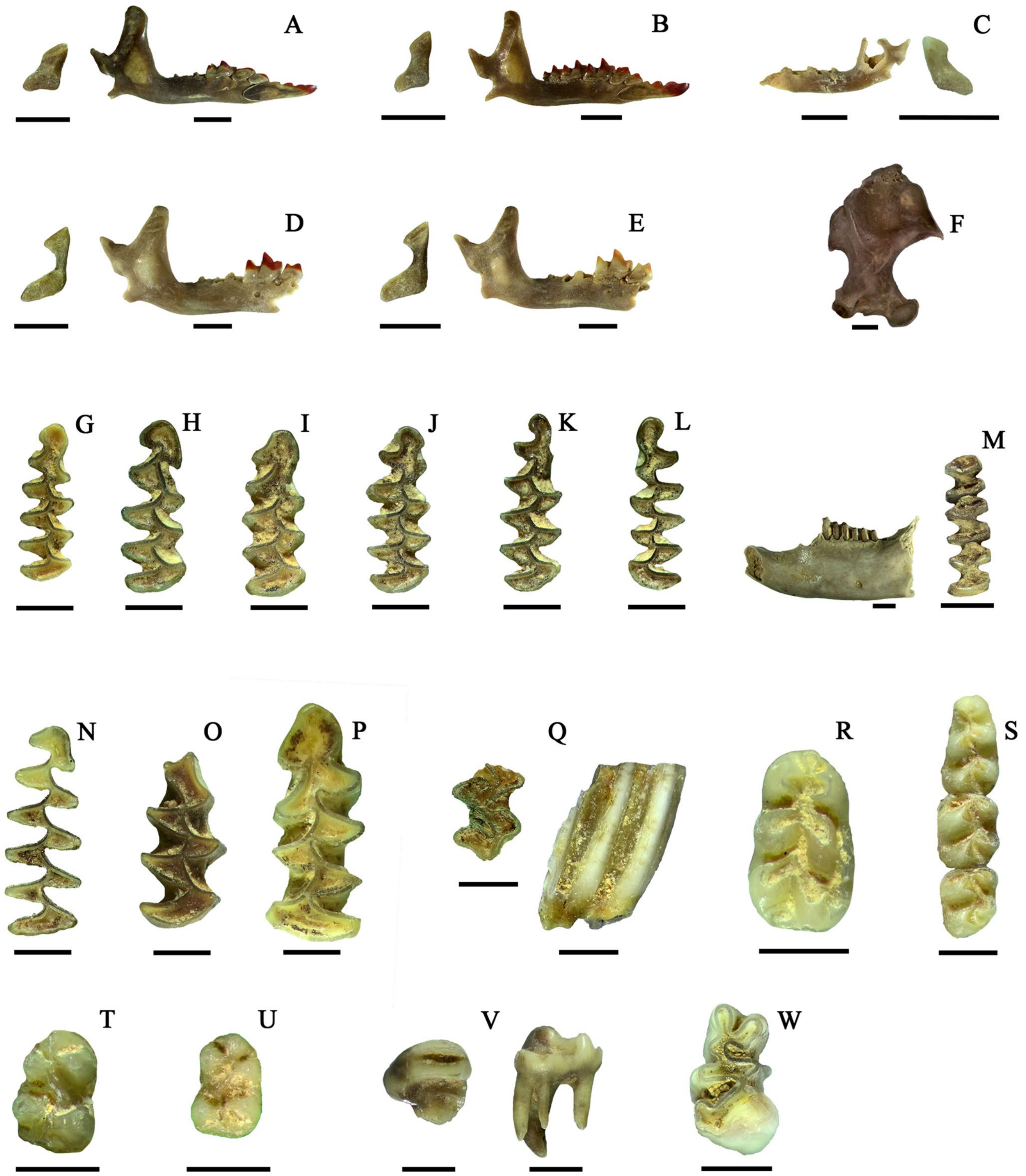
To summarize, the landscape surrounding Hohle Fels during the deposition of the Middle Paleolithic Horizons was dominated by open environments, with forest components always present, due to the influence of the Ach River. GH 15 presents as relatively temperate and humid; GH 14 as more temperate and humid; GH 13 less temperate and humid; GH 12 and 11 cold and arid but relatively more temperate than the following periods; GH 10 is still cold but less arid; GH 9 clearly colder and arid.

The data from the bioclimatic model are consistent with our environmental reconstruction (Table 6). The MATs inferred for the sequence are always lower than modern temperatures, between 4.2 (GH 14) and 9.48 °C (GH 9) less than the present. Ps are also significantly lower, between 638 (GH13) and 672.73 mm (GH9) less than present mean annual precipitation. After a relatively temperate and humid period (GH 13–15), climatic conditions became increasingly colder and more arid (GH 9–12). These results confirm the trend already observed by Rhodes and Conard (2021) for GH 9–12. Furthermore, our reconstruction also coincides with the paleoclimatic data obtained from micromorphology analysis of GH 9–12 (Miller 2015), which showed a gradual decrease in temperate and humid conditions throughout the Middle Paleolithic layers excavated at the time.

Based on the limited radiocarbon dates available at the time for the lower GHs, Rhodes (2019) suggested that the shift in climatic conditions between GH 12 and 11 might take place around the time of the Greenland Interstadial (GI) 12, at ca. 47 ka cal BP. Using the new ESR dates available for GH 12 and the radiocarbon dates for the upper Middle Paleolithic Horizons, we can tentatively try to relate the different GHs to the oxygen isotope curve for the Late Pleistocene (Fig. 7). GH 12, dated at 62.5 ± 4 ka (Conard et al. 2021), corresponds to the end of Marine Isotope Stage (MIS) 4—beginning of MIS 3. Given its relatively temperate signal, it might correspond to the GI 18 (ca. 64 ka BP) or to the beginning of MIS 3 (ca. 59–57 ka BP) (after Rasmussen et al. 2014). Consequently, GH 15 to 13 probably correspond to the end of MIS 5 (ca. 87–71 ka BP, after Rasmussen et al. 2014), and we can cautiously assign GH 14, with the highest MAT, to GI 21, 20, or 19, while GH 15 and 13 to the cooling periods preceding and following it (as described in Wohlfarth 2013). GH 11 to 9 show a trend toward colder and more arid conditions, typical of MIS 3, but it is not possible at the time to correlate these GHs to any particular point of the curve.

## Small mammals: biochronological inferences

Furthermore, the stage of evolution of the water vole *Arvicola amphibius* as quantified by the Schmelzband-Differenzierung-Quotient (SDQ) can help with the chronological attribution of the lower Middle Paleolithic Horizons. A general decrease in the value of SDQ index is observed in water vole populations all across Europe during the Middle and Late Pleistocene (Heinrich 1990; van Kolfschoten 1992; Koenigswald von 1994; van Kolfschoten and Turner 1996; Desclaux et al. 2000; Maul et al. 2000; Paunescu et al. 2004; Kalthoff et al. 2007; Cuenca-Bescós et al. 2010). However, this trend is not perfectly smooth through time or synchronous in all regions (Maul and Markova 2007; Maul et al. 2007, 2014; Masini et al. 2020). Hence, criticisms have been made about the use of the SDQ index as a tool for specific determination and/or stratigraphic correlations (Escudé et al. 2008; Martin 2014). The SDQ pattern is in fact influenced by factors including climate, geography, altitude, latitude, and migration (Kratochvil 1981; Röttger 1987; van Kolfschoten 1992; Ruddy 2011) but, even considering its limits, the SDQ index remains a very powerful descriptive tool and, given the amount of study and analysis presented in literature, a solid base for comparison.



Furthermore, once the context is taken into account (i.e., the small mammal assemblage as a whole, the geographic position, the possibility of contact between different populations, and the morphology of the molars), it is possible to use the SDQ index to obtain a reliable biochronological indication for the relative age of a site.

Only GH 15, 14, 13, and 12 at Hohle Fels present complete first lower molars of *A. amphibius* which could be measured (Table 7). Although the number of specimens analysed is limited, it is possible to see that the values for the index in GH 15, 14, and 13 are > 90, while the value of the sample from GH 12 is only 84.2. Compared with SDQ values of populations from

◀**Fig. 5** **A** *Sorex* ex gr. *araneus*, condylar process and right mandible, HF_25-GH12-154; **B** *Sorex tundrensis*, condylar process and right mandible, HF_25-GH12-155; C: *Sorex minutus*, left mandible and condylar process, HF_28d_GH13-432; **D** *Neomys fodiens*, condylar process and right mandible, HF_28c-GH15-n4001; **E** *Neomys anomalus*, condylar process and right mandible, HF_27a-GH15-n3434; **F** *Talpa europaea*, left humerus, HF_27b-GH15-n3411. Scale 2 mm. **G** *Microtus arvalis*, right m1, HF_27b-GH15-672; H: *Chionomys nivalis*, right m1, HF_27b-GH9-345; **I** *Alexandromys oeconomus*, right m1, HF_26a-GH15-115; **J** *Lasiopodomys anglicus*, right m1, HF_27b-GH9-355; **K** *Lasiopodomys anglicus*, right m1, HF_27b-GH9-356; **L** *Lasiopodomys anglicus*, left m1, HF_27b-GH9-357; **M** *Ochotona pusilla*, left mandible, lateral and occlusal view, HF_26a-GH14-n1887; **N** *Dicrostonyx torquatus,* right m1, HF_26a-GH15-117; **O** *Lemmus lemmus*, right m1, HF_25-GH12-77; **P** *Arvicola amphibius*, left m1, HF_27a-GH15-25; **Q** *Clethrionomys glareolus*, left M2, occlusal and lateral view, HF_27b-GH9-316; **R** *Apodemus* cf *sylvaticus*, right m1, HF_27a-GH14-505; **S** *Allocricetus* vel *Cricetulus* sp., left m1, m2, m3, HF_25d-GH15-329; **T** *Sicista* cf. *subtilis*, left m1, HF_27a-GH14-506; **U** *Sicista* cf. *betulina*, left m1, HF_28-GH13-446; **V** *Spermophilus* cf. *superciliosus*, right M3, occlusal and lateral view, HF_25d-GH15-42; **W** *Allactaga* cf. *major*, right m1, HF_25c-GH 14.1–187. Scale 1 ms

Central Europe (Heinrich 1990; Kalthoff et al. 2007; Maul et al. 2014), our data suggest that GH 15 to 13 might be related to the Early Weichselian (MIS 5d-5a) while GH 12 belongs to a later period, in accordance with the ESR dates obtained for GH 12 and with our paleo-environmental and -climatic reconstruction.

## Were Neanderthal occupations at Hohle Fels influenced by climatic and environmental changes?

### Neanderthal subsistence practices in freshwater ecosystems

Several authors presented evidence of aquatic resources exploitation during the Lower Paleolithic in Africa (Brooks et al. 1995; Yellen et al. 1995) and Neanderthal marine coastal adaptation, including fishing activities, in the Iberian Peninsula and the Atlantic coast (e.g., Morales-Muñiz and Roselló-Izquierdo 2005; Stringer et al. 2008; Brown et al. 2011; Zilhão et al. 2020). Nevertheless, the possibility of the exploitation of continental freshwater ecosystems in Western-Central Europe by Neanderthal groups has not often been the subject of systematic research. This is partially due to the lack of well-preserved, abundant assemblages. However, the study of inland fishing activities, occurring close to rivers or lakes, during the Middle Paleolithic has been shown to have great potential by authors who have already analysed this topic with interesting results (e.g., Blanco-Lapaz 2019; Guillaud et al. 2021).

Our analysis shows that the freshwater ecosystem around this site was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters inhabited by preys suitable to humans, due to their relatively larger size and weight (Morales-Muñiz and Roselló-Izquierdo 2005). Other Middle Pleistocene sites in Western Europe show smaller fish accumulations, indicating probably that this abundance of fish results from birds of prey or small-medium carnivores (Guillaud et al. 2021). Based on our preliminary results on the Hohle Fels fish remains, we cannot discard fishing as part of the subsistence practices of Paleolithic hunter-gatherers in Central Europe. However, future studies on fish remains would be necessary to better understand the local freshwater ecosystems, the taphonomic history of fish accumulation, and how fish constitute part of the human diet. In an effort to address some of these issues, additional studies from other Swabian Palaeolithic sites are underway. Exploring more fish assemblages from Middle Paleolithic sites could also help to investigate, and possibly refute, the existing paradigm that Neanderthals were unable to use fishes as a resource in continental waters (Morales-Muñiz and Roselló-Izquierdo 2005; Conard et al. 2013; Guillaud et al. 2021; Blanco-Lapaz et al. 2021).

### Neanderthal occupations at Hohle Fels Cave

The upper units attributed to the Middle Paleolithic, corresponding to AH VI-IX / GH 9–12, are relatively poor in anthropogenic finds (i.e., lithic industries, burned bones, modified bones) (Conard et al. 2012). Going from bottom to top, the density of the finds decreases and the layer underlying the first Aurignacian proved to be essentially sterile (Conard and Bolus 2008). This led to the hypothesis that the last Neanderthal groups and the first modern human inhabited the cave with little or no overlaps (Conard et al. 2006). The low density of finds in AH VI-IX might indicate frequent moves and few long-term occupations by large groups of Neanderthals and, although well-adapted to the steppe environment, population density also appears to be low (Conard et al. 2012). On the other hand, the new lower Middle Paleolithic units, corresponding to AH X-XI / GH 13–15, present a relatively high finds density, not comparable with the density of the Aurignacian layers, but remarkably higher than those of AH VI-IX (Conard et al. 2021). This increase in anthropogenic findings coincides with the more temperate climatic phase detected by the analysis of the small mammal assemblage. This suggests that Neanderthals used the cave more intensely during periods with less harsh conditions. The increased levels of all classes of anthropogenic materials reflect the presence of larger groups, occupations for longer periods, or both. The archaeological signal might also point to higher population density at the end MIS 5 than during MIS 3. Changes in sedimentation rates and taphonomic factors including biological, geological, and/or anthropogenic influences might also contribute to the differences in anthropogenic signals between AH VI-IX and AH X-XII. Thus, more studies are ongoing to ascertain the characteristics of the newly excavated AHs. Here, it is important to note that the deepest part of the excavation currently corresponds to only 6m$^2$, and a far greater sample is needed to confirm or refute these trends.

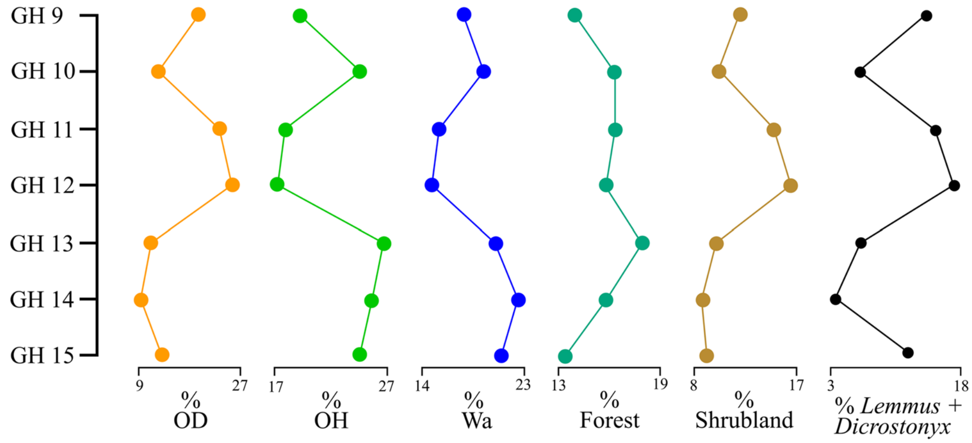


**Fig. 6** Paleoenvironmental reconstruction for the Middle Paleolithic Horizons of Hohle Fels. GH: geological horizons; OD: open dry; OH: open humid; Wa: water-related environment. % of *Lemmus* + *Dicrostonyx* indicates subarctic and tundra environments

**Table 4** Paleoenvironmental reconstruction based on ecological preferences of rodents and insectivores. GH: geological horizons; OD: open dry; OH: open humid; OW: open woodland; Wo: woodland; R: rocky environment; Wa: water-related environment. Values are expressed in percentages

| | OD | OH | OW | Wo | R | Wa |
|---|---|---|---|---|---|---|
| GH 9 | 19.29 | 19.18 | 25 | 3.02 | 15.52 | 18 |
| GH 10 | 12.65 | 24.24 | 22.41 | 3.35 | 17.53 | 19.82 |
| GH 11 | 24.31 | 17.41 | 26.21 | 2.67 | 13.62 | 15.78 |
| GH 12 | 26.17 | 16.54 | 27.73 | 1.84 | 12.69 | 15.03 |
| GH 13 | 11.77 | 26.18 | 21.26 | 3.25 | 16.48 | 21.05 |
| GH 14 | 9.05 | 25.28 | 21.46 | 4.29 | 17.26 | 22.67 |
| GH 15 | 13.42 | 23.99 | 20.94 | 3.69 | 16.65 | 21.31 |

**Table 5** Paleoenvironmental reconstruction based on habitat suitability of rodents and insectivores. GH: geological horizons. Values are expressed in percentages

| | Forest | Shrubland | Grassland | Wetland | Rocky | Desert |
|---|---|---|---|---|---|---|
| GH 9 | 14.17 | 12.14 | 64.22 | 8.00 | 1.29 | - |
| GH 10 | 16.79 | 10.25 | 60.30 | 8.84 | 3.66 | - |
| GH 11 | 16.85 | 15.07 | 56.55 | 8.87 | 2.41 | - |
| GH 12 | 15.90 | 16.50 | 57.26 | 8.52 | 1.56 | - |
| GH 13 | 17.94 | 10.16 | 58.04 | 10.63 | 3.05 | 0.04 |
| GH 14 | 15.87 | 8.87 | 62.95 | 9.74 | 2.24 | 0.21 |
| GH 15 | 13.50 | 9.06 | 65.84 | 10.17 | 1.11 | 0.22 |

