





Review

An Updated Review of The Quaternary Hippopotamus Fossil Records from the Iberian Peninsula

Dário Fidalgo ^{1,*}, Joan Madurell-Malapeira ^{2,3}, Roberta Martino ^{4,5}, Luca Pandolfi ⁶ and Antonio Rosas ¹

¹ Department of Palaeobiology, Museo Nacional de Ciencias Naturales (CSIC), st/José Gutiérrez Abascal 2, 28006 Madrid, Spain; arosas@mncn.csic.es

² Earth Science Department, University of Florence, 50121 Firenze, Italy; joan.madurell@uab.cat

³ Department of Geology, Campus de la UAB, Universitat Autònoma de Barcelona, Edifici C, 08193 Cerdanyola del Vallès, Barcelona, Spain

⁴ Department of Earth Sciences, GeoBioTec, School of Science and Technology, FCT-NOVA, Campus de Caparica, Universidade NOVA de Lisboa, 2829-516 Caparica, Portugal; roberta.aska@gmail.com

⁵ Museu da Lourinhã, R. João Luís Moura, 95, 2530-158 Lourinhã, Portugal

⁶ Department of Science, University of Basilicata, viale dell'Ateneo Lucano 10, 85100 Potenza, Italy; luca.pandolfi@unibas.it

* Correspondence: dfidal01@ucm.es

Abstract: This work presents a comprehensive review of the Quaternary fossil records of hippopotamuses from the Iberian Peninsula, unveiling biogeographical insights of global significance. The results presented herein include the inference of a delayed arrival of *Hippopotamus* (*Hippopotamus antiquus*) populations onto the Iberian Peninsula compared to other European Mediterranean regions, with an estimated age of ca. 1.7 Ma, in contrast to 2.1–2.2 Ma elsewhere. Moreover, we hypothesize the possibility of a short-lived coexistence between *H. antiquus* and *Hippopotamus amphibius*, close to the extinction of the former taxon (ca. 0.45 Ma). The local extinction of all hippopotamus populations on the Iberian Peninsula between MIS 5 and 3 is suggested here, mirroring proposals made for the Italian peninsula. Notable aspects of this fossil record include the abundance of specimens, previously undocumented anatomical elements, and partially complete individuals with articulated body segments. The remains analyzed herein also present different ontogenetic stages and sexual dimorphism. Moreover, the presence of specimens displaying paleopathologies provides valuable insights into ethological and paleoecological studies. The exceptional record of at least three events of human exploitation of hippopotamus stands out, with this being a rarity in the broader context of the archaeological and paleontological record of the European continent.

Keywords: Pleistocene; Mediterranean; Spain; Portugal; biogeography; *Hippopotamus antiquus*; *Hippopotamus amphibius*



Citation: Fidalgo, D.; Madurell-Malapeira, J.; Martino, R.; Pandolfi, L.; Rosas, A. An Updated Review of The Quaternary Hippopotamus Fossil Records from the Iberian Peninsula. *Quaternary* **2024**, *7*, 4. <https://doi.org/10.3390/quat7010004>

Academic Editor: Juan Rofes

Received: 29 October 2023

Revised: 1 December 2023

Accepted: 18 December 2023

Published: 10 January 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Despite their putative restrictive environmental necessities, fossil records suggest that *Hippopotamus* inhabited continental Europe for at least 2 million years during the Quaternary period [1–3]. According to the current data, changes in the African and European ecosystems as well as in their interconnecting areas allowed the passage and the following establishment of hippopotamus populations between these zones, forming a complex phylogeographical context [4]. In order to unravel these paleobiological networks, approaches at different scales are necessary, from a global approach that interrelates existing regional data to the evaluation of specific cases that provide a geographical and chronological basis for biological information. In the case of hippopotamuses, there has been an inertia in this type of work in the last few decades. Since the end of the last century, different studies focused on hippopotamus occurrences have been carried out. These works include Stuart and Gibbard [5] for the United Kingdom, Pandolfi and Petronio [6] and Martino and

Pandolfi [2] for the Italian peninsula, Athanassiou [7] for Greece, and Martino et al. [8] for the Portuguese record.