**Table 6** Paleoclimatic reconstruction based on the Bioclimatic Model. GH: Geological Horizons; MAT: mean annual temperature (fit); P: mean annual precipitations (fit), with lower (lwr) and upper (upr) limit values. ΔT: difference between the obtained MAT and the current mean annual temperature. ΔP: difference between the obtained P and the current mean annual precipitation

| | MAT (°C) | | | | P (mm) | | | |
|---|---|---|---|---|---|---|---|---|
| | fit | lwr | upr | ΔT | fit | lwr | upr | ΔP |
| GH 9 | −1.18 | −7.37 | 5.02 | −9.48 | 386.27 | −177.77 | 950.33 | −672.73 |
| GH 10 | 1.07 | −5.23 | 7.37 | −7.23 | 403.93 | −169.93 | 977.80 | −655.07 |
| GH 11 | 1.19 | −5.12 | 7.50 | −7.11 | 405.52 | −168.67 | 979.72 | −653.48 |
| GH 12 | 2.49 | −3.78 | 8.76 | −5.81 | 404.74 | −166.24 | 975.74 | −654.26 |
| GH 13 | 3.09 | −3.28 | 9.46 | −5.21 | 421.51 | −158.49 | 1001.52 | −637.49 |
| GH 14 | 4.10 | −2.19 | 10.39 | −4.20 | 417.49 | −155.06 | 990.05 | −641.51 |
| GH 15 | 3.24 | −3.04 | 9.51 | −5.06 | 407.94 | −163.06 | 978.94 | −651.06 |

**Fig. 7** Bioclimatic reconstruction for the Middle Paleolithic Horizons of Hohle Fels with tentative correlation to the Isotope Curve (after Lisiecki and Raymo 2005). MAT: mean annual temperature; P: mean annual precipitations

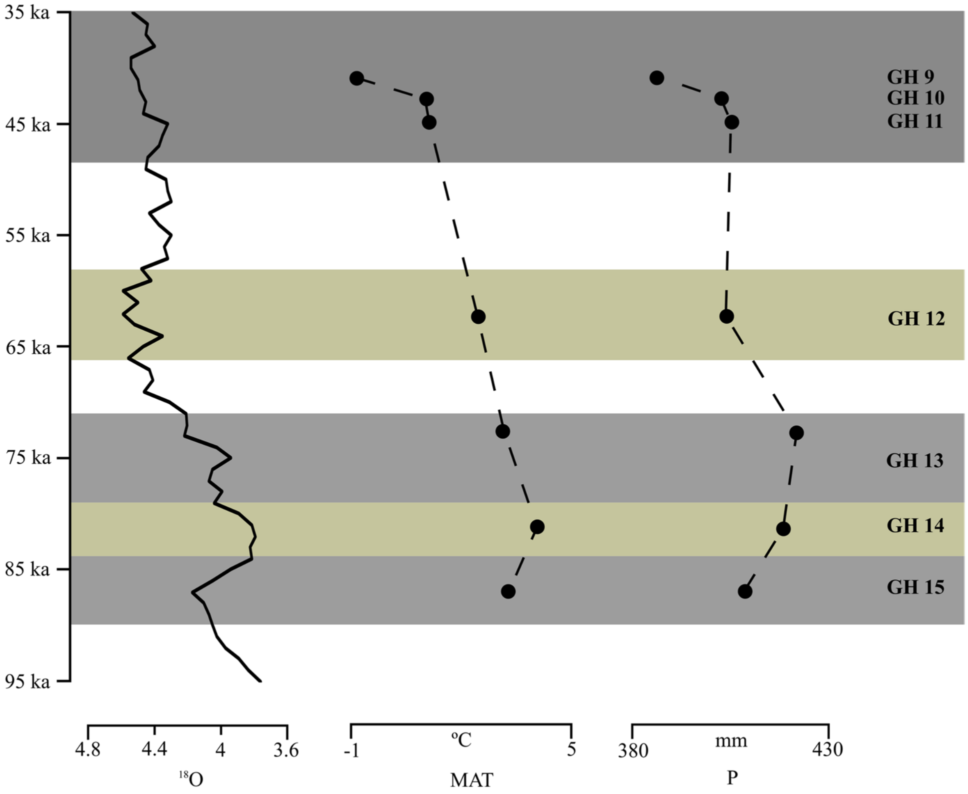


**Table 7** SDQ values for *Arvicola amphibius*. GH: geological horizons; n: number of specimens; min: minimum value; max: maximum value; SD: standard deviation

| | *n* | Mean | Median | Min | Max | SD |
|---|---|---|---|---|---|---|
| GH 12 | 8 | 84.57 | 84.2 | 73.52 | 92.42 | 5.81 |
| GH 13 | 7 | 88.73 | 91.13 | 76.19 | 97.1 | 7.39 |
| GH 14 | 9 | 97.84 | 98.03 | 89.06 | 105.55 | 4.51 |
| GH 15 | 12 | 90.70 | 91.6 | 81.8 | 100.69 | 6.23 |

Among the findings from AH X, the most remarkable is the presence complete leaf point, the first one recovered in situ in the Swabian Jura after the 1936 excavation at Haldenstein (Lone Valley) conducted by Riek (Riek 1938). The leaf point is 7.6 cm long, 4.1 cm wide, 0.9 cm thick, made from locally available, grey Jurassic chert from the Swabian region. It was hafted at the less pointy end, probably used as a projectile during hunting, and discarded after a failed attempt at resharpening (Rots et al. 2021). In Germany, leaf points are referred to as "Blattspitzen" and until now, the Blattspitzengruppe, the cultural unit to which the leaf points belong, has been assigned to the final Middle Paleolithic (Bosinski 1967; Conard and Fischer 2000; Bolus 2004, 2011). The new dates for GH 12, combined with the biostratigraphic signal of *A. amphibius* and the climatic reconstruction here presented, would place the leaf point of Hohle Fels at a much earlier time than expected and thereby questioning the traditional cultural chronology of Swabian Jura. Here, it is important to reiterate that our biostratigraphic arguments are consistent with new radiometric dates (Conard et al. 2021). A reappraisal of this cultural unit and its chronological attribution is needed to document Middle Paleolithic technology and hunting strategies, as well as to refine our understanding of the circumstances that led to the extinction of Neanderthals. Every indication suggests that the ongoing excavations at Hohle Fels will continue to contribute to these research questions.

## Neanderthal occupations at Hohle Fels Cave in the context of Central-Western Europe (Germany, Belgium, Poland, and France)

The small mammal assemblages related to the Middle Paleolithic GHs at Hohle Fels provide a fundamental regional reference for this chronology, for its sample size, and for the reliable dates available for the sequence. The assemblage of Geißenklosterle (GHs 23–18, Ach Valley, Rhodes et al. 2018) is dated to the end of MIS 5 up to MIS 3 (Richard et al. 2019b). It is smaller in size, but consistent in faunal composition with the Hohle Fels one. The assemblage of Stadel-Höhle at Hohlenstein (Lone Valley, Ziegler 2019) is dated to the MIS 3 (Richard et al. 2019a) and it differs from the Hohle Fels one for the presence, although sporadic, of *Clethrionomys glareolus*, *Glis glis*, *Sciurus vulgaris*, *Apodemus* sp., indicators of woodland and forest patch, and of *Ochotona pusilla* and large- and small-size hamsters, indicators of open and arid environments. These differences might indicate that micro-environmental and micro-climatic conditions were not the same in the two valleys during the last Neandertal occupations.

A recent publication by Rhodes and Conard (2021) suggests that climatic conditions in the Ach Valley were colder and more arid than in other Central European sites with the same chronology as GHs 12–7 of Hohle Fels. The present study confirms these results also for the lower GHs 15–13. The small mammal assemblage from Sesselfelsgrotte (Germany, layers L-G, MIS 4–3; van Kolfschoten 2014) indicates generally more temperate conditions than those registered at Hohle Fels, due to the relative dominance of *M. arvalis/agrestis* over *L. anglicus* (=*Microtus gregalis*) and the presence of *C. glareolus*. Data from small mammal assemblages directly related to Middle Paleolithic occupations at Scladina Cave (MIS 5–3, López-García et al. 2017a, 2017b) and Marie-Jeanne Cave (MIS 3, López-García et al. 2017a), both located in Belgium, indicate more temperate conditions than at Hohle Fels, testified by the presence of *C. glareolus*, *Microtus* (*Terricola*) *subterraneus*, *Glis glis*, and *Apodemus* gr. *sylvaticus/flavicollis*. During MIS 5, the landscape at Scladina and Marie-Jeanne Caves was always dominated by woodland, while that at Hohle Fels open environment is always dominant. During both MIS 5 and MIS 3, the mean annual precipitation indicates more humid conditions than at Hohle Fels. Similar comparisons can be drawn between the Hohle Fels assemblage and the assemblage from Biśnik Cave (MIS 5–3, layers 13 to 9; Socha 2014) in Poland. Both faunal composition and bioclimatic reconstructions indicate more temperate and humid conditions than at Hohle Fels. The small mammals from Obłazowa Cave (Poland, early MIS 3; Valde-Nowak and Nadachowski 2014) also indicate more humid conditions, due to the relatively high percentage of *A. oeconomus*. Another recent study concerning small mammal assemblages in Middle Paleolithic contest at Koziarnia Cave (Poland, Berto et al. 2021) indicates a general dominance of the open environment, but the sample size does not allow for further comparisons. According to the environmental reconstructions of Discamps and Royer (2017), the conditions at Hohle Fels seem to be close to those of the sites of the Atlantic region (i.e. Charente-Maritime, Charente, and Gironde, see Fig. 1), with *L. anglicus* dominant over *M. arvalis/agrestis* and generally dry and open landscape, while in the rest of southern France conditions seem more humid and temperate, with a higher component of shrubland and woodland.

In this context, the Middle Paleolithic occupations registered at Hohle Fels both during MIS 5 (GHs 15- 13) and MIS4-3 (GHs 12–9) took place in a more arid and colder environmental setting than those registered in Sesselfelsgrotte, Poland, and Belgium. Further studies are needed to clarify if this is a local (Ach Valley) or regional (Swabian Jura) peculiarity.

## Conclusions

The joint study of fish and small mammal assemblages from the Middle Paleolithic of Hohle Fels provided insights into the climatic and environmental conditions faced sby Neanderthals in the Ach Valley. The freshwater ecosystem around this site was characterized by a pre-mountain river system with the presence of permanent, oxygen-rich, and cold running waters. The landscape was dominated by an open environment, and thanks to the presence of the Ach river, the forest component was always relatively stable throughout the sequence. Our research has identified two major climatic oscillations: one more temperate corresponding to Neanderthal occupations of relatively high intensity, the other colder and more arid, presenting a trend toward increasingly harsher conditions, characterized by low-intensity Neanderthal occupations. Future studies, including additional material from Aurignacian, Gravettian, and Magdalenian units of Hohle Fels (already ongoing) will provide further knowledge about the changes in climate and environment during the human occupations at Hohle Fels. This ongoing research will document how human groups interacted with and adapted to the different climatic settings and will further illuminate their use of freshwater resources.

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**Author contributions** E. Luzi and S. Rhodes analysed the small mammal assemblage. Á. Blanco-Lapaz analysed the fish assemblage. N. Conard directs the excavation at Hohle Fels provided archaeological and geological context and funding. The manuscript was written by E. Luzi. All authors contributed to sections of the manuscript. All authors reviewed and approved the manuscript before submission.

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**Data availability** Raw data are available upon request. Corresponding author contact: elisa.luzi@ifu.uni-tuebingen.de.

## Declarations

**Competing interests** The authors declare no competing interests.

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## Appendix 6

**Blanco-Lapaz, A**., Marín-Arroyo, A.B., Gutiérrez-Zugasti, I., González-Echegaray de Yarto., F., González-Morales, M.R. 2023b. Coastal and Inland subsistence strategies during the Gravettian in the Cantabrian Region (northern Iberian Peninsula). Quaternary Science Advances, 12: 100106. https://doi.org/10.1016/j.qsa.2023.100106

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# Coastal and Inland subsistence strategies during the Gravettian in the Cantabrian Region (northern Iberian Peninsula)

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## ABSTRACT

The Gravettian site of Fuente del Salín Cave is located in the northern Iberian Peninsula (Cantabrian Region, Spain). In 2016, excavations conducted at the site yielded numerous faunal remains, including mammals and fish. Researchers also recovered molluscs remains during the 1990, 1991, and 2000 campaigns. This study presents the results of the archaeozoological and taphonomical analyses of the large mammals and fish remains recovered during these excavations. At Fuente del Salín Cave, a high level of bone fragmentation and the presence of burning damage characterizes the faunal assemblage. Taxonomy of large game shows diverse habitat exploitation, such as coastal valleys and plains (red deer, *Cervus elaphus*; horse, *Equus ferus*) as well as rocky landscapes (Iberian ibex, *Capra pyrenaica*; and chamois, *Rupicapra rupicapra*). Additionally, fish remains show the presence of salmonids (*Salmo* sp.), cyprinids, and haddock (*Melanogrammus aeglefinus),* indicating the exploitation of coastal, demersal, and riverine species. The taphonomic analysis of the mammals revealed burning damage concentrated on axial elements and epiphyses, characterized by temperatures typical of carbonization or calcification. The scarcity of carnivore gnawing marks and the presence of butchering marks prove that humans were the main accumulators at Fuente del Salín Cave. Concerning fish, most remains correspond to spines, branchial spines, ribs, and vertebrae, indicating humans processed fish by removing these elements for consumption. Based on our results, Fuente del Salín Cave provides an essential record of the subsistence strategies of the inhabitants of the Cantabrian Region during the Gravettian.

## 1. Introduction

At the beginning of the 20th century, Breuil (1912) first described the term Gravettian in his work: “Les subdivisions du Paléolithique supérieur et sa signification” during the International Congress of Prehistoric Anthropology and Archaeology of Genève. Modern research shows that the Gravettian covers an extended period (ca. 28–20 kyr $^{14}$C BP) characterized by widely fluctuating climatic conditions, with long cold phases punctuated by short, milder periods (Dansgaard/Oeschger interstadials) (Heinrich stadials; Rufí et al., 2019), which encompassed the final stage of the stadial Marine Isotopic Stage (MIS) 3 and the entirety of MIS 2. Bicho et al. (2017) observed the permanent occupation of even Europe’s peripheral regions by Anatomically Modern Humans between c.37 and 30 ka ago.

During the Gravettian, rapid climatic fluctuations associated with significant territorial increment led to diverse subsistence strategies extending from the Atlantic coast of the Iberian Peninsula to Siberia (Foucher, 2013). In this context, several authors identified subsistence strategies focused on cold-adapted animals, such as the woolly mammoth (*Mammuthus primigenius*) in eastern Gravettian sites like Yudinovo (Siberia; Vereshchagin and Kuz’mina, 1977) and Předmostí (Czech Republic; Bocherens et al., 2015). Similarly, authors such as Boyle (2017) and Lacarrière (2015) observed a hunting focus on reindeer (*Rangifer tarandus*).

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Moving to the Iberian Peninsula, particularly in the Cantabrian Region, Marín-Arroyo et al. (2018) conducted a recent review of the regional duration of the Gravettian, suggesting dates between 36,800–35,000 cal BP and 26,000 cal BP. The Gravettian lithic record is characterized by the presence of Noailles burins, La Gravette points, Font Robert points, and scrapers (Rasilla and Straus, 2004; Rasilla-Vives and Santamaría-Álvarez, 2006; Bradtmöller, 2014). Fortea (1992) conducted a systematic study of the Gravettian in the Cantabrian Region, which shows two main phases: one defined by the presence of Noailles burins and the other by more generic industries similar to the Font-Robert point morphotype. Later, Rasilla and colleagues (Rasilla and Straus, 2004) also characterized the Cantabrian Gravettian into two phases, the first dominated by the Noailles burin and the second characterized by a decrease in Noailles burins and an abundance of pedunculated Isturitz type points. The authors also described the presence of similar proportions of blade and bladelet tools and La Gravette points.

The Cantabrian Region (Fig. 1), comprised of Asturias, Cantabria, Basque Country, and the northern Navarre autonomous administrative regions, is located in north of Iberia. The region is nowadays characterized by its Atlantic coastline, which lies only c. 5–12 km south of the Late Glacial shoreline. This relative stability is due to the strait continental shelf and the steep, peaks and massifs of the Cantabrian Cordillera and the Picos de Europa range, which lie parallel to the coast. In this small area of the northern Iberian Peninsula, a wide range of habitats are present, including the shore, coastal zone, low hills, high mountain slopes, and valleys with different orientations, all of which are easily accessible within short distances. Long-distance movements were thus not required to exploit a wide range of resources during different seasons (e.g., Marín-Arroyo et al., 2023). In this context, archaeologists discovered and studied several relevant Paleolithic sites in the Cantabrian Region, yielding rich lithic and faunal assemblages and remarkable artistic manifestations, such as cave paintings and portable art (e.g., Bernaldo de Quirós, 1982; Bicho et al., 2007; Arias and Ontañón, 2013; Bradtmöller, 2014).

For the Cantabrian Gravettian, along with recent sub-regional studies (Rasilla and Straus, 2004; Martínez and Rasilla, 2012; Foucher, 2013) we have some syntheses mainly focused on lithic industries (de la Peña, 2009; Ríos-Garaizar et al., 2011; Arrizabalaga and de la Peña, 2012), plus different site studies that record the variability of Gravettian occupations in the area; general overview appears in the proceedings of the Altamira meeting on the Gravettian in 2011 (de las Heras et al., 2012). The main problem still present is the poor definition of several of them, especially in the case of old excavations; in other situations, the information is biased by the limited surface excavated. The distribution of Gravettian sites is presented in Fig. 1.

From the paleoenvironmental point of view, during the Gravettian (de la Peña, 2009), authors such as Andersen et al. (2006) and Fernández-García et al. (2023) observed an increase in cooler climatic conditions throughout Europe during the Gravettian. This change led to the migration of hunter-gatherer populations and an increase in the number of sites compared to prior periods. Based on the genetic record, Fu et al. (2016) and Posth et al. (2023) similarly observed that, during the Last Glacial Maximum, human populations retreated to glacial refugia on the southern edge of Europe (Iberian Peninsula and France), coinciding with the development of Solutrean technology. This model of human population continuity between western Gravettian and Solutrean is supported by Villalba-Mouco et al. (2023).

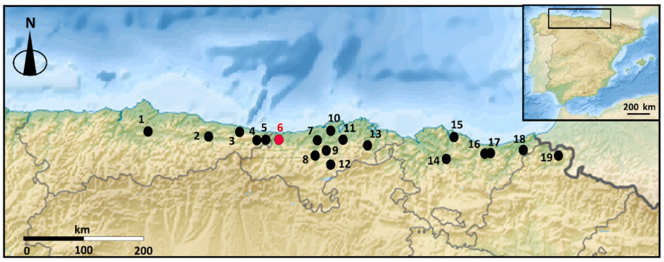

**Fig. 1.** General location of the Fuente del Salín Cave and the most important Gravettian sites within the Cantabrian Region. In Asturias: 1. La Viña, 2. Sopeña, 3. Cueto de la Mina, 4. Coímbre B, 5. Llonín; In Cantabria: 6. Fuente del Salín, 7. Altamira cave, 8. Hornos de la Peña, 9. El Castillo, 10. El Pendo, 11. Morín, 12. La Garma A, 13. El Mirón; In the Basque Country: 14. Bolinkoba, 15. Antoliñako, 16. Irikaitz, 17. Amalda, 18. Aitzbitarte III; Navarre: 19. Alkerdi.

Palynological studies at the Gravettian levels of Aitzbitarte III (31-28 kyr cal BP; Altuna et al., 2011) and Amalda (28 kyr cal BP; Altuna et al., 1990), both sites located in Guipúzcoa, confirm the decreased presence of forests with a dominance of grass taxa in cold contexts. Jones et al. (2018) confirmed, based on isotope analysis (carbon and nitrogen-stable isotopes collected from herbivores consumed by humans), a predominance of steppe taxa at both sites, such as *Pinus*, Cupressaceae, Poaceae, Anthemidae, and Cichoriae (Iriarte-Chiapusso, 2011). Previous archaeozoological studies of several sites in the Cantabrian Region, such as Lezetxiki, Morín, Labeko Koba, Amalda, Aitzbitarte, Cueto de la Mina, El Castillo, and Covalejos, indicate the presence of mammals from cold (such as seals, *Pusa hispida* or *Phoca vitulina;* wolverines, *Gulo*; reindeer, *Rangifer tarandus*; and arctic foxes, *Alopex lagopus*), open (such as red deer, *Cervus elaphus;* aurochs, *Bos primigenius*; and bison, *Bison priscus*), and rocky (Iberian ibex, *Capra pyrenaica*; chamois, *Rupicapra rupicapra*) environments during the Aurignacian-Gravettian (e.g., Álvarez-Lao & García, 2011; Altuna et al., 2013; Sánchez-Romero et al., 2021). Additionally, cold-adapted birds also are present in the Cantabrian Region, such as rock ptarmigan (*Lagopus mutus*) (Altuna et al., 2013).

### *1.1. Terrestrial resources during the Gravettian*

Exhaustive archaeozoological studies from various sites in Cantabria indicate a dominance of red deer (*C. elaphus)* during the Gravettian (Altuna, 1972; Freeman, 1973; Straus, 1977; Bernaldo de Quirós, 1982; Marín-Arroyo and Sanz-Royo, 2021), which characterize the subsistence strategies of this region. This signal differs from that of France, where reindeer (*R. tarandus*) prevailed due to local environmental and geographical conditions (e.g., Quesada López, 1995, 1997a,b,c; Mellars, 2002; Discamps et al., 2011). In the Cantabrian Region, humans also exploited Iberian ibex (*C. pyrenaica*) and other occasional herbivorous such as aurochs (*B. primigenius*), bison (*B. priscus*), horse (*E. ferus*/sp.), chamois (*R. rupicapra*), and exceptionally roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*) during this time. From the Aurignacian onwards, the frequency of horse and large bovid decrease, becoming notable in the Magdalenian. Although, the presence and abundance of some taxa are determined by the environmental conditions (González-Echegaray de Yarto, 2020), humans may have preferred specific resources.

Among the ungulates hunted by Gravettian populations, the acquisition appears more linked to environmental availability. However, the proximity to the coast meant that hunter-gatherer groups were in an advantageous position, by following the migratory movements of animals to obtain resources more effectively. Despite this, and as previously mentioned, the main prey in central and eastern Cantabria is red deer (*C. elaphus*), followed by medium-size caprines (*C. pyrenaica* and *R. rupicapra*) in mountain or mid-mountain areas and large bovids in the eastern part of the Basque Country, as in Aitzbitarte III (e.g., Quesada López, 1997c; Altuna et al., 2011; Altuna et al., 2013; González-Echegaray de Yarto, 2020).

In addition to ungulates, the carnivore taxa in the Cantabrian Region include bears (*Ursus* sp.), large felids (*Panthera* sp.), wolves (*Canis lupus*), red fox (*Vulpes vulpes*), and European badger (*Meles meles*) (Yravedra, 2002; Normand et al., 2012; Iriarte-Chiapusso and Arrizabalaga, 2012; González-Morales and Straus, 2012; Marín-Arroyo and Sanz-Royo, 2021).

### 1.2. Aquatic resources during the Gravettian

Aquatic resources, especially molluscs, were traditionally considered low-ranked and only consumed during periods of dietary stress (Osborn, 1977; Parmalee and Klippel, 1974). From the perspective of the Broad Spectrum Revolution, these resources were only consumed intensively during the Mesolithic, a sign of diversification and intensification, which occurred as a response to increasing population size and rising pressure on land resources (Binford, 1968; Flannery, 1969). However, in the last two decades, new models have proposed that the use of aquatic resources during the Upper Paleolithic has been underestimated (Bailey and Milner, 2002; Bicho and Haws, 2008; Bailey and Flemming, 2008; Bicho and Esteves, 2022). These models emphasize the bias produced by sea level rise, which covered Upper Paleolithic coastal areas and, therefore, a significant portion of coastal settlements. Despite this underrepresentation, and thanks to intense research efforts, today, there is plenty of evidence of the use of marine resources throughout the Upper Paleolithic across the coastal areas of Atlantic and Mediterranean Europe (Colonese et al., 2011; Gutiérrez-Zugasti et al., 2011). In some regions, such as the Atlantic coast of Portugal, marine productivity was even higher than in the Holocene. Thus, human populations could have benefited from the abundance, predictability, and ease of access to intertidal resources, such as molluscs. Moreover, current evidence suggests that diversification and intensification primarily began during the early Upper Paleolithic (e.g., Bicho and Haws, 2008) as seen, for example, at the Gravettian site of Vale Boi where coastal adaptations have been recently described (Bicho and Esteves, 2022). New investigations (e.g., Zilhão et al., 2020; Nabais et al., 2023) observed that an intensification of marine resources such as fish, molluscs, and crabs, was already incipient during the Middle Paleolithic. In the north of the Iberian Peninsula, the role of aquatic resources as part of human subsistence strategies during the Upper Paleolithic has gained importance in recent years (Freeman, 1973; Straus, 1977; Straus and Clarck, 1986; Álvarez-Fernández, 2011a; Gutiérrez-Zugasti et al., 2011). However, even though 12 sites show evidence of aquatic resource exploitation during the Gravettian, only a few have been thoroughly studied, and only Fuente del Salín Cave and La Garma A have essential quantitative and qualitative studies based on malacofauna (Álvarez-Fernández, 2007; Gutiérrez-Zugasti et al., 2012, 2013). These studies show the use of marine molluscs as food, attested by the collection of edible species, such as the common limpet (*Patella vulgata*), the common periwinkle (*Littorina littorea*), and the mussel (*Mytilus* sp.), but also as ornaments, which is suggested by the presence of pierced flat periwinkle (*L. obtusata)* and cowrie (*Trivia* sp.) shells. Other sites, such as Altamira cave, also show evidence of shell collection for food (de las Heras et al., 2012), while Aitzbitarte III presents a few molluscs from each level (edible and ornamental). Still, they are present across the entire Gravettian sequence of the site (Álvarez-Fernández, 2011b), reflecting a continuous collection throughout the period. At other sites only a few ornamental shells have been recorded, such as at Coímbre cave (Álvarez-Fernández, 2017). Thus, data from these and other sites (Table 1) indicate a significant and stable collection of molluscs on rocky intertidal shores. Finally, the importance of molluscs for Gravettian societies is also evidenced at Fuente del Salín and Altamira caves through the use of marine shells as tools, especially for getting ocher powder likely destined to paint the exceptional rock art present in both caves (Cuenca-Solana, 2013, 2016). Overall, data from northern Iberia also suggest the occurrence of coastal adaptations (or at least a systematic use of marine resources) since the Early Upper Paleolithic.

If we talk about recovered and studied fish remains from Gravettian sites in the Cantabrian Region, few pieces of evidence are described in detail. At Aitzbitarte III, Roselló-Izquierdo and Morales-Muñiz (2011). defined the presence of Atlantic species such as the poor cod (*Trisopterus minutus,* an inhabitant of waters closes to the coast), the mackerel (*Scomber* sp., which is common in the Cantabrian Sea during the spring), the blenny (*Blenius* sp., typical from rocky areas close to the coast), and the European flounder (*Platichtys flesus*, present in sandy soils). Also, the authors documented the presence of remains from salmonids (*Salmo* sp.) and anguillids. The last two families are also recorded at La Garma A (Dr. Sónia Gabriel, Directorate-General for Cultural Heritage (DGPC), Lisboa, Portugal, com. pers.). Ongoing excavations at both sites will provide more comprehensive information about the role of fish in the human diet. At Coímbre B (Asturias), Gabriel (2017) observed the presence of two brown trout (*Salmo* cf. *trutta*) remains from the Gravettian layer Co. B.6.

Marine mammals are less frequent in the Gravettian-Solutrean record of the Cantabrian Region. Evidence corresponds to a seal (*P. hispida* or *P. vitulina*) canine from level E and a dolphin (*Tursiops truncatus*) tooth

**Table 1**
Sites presenting Gravettian layers from the Cantabrian Region with malacofauna lists. Modified from Castaños and Álvarez-Fernández (2012).

| Taxa | Gravettian Cantabrian archaeological sites | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | C.Mina | F.Salín | Pendo | Altamira | Morín | Garma A | Castillo | Bolinkoba | Amalda | Aitz. III | Alkerdi | Coímbre B |
| *P. vulgata* | + | + | + | + | + | + | + | | | + | | |
| *P. depressa* | | | | | | | | | | | | |
| *Patella* sp. | | | | | + | | | | + | + | + | |
| *L. littorea* | + | + | | + | | + | + | + | | + | | |
| *Mytilus* sp. | | | | | | + | | | | | | |
| *P. lineatus* | | | | | | + | | | | | | |
| *Ostrea* sp. | | | | | + | | | | | | | |
| *Trivia* sp. | | + | | | | + | | + | + | | | |
| *L. obtusata* | + | + | | | + | + | | + | + | + | + | + |
| *L. fabalis* | | | | | | | | | | + | | + |
| *L. saxatilis* | | | | | | + | | | | | | |
| *Littorina* sp. | | | | | | + | | + | + | + | | |
| *T. reticulata* | | | | | + | + | | | | | | |
| *N. lapillus* | | | | | | + | | + | + | | | |
| *Turritella* sp. | | | | | | | | + | | | + | |
| *L. lurida* | | | | | | | | | | | | |
| *Colus* sp. | | | | | | + | | | | | | |
| *S. saburon* | | | | | | + | | | | | | |
| Gast. Indet. | | | | | | + | | | | | | |
| *Antalis* sp. | | | | | | | | | | | + | |
| Cardiidae | | | | | + | + | | | | | | |
| Neritidae | | | | | | + | | | | | | |
| *A. islandica* | | | | | | + | | | | | | |
| Mol. Indet. | | | | | | | | | + | + | | |

from level G of La Garma (the piece exhibits a perforation probably used as an ornament; Álvarez-Fernández, 2011a), a canine tooth belonging to an undetermined seal from Altamira (Breuil and Obermaier, 1935; Álvarez-Fernández and Fernández-García, 2011), and a phalange of *P. vitulina* (Altuna and Straus, 1976) alongside two unidentified seal bones from levels 4 and 7 at La Riera (Altuna and Straus, 1976).

This study aims to provide new and relevant data on the subsistence strategies of the hunter-gatherers of the Cantabrian Region during the Gravettian. We focus, in particular, on the Fuente del Salín Cave as an example of a site between the coast and the mountains. Due to the small number of multi-taxa (large game, fish, and molluscs) and multi-proxy (taphonomy, seasonality, paleoenvironment) studies, we improve our knowledge of subsistence during the Gravettian period in this area. Additionally, this region is particularly interesting for understanding how subsistence strategies evolve and change concerning environment, landscape, and geography.

## 2. Fuente del Salín Cave

Fuente del Salín is a cave in Muñorrodero (Val de Sal Vicente) on the western edge of the Autonomous Region of Cantabria (North Iberia, Fig. 1). The site, discovered in 1985 (González-Morales and Moure-Romanillo, 2000), lies at an altitude of 15 m.a.s.l., ca. 40 m above the base of the Rucao mountain, and is situated around 20 m from the Nansa river. The cave is currently located 3 km from the open shore (Cuenca-Solana, 2013) but less than one from the inner edge of the estuary.

The cave is characterized by a lower and a middle gallery, both with circulating water, which is still active today. Since Fuente del Salín Cave is close to the Nansa River, its geological context presents several fluvial terraces. Several tributaries, located in Peña Labra and Peña Sagra mountains, are the primary source of the Nansa River.

The original entrance is blocked, and the cave is only accessible from the lower galleries (González-Morales and Moure-Romanillo, 2008). The main gallery where the archaeological deposit was found is located on the upper level of the cave, which also exhibits wall paintings (Fig. 2).

Discovered in 1985 by explorers of "Sociedad de Actividades Espeleológicas de Cantabria (SAEC)" caving group, the site includes an exceptional set of hand stencils painted in red, along with two positive ones and three others in black. These Palaeolithic representations were located close to the cave's original entrance; initial excavations developed in 1990 and 1991 confirmed the presence of a single archaeological layer of the Gravettian. The stratigraphy of the excavated section includes three sedimentary levels. Level 1 comprises three sublevels corresponding to a thin layer of dark clay (sublevel 1.1), which sealed a thin stalagmitic crust underneath (sublevel 1.2). Below sublevel 1.2 is sublevel 1.3, which is characterized by a soft and disintegrated stalagmitic fill. Under this, a virtually sterile stalagmitic package, lies a deposit (Level 2) with dark sediment (Fig. 1). This level corresponded to a large hearth, alternating layers of burnt clay and charcoal beds, abundant mammals and fish remains, and many molluscs. The presence of tools and worked bones were scarce. The excavation stopped at the base of the hearth, wherein an archeologically sterile layer (3) was encountered. The radiocarbon dates place the duration of the occupation (28,080–26,640 cal BP) in the Gravettian (González-Morales and Moure-Romanillo, 2008, Fig. 3, Table 2), in accordance following the characteristics of lithic and bone/antler industries. Seven radiocarbon dates were undertaken to provide a chronology for the Gravettian level 2 located inside the cave. Two dates were made on bone collagen, one in shell and three in charcoal recovered in the hearth. Samples were measured at Geochron laboratories, the University of Groningen, the Oxford Radiocarbon Accelerator Unit (ORAU) the Centre for Applied Isotope Studies (CAIS) at the University of Georgia (USA), and the International Chemical Analysis Inc. (ICA). (Table 2). A Bayesian age model was built for the site using OxCal4.4.2 software (Bronk Ramsey, 2009a), with the INTCAL20 calibration curve (Reimer et al., 2020).

A Delta-R of −577 ± 131 was used for calibration of marine samples. This value was calculated following the method established by Soares et al. (2016) and using the Marine20 calibration curve.

Considering the stratigraphic information of the site, the dates were modelled in a sequence model with the stratigraphic level represented a phase, with a start and end boundaries. All radiocarbon determinations were given a 5 per cent prior likelihood of being an outlier within the General t-type Outlier Model (Bronk Ramsey, 2009b), so that the model

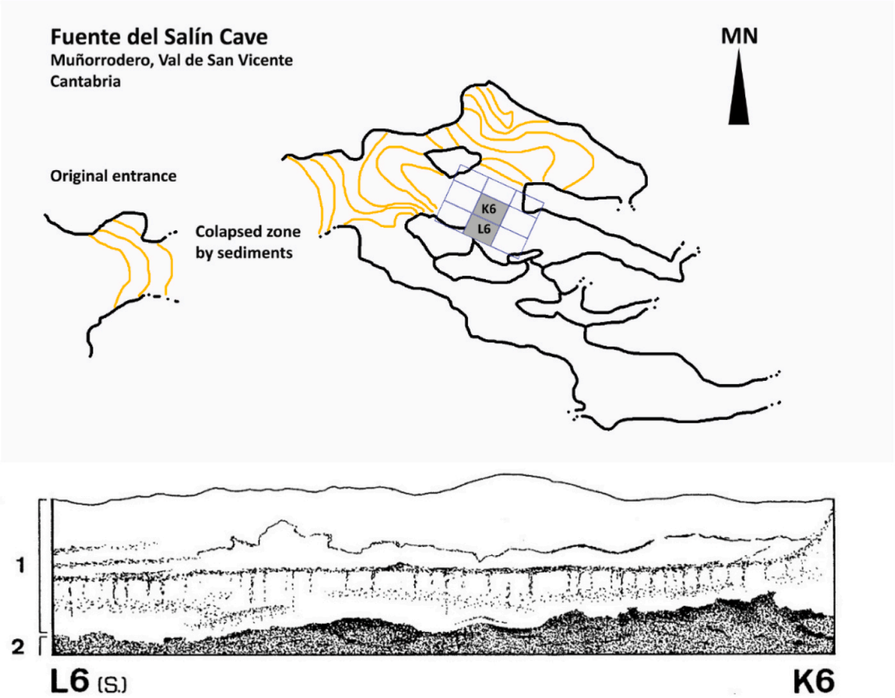

**Fig. 2.** Plan of the cave with the two excavated squares, the origin of the materials of this study in grey (K6 and L6), and the stratigraphic section below. Modified from González-Morales and Moure-Romanillo (2008).