During the Quaternary, at least two hippopotamus dispersals into continental Europe are inferred, both from taxa belonging to the genus *Hippopotamus* [9]. *Hippopotamus antiquus* is a species erected on specimens from the Upper Valdarno (Tuscany, Italy) ([2] and references therein). The first appearance datum (FAD) of *H. antiquus* can probably be traced back to the Middle–Late Villafranchian boundary, probably before 2 Ma [2,10]. Its origin is still disputed, although it seems closely related to the large African species *Hippopotamus gorgops* [11]. *H. antiquus* has a wide paleogeographic distribution range, extending from the Iberian Peninsula to Georgia and reaching the United Kingdom and the entire Italian Peninsula [2,5,8,12]. The last records of this taxon in Europe are referred to in the mid-Middle Pleistocene and are rather conflicting [8], with the taxon *Hippopotamus tiberinus* (= *H. ex gr. H. antiquus* in [13]) being considered to encompass the last forms of this lineage or it could represent a new interaction with African populations (see [4,14]).

More limited are the fossil records of *Hippopotamus amphibius*, and its dispersal towards the European continent is still poorly documented [8]. However, it is generally considered that between 0.5–0.4 Ma, specimens belonging to this species were present in Europe [15]. This chronological range would allow a presumed co-occurrence of *H. amphibius* with *H. antiquus* in areas such as the Italian peninsula [2]. Even so, the specific discrimination of most of the skeletal elements of both species is complex. Some complete skulls and postcranial material of *H. amphibius* were collected from the English locality of Barrington [16], and a skull assigned to *H. amphibius* was described from the Italian locality of Tor di Quinto [15,17]. The last recorded occurrences of this taxon go as far as MIS 5–MIS 3 in Italy [6], without a clear assessment of the conditions that led to its extinction across Europe. Probably in Greece, *H. amphibius* survived until ca 30 ka since its presence is reported from Dyrós Cave [7]. An analysis of the fossil and archaeological records of the Levantine corridor shows that the last populations of hippopotamuses persisted in this area until historical times [18].

The long paleontological and archaeological research traditions of the Iberian Peninsula have favored a rigorous method for excavation and contextualization of the fossil and archaeological records. This, together with the presence of large basins with Quaternary sedimentary deposits and areas with karstic activity [19], creates very favorable conditions to house a fossil record of great interest. A better understanding of the spatiotemporal distribution of hippopotamuses on the Iberian Peninsula is necessary to improve the paleoenvironmental interpretation of their habitats at times of coexistence with human populations and to better understand how their ecosystems changed. Under these premises, this paper compiles, re-evaluates, and provides new data on the fossil record of hippopotamuses on the Iberian Peninsula during the Quaternary. Special attention is paid to paleobiological parameters, also contextually including the relevant archaeological information.

2. Materials and Methods

In order to carry out an exhaustive update of the Iberian fossil records of hippopotamuses, a four-stage methodology was applied:

1. Compilation and consultation of all of the available bibliographies on hippopotamus fossils on the Iberian Peninsula and the sites where they have been found. The key references for each case are listed in Table S1.
2. Direct consultation with the researchers responsible for excavations on the findings. Data from this type of consultation are referenced as “pers. comm.”.
3. Review of previously published historical collections and unpublished material deposited in numerous Iberian institutions. Museo Nacional de Ciencias Naturales (MNCN), Museo Geominero (IGME), Museo Arqueológico y Paleontológico de Madrid (MAR), Museo Arqueológico Nacional (MAN), Museo de San Isidro (MSI), Catedral de Astorga, Museo de la Rinconada, Institut Català de Paleocologia Humana

i Evolució Social (IPHES), Institut Català de Paleontologia (ICP), Museu Arqueològic Comarcal de Banyoles, Museu de Ciències Naturals de Barcelona, Museu del Seminari Conciliar de Barcelona, Museu d'Arqueologia de Catalunya, Museu d'Història de València, Museo Paleontológico de Elche, Museo de Arqueología de Murcia, Museo Arqueológico de Cartagena, Museo Arqueológico y Etnológico de Granada, and Museu Geológico de Lisboa (MG).