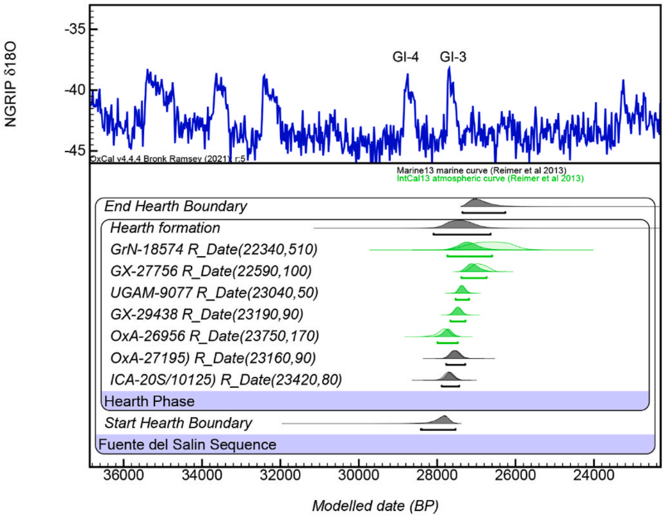

**Fig. 3.** Radiocarbon dates for the Gravettian assemblages of Fuente del Salín Cave calibrated against IntCal20 in OxCal v.4.4, assuming each sample has a 5% prior probability of being an outlier within the general t-type outlier model. Aoverall = 85. the duration phase of the hearth is between 28,080 and 26,640 cal BP.

**Table 2**
Radiocarbon dates from Fuente del Salín Cave.

| Sample area | Material | method | 14C age BP | ± | Laboratory reference |
|---|---|---|---|---|---|
| Black negative hand | Charcoal | AMS | 18,200 | 70 | GX-27757 |
| Hearth surface | Bone | ? | 23,190 | 900 | GX-29438 |
| Charcoal in the hearth | Charcoal | ? | 22,340 | 510/ 480 | GrN-18574 |
| Charcoal in the hearth | Charcoal | AMS | 22,580 | 100 | GX-27756 |
| In the hearth | Bone | ? | 23,040 | 50 | UGAMS-9077 |
| In the hearth | Shell | ? | 23,160 | 90 | OxA-27195 |

could test their reliability. Convergence was greater than 95 per cent, and the model agreement index was 87.4 per cent. The results were compared with the Greenland ice-core oxygen isotope record (NGRIP) (Andersen et al., 2006; Svensson et al., 2008), used as a global climatic record to correlate each culture with the different climatic phases.

## 3. Material and methods

This paper includes fish and macromammal remains collected during the 2016 excavation campaign from a 2 $m^2$ area (squares K6, sectors 1–9; and L6, sectors 1–9) (Fig. 2). All fish material belongs to level 2. Although excavators sometimes denoted the sublayer “2-Fondo”, all remains were analyzed together.

While investigating this material, we used a binocular EXACTA OPTECH model LFZ s/n 201030 20 W, LEICA S8 APO stereoscope, and a Dino-Lite Edge Digital Microscope.

### 3.1. *Taxonomy*

We analyzed the macromammal material following standard archaeozoological methods. Most specimens were identified to genus/species, whereas fragments with no-diagnostic attributes were assigned to body size categories.

Due to the lack of specific landmarks and high fragmentation, we grouped the taxonomically unidentifiable specimens based on their body size into five categories of mammals: size 1, smaller than rabbit/hare; size 2, small mammals weighing <20 kg (lagomorphs, rodents, and small carnivores); size 3, medium mammals between 20 and 100 kg (*C. pyrenaica*, *R. rupicapra*, *C. capreolus*, *C. lupus*); size 4, medium/large mammals between 100 and 300 kg (*C. elaphus*, Ursidae); and size 5, large mammals of >300 kg (large bovids).

We quantified the assemblage using the following indices: Number of Remains (NR), Number of Identified Specimens (Grayson, 1984; Lyman, 2008), Minimum Number of Individuals (MNI; Grayson, 1984; Lyman, 1994, 2008), Minimum Number of Skeletal Elements (MNE) and Minimum Animal Units (MAU) following Marín-Arroyo (2009).

We used the osteological comparative collection at the EvoAdapta Laboratory, University of Cantabria.

We conducted anatomical and taxonomical classifications for fish remains using the modern reference collection at the University of Tübingen and several osteological atlases (Conroy et al., 2005; Lepiksaar, 1994; Watt et al., 1997). We employed the taxonomic nomenclature from Cannon (1987) and Wheeler and Jones (2009). However, we considered indeterminate fragments in the taphonomic analysis. Some elements were indeterminate due to poor preservation. For this paper, when osteometric models to estimate the fish size was not available, it was visually estimated through direct comparison (Guillaud et al., 2017, 2020) with specimens of known length data from the modern comparative collection based at the Senckenberg Center for Human Evolution and Palaeoenvironment, University of Tübingen.

### 3.2. *Taphonomy and skeletal representation*

We examined bone surface damage in detail to determine the principal accumulation agent and/or modification (carnivores and birds of prey versus humans) and post-depositional processes. We followed Behrensmeyer (1978) and Fisher (1995) to document natural surface damages and weathering, such as flaking, cracks, and exfoliation on bones (González-Echegaray de Yarto, 2020). In addition, we recorded the presence of taphonomical signals such as chemical weathering and root etching. Other indications that we analyzed for each specimen were rodent and carnivore gnawing, epiphyseal fusion, tooth wear, burning, and butchery damage (Stiner, 1994, 2005; Stiner et al., 1995). Additionally, we had to prove that fish accumulation in Fuente del Salín Cave could be attributed to human activities before making inferences about human behavior, such as seasonality and subsistence strategies (Butler, 1990; Russ, 2010a, 2011; Hardy and Moncel, 2011; Guillaud et al., 2018, 2020; Blanco-Lapaz et al., 2021). To do so, it was necessary to consider different aspects of the fish assemblage, such as the biology of the sample (ecology, species diversity, and fish size), diversity, taphonomy (element representation, element fragmentation, bone surface modifications, digestion marks, and spatial distribution), and species seasonality to determine the principal agent responsible for the accumulation of the fish remains.

We analyzed bone surface modifications for the fish remains, such as digestion marks, compression, uniaxial mechanical deformation, and gnawing marks (Guillaud et al., 2018; Frontini et al., 2021). We identified evidence of burning using five stages of thermally-induced discoloration following Cáceres et al. (2002). These are based on heat-induced color alterations described by Shipman et al. (1984) and Stiner et al. (1995) for large mammal bones (see also Lloveras et al., 2009; Medina et al., 2012; Walker et al., 2016 for applications to microvertebrates). The stages correspond to 0 (no discoloration), 1 (yellowish with reddish-brown spots; <100 °C to 300 °C), 2 (dark brown to black; <400 °C to 550 °C), 3 (charred bone: dark black or blue over 50–100% of the surface; 500 °C to <700 °C), 4 (grey-white coloration, partial calcination; 650 °C to <950 °C), and 5 (calcined bone: white coloration over 50–100% of the surface; >700 °C).

### 3.3. *Distribution, capture areas, and seasonality*

Determining the seasonal variations in the consumed species helps us to determine an occupation period and also provide us with data on a particular type of different protein production and use. In addition, species-specific birth periods allow us to identify the duration of occupation of the site.

The birth period of each wild species is constant, so the age at which an animal was hunted provides a date of birth and, therefore, information on the occupational duration of the site.

Ungulate mortality patterns were assessed using dental eruption, wear stage, and bone fusion. For cervids, we followed Mariezkurrena (1983), Azorit et al. (2002), and Tomé and Vigne (2003). For caprids, we used Couturier (1962), Pflieger (1982), and Habermehl (1992). Once we determined the age of death, we grouped individuals into five age groups: Foetal/Neonatal; Juvenile: light wear on deciduous teeth and erupted M1; sub-Adult: moderate wear on deciduous teeth and erupted M2; Adult: all permanent teeth erupted with any wear; Old Adult or Senile: advanced wear. We estimated the ratio between juvenile and adult individuals to measure the pressure on low-return younger prey and the type of exploited prey.

Additionally, we applied a Bayesian method based on a Monte Carlo Markov Chain sampling that uses the available skeletal information to constrain the possible degrees of attrition and carcass processing strategies (Marín-Arroyo and Ocio, 2017). This method considers two parameters, alpha ($\alpha$) and beta ($\beta$), active during the assemblage formation and history. $\alpha$ informs about the transport preference based on butchering efficiency in skeletal elements, and it can take any value between $-1$ ($>$ axial contribution) and 1 ($>$ appendicular contribution). The degree of attrition ($\beta$) follows the definition established by Rogers (2000a,b), which relates the survivorship of bone elements to their maximum bone density. This method aims to overcome the problem of equifinality in skeletal profile interpretations by analyzing the two factors simultaneously (e.g., Marín-Arroyo and Ocio, 2017; R code in Marín-Arroyo et al., 2022).

For fish, to determine the possible capture areas and their proximity to the site, we analyzed the geographical distribution and habitats of the fish species based on modern and ancient reconstructions (Kettle et al., 2010; Lloris, 2015). We also compared our results with other studies based on malacofauna (species, size, and age), the reconstructions of the coastline, and the sea level near Fuente del Salín Cave during the Gravettian (Gutiérrez-Zugasti et al., 2012).

## 4. Results

### 4.1. Taxonomy of large mammalian game

A total of 2888 macrofaunal remains were identified, corresponding to 2509 unidentified remains (86.9%) and 379 classified to species/genus level (13.1%). From the classified remains, we taxonomically identified 227 (7.9%) and 152 (5,3%) to size class. Seven taxa are present in Fuente del Salín Cave assemblage, such as red deer (*C. elaphus,* NISP = 156, 68.7%), Iberian ibex (*C. pyrenaica,* NISP = 51, 22.54%), chamois (*R. rupicapra,* NISP = 9, 3.9%), horse (*E. ferus,* NISP = 5, 2.2%), roe deer (*C. capreolus,* NISP = 4, 1.7%), red fox (*V. vulpes,* NISP = 1, 0.4%), and wild cat (*Felis sylvestris,* NISP = 1, 0.4%) (Table 3).

### 4.2. Taxonomy of fish

Fig. 4 presents the identified taxa at Fuente del Salín Cave (see Table 5).

We identified 1602 fish remains, 1503 (93.8%) of which were classified as unidentified Teleostei due to their poor preservation and fragmentation level. Eleven remains (0,7%) correspond to the family Cyprinidae, most corresponding to vertebrae. The Salmonidae family (salmon and trout) is present in the assemblage, with 84 specimens (5,2%) belonging to the *Salmo* genus. Due to the fragmentary nature of the material, it was impossible to classify the remains to species level. The only species-level classification in Fuente del Salín Cave corresponds to the haddock (*Melanogrannus aeglifinus*), represented by four remains (0,2%).

Due to the poor preservation, estimating fish size was impossible. Using the modern comparative collection of the University of Tübingen, all remains belonging, for example, to *Salmo* sp. might correspond to large animals with a total length of around 60–70 cm. The Cyprinidae elements correspond to vertebrae, which cannot be attributed to genus or species level due to the high diversity and morphological similarity within this family (Roselló-Izquierdo and Morales-Muñíz, 2005).

Most elements classified as unidentified Teleostei correspond to ribs, vertebrae, and neural and branchial spine fragments showing a high fragmentation level, which makes taxonomic determination impossible.

### 4.3. Taphonomy and skeletal representation. Large game

#### 4.3.1. Anthropogenic fragmentation

A high fragmentation rate characterizes the macrofauna assemblage at Fuente del Salín Cave, since most remains are smaller than 3 cm (87.4%). Only 1.4% correspond to complete elements, usually phalanges and sesamoids. From the remains smaller than 3 cm, 21.6% corresponds to axial elements, 6% to posterior extremities, 2.9% to anterior extremities, and 3.1% to cranial elements. The abundance of less dense bones indicates a high degree of anthropogenic modification at the site. Overall, specimens exhibiting burning damage are frequent (1103 bones, 50.4%), as well as anthropic breakage for marrow extraction (14.5%). No anthropogenic marks are present on the remains of either carnivore (red fox and wild cat), possibly excluding humans as their agent of accumulation (González-Echegaray de Yarto, 2020, Table 4).

**Table 3**

Macrofaunal remains of Fuente del Salín. Number of identified specimens (NISP), remains (NR), Minimum Number of Individuals (MNI), and relative proportions (%).

| Taxa | NISP/NR | % | MNI | % | MNI | | | |
|---|---|---|---|---|---|---|---|---|
| **Ungulates** | | | | | **Infantile** | **Juvenile** | **Subadult** | **Adult** |
| Horse (*E. ferus*) | 5 | 0,2 | 1 | 10 | | 1 | | |
| Red deer (*C.elaphus*) | 156 | 5,4 | 3 | 30 | 1 | 1 | | 1 |
| Roe deer (*C. capreolus*) | 4 | 0,1 | 1 | 10 | | 1 | | |
| Iberian ibex (*C. pyrenaica*) | 51 | 1,8 | 2 | 20 | 1 | | 1 | |
| Chamois (*R. rupicapra*) | 9 | 0,3 | 1 | 10 | | | 1 | |
| **Carnivores** | | | | | | | | |
| Red fox (*V. vulpes*) | 1 | 0,0 | 1 | 10 | | 1 | | |
| Wild cat (*F. sylvestris*) | 1 | 0,0 | 1 | 10 | | | | 1 |
| Large mammal-size | 4 | 0,1 | | | | | | |
| Medium mammal-size | 122 | 4,2 | | | | | | |
| Small mammal-size | 26 | 0,9 | | | | | | |
| Unidentified | 2509 | 86,9 | | | | | | |
| **Total** | **2888** | **100** | **10** | **100** | **2** | **4** | **2** | **2** |

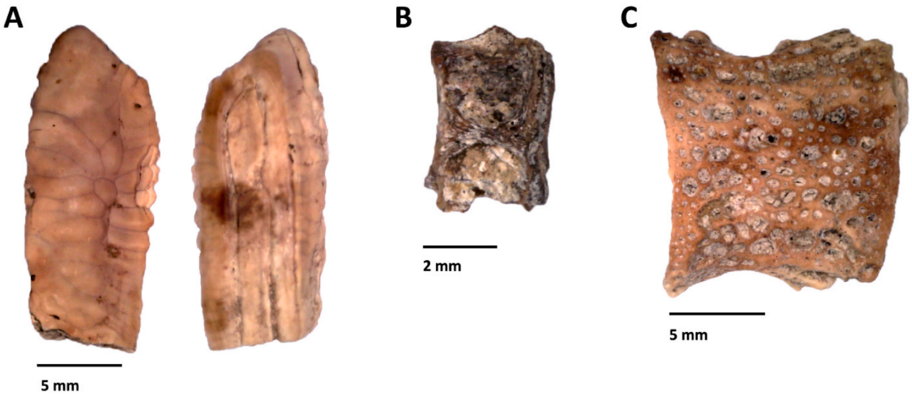

**Fig. 4.** **A.** Haddock (*M. aeglefinus*), left otolith (Salín 2016 N.399 L6 Sc.2 UE.2 Tr.1); **B.** Cyprinidae unidentified, caudal vertebra (Salín 2016 N.405 L6 Sc.1 UE.2 Tr.1); **C.** Salmonid (*Salmo* sp.), vertebra fragment (Salín 2016 N.393 K6 Sc.7 UE.2 BASE).

**Table 4**
Taphonomical modifications identified in the macrofaunal assemblage at Fuente del Salín.

| | Total | |
|---|---|---|
| | NR | % |
| Biostratinomic alterations | | |
| Fresh breakage | 320 | 14.6 |
| Cut marks | 22 | 1.0 |
| Burning | 1103 | 50.4 |
| Granwing marks | 1 | 0 |
| Rodents | | |
| Trampling | 3 | 0.1 |
| Weathering | 16 | 0.7 |
| Digestion | 1 | 0 |
| **Subtotal** | **1466** | **67.0** |
| Diagenetic alterations | | |
| Concretions | 164 | 7.5 |
| Iron oxides | 241 | 11.0 |
| Manganese | 104 | 4.8 |
| Water dissolution | 203 | 9.3 |
| Peeling | | |
| Bacteria | 9 | 0.4 |
| Root etching | | |
| **Subtotal** | **721** | **33.0** |
| **Total** | **2187** | **100** |

### 4.3.2. *Burning damage*

Most bones showing burning damage (82.5%) endured a firing temperature of between 525 °C and +940 °C (Stages 3–5), which indicates direct exposure to fire. 17.5% of bones show stages 1–2 (185°C-525 °C), indicating a non-direct exposure, probably linked to cooking activities (González-Echegaray de Yarto, 2020). Of the identifiable taxa, we observed black coloration on 79 red deer (*C. elaphus*) bones, indicating temperatures of between 525 °C and 645 °C. No burning damage is recorded on roe deer (*C. capreolus*) or horse bones (González-Echegaray de Yarto, 2020).

### 4.3.3. *Skeletal profiles*

For the most commonly identified taxa in the assemblage, the red deer (*C. elaphus*), all anatomical parts appear in different proportions. The extremities (phalanges, metapodials, and sesamoids) are most frequently represented (35.5%), followed by axial bones (23.7%), anterior (12.8%) and posterior (18.6%) long bones, and cranial elements (9%). Therefore, it shows all elements were transported, but there was a preference for those of higher nutritional value, that is, appendicular elements, especially to the detriment of crania. The Bayesian model that gives us information about transport preferences (Fig. 5) indicates a complete transport of animals to the site (α = 0.13).

All skeletal parts of the second most abundant species, the Iberian ibex (*C. pyrenaica*), are present in Fuente del Salín Cave. The extremities (phalanges, metapodials, and sesamoids) are the most represented (49%), followed by long anterior bones (19.6%), axial bones (13.7%), long posterior bones (11.8%), and cranial elements (9%). Anthropogenic marks are present on 37.2% of remains, highlighted by longitudinal fractures. A total of 14 bones show burning damage, indicating temperatures of between 525 °C and 645 °C. The bones of chamois indicate a similar pattern since 66.7% correspond to extremities and 11% to cranial elements. No axial bones are present. All roe deer (*C. capreolus*) elements correspond to extremities. Horse (*E. ferus*) also follow the previous patterns, with the extremities being most represented.