4. Collaboration in the evaluation of new finds. Barranc de la Boella, Vallparadís Estació, Cal Guardiola, Incarcàl Complex (I, II and V), Las Jarillas, Bòbila Ordis, Barranco León D, Fuente Nueva-3, and Venta Micena.

The large volume of fossil material evaluated (either directly, bibliographically or by personal communication) cannot be described in detail in this paper. Nevertheless, in the following sections, some of the specimens and fossil assemblages with the greatest paleobiological, archaeological, or heritage value will be highlighted. In turn, the fossil assemblages are summarized in the data associated with the locality or archaeo-paleontological level of the find (Table S1). These sites and geological layers will be treated as cases for the analysis of the fossil records.

The taxonomic determinations of the hippopotamus specimens included were reviewed, accepting those determinations that are sufficiently justified and based on discriminating anatomical elements. In this work, we considered the taxonomy proposed by Petronio [9]; we therefore accepted the validity of *H. antiquus* (= *H. major*) and *H. amphibius*, and we avoided using *H. tiberinus*, *H. ex gr. antiquus*, or *H. incognitus*.

The most current geochronology and stratigraphic framework proposed for each find included has been respected. Geochronologic ages are given in thousand or million years before the present, abbreviated as “ka” or “Ma”, respectively.

3. Results

The review carried out in this work highlights the appraisal of at least forty-eight different localities or deposits with the occurrence of hippopotamuses on the Iberian Peninsula. Most of these localities are distributed parallel to the Mediterranean coast, although there are records from the center of the peninsula, the western part of the Atlantic coast, and a few specimens from the northern part of the peninsula (Figure 1).

A total of twenty-five deposits with hippopotamuses have been dated to the Early Pleistocene, while fifteen belong to the Middle Pleistocene and only two belong to the Late Pleistocene (Figure 2). Six of the cases in our dataset could not be assigned to a more precise chronology than the undifferentiated Pleistocene. The earliest record found on the Iberian Peninsula, the Mencal-9 site, is associated with a chronology of ca. 1.7 Ma (Figure 3j). On the other hand, the last records of hippopotamuses on the peninsula are ascribed to the Late Pleistocene, between MIS 5 and MIS 3, at the sites of Cueva del Toll and Sima de las Palomas de Cabezo Gordo (Figure 3k). If we focus on the taxa considered, the oldest specimens reliably determined as *H. antiquus* are found at Venta Micena (1.6–1.4 Ma), and the latest are found at Condeixa (ca. 0.45 Ma). According to the records from Solana de Zamborino and Las Jarillas, *H. amphibius* may have made its appearance in the records 0.48–0.4 Ma ago, surviving until the Late Pleistocene (Figure 2).

If we evaluate the geographic and chronological data of all hippopotamus occurrences, we can observe a wide distribution area of hippopotamuses in the Early Pleistocene that would extend from the southwest of the peninsula (Algoz) and the eastern Pyrenees (Incarcàl Complex and Bòbila Ordis) to the center–north of the peninsula (Atapuerca Complex), including the entire Mediterranean coast (Figure 1). During the Middle Pleistocene, this extension remained constant, increasing the records in the center of the peninsula and in the central part of the Atlantic coast. At the end of the Middle Pleistocene and during the Late Pleistocene, hippopotamus records were much more limited and only located on the Mediterranean coast (Figure 1).

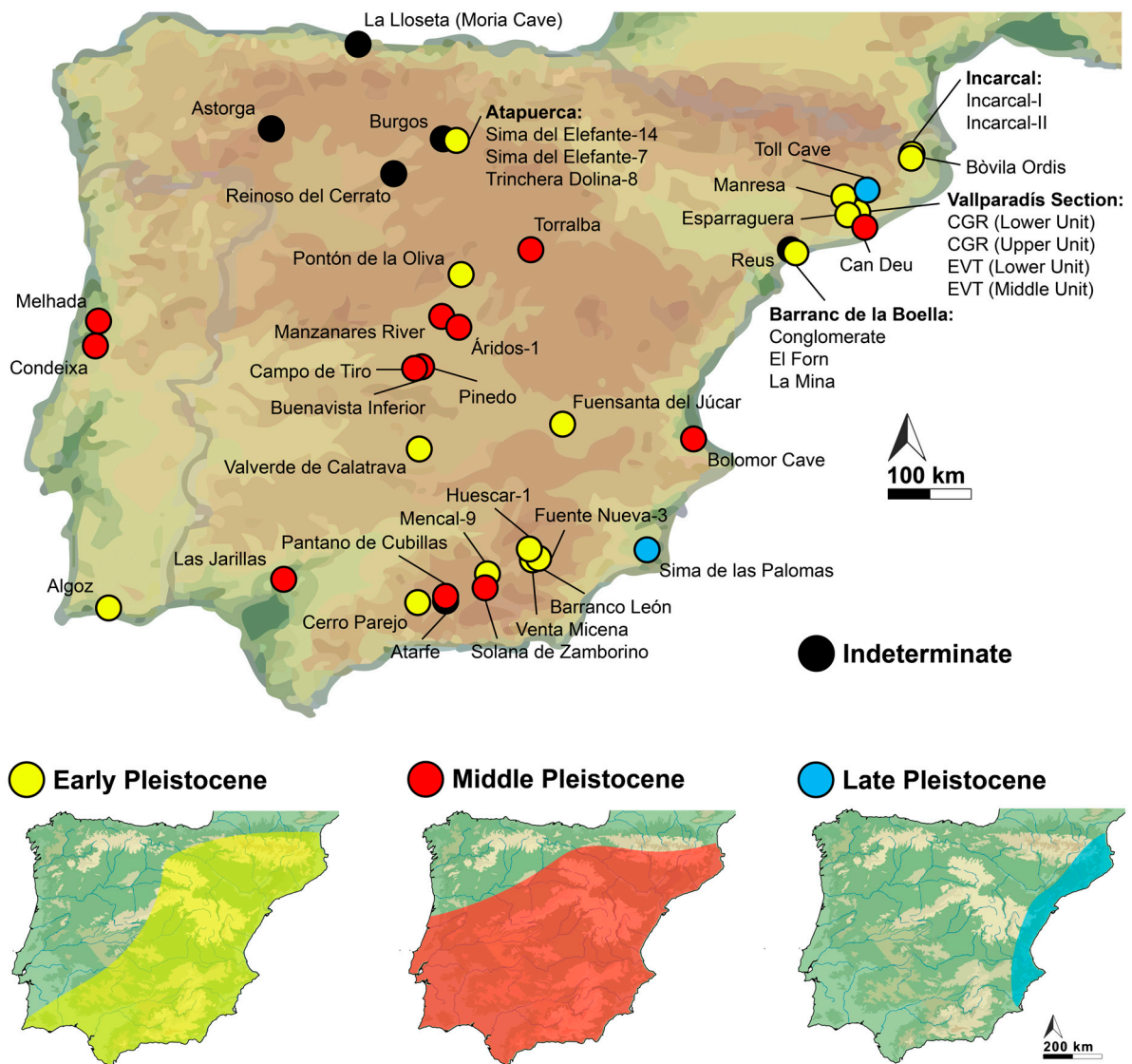


Figure 1. Schematic map of the Iberian Peninsula with the localities where *Hippopotamus* specimens have been found. In the lower part of the map, the minimum geographic distribution range that hippopotamus populations would reach in each sub-epoch according to their fossil records is highlighted.