## 4.4. *Taphonomy and skeletal representation. Fish remains*

### 4.4.1. *Anthropogenic fragmentation*

Taphonomic analysis indicates no mechanical deformation, rounding, or polishing due to compression during digestion (Blanco-Lapaz et al., 2021; Frontini et al., 2021; Morales-Muñiz et al., 2021). The lack of rounded or abraded bones and surface weathering suggest water transport is an unlikely scenario for accumulation at Fuente del Salín Cave. Instead, the bones were deposited at the site and quickly covered by sediment (e.g., Rhodes et al., 2016). Gnaw, crush, and digestive marks are also absent from all fish remains, which means that carnivores or birds of prey can be ruled out (Nicholson, 1993). The lack of carnivore modifications indicates that species, such as red foxes, cats, and birds of prey, infrequently visited the cave (González-Echegaray de Yarto, 2020) and were not the agents of accumulation. This also suggests that the high degree of fragmentation in the fish assemblage corresponds to anthropogenic activity.

### 4.4.2. *Burning damage*

The burning analysis of the fish remains revealed 181 remains (11.3%) corresponding to stage 0, 1203 (75.1%) to stage 1, 154 (9.6%) to stage 2, and 54 (3.4%) to stage 3. Only 4 (0.7%) remains correspond to stage 4, and no remains show stage 5 (Table 5, Fig. 6). Based on the thermal discoloration stages, we confirm that most remains (75,1%) indicate a firing temperature between 100 and 300 °C (Stage 1). However, some bones indicate higher temperatures of no more than 700 °C (Shipman et al., 1984).

### 4.4.3. *Skeletal profiles*

The recovered fish from Fuente del Salín Cave are characterized by postcranial elements, namely vertebrae, spines, branchial spines, and ribs (NISP = 1578; 98.5%) (Table 6). Cranial bones (NISP = 24; 1.5%) are underrepresented. By taxon/group, unidentified Teleostei make up most of the sample. Vertebrae fragments (NISP = 169; 11.2%), spines (NISP = 970; 64.5%), branchial spines (NISP = 286; 19%), and ribs

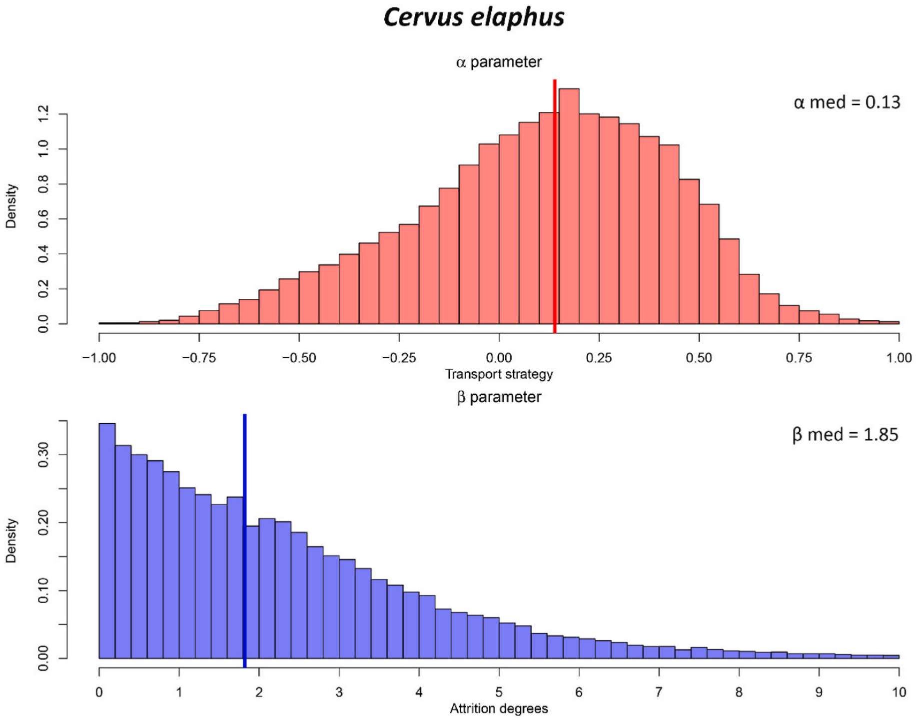

**Fig. 5.** Results of the Bayesian method to evaluate the model of transport and the degree of attrition in red deer (*C. elaphus*; α = 0.13 β = 1.83). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

**Table 5**
The number of fish remains and burning stages observed in Fuente del Salín fish remains.

| Taxa | Burning stages | | | | | Total |
|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | |
| Teleostei | 162 | 1161 | 133 | 43 | 4 | 1503 |
| *Salmo* sp. | 11 | 47 | 18 | 8 | | 84 |
| Cyprinidae | 6 | | 2 | 3 | | 11 |
| *M. aeglifinus* | 2 | 1 | 1 | | | 4 |
| **Total** | 181 (11,3%) | 1209 (75,5%) | 154 (9,6%) | 54 (3,4%) | 4 (0,2%) | **1602** |

**Fig. 6.** Burning stages observed in Fuente del Salín Cave based on salmonid remains. From stages 0–4 corresponding to Salín 2016 N.397 L6 Sc.7 UE.2 FONDO, stage 4 belongs to Salín 2016 N.399 L6 Sc.2 UE.1 Tr.1.

(NISP = 58; 3.9%) are the most common elements, representing 88.6% of the total. The most common elements belonging to *Salmo* sp. include fragments of vertebrae (NISP = 79; 94%) and just three teeth (3.6%). Vertebrae are the only elements recovered for cyprinids (NISP = 11). Vertebrae (NISP = 3) are the most common elements of the haddock (*M. aeglifinus*), although an otolith is also present (Table 6, Figs. 3 and 7).

## 5. Discussion

### 5.1. Taxonomy

The pattern of ungulate exploitation at Fuente del Salín Cave during the Gravettian shows red deer (*C. elaphus*) were the most exploited species at the site, e characteristic of coastal valleys and plains. Marín-Arroyo and Sanz-Royo (2021) observed the same, since this species is the most exploited in the Vasco-Cantabrian region during the Middle Paleolithic-Upper Paleolithic transition. In Fuente del Salín Cave, this

**Table 6**
Taxa, number and percentage of the anatomical element recovered in Fuente del Salín Cave. Ce, Cranial element; Cv, Caudal vertebra; Tv, Thoracic vertebra; Fv, Fragment of vertebra; Sp, Spine; Bs, Branchial spine; R, Rib.

| Taxa | Skeletal elements | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | Ce | Cv | Tv | Fv | Sp | Bs | R | |
| Teleostei | 20 (1,3%) | | | 169 (11,2%) | 970 (64,5%) | 286 (19%) | 58 (3,9%) | 1503 |
| *Salmo* sp. | 3 (3,6%) | | 2 (2,4%) | 79 (94%) | | | | 84 |
| Cyprinidae | | 8 (72,7%) | 3 (27,3%) | | | | | 11 |
| *M. aeglifinus* | 1 (25%) | 1 (25%) | 2 (50%) | | | | | 4 |
| **Total** | 24 (1,5%) | 9 (0,6%) | 7 (0,4%) | 248 (15,5%) | 970 (60,5%) | 286 (47,5%) | 58 (3,6%) | **1602** |

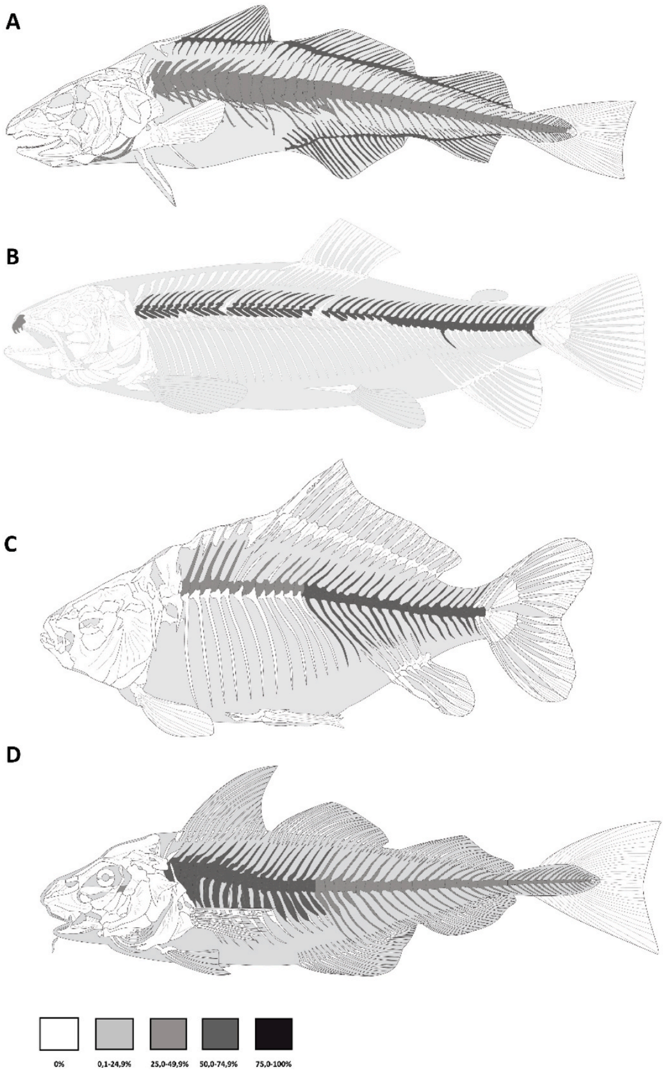

**Fig. 7.** Percentage of the skeletal element present in Fuente del Salín Cave. **A:** Cod skeleton representing the Teleostei unidentified remains, **B:** Atlantic salmon (*Salmo salar*) skeleton representing the *Salmo* sp. remains, **C:** Carp skeleton (*Cyprinus carpio*) representing the Cyprinidae remains, D: Haddock skeleton (*Melanogrannus aeglefinus*). Modified from Michel Coutureau and Philippe Béarez (collab.), 2017/ArcheoZoo.org (License CC BY NC SA 4.0 International).

species is followed by the Iberian ibex (*C. pyrenaica*) and the chamois (*R. rupicapra*), indicating the exploitation of steep, rocky landscapes. The scarcity of carnivores excludes the alternation between human and animal occupation at Fuente del Salín Cave.

During the Upper Paleolithic in the Cantabrian Region, a diversity of fish species in assemblages is generally rare, represented mostly by salmonids (*Salmo* sp.) and cyprinids (e.g., Straus, 1983; Straus and Clarck, 1986; Russ, 2010b; Roselló-Izquierdo and Morales-Muñiz, 2011; Aura-Tortosa et al., 2019; Blanco-Lapaz et al., 2021; Álvarez-Fernández et al., 2022) (Table 7). The brown trout is the most common salmonid in the Iberian Peninsula (e.g., Russ, 2010b; Aura-Tortosa et al., 2019; Blanco-Lapaz et al., 2021). However, researchers have also described the presence of the Atlantic salmon (*S. salar*) since the Middle-Upper Paleolithic (e.g., Russ, 2010b; Álvarez-Fernández et al., 2022).

In this paper, we described large-sized salmonids at Fuente del Salín Cave. Large-sized animals are more characteristic of the Atlantic salmon (*S. salar*) than the common brown trout (*S. trutta*) in the Iberian Peninsula, which rarely exceeds 60 cm and 10 kg (the maximum for the trout in Central Europe corresponds to 100 cm and around 20 kg; Consuegra et al., 2002; Doadrio et al., 2011). Although this could indicate that all Fuente del Salín Cave salmonid remains correspond to Atlantic salmon (*S. salar*), we cannot confirm this hypothesis due to the fragmentary nature of the assemblage and difficulty in distinguishing Atlantic salmon and trout.

Additionally, we describe the presence of large haddock specimens (>50 cm total length), indicating that the presence of large-sized fishes is probably due to anthropogenic activity (Morales-Muñíz and Roselló-Izquierdo, 1990; Roselló-Izquierdo and Morales-Muñíz, 2005).

### 5.2. *Taphonomy*

At Fuente del Salín Cave, archaeologists observed that the cave walls and roof were significantly damaged. This damage is located 2 m high around the large hearth and probably resulted from a significant concentration of high temperatures. The mechanical alteration of the limestone was caused by a temperature between 600 °C and 900 °C (González-Echegaray de Yarto, 2020).

In general, the burning damage on mammal bones is located primarily on axial elements and epiphyses, where the possible use of these remains as combustion material joined with wood cannot be ruled out (Yravedra et al., 2017).

Based on the mammal remains, 82.5% showed burning damage, indicating temperatures typical of carbonization or calcification with black and grey colors. Together with the high degree of fragmentation (more than 70%) and the higher burning frequency on elements rich in fat (epiphyses and axial elements), this evidence suggests bone burning would serve to increase the duration of the fire. This combination at the hearth would offer constant high temperatures either to eliminate organic elements or for use as fuel. Lastly, the alternating layers of clay and coal in the central area of the hearth, together with the location of the deposit, lead us to suggest the everyday use of firewood and bones for a repeatedly lit hearth (González-Morales and Moure-Romanillo, 2000; González-Echegaray de Yarto, 2020).

Our archaeozoological and taphonomical analyses, based on mammal bones from Layer 2 at Fuente del Salín Cave, prove the anthropogenic nature of the site. The scarcity of carnivore gnawing marks and the taphonomic alterations typical of butchery processing indicates that humans were the main accumulators at Fuente del Salín Cave, where the high degree of fragmentation and fresh breakage also indicates an intensive use by its inhabitants.

**Table 7**
Gravettian sites from the Cantabrian Region with fish remains lists. Aitz. = Aitzbitarte.

| **Taxa** | Cantabrian Region Sites | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | C. Mina | F. Salín | Pendo | Morín | Garma A | Castillo | Bolinkoba | Amalda | Aitz. III | Alkerdi | Coímbre B |
| *Teleostei* | | + | | | + | | | | + | | |
| *Blenius* sp. | | | | | | | | | + | | |
| *Scomber* sp. | | | | | | | | | + | | |
| *P. flesus* | | | | | | | | | + | | |
| *M. aeglifinus* | | + | | | | | | | | | |
| *Salmo* sp. | | + | | | + | | | | + | | |
| cf. *S. trutta* | | | | | | | | | | | + |
| *Cyprinidae* | | + | | | | | | | | | |
| *Anguillidae* | | | | | + | | | | | | |

The taphonomic analyses based on fish remains indicate an abundance of spines, branchial spines, ribs, and vertebrae fragments (NISP = 1578; 98,5%), suggesting that humans removed the spines and branchial spines for consumption. Although there is no direct evidence of fishing implements such as hooks, leisters, gorges, harpoons or fishing nets, humans likely used composite tools or fishing traps made of wood or plant fibers, which were not preserved in the cave's wet, humid conditions.

### 5.3. *Marine, estuarine, riverine and terrestrial exploitation*

The collection of molluscs for food at Fuente del Salín Cave almost exclusively includes the limpet *P. vulgata*. Oxygen stable isotope analysis indicates these limpets were collected in spring, summer, and late fall-early winter (unpublished data). The study of shell collection areas suggest that the inhabitants of the cave primarily collected the molluscs on the upper intertidal zone of sheltered shores. Although limited, the presence of sea urchins and crab remains shows that other intertidal resources were also collected for food.

During the Gravettian, the distance from Fuente del Salín Cave to the coast was between 9 and 11 km, which is within the limits of an acceptable distance for coastal resource exploitation among hunter-fisher-gatherers (Gutiérrez-Zugasti et al., 2012, 2013). However, the closer areas of the inner estuary could have also been exploited.

Ornamental species, such as *L. obtusata* and *Trivia* sp. (as well as the presence of unmodified *L. saxatilis*), reflect how shells were also used for symbolic purposes. At the same time, prior functional analysis demonstrated that *P. vulgata* were also used as tools (Cuenca-Solana et al., 2013; 2016). Therefore, shells were used for different purposes, indicating that these resources played an important role for Gravettian populations living in coastal areas.

From an environmental point of view, all mollusc species identified at the site indicate cold waters (Gutiérrez-Zugasti, 2009), which is in agreement with environmental conditions reflected by other proxies for this period. In the present study, salmonids (*Salmo* sp.) and the haddock (*M. aeglifinus*), a boreal gadid species, also confirm this finding.

Haddock (*M. aeglefinus*) is a demersal species that prefer cold waters (4–10 °C) and are located at depths between 10 and 450 m, although they live more frequently between 80 and 200 m. Several authors (e.g., Casaretto et al., 2014, 2015) observed that the spawning season of haddock occurs generally between January and June. This species is currently present in Northwest Europe with a southernmost range in the Bay of Biscay (Withehead et al., 1986). Rodrigo (1994) also reported the presence of haddock and salmonids in Nerja cave (Málaga, Southern Spain) during the LGM.

Concerning salmonids, two species are present in the Iberian Peninsula: Atlantic salmon (*S. salar*) and brown trout (*S. trutta*). Atlantic salmon (*S. salar*) reproduce in cold and well-oxygenated waters. Their entrance to the rivers occurs from October to August (Doadrio et al., 2011). In northwestern Europe, the current southernmost range of Atlantic salmon is northern Portugal. However, Kettle et al. (2010) also studied the presence of this species in southern Spain during the LGM (Nerja cave in particular), indicating that immigrant populations would have passed through the Straits of Gibraltar when temperatures in southern Spain were similar to present day northern Europe. Like the Atlantic salmon, the brown trout (*S. trutta*) also lives in cold and rapid waters. Their reproduction period is between November and January when the water temperature oscillates between 5 and 10 °C (Doadrio et al., 2011).