Among the most important features of these fossil records, there is a great number of hippopotamus specimens from sites such as Vallparadís Estació, with more than 3000 fossils. The studied fossil assemblages contain several complete or partial skulls and mandibles (e.g., the Cal Guardiola Lower Unit, La Mina, Bòbila Ordis, the Vallparadís Estació Upper Unit, Incarcàl-I, or Condeixa; Figure 3a–i) and partial skeletons (e.g., the Cal Guardiola Lower Unit or Incarcàl-I; Figure 3n) including anatomical element such as the hyoid bone (e.g., Incarcàl-I), together with specimens belonging to different age classes and sexes (e.g., the Vallparadís Section; Figure 3a–d). In addition to valuable data for the autoecological analysis of the hippopotamus populations, at some sites, we found information on the biotic (plant and faunal) and abiotic context in which these populations lived (e.g., Barranc de la Boella [10]). In some of the localities, direct interaction of other organisms with hippopotamuses was detected, such as marks on the bones of exploitation by carnivores (e.g., Barranco León [20] or the Vallparadís Section [21]; Figure 3m) or cutmarks by humans (Barranco León, Fuente Nueva-3 [20], and Cueva de Bolomor [22]; Figure 3l).

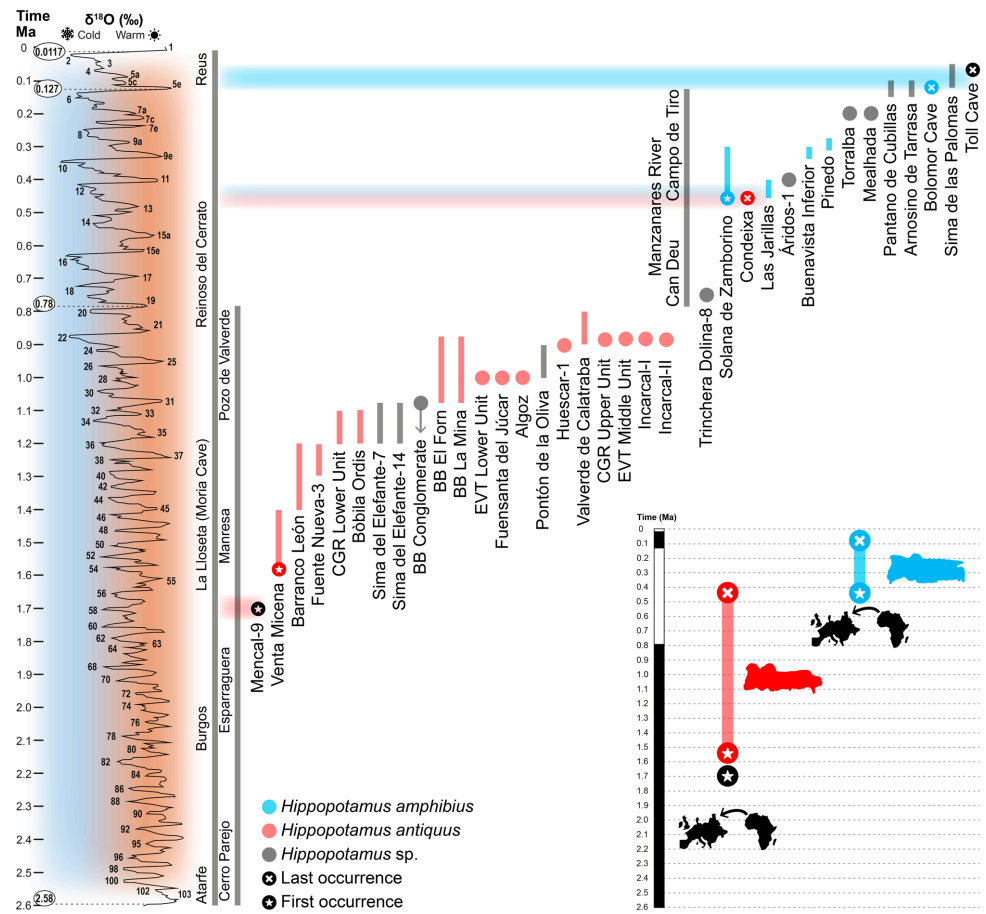


Figure 2. Chronological representation of *Hippopotamus* finds from the Iberian Peninsula and their taxonomic approximation. On the right, the estimated biochronological range of each species on the Iberian Peninsula is indicated with respect to its estimate for Europe as a whole.

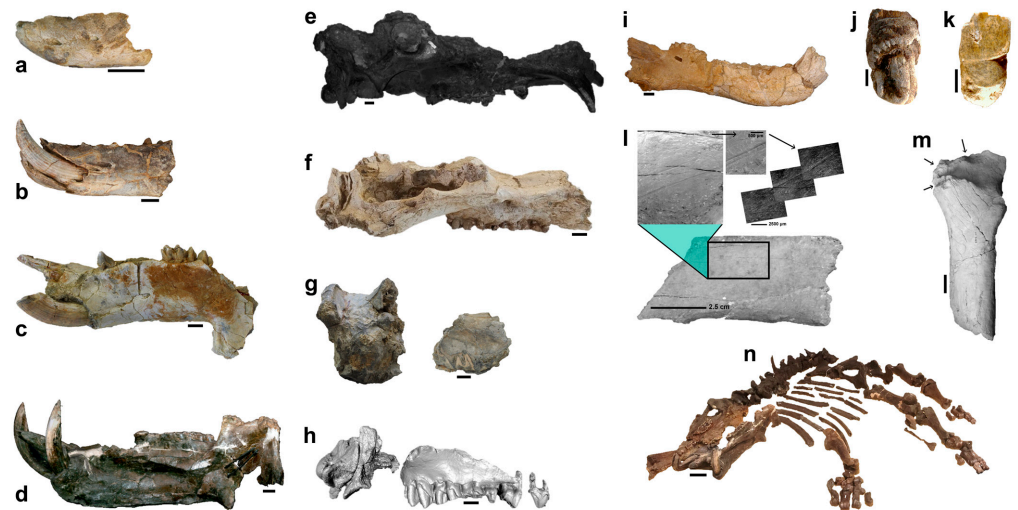


Figure 3. Some of the most outstanding finds of hippopotamuses on the Iberian Peninsula: (a–d) ontogenetic series of jaws of *Hippopotamus antiquus* from the Vallparadís Section, (a) infant jaw from Vallparadís Estació (EVT; IPS99003), (b) juvenile jaw from EVT (IPS127115), (c) young adult

jaw from EVT (IPS127243), and (d) adult jaw from Cal Guardiola (IPS14513); (e) skull of *H. antiquus* from Cal Guardiola (IPS14960); (f) skull of *H. antiquus* compressed dorso-ventrally found in the Vallparadís Estació layer EVT7 (IPS127242); (g) reconstruction of the skull of *H. antiquus* found in Bòbila Ordis; (h) reconstruction of the skull of *H. antiquus* found in Barranc de la Boella [10]; (i) mandible of *H. antiquus* found in Condeixa, assigned to the last recorded presence of the species on the Iberian Peninsula [8]; (j) fragment of a molar from Mencil-9, assigned to the oldest recorded presence of *Hippopotamus* on the Iberian Peninsula (Arribas, pers. comm.); (k) incisor fragment determined as *Hippopotamus amphibius* found in the Sima de las Palomas de Cabezo Gordo, assigned to one of the last recorded presences of hippopotamuses on the Iberian Peninsula (Walter, pers. comm.); (l) cut mark reported on a bone of *H. antiquus* at the locality of Fuente Nueva (modified from [20]); (m) femur of *H. antiquus* with marks of exploitation by hyenas found at Fuente Nueva (modified from [20]); and (n) partial skeleton of *H. antiquus* found at Cal Guardiola. Scale bar (a–i) 3 cm, (j–k) 1 cm and (n) 10 cm.