Cyprinids present in the assemblage would indicate an availability all year round. In general, this family is distributed in most water types (Doadrio et al., 2011), and the presence of salmonids and cyprinids would suggest exploitation of different areas in the Nansa River and, not only in fast-water portion, where salmonids are mostly present (Doadrio et al., 2011) However, we cannot conclude this hypothesis due the difficulty to identify cyprinids to species level based on their vertebrae (Roselló-Izquierdo and Morales-Muñíz, 2005).

Based on the recovered fish remains, salmonids (probably Atlantic salmon, *S. salar*) and cyprinids indicate extensive fish exploitation at Fuente del Salín Cave, since their presence in the fluvial/estuarine system occurs from fall to summer. In addition, the presence of haddock (*M. aeglifinus*) supports this pattern since their spawning season also takes place from winter to summer.

Concerning terrestrial resources, red deer (*C. elaphus*) are the most useful to estimate the period of occupation and seasonality at Fuente del Salín Cave. We observed a predominance of juvenile and infant individuals, mostly indicating a fall-winter hunting period. The first molar of an Iberian ibex (*C. pyrenaica*) also indicates a winter occupation. However, horse remains and a neonatal Iberian ibex (*C. pyrenaica*) indicate a spring component. Unfortunately, we could not determine if the cave was used by humans in a single event or over several occupations. However, the seasonality results and the hearth stratigraphy indicate a short-term occupation. Overall, in Fuente del Salín Cave, we argue that hunting was episodic, but occurred mainly during fall/winter.

Our results based on aquatic (fish and molluscs) and inland (large game) resources indicate that Gravettians exploited large mammals mainly during fall/winter and fish from fall to summer. Limpet shells of *P. vulgata* were collected in spring, summer and late fall-early winter (unpublished data). These results expand our knowledge of seasonal occupation at the site and in the Cantabrian Region during the Upper Paleolithic. Additionally, considering the short-term nature of the occupations, it is important to highlight the high diversity of prey for human subsistence in Fuente del Salín Cave.

## 6. Conclusions

Fuente del Salín Cave, located on the southwestern slope of a ridge above the spur that enters the mouth of the Nansa River, presents an excellent location for hunting, fishing, and gathering in various biotypes. The site exhibits human subsistence dominance of red deer, which was supplemented by other resources provided by the river and the coast, such as fish and molluscs.

The fish and mollusc remains located in the Gravettian layers of Fuente del Salín Cave prove that aquatic resource exploitation was a strategy within a diversified human diet during the beginning of the Upper Paleolithic. During the Gravettian, only two other sites point towards fish exploitation in the Cantabrian Region (Aitzbitarte III and La Garma A), with salmonids being most commonly recovered. Our taxonomic, palaeoecological, and taphonomic results indicate that, in Fuente del Salín Cave, humans mainly exploited two fish taxa, salmonids (*Salmo* sp.) and (much less) haddock (*M. aeglefinus*). These taxa indicate capture areas close to the coast and the river mouth, although the presence of haddock could show some fishing far from the coastline.

Red deer (*C. elaphus*) and Iberian ibex (*C. ibex*), together with limpets (*P. vulgata*), salmonids (*Salmo* sp.), cyprinids, and haddock (*M. aeglifinus*), were transported to the site whole and subsequently cooked, as indicated by frequent burning damage, which suggests indirect exposure to fire. Once consumed, their remains were abandoned in the vicinity of the habitation area, perhaps during domestic cleaning tasks.

Our results indicate that fish exploitation complemented the human diet during the summer periods, while humans exploited larger game during the spring and fall-winter periods, and molluscs in all of these seasons. Layer 2 of Fuente del Salín Cave hosts a record of short-term occupations, where humans transported mostly complete ungulate prey to the site, combined with molluscs and fish. The diversity of recovered taxa was likely stimulated by the site's proximity to various coastal and mountainous biotopes, and reflects the topographic characteristics and vegetation cover of the surrounding paleoenvironment.

Studies of fish exploitation in the Cantabrian Region during the Gravettian are limited in comparison with works related to Solutrean and Magdalenian sites, making it hard to reconstruct human fishing activities during this period. Exploring fish assemblages from other sites in the region could help to improve our knowledge of fishing strategies as part of human subsistence practices during the Upper Paleolithic in the North Iberian Peninsula.

## Author contributions

A. B-L. analyzed and studied the fish assemblage. F. G-E. and A.B. M-A. analyzed and studied the large game assemblage. I.G-Z previously analyzed the mollusc assemblage. I. G-Z, M.R. G-M., IG-Z, and A.B.M-A. provided archaeological, archaeozoological, and geological contexts. A-B-L. primarily wrote the manuscript, but all authors contributed to all sections. All authors reviewed and approved the manuscript before submission.

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## Institutional review board statement

Not applicable.

## Informed consent statement

Not applicable.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The authors do not have permission to share data.

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## Supplementary Material

References by site, region, period, species, and accumulation agent.

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| 🟦 | **Lower Paleolithic** |
| 🟧 | **Middle Paleolithic** |
| ⬜ | **Upper Paleolithic** |

**Note:** Numbers between brackets indicate the number of fish specimens

| Site | Region | Date | Species | Accumulation agent | References |
|---|---|---|---|---|---|
| Barranco León | Iberian Peninsula | Lower Paleolithic | *Luciobarbus cf. bocagei (1)*<br>*Luciobarbus cf. sclateri (10)*<br>*Squalius cf. cephalus (1)*<br>*Squalius cf. pyrenaicus (23)* | Natural? | (Doadrio and Casado, 1989; Agustí et al. 2015; Blain et al. 2016) |
| Gran Dolina | Iberian Peninsula | Lower Paleolithic<br>Middle Paleolithic | *Salmo trutta (966)*<br>*Anguilla anguilla (16)*<br>*Squalius sp. (5),* Cyprinidae (94), Salmonidae (4)<br>Teleostei (2) | Natural<br>*Bubo bubo* | (Aguirre 1995; Blanco-Lapaz et al. 2021a) |
| Sima del Elefante | Iberian Peninsula | Lower Paleolithic | *Salmo sp.*<br>*Leuciscus sp.* | Natural<br>*Haliaeetus albicilla* | (Cuenca-Bescós et al. 2015; Huguet et al. 2015) |
| Lazaret | France | Lower Paleolithic<br>Acheulean | *Salmo trutta, Anguilla anguilla,* Percidae, Gadidae Sparidae | Natural | (Desse and Granier 1976) |
| Grotte du Vallonnet | France | Lower Paleolithic | Sparidae, Labridae | Natural | (Cleyet-Merle 1990) |
| Orgnac | France | Lower Paleolithic<br>Acheulean | *Salmo trutta*<br>*Barbus sp., Salvelinus sp.* | No data | (Desse and Granier 1976; Cleyet-Merle 1990) |
| Durfort | France | Lower Paleolithic | *Salmo trutta*<br>Cyprinidae<br>*Esox lucius* | Natural | (Desse and Granier 1976) |
| Grottes du Mas de Caves | France | Lower Paleolithic<br>Middle Paleolithic | Teleostei | No data | (Cleyet-Merle 1990) |
| Bilzingsleben | Germany | Lower Paleolithic | *Phoxinus cf. phoxinus*<br>*Tinca tinca, Lota lota*<br>*Silurus glanis,* Cyprinidae<br>*Cottus cf. gobio* | Natural | (Böhme 1998) |
| Schöningen 13 II | Germany | Lower Pleistocene/Lower Paleolithic | *Esox lucius (+2000)*<br>*Albrunus alburnus (1)*<br>*Carassius carassius (88)*<br>*Gobio gobio (1)*<br>*Leucaspius delineatus (2)*<br>*Rutilus rutilus (3)*<br>*Scardinius erythrophthalmus (273), Tinca tinca (4)*<br>*Misgurnus fossilis (1)*<br>*Salmo cf. trutta (1)*<br>*Lota lota (35)*<br>*Gasterosteus aculeatus (4)*<br>*Pungitius pungitius (4)*<br>*Perca fluviatilis (2)* | Natural | (Böhme 2015) |
| Navalmaíllo Rockshelter | Iberian Peninsula | Middle Paleolithic | *Salmo trutta (10)*<br>*Cyprinidae (5)* | Natural<br>*Bubo bubo* | (Blain et al. 2022) |
| Cova dels Ermitons | Iberian Peninsula | Middle Paleolithic<br>Mousterian | *Salmo trutta fario (1)* | Not discussed | (Roselló-Izquierdo and Morales-Muñiz |

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| | | | | | 2005; Russ 2010b) |
| Cueva de Amalda | Iberian Peninsula | Middle Paleolithic | *Salmo sp. (3)* | Not discussed | (Rosello-Izquierdo and Morales-Muñiz 2005; Russ 2010b) |
| Cueva del Castillo | Iberian Peninsula | Middle Paleolithic<br>Upper Paleolithic | *Salmo sp. (22)*<br>*Anguilla anguilla (3)* | Not discussed | (Russ 2010b) |
| Sima de los Huesos | Iberian Peninsula | Middle Paleolithic | *Salmo sp.*<br>*Squalius (Leuciscus) sp.* | No discussed | (Cuenca-Bescós et al. 1997) |
| Cova Eirós | Iberian Peninsula | Middle Paleolithic | *Salmo trutta (8)*<br>Teleostei (1) | No discussed | (Rey-Rodríguez et al. 2016) |
| Arbreda cave | Iberian Peninsula | Middle Paleolithic<br>Mousterian<br>Solutrean | *Salmo sp. (11), Samo salar (4), Salmo trutta (108)*<br>*Anguilla anguilla (149)*<br>*Barbus sp. (78)*<br>*Leuciscus sp. (42)*<br>Teleostei (86)<br>*Salmo trutta (27), Rutilus sp. (4), Leuciscus sp. (5)*<br>*Barbus sp. (13)* | Human<br>Associated with artefacts<br>Only vertebrae | (Muñoz and Casadevall 1997; Roselló-Izquierdo and Morales-Muñiz 2005<br>Solutrean (Aura-Tortosa et al. 2019) |
| Tito Bustillo | Iberian Peninsula | Middle Paleolithic<br>Magdalenian | *Salmo trutta (123)*<br>*Salmo salar (1)*<br>Pleuronectidiae (1) | Human | (Morales-Muñiz 1984) - Middle Paleolithic<br>(Straus 1983b; Adán et al. 2009) - Upper Paleolithic |
| Bolomor Cave | Iberian Peninsula | Middle Paleolithic | Teleostei | Human? | (Blasco and Peris 2009) |
| Cueva Millán | Iberian Peninsula | Middle Paleolithic | *Salmo trutta fario* (194)<br>*Anguilla anguilla* (29)<br>*Chondrostoma polylepis* (51)<br>Teleostei (10) | Human | (Morales-Muñiz 1984; Roselló-Izquierdo 1992; Roselló-Izquierdo and Morales-Muñiz 2005; Guillaud et al. 2020) |
| Vanguard Cave | Iberian Peninsula | Middle Paleolithic | *Diplodus sargus/vulgaris (1)* | Unknown | (Stringer et al. 2008; Brown et al., 2011) |
| Sopeña Rockshelter | Iberian Peninsula | Middle Paleolithic<br>Upper Paleolithic | Teleostei (1) | No discussed | (Pinto-Llona et al. 2012) |
| Abri des Pêcheurs | France | Upper Paleolithic<br>Magdalenian<br>Middle Paleolithic | *Anguilla anguilla (1)*<br>*Salmo trutta (2)*<br>*Thymallus thymallus (6)*<br>Teleostei (1) | Human | (Cleyet-Merle 1990; Guillaud et al. 2021) |
| Payre | France | Middle Paleolithic | Teleostei | Human<br>Residues on lithics | (Hardy and Moncel 2011) |
| Vaufrey Cave | France | Middle Paleolithic<br>Mousterian | *Salmo salar (13), Salmo trutta (85), Anguilla anguilla (4), Thymallus thymallus (10)*<br>*Esox lucius (1), Perca fluviatilis (8), Leuciscus leuciscus, Squalius cephalus*<br>*Rutilus rutilus,* Cyprinidae (177), Teleostei (106) | No data | (Le Gall 1984; 1992b; Guillaud et al. 2021) |
| Baume Moula-Guercy | France | Middle Paleolithic | *Anguilla anguilla (209), Alosa agone (1), Phoxinus phoxinus (3), Rutilus* | Human | (Guillaud et al. 2021) |

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| | | | *rutilus (2), Squalius cephalus (2)*<br>Cyprinidae (196), *Esox lucius (13)*, *Lota lota (589)*<br>*Salmo trutta (97)*<br>*Thymallus thymallus (15)*<br>Teleostei (171) | | |
| Abri du Maras | France | Middle Paleolithic | *Squalius sp. (13),* Cyprinidae (21), *Perca fluvialitis (12)*<br>Teleostei (121) | Human | (Daujeard et al. 2019; Guillaud et al. 2021) |
| Barasses II | France | Middle Paleolithic | *Anguilla (2), Lota lota (4)*<br>*Perca fluviatilis (1), Salmo trutta (12),* Teleostei (29) | Human | (Béarez and Guillaud 2019; Guillaud et al. 2021) |
| Bauma Vallée | France | Middle Paleolithic | *Salmo trutta (20)*<br>Teleostei (4) | Human | (Guillaud et al. 2021) |
| Grotte Mandrin | France | Middle Paleolithic Mousterian | Salmonidae | No data | (Cravinho 2009) |
| Unnamed site in Sonnaz | France | Middle Paleolithic Mousterian | *Esox lucius* | No data | (Desse and Granier 1976) |
| Grottes de la Cure | France | Middle Paleolithic<br>Upper Paleolithic | Salmonidae<br>*Thymallus thymallus* | No data | (Baffier et al. 2005) |
| Erguillère-Port-Racine | France | Middle Paleolithic Mousterian | *Teleostei* | No data | (Cleyet-Merle 1990) |
| Abri Olha | France | Middle Paleolithic Mousterian | Salmonidae<br>Cyprinidae<br>*Anguilla* | No data | (Le Gall 1992b; 2000) |
| Baume de Gingy | France | Middle Paleolithic Mousterian | *Salmo trutta,* Cyprinidae<br>*Esox lucius, Thymallus thymallus, Lota lota* | No data | (Desse and Desse 1989) |
| Les Fieux | France | Middle Paleolithic Mousterian | Salmonidae, Cyprinidae<br>*Anguilla anguilla, Esox lucius* | No data | (Le Gall 1992b; 2000) |
| Gortte du Noisetier | France | Middle Paleolithic Mousterian | Salmonidae<br>Cyprinidae | No data | (Le Gall 1992b; 2000) |
| Grotte de la Carrière | France | Middle Paleolithic Mousterian | *Salmo trutta*<br>*Anguilla anguilla*<br>*Lota lota* | No data | (Desse and Granier 1976; Le Gall 1992b; 2000) |
| Caverne Marie-Jeanne | Belgium | Middle Paleolithic | *„Perch sp"*<br>*Cottus gobio (6)*<br>*Barbus sp. (1)*<br>*Lota lota (2)*<br>*Salmo trutta (4)*<br>Teleostei (81) | Human<br>Not discussed for the fish | (Gautier and Heinzelin 1980: 15; Van Neer 1997)<br>(Guillaud et al. 2021) |
| Scladina | Belgium | Middle Paleolithic | *Acipenser sturio (32)*<br>*Esox lucius (3)*<br>Teleostei (39) | Human | (Guillaud et al. 2021) |
| Walou Cave | Belgium | Middle Paleolithic | *Cottus gobio (24),* Cyprinidae (8), *Esox lucius (1)*<br>*Lota lota (41), Barbatula barbatula (28), Salmo trutta (103), Thymallus thymallus (72),* Teleostei (76) | Human | (Van Neer and Wouters 2010; Guillaud et al. 2021) |
| Castelcivita cave | Italy | Middle Paleolithic | *Anguilla anguilla*<br>*Salmo trutta*<br>*Squalius sp.* | Human | (Cassoli et al. 1997) |
| Kogelstein | Germany | Middle Paleolithic | *Thymallus thymallus (53)*<br>*Lota lota (31), Cottus gobio (5),* Salmonidae (3)<br>Teleostei 82) | No data | (Böttcher et al. 2000) |

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| Hohlenstein-Stadel | Germany | Middle Paleolithic<br>Aurignacian | *Lota lota (71)*<br>*Thymallus thymallus (90)*<br>*Cottus gobio (38),*<br>Cyprinidae (2),<br>Salmonidae (3)<br>Teleostei (95) | Human<br>Seasonality | (Blanco-Lapaz 2019; Blanco-Lapaz et al. 2021b) |
| Sesselfeslgrotte VI | Germany | Middle Paleolithic | *Acipenser sp. (8)*<br>*Esox lucius (11)*<br>*Hucho hucho (25)*<br>*Coregonus sp. (7)*<br>*Thymallus thymallus (42)*<br>*Lota lota (7)*<br>*Zingel zingel (2)*<br>*Cottus gobio (11)*<br>*Barbus barbus (5)*<br>*Chondrostoma nasus (39)*<br>*Leuciscus leuciscus (13)*<br>*Vimba vimba (1)*<br>*Barbatula barbatula (3)* | | (Bötcher 2014) |
| Höhlenruine Hunas | Germany | Middle Paleolithic | *Cottus gobio*<br>*Phoxinus phoxinus*<br>*Salmo trutta*<br>*Lota lota*<br>*Thymallus thymalllus* | No data | (Bötcher et al. 2001) |
| Figueira Brava | Portugal | Middle Paleolithic | *Alosa sp.*<br>*Sparus aurata*<br>Sparidae<br>Clupeidae<br>*Anguilla anguilla*<br>*Conger conger* | Human | (Antunes, 1991; Zilhão et al. 2020) |

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| Hohle Fels | Germany | Upper Paleolithic<br>Magdalenian<br>Gravettian<br>Aurignacian<br>Middle Paleolithic | Upper Paleolithic<br><br>*Squalius cephalus*<br>*Cobitidae*<br>*Salmonidae*<br>*Salmo trutta*<br>*Thymallus thymallus*<br>*Esox lucius*<br>*Squalius cephalus*<br>*Cottus gobio*<br>*Phoxinus sp.*<br>*Lota lota*<br>*Salvelinus sp.*<br><br>Middle Paleolithic<br><br>*Chondrostoma nasus*<br>*Thymallus thymallus*<br>*Lota lota*<br>*Squalius sp.*<br>*Cottus gobio*<br>*Esox lucius* | Human? | (Torke 1981; 1998; Hahn 2000; Hockett and Haws 2005; Smith 2007; Conard et al. 2013; Luzi et al. 2022)<br>Under study by Blanco-Lapaz |
| Gorham's Cave | Iberian Peninsula | Upper Paleolithic | *Thunnus sp. (1)*<br>*Scomber scombrus (1)* | Unkown | (Carrión et al., 2008) |
| La Riera, Asturias | Iberian Peninsula | Upper Paleolithic<br>Solutrean<br>Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>Sparidae<br>*Solea sp.* | Human<br>Mostly vertebrae<br>Associated with self-barbed harpoons | (Straus et al. 1981; González Morales 1982: 72; Clark 1983: 143-144; Straus 1983a: 52; 1983b: 101; Straus and Clark 1986; Pokines and Krupa 1997: 249; Straus 2005: |

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| | | | | | 155; Adán et al. 2009) |
| Coberizas Cave | Iberian Peninsula | Upper Paleolithic | Teleostei | Human<br>Not considered an important dietary resource, | (Clark and Cartledge 1973; González Morales 1982: 72; Clark 1983: 114-116) |
| Ambrosio Cave, Almería | Iberian Peninsula | Upper Paleolithic<br>Solutrean | *Salmo trutta (46)* | Unknown | (Aura-Tortosa et al. 2019) |
| Santa Maira Cave, Valencia | Iberian Peninsula | Solutrean | *Salmo trutta (1)*<br>*Anguila anguila (1)* | Human | (Aura-Tortosa et al. 2019) |
| Reclau Viver, Catalonia | Iberian Peninsula | Solutrean | *Salmo salar (1)*<br>*Salmo trutta (13), Rutilus sp. (1), Barbus sp. (4)* | | (Aura-Tortosa et al. 2019) |
| Davant Pau Cave, Catalonia | Iberian Peninsula | Solutrean | *Salmo salar (1)*<br>*Salmo trutta (2)* | | (Aura-Tortosa et al. 2019) |
| Cueto de la Mina, Asturias | Iberian Peninsula | Solutrean<br>Aurignacian | Teleostei<br>Salmonidae?<br>*Condrichtyies*<br>*Raja sp.* | Human<br>Associated self-barbed harpoons | (Straus 1983a: 92, 97; Rasilla Vives 1990; Pokines and Krupa 1997: 249; Rosello-Izquierdo and Morales-Muñiz 2005; Adán et al. 2009) |
| Cueto de la Mina, Asturias | Iberian Peninsula | Solutrean<br>Aurignacian | Teleostei<br>Salmonidae?<br>Condrichtyies<br>*Raja sp.* | Human<br>Associated self-barbed harpoons | (Straus 1983a: 92, 97; Rasilla Vives 1990; Pokines and Krupa 1997: 249; Rosello-Izquierdo and Morales-Muñiz 2005; Adán et al. 2009) |
| Chufín cave, Santander | Iberian Peninsula | Solutrean | Teleostei<br>Salmonidae? | Human | (Straus 1983a: 56, 97) |
| Bolinkoba | Iberian Peninsula | Upper Paleolithic<br>Lower Magdalenian | Teleostei | No data | (Utrilla 1981; Pokines and Krupa 1997: 249) |
| Praileaitz I | Iberian Peninsula | Solutrean<br>Epipaleolithic | *Salmo sp. (31)* | Human | (Morales-Muñiz 2017) |
| El Pindal | Iberian Peninsula | Upper Paleolithic | Teleostei (1) | Human | (Ávarez-Fernández et al. 2015) |
| Cuevona de Avín | Iberian Peninsula | Magdalenian | Teleostei<br>Salmonidae | No data | (Álvarez-Fernández et al. 2022) |
| La Lloseta | Iberian Peninsula | Upper Paleolithic<br>Lower Magdalenian | Teleostei | No data | (Pokines and Krupa 1997: 249; Adán et al. 2009) |
| Arangas Cave | Iberian Peninsula | Upper Paleolithic | Salmonidae (2)<br>Teleostei (4) | Human and Natural | (Álvarez-Fernández et al. 2020) |
| Alkerdi | Iberian Peninsula | Gravettian | Teleostei | Under study | (Cava et al. 2009) |
| Ekain | Iberian Peninsula | Upper Paleolithic<br>Lower Magdalenian | Teleostei | No data | (Pokines and Krupa 1997: 249) |
| El Cierro Cave | Iberian Peninsula | Upper Paleolithic | Salmonidae (5)<br>*Aguilla anguilla (1)*<br>Teleostei (5) | Human | Álvarez-Fernández et al. 2020) |
| Cueva de Nerja | Iberian Peninsula | Upper Paleolithic<br>Epipaleolithic | *Acipenser sturio (1)*<br>*Phycis sp. (1)*<br>*Belone belone (2)* | Human | (Morales-Muñiz et al. 1994; Roselló et al. |

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| | | | *Trachurus trachurus (18)*<br>*Epinephelus guaza (1)*<br>*Sparidae (65)*<br>*Dentex gibosus (1)*<br>*Diplodus vulgaris (7)*<br>*Pagellus erythrinus (89)*<br>*Pagrus pagrus (6)*<br>*Sparus aurata (9)*<br>*Labrus merula (2)*<br>*Scomber scrombrus (3)* | | 1995; Morales-Muñiz and Roselló-Izquierdo 2004) |
| Fonfría | Iberian Peninsula | Upper Paleolithic | *Solea sp.*<br>Teleostei | Human alternate accumulation agents not considered | (González Morales 1982: 72; Clark 1983: 114-116; Adán et al. 2009) |
| Bricia A | Iberian Peninsula | Upper Paleolithic | *Solea sp.*<br>Teleostei | Human alternate accumulation agents not considered | (González Morales 1982: 72; Clark 1983: 114-116) |
| Balmori | Iberian Peninsula | Upper Paleolithic Magdalenian | *Solea sp.*<br>Teleostei | Human alternate accumulation agents not considered | (Clark 1974-75; 1976; 1983: 114-116; Straus 1983b: 101; Pokines and Krupa 1997: 249; Adán et al. 2009) |
| Penicial Conchero | Iberian Peninsula | Upper Paleolithic | Teleostei | Human alternate accumulation agents not considered | (González Morales 1982: 72; Clark 1983: 114-116) |
| Arnero A | Iberian Peninsula | Upper Paleolithic | Teleostei | Human alternate accumulation agents not considered | (González Morales 1982: 72; Clark 1983: 114-116; Adán Álvarez 1997; Adán et al. 2009 |
| Sofoxo | Iberian Peninsula | Upper Paleolithic | *Salmo salar*<br>Salmonidae | Human alternate accumulation agents not considered | (Straus 1983b: 101; Adán et al. 2009: 897) |
| Altamira | Iberian Peninsula | Upper Paleolithic Magdalenian | Salmonidae<br>Pleuronectidae<br>Elasmobranchii | Human alternate accumulation agents not considered | (Breuil and Obermaier 1935; Altuna and Straus 1976; Straus 1983b: 101; Pokines and Krupa 1997: 249; Russ 2010) |
| El Juyo | Iberian Peninsula | Upper Paleolithic | Salmonidae<br>Pleuronectidae<br>*Raja sp.* | Human alternate accumulation agents not considered | (Straus 1983b: 101; Freeman et al. 1988: 13; Pokines and Krupa 1997: 243; Russ 2010) |
| Rascaño | Iberian Peninsula | Upper Paleolithic | *Salmo sp.*,<br>Pleuronectidae<br>Elasmobranchiii | Human | (González Echegaray and Barandiaran Maestu 1981: 348; Straus 1983b: 101; Pokines and |

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| | | | | | Krupa 1997: 249; Russ 2010) |
| El Otero | Iberian Peninsula | Upper Paleolithic | Teleostei (1) | Human | (Madariaga 1966; Straus 1983b: 101) |
| La Chora | Iberian Peninsula | Upper Paleolithic | Teleostei | Human | (Madariaga 1963; Straus 1983b: 101) |
| Lumentxa | Iberian Peninsula | Upper Paleolithic | Teleostei | Human | (Straus 1983b: 101) |
| Isturitz | Iberian Peninsula | Upper Paleolithic | Teleostei | Human | (Straus 1983b: 101) |
| El Valle | Iberian Peninsula | Upper Paleolithic | Teleostei | Human, not discussed | (Straus et al. 2002: 1408) |
| El Mirón | Iberian Peninsula | Upper Paleolithic | *Salmo salar*<br>*Salmo trutta* | Human, not discussed | (Straus et al. 2001; Straus et al. 2002: 1410) |
| Cueva Oscura | Iberian Peninsula | Upper Paleolithic | Salmonidae | Human | (Adán Álvarez et al. 2000; Adán et al. 2009) |
| El Buxu | Iberian Peninsula | Upper Paleolithic<br>Solutrean | *Salmo trutta*<br>*Salmo salar* | Human, not discussed | (Soto Rodríguez 1984: 804; Adán et al. 2009) |
| El Cierro | Iberian Peninsula | Upper Paleolithic | Teleostei | Human, not discussed | (Clark 1976; Adán et al. 2009) |
| La Güelga | Iberian Peninsula | Upper Paleolithic | Teleostei | Human, not discussed | (Turrero 2007; Adán et al. 2009) |
| La Lluera | Iberian Peninsula | Upper Paleolithic<br>Magdalenian | Salmonidae | Human, not discussed | (Adán et al. 2009: 896) |
| La Paloma | Iberian Peninsula | Upper Paleolithic | Teleostei | Human, not discussed | (Hernández Pacheco 1919; Adán et al. 2009) |
| Las Caldas | Iberian Peninsula | Upper Paleolithic<br>Magdalenian | Salmonidae | Human, not discussed | (Corchón et al. 1981; Adán et al. 2009 |
| Les Pedroses | Iberian Peninsula | Upper Paleolithic | Teleostei | Human, not discussed | (Clark 1976; Adán et al. 2009) |
| Los Azules | Iberian Peninsula | Upper Paleolithic | *Salmo salar*<br>Teleostei | Human, not discussed | (Fernández-Tresguerres and Rodríguez Fernández 1990; Adán et al. 2009) |
| Mazaculos | Iberian Peninsula | Upper Paleolithic | Teleostei | Human, not discussed | (González Morales 1982: 72; Adán et al. 2009) |
| La Meaza | Iberian Peninsula | Upper Paleolithic | Teleostei | Human, not discussed | (Clark 1983: 114-115) |
| Aitzbitarte III | Iberian Peninsula | Upper Paleolithic<br>Solutrean | *Salmo sp. (126)*<br>*Anguilla anguilla (19)*<br>*Trisopterus minutus (1)*<br>*Perciforme (1)*<br>*Blennius sp. (3)*<br>*Platichtys flesus (1)*<br>Teleostei (4) | Natural<br>*Lutra lutra* | (Altuna 1997; Morales- Muñiz 2009; Roselló-Izquierdo and Morales-Muñiz 2011) |
| Fuente del Salín | Iberian Peninsula | Gravettian | *Melanogrammus aeglifinus (4),* Cyprinidae (11)<br>*Salmo sp. (84)*<br>Teleostei (1503) | Human | (Blanco-Lapaz et al. 2023, for submission) |

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| La Garma A | Iberian Peninsula | Gravettian | *Salmo sp.*<br>*Anguilla anguilla* | No discussed | (Castaños and Álvarez-Fernández 2012) |
| Áridos | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Bora Gran d’en Carrera | Iberian Peninsula | Upper Paaeolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Cueva de Abauntz | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Cueva de Los Canes | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Davant Pau | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| El Cingel Vermell | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Laminak II | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Mollet I | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Recalu Viver | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Santa Catalina | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Santimamiñe | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Tossal de la Roca | Iberian Peninsula | Upper Paleolithic | Teleostei | Not discussed | (Morales-Muñiz 2009) |
| Salitre | Iberian Peninsula | Upper Paleolithic | *Salmo sp. (2)* | No data | (Russ 2010) |
| Fariseu | Iberian Peninsula | Upper Paleolihtic | *Alosa alosa*<br>*Cyprinidae* | Human | (Gabriel and Béarez 2009) |
| Le Flageolet | France | Aurignacian | *Salmo trutta*<br>*Esox lucius* | Human | (Cleyet-Merle 1990: 28) |
| Grotte du Pape | France | Upper Paleolithic | *Esox lucius* | Human | (Cleyet-Merle 1990: 28) |
| Sainte-Anastasie | France | Aurignacian | *Barbus sp.*<br>*Rutilus rutilus*<br>*Leuciscus leuciscus* | Human | (Cleyet-Merle 1990: 28) |
| Gatzarria | France | Aurignacian | Teleostei | Human<br>Perforated-adornment | (Vanhaeren and d'Errico 2006: 1109) |
| Roc de Combe | France | Aurignacian | Teleostei | Human<br>Perforated-adornment | (Vanhaeren and d'Errico 2006: 1110) |
| La Grotte des Eglises | France | Upper Paleolithic | *Salmo salar*<br>*Salmo trutta* | Human | (Delibrias and Erin 1974; Clottes et al. 1983; Straus 1983b: 101; Le Gall 1984; Cleyet-Merle 1990: 29) |
| Pont d’Ambon | France | Upper Paleolithic | *Leucsicus cephalus*<br>*Leuciscus leuciscus*<br>*Anguilla anguilla*<br>*Esox lucius*<br>Salmonidae | Human | (Le Gall 1984; Cleyet-Merle 1990; Célérier 1998: 28; Drucker and Bocherens 2004) |
| Grotte des Eyzies | France | Upper Paleolithic | *Salmo sp.*<br>*Salmo salar*<br>*Salmo trutta*<br>*Esox Lucius*<br>*Rutilus rutilus*<br>*Leuciscus sp.*<br>*Leuciscus cephalus*<br>*Leuciscus leuciscus*<br>Cyprinidae | Human?<br>Heated? | (Coulston 2000) |

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| Abri Pataud | France | Aurignacian | *Salmo salar*<br>*Salmo trutta*<br>*Anguilla anguilla*<br>*Thymallus sp.* | Human | (Cleyet-Merle 1990: 28) |
| La Baulauziére | France | Aurignacian | Teleostei | Human | (Cleyet-Merle 1990: 28) |
| Fourneau du Diable | France | Solutrean | Teleostei | Human | (Cleyet-Merle 1990: 28) |
| Badegoule | France | Solutrean | *Salmo salar*<br>Cyprinidae | Human | (Cleyet-Merle 1990: 28) |
| Liveyre | France | Solutrean | *Salmo salar* | Human | (Cleyet-Merle 1990: 28) |
| Lachaud | France | Solutrean | Cyprinidae<br>Teleostei | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Laugerie Haute | France | Proto-Magdalenian | Salmonidae<br>Teleostei | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Abri Fritisch | France | Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>*Thymallus sp.* | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Le Peyrat | France | Magdalenian | Cyprinidae<br>Salmonidae<br>*Esox lucius* | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Lachaud | France | Proto-Magdalenian | Teleostei, *Salmo salar*<br>*Salmo trutta,* Cyprinidae<br>Salmonidae | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Bois des Brousses | France | Magdalenian | *Salmo trutta, Anguilla*<br>*Thymallus sp.,Lota lota* | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Laroque | France | Magdalenian | *Salmo trutta* | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Cave of Rey | France | Upper Paleolithic | Teleostei | Human, perforated | MacCurdy 1923) |
| La Madeleine | France | Upper Paleolithic | Cyprinidae (1) | Human<br>Fishing gear in a burial | (MacCurdy 1924) |
| Abeurador | France | Upper Paleolithic<br>Epipaleolithic | *Salmo salar* | Human, not discussed | (Le Gall 1984; Cleyet-Merle 1990: 29; Muñoz and Casadevall 1997) |
| Duruthy | France | Upper Paleolithic<br>Magdalenian | *Salmo salar* | Human | (Straus 1983b: 101; Rigaud 1984; Cleyet-Merle 1990: 28-29) |
| Dufaure | France | Upper Paleolithic<br>Magdalenian | *Salmo salar*<br>*Esox lucius*<br>Salmonidae | Human | (Straus 1983b: 101; Cleyet-Merle 1990: 29) |
| Lespugue | France | Upper Paleolithic | *Teleostei* | Human<br>alternate accumulation agents not considered | (Straus 1983b: 101) |
| Gourdan | France | Upper Paleolithic | *Teleostei* | Human<br>alternate accumulation agents not considered | (Straus 1983b: 101) |
| Mas d'Azil | France | Upper Paleolithic | *Teleostei* | Human<br>alternate accumulation agents not considered | (Straus 1983b: 101) |
| Aurensan | France | Upper Paleolithic<br>Magdalenian | *Salmo salar*<br>*Leuciscus sp.* | Human<br>alternate accumulation agents not considered | (Straus 1983b: 101; Cleyet-Merle 1990: 28) |