4. Discussion

4.1. Phylogenetic and Biogeographical Relationships of *Hippopotamus* of the Iberian Peninsula

Considering the data obtained, the oldest chronological record of specimens assignable to the genus *Hippopotamus* on the Iberian Peninsula was found at the Mencil-9 site. Despite the fragmentary nature of the remains found at Mencil-9 (two fragmented incisors (M9-2009-0012 and M9-2009-0059) and a fragmented molar [Figure 3j]), their taxonomic attribution to the genus *Hippopotamus* is reliable (Garrido and Arribas, pers. comm.). Chronologically, the Mencil-9 deposits have been dated to ca. 1.7 Ma by magnetostratigraphic and biochronological techniques [23] (Garrido and Arribas, pers. comm.). Some interesting specimens originally assigned to *H. antiquus* were also found in Venta Micena layers dated ca. 1.6–1.4 Ma [24]. Possibly, the remains from these two localities represent some of the earliest populations of *H. antiquus* that would have entered the Iberian Peninsula slightly later than in other Mediterranean areas: ca. 2 Ma in Greece (Elis [25]), ca. 2.2–2.1 Ma in Italy (e.g., Coste San Giacomo [26]), or ca. 2.2–2.1 Ma in France (Senèze [27]; J.M.-M. unpublished data). According to the hypothesis of van der Made et al. [14], these populations could correspond to an initial influx of African forms related to the controversial taxon *Hippopotamus kaisensis* (referred to as *H. antiquus* in Europe). Subsequently, these populations would have disappeared, leading to a period without hippopotamuses in Europe, which would have probably ended ca. 1.4 Ma ago with the arrival of populations of *Hippopotamus gorgops* (referred to as *Hippopotamus tiberinus* in Europe). However, the relatively close chronologies of the Barranco León site (ca. 1.4–1.2 Ma), where hippopotamus fossils have also been found [28], and the general scarcity of fossil sites from this time span (1.6–1.4 Ma) on the Iberian Peninsula [29] do not particularly support the previously mentioned hypothesis.

The number of hippo sites increased enormously during the so-called ‘Early-Middle Pleistocene Transition’, from the end of the Jaramillo subchron to the end of the Early Pleistocene. In this chronological timespan, *H. antiquus* populations extended from the southwesternmost tip of the peninsula (Algoz [30]) to its northeastern boundary (Incarcal Complex and Bòbila Ordis [31,32]). This increase in the fossil records of hippopotamuses is also shared in other areas of Europe, such as the Italian peninsula [2], where fossil assemblages, such as Collecorti, with more than five hundred specimens of this taxon were described by Mazza and Ventra [33]. With the transition to the Middle Pleistocene, the abundance of fossil sites with hippopotamus specimens decreased again. Indeed, Mazza [4] recognized a phenotypic trend in *H. antiquus* populations from ca. 1 Ma onwards that described as a new species *Hippopotamus tiberinus*. The validity of this taxon is disputed but a discussion on this topic is beyond the scope of this paper. However, it should be noted that van der Made et al. [34] noted a certain affinity between the specimens found in level TD8 from Gran Dolina (Atapuerca) and the specimens determined by Mazza [4] as *H. tiberinus*.

The last reliable occurrences of *H. antiquus* in Europe were recorded in the mid-Middle Pleistocene. Martino et al. [8] re-evaluated the specimens collected from Condeixa dated to ca. 0.45 Ma and confirmed their attribution to *H. antiquus*. If we consider as the earliest occurrence of *H. amphibius* in Europe the record from Tor di Quinto (most likely Cava Montanari [17]) dated ca. 0.55–0.45 Ma [15], a brief overlap of both taxa in Europe seems likely. On the Iberian Peninsula, there is no record of *H. amphibius* sufficiently informative to be sure of the chronological range of its presence. However, specimens from Solana de Zamborino (0.48–0.3 Ma [35]) and Las Jarillas (0.45–0.4 Ma [36]) have been determined as *H. amphibius*. If these determinations are confirmed, we should consider the possibility of the coexistence of *H. antiquus* and *H. amphibius* in a limited geographical area as the south and west of the Iberian Peninsula.