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| Bédeilhac | France | Upper Paleolithic | Teleostei | Human alternate accumulation agents not considered | (Straus 1983b: 101) |
| Fontanet | France | Upper Paleolithic | Teleostei | Human alternate accumulation agents not considered | (Desse and Desse 1976b; Straus 1983b: 101) |
| Rhodes II | France | Upper Paleolithic | *Salmo salar*<br>*Salmo trutta* | Human alternate accumulation agents not considered | (Straus 1983b: 101; Cleyet-Merle 1990: 29) |
| La Vache | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta*<br>*Salmonidae*<br>Teleostei | Human alternate accumulation agents not considered | (Straus 1983b: 101; Cleyet-Merle 1990: 28) |
| Grotte de l'Oeil | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta*<br>*Alosa sp.* | Human alternate accumulation agents not considered | (Straus 1983b: 101; Cleyet-Merle 1990: 28) |
| Bevis | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta*<br>*Salmo salar* | Human alternate accumulation agents not considered | (Straus 1983b: 101; Le Gall 1984; Cleyet-Merle 1990: 29; Muñoz and Casadevall 1997: 114) |
| Gare de Conduché | France | Upper Paleolithic<br>Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>*Leuciscus sp.* | Human | (Cleyet-Merle 1990: 28) |
| Les Peyrugues | France | Upper Paleolithic<br>Magdalenian | Salmonidae, *Leuciscus leuciscus*, *Salmo salar*<br>*Salmo trutta,* Cyprinidae<br>*Anguilla anguilla* | Human, not discussed | (Cleyet-Merle 1990: 28-29) |
| Canecaude | France | Magdalenian | *Salmo trutta* | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Cottier | France | Magdalenian | *Salmo trutta* | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Reignac | France | Upper Paleolithic<br>Magdalenian | Salmonidae | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Saut-du-Perron | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Le Calvaire | France | Upper Paleolithic | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Espelugues | France | Upper Paleolithic<br>Magdalenian | Cyprinidae<br>Teleostei | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Grotte des Fées | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 28) |
| La Colombière | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Bruniquel | France | Upper Paleolithic<br>Magdalenian | *Salmo sp.* | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Casteljau | France | Upper Paleolithic<br>Magdalenian | Salmonidae | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Faustin | France | Upper Paleolithic<br>Magdalenian | Salmonidae<br>Cyprinidae | Human, not discussed | (Cleyet-Merle 1990: 28) |
| Couze | France | Upper Paleolithic<br>Magdalenian | *Rutilus rutilus* | Human, not discussed | (Desse and Desse 1976b; Cleyet-Merle 1990: 29) |
| Bois Ragot | France | Upper Paleolithic<br>Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>*Thymallus sp.*<br>*Leuciscus leuciscus* | Human, not discussed | (Cleyet-Merle 1990: 28) |

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| | | | *Perca fluviatilis*<br>*Anguilla anguilla* | | |
| Laroque | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Grotte de Harpons | France | Upper Paleolithic<br>Magdalenian | *Esox lucius*<br>*Leuciscus cephalus* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Limeuil | France | Upper Paleolithic<br>Magdalenian | Cyprinidae<br>*Salmo salar* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Rochereil | France | Upper Paleolithic<br>Magdalenian | *Esox lucius*<br>*Rutilus rutilus*<br>*Leuciscus cephalus* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Laugerie Basse | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Pegourie | France | Upper Paleolithic<br>Magdalenian | *Alosa sp.* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Le Courbet | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Morin | France | Upper Paleolithic<br>Magdalenian | *Esox lucius*<br>*Salmo trutta* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Rocamadour | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Fontalès | France | Upper Paleolithic<br>Magdalenian | Salmonidae | Human, not discussed | (Cleyet-Merle 1990: 29) |
| La Garenne | France | Upper Paleolithic<br>Magdalenian | *Salmo salar*<br>*Salmo trutta* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Le Peyrat | France | Upper Paleolithic<br>Magdalenian | *Rutilus rutilus, Salmo trutta*<br>*Anguilla anguilla, Leuciscus cephalus,*<br>Cyprinidae<br>Salmonidae | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Souilhac | France | Upper Paleolithic<br>Magdalenian | *Tinca tinca* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| La Tourasse | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Villepin | France | Upper Paleolithic<br>Magdalenian | Teleostei | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Rochedane | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta, Thymallus sp*<br>*Lota lota, Rutilus rutilus* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| Pierre Chatel | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta, Lota lota*<br>*Leuciscus leuciscus*<br>*Coregonus sp.* | Human, not discussed | (Cleyet-Merle 1990: 29) |
| La Grotte du Bourrouilla | France | Upper Paleolithic<br>Mesolithic | Salmonidae, *Esox lucius*<br>Cyprinidae, *Anguilla anguilla* | Human | (Chauchat et al. 1999; Le Gall 1999c) |
| La Grotte du Taillis des Coteaux | France | Upper Paleolithic<br>Magdalenian | *Thymallus thymallus (5342)*<br>*Salmo sp., Coregonus sp.*<br>Cyprinidae<br>*Anguilla anguilla* | Human and nonhuman | (Rambaud and Laroulandie 2009; Guillaud et al. 2017b) |
| Sous-Blame | France | Upper Paleolithic | *Salmo trutta, Anguilla Anguilla, Alosa alosa*<br>*Squalius cephalus*<br>*Leuciscus leuciscus* | Human, not discussed | (Le Gall 1993) |
| Chenelaz | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta*<br>*Thymallus thymallus* | Human, not discussed | (Le Gall 1999a) |
| Romains de Pierre-Chatel | France | Upper Paleolithic<br>Magdalenian | *Salmo trutta*<br>*Lota lota*<br>*Coregonus sp.*<br>*Leuciscus leuciscus* | Human, not discussed | (Le Gall 1992a; b; 1999a) |
| La Crouzade | France | Upper Paleolithic | *Salmo trutta*<br>Sparidae | No data | (Desse and Granier 1976; Cleyet-Merle 1990; Le Gall 1992b; 1999a) |
| Grotte Gazel | France | Upper Paleolithic<br>Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>Cyprinidae | No data | (Cravinho 2009) |

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| Grottes d’Abzac | France | Upper Paleolithic Magdalenian | Salmonidae | No data | (Le Gall 1992a; b) |
| Font-Brunel | France | Upper Paleolithic Magdalenian | *Salmo salar*<br>Cyprinidae | No data | (Capitan and Bouyssonie 1924; Cleyet-Merle 1990; Le Gall 1992b) |
| La Combe Saunière | France | Upper Paleolithic Solutrean | *Salmo salar*<br>Cyprinidae | No data | (Le Gall 1992b) |
| Abri Castanet | France | Upper Paleolithic Aurignacian | *Salmo salar*<br>*Salmo trutta* | No data | (Cravinho 2009) |
| Jolivet | France | Upper Paleolithic Magdalenian | Teleostei | No data | (Le Gall 1992a; b) |
| Baume du Monclus | France | Upper Paleolithic Magdalenian | Teleostei | No data | (Escalon De Fonton 1976; Le Gall 1992a; b) |
| Grotte du Salpêtre | France | Middle Paleolithic Mousterian | *Salmo trutta*<br>*Anguilla anguilla* | No data | (Le Gall 1992b) |
| Grotte de l’Esquicho-Crapaou | France | Upper Paleolithic Aurignacian | *Leuciscus leuciscus*<br>*Barbus barbus*<br>*Rutilus rutilus* | No data | (Cleyet-Merle 1990; Le Gall 1992b) |
| La Balauzière | France | Upper Paleolithic Aurignacian | *Raja sp.* | No data | (Cleyet-Merle 1990) |
| Abri du Vidon | France | Upper Paleolithic Magdalenian | Teleostei | No data | (Le Gall 1992a; b) |
| Roc de Marcamps | France | Upper Paleolithic Magdalenian | *Salmo salar, Salmo trutta* | No data | (Le Gall 1992a; b) |
| Pair-Non-Pair | France | Middle Paleolithic Mousterian | Teleostei | No data | (Le Gall 1992b) |
| Abri de Buholoup | France | Upper Paleolithic | Salmonidae, Cyprinidae<br>*Anguilla anguilla, Esox lucius* | No data | (Le Gall 1993) |
| Rond-du-Barry | France | Upper Paleolithic Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>*Esox lucius* | No data | (Le Gall 1992a; b) |
| Abri de la Vieille Eglise | France | Upper Paleolithic | *Salmo trutta* | No data | (Bintz et al. 1995) |
| Grotte abri du Moulin | France | Upper Paleolithic Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>*Esox lucius*<br>*Squalius cephalus* | No data | (Barbaza 1988; Le Gall 1993) |
| Abri-sous-roche de la Pointe du Rozel | France | Upper Paleolithic Magdalenian | Labridae | No data | (Cleyet-Merle 1990) |
| Embulla | France | Upper Paleolithic Solutrean | *Salmo trutta* | No data | (Le Gall 1999a) |
| Jean Pierre I and II | France | Upper Paleolithic Magdalenian | *Salmo salar*<br>*Salmo trutta*<br>*Lota lota* | No data | (Desse and Granier 1976; Bintz et al. 1995) |
| Grotte du Renne | France | Châtelperrronien | *Thymallus thymallus* | No data | (Baffier et al. 2005 |
| Monruz | Switzerland | Upper Paleolithic Magdalenian | *Lota lota (2)*<br>*Cf. Salvelinus alpinus (1)*<br>*Thymallus thymallus (>700)*<br>Salmonidae (1)<br>Teleostei (121) | Human | (Müller 2008) |
| Champréveyres | Switzerland | Upper Paleolithic Magdalenian | *Lota lota (78), Salmo trutta (1), Thymallus thymallus (2)*<br>Salmonidae (1), *Rutilus rutilus (1)*, Teleostei (27) | Human | (Müller 2008) |
| Néviau | Belgium | Upper Paleolithic Magdalenian | *Silurus glanis* | No data | (Giltay 1931; Van Neer 1997) |

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|---|---|---|---|---|---|
| Grotte Walou | Belgium | Upper Paleolithic<br>Aurignacian | *Thymallus thymallus (26)*<br>*Lota lota (8), Salmo trutta (4)*<br>Salmonidae (44) | Animal (small fish)<br>Human (large fish) | (Van Neer and Wouters 2007; Le Gall 2008) |
| Grotte de la Princesse | Belgium | Aurignacian | Freshwater fish | Unknown | (Gautier 1981; Van Neer 1997) |
| Bois de Laterie | Belgium | Upper Paleolithic<br>Magdalenian | *Salmo trutta fario (41)*<br>*Thymallus thymallus (3)*<br>*Lota lota (23)* | Human<br>No taphomical studies | (Van Neer 1997) |
| Trou de Chaleux | Belgium | Upper Paleolithic | *Chondrostoma nasus (1)*<br>*Cf. Leuciscus (1), Esox lucius 81), Thymallus thymallus (7)*<br>*Salmo trutta fario (5)*<br>*Lota lota (1)* | Human | (Van Neer et al. 2007) |
| Trou du Sureau | Belgium | Upper Paleolithic | Cyprinidae (3)<br>*Thymallus thymallus (37)*<br>*Salmo trutta fario (16)*<br>Salmonidae (9)<br>*Lota lota (10),* Teleostei (2) | Human | (Van Neer et al. 2007) |
| Trou du Frontal | Belgium | Upper Paleolithic | *Anguilla anguilla (3), Cf. Barbus barbus (3), Cf. Leucsiscus 83),* Cyprinidae (17), *Esox Lucius (4)*, *Thymallus thymallus (9)*<br>*Salmo salar/trutta (5)*<br>*Salmo trutta fario (9)*<br>Salmonidae (2), *Lota lota (37),* Teleostei (4) | Human | (Van Neer et al. 2007) |
| Grotta di Pozzo | Italy | Upper Paleolithic | *Salmo trutta (7048)* | Human<br>Low species diversity, spatial distribution, size, seasonality | (Mussi et al. 2004; Russ 2006; 2008; Russ et al. 2008; Russ and Jones 2009; Russ 2010) |
| Maurizio shleter | Italy | Upper Paleolithic | *Salmo trutta (1)* | Human | Radmilli 1963; Wilkens 1994; Russ 2010) |
| Ciccio Felice Cave | Italy | Upper Paleolithic | *Salmo trutta (1)* | Human | (Radmilli 1956b; Wilkens 1994; Russ 2010) |
| La Punta Cave | Italy | Upper Paleolithic | *Salmo trutta (43)* | Human | (Cremonesi 1968b; Bietti 1990: 111; Wilkens 1994; Russ 2010) |
| Ortucchio Cave | Italy | Upper Paleolithic | *Salmo trutta (743)* | Human | (Cremonesi 1968b; Bietti 1990: 111; Wilkens 1994; Russ 2010) |
| Maritza Cave | Italy | Upper Paleolithic | *Salmo trutta (51877)* | Human | Grifoni and Radmilli 1964; Bietti 1990: 111; Wilkens 1994; Russ 2010) |
| Grotta della Madonna | Italy | Upper Paleolithic | *Salmo trutta*<br>*Anguilla anguilla*<br>*Sparus aurata*<br>*(7743)* | Human<br>Large specimens only | (Durante 1978; Bietti 1990: 116; Fiore et al. 2004; Phoca-Cosmetatou |

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|---|---|---|---|---|---|
|  |  |  |  |  | 2009; Russ 2010) |
| Grotta delle Prazziche | Italy | Upper Paleolithic | Teleostei | Unknown | (Milliken 1998: 279; Russ 2010) |
| Grotta dell'Uzzo | Italy | Upper Paleolithic | Teleostei | Unknown | (Piperno et al. 1980: 279; Bietti 1990: 116; Russ 2010) |
| Barma Grance Cave | Italy | Upper Paleolithic | *Salmo salar*<br>*Salmo trutta*<br>*cf Anguilla anguilla* | Human, perforated | (De Villeneuve et al. 1906-1919; MacCurdy 1923; Cleyet-Merle 1990: 29; Mussi 2001) |
| Achille Graziani | Italy | Upper Paleolithic Final Eipgravettian | Teleostei | Human | (Radmilli 1955; 1977; Phoca-Cosmetatou 2009: 7) |
| Riparo di Biarzo | Italy | Upper Paleolithic Final Eipgravettian | Teleosei (2) | Human | (Rowley-Conwy 1996; Albertini and Tagliacozzo 2004a; Phoca-Cosmetatou 2009) |
| Riparo Cogola | Italy | Upper Paleolithic Final Eipgravettian | *Leucisucs cephalus (3)*<br>Cyprinidae *(13)*<br>*Esox lucius (2)*<br>Teleostei (78) | Carnivore/Owl Base on spatial distribution/species | (Albertini and Tagliacozzo 2004b; Phoca-Cosmetatou 2009) |
| Riparo Dalmeri | Italy | Upper Paleolithic Final Eipgravettian | *Barbus plebejus (46)*<br>*Leuciscus cephalus (64)*<br>Cyprinidae (325)<br>*Salmo trutta/marmoratus (27)*<br>*Thymallus thymallus (22)*<br>*Esox lucius (2)*<br>Teleostei (1769) | Human | (Albertini and Tagliacozzo 2004a; Phoca-Cosmetatou 2009) |
| Grotta delle Mura | Italy | Upper Paleolithic Final Eipgravettian | Teleostei | Human, not discussed | (Phoca-Cosmetatou 2009) |
| Grotta Romanelli | Italy | Upper Paleolithic Final Eipgravettian | Teleostei (496) | Human, not discussed | (Tagliacozzo 2003; Phoca-Cosmetatou 2009) |
| Riparo Slavini | Italy | Upper Paleolithic Final Eipgravettian | Teleostei | Human, not discussed | (Phoca-Cosmetatou 2009) |
| Grotta della Serratura | Italy | Upper Paleolithic Final Eipgravettian | Teleostei (346) | Human, not discussed | (Phoca-Cosmetatou 2009) |
| Riparo Soman | Italy | Upper Paleolithic Final Eipgravettian | Teleostei (7) | Human, not discussed | (Tagliacozzo and Cassoli 1994; Albertini and Tagliacozzo 2004a; Phoca-Cosmetatou 2009) |
| Pradestel | Italy | Late Glacial | Teleostei | Human, not discussed | (Albertini and Tagliacozzo 2004a) |
| Romagnano III | Italy | Late Glacial | Teleostei | Human, not discussed | (Albertini and Tagliacozzo 2004a) |
| Zigeunerfels | Germany | Upper Paleolithic | Salmonidae | No data | (Torke 1998) |

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|---|---|---|---|---|---|
|  |  | Magdalenian | *Salmo trutta*<br>*Thymallus thymallus*<br>*Hucho hucho*<br>*Esox Lucius*<br>*Cottus gobio*<br>*Lota lota*<br>*Squalius cephalus*<br>*Chondrostoma polyleps*<br>*Barbus barbus*<br>*Gymnocephalus cernuus* |  |  |
| Burghöhle | Germany | Upper Paleolithic<br>Magdalenian | Salmonidae<br>*Salmo trutta*<br>*Thymallus thymallus*<br>*Hucho hucho*<br>*Squalius cephalus*<br>*Chondrostoma polyleps*<br>*Barbus barbus*<br>*Cottus gobio*<br>*Gymnocephalus cernuus cf.*<br>*Lota lota* | No data | (Torke 1998) |
| Brillenhöhle | Germany | Late Magdalenian<br>Gravettian | Teleostei<br>Salmonidae<br>*Hucho hucho (2)*<br>*Thymallus thymallus (10)*<br>*Salvelinus alpinus (11)*<br>*Lota lota (44)* | No data | (Lepiksaar 1973; Torke 1981; 1998; Hahn 2000; Hockett and Haws 2005; Smith 2007) |
| Geißenklösterle | Germany | Upper Paleolithic<br>Magdalenian<br>Gravettian<br>Aurignacian | Salmonidae<br>*Salmo trutta*<br>*Thymallus thymallus*<br>*Hucho hucho*<br>*Esox lucius*<br>*Cottus gobio*<br>*Phoxinus sp., Lota lota*<br>*Salvelinus sp.* | No data | (Torke 1981; Hahn 1988; Torke 1998; Münzel 2001; Münzel and Conard 2004; Böhme, 2019) |
| Malerfels | Germany | Upper Paleolithic<br>Magdalenian | Salmonidae<br>*Salmo trutta*<br>*Thymallus thymallus*<br>*Hucho hucho*<br>*Esox lucius*<br>*Cottus gobio*<br>*Phoxinus sp.*<br>*Lota lota* | No data | (Torke 1998) |
| Felsställe | Germany | Upper Paleolithic<br>Magdalenian | Salmonidae<br>*Salmo trutta*<br>*Thymallus thymallus*<br>*Hucho hucho*<br>*Esox lucius*<br>*Cottus gobio*<br>*Phoxinus sp.*<br>*Lota lota* | No data | (Torke 1998) |
| Spitzbubenhöhle | Germany | Upper Paleolithic<br>Magdalenian | *Squalius cephalus,*<br>Cobitidae | No data | (Torke 1998) |
| Schmiechtal | Germany | Late Magdalenian | *Esox lucius* | No data | (Schmidt, 1912) |
| Buttentalhöhle | Germany | Upper Paleolithic<br>Magdalenian | *Squalius cephalus,*<br>Cobitidae | No data | (Torke 1998) |