During the second half of the Middle Pleistocene, there are few sites where hippopotamuses are present, but unfortunately, their record is rather fragmentary. Despite this, the known finds point to the greatest geographical extension of this taxon, from the central-west (Condeixa and Melhada [8]) to the northeast (Can Deu [37]) of the peninsula. The group of fluvial terrace sites on the central and southern peninsula also highlight a constant presence of *H. cf. amphibius* populations until the end of the Middle Pleistocene (Áridos-1 [38], Campo de Tiro [39], Buenavista Inferior [39], or Las Jarillas [36]). A record with a slightly higher abundance of this taxon was found at the end of the Middle Pleistocene (MIS 5e) in the Bolomor Cave site [40] (Fernández Peris and Blasco, pers. comm.), although a detailed paleobiological study of these materials has not yet been carried out. These time periods coincide with those proposed for the findings of the largest accumulation of *H. amphibius* specimens at the Barrington locality (UK, ca. 0.13–0.115 Ma [16]). Faure [41], based on the English specimens, erected the disputed taxon *Hippopotamus incognitus*, listed as invalid by Petronio [9].

The local extinction of *H. amphibius* is poorly recorded on the Iberian Peninsula. The most recent findings of this taxon point to its last occurrences around MIS 4. Even so, these findings present a very limited stratigraphic and chronological contextualization. The specimens cited by Donner and Kurtén [42] at the Toll Cave site, and dated to MIS 4, have not been located in subsequent revisions (Blasco, pers. comm.). On the other hand, the specimen cited at the Sima de las Palomas de Cabezo Gordo site was found thirty years ago in the Upper Cuttin, without any stratigraphic context (Walker, pers. comm.). Estimation of the original stratigraphic position of the specimen has allowed us to assess a chronological range for its deposition between MIS 5 and MIS 3 [43]. These last local presences' chronologies also approximate the timing of the extinction of *H. amphibius* populations across Europe. Although specimens from the Italian site of Grotta Romanelli dated to MIS 3 were considered the last occurrence of hippopotamuses in continental Europe by Martino and Pandolfi [2], recently, Pieruccini et al. [44] re-dated the IUS3 to MIS 5e.

4.2. Paleoeological Considerations

Although the niche parameters of *H. antiquus* are still under discussion [10,45,46], the need for permanent bodies of water for its survival [47] and the presence of more or less open areas with grasslands [46] seem a clear requirement. Although these inferences are not very precise, they provide information on the minimum climatic parameters for its arrival in Europe and, specifically, for its dispersal across the Iberian Peninsula. The extension of the distribution area from Africa to the Iberian Peninsula in the middle of the Early Pleistocene raises two possible scenarios: (1) the presence of sufficient water bodies and an orographically traversable terrain for its passage through the Levantine corridor and the crossing of the entire European continent or (2) the reconsideration of a possible aquatic entry from North Africa through the western Mediterranean.

Once the populations of *H. antiquus* were established on the Iberian Peninsula, a continuous period of more than one million years of presence in this area was observed. The stability of these populations on a large part of the peninsula is surprising, as climatic

conditions were progressively becoming harsher. These changes, known as the ‘*Early-Middle Pleistocene Transition*’, were characterized by a gradual increase in the severity and duration of glacial cycles, along with an increase in seasonality and aridity [48,49]. Equally surprising is the possibility of a very brief coexistence of *H. antiquus* and *H. amphibius* in a restricted geographical area in the mid-Middle Pleistocene. This phenomenon has been previously proposed for the Italian peninsula as well [2]. More information on the niche differences between the two hippopotamuses is needed to assess the possible role of *H. amphibius* in the extinction of *H. antiquus*. The same can be said regarding the environmental conditions that may have led to a shift from the European to the extant hippopotamus, as it has been hypothesized that both taxa had the same dietary and climatic constraints.

The Middle Pleistocene is characterized by the presence of rapid cyclicity between glacial and interglacial intervals [50]. The arrival into the Northern Hemisphere of *H. amphibius*, classically associated with warm and wet conditions, is remarkable [47]. Even more surprising is its persistence in Europe until the Late Pleistocene, with an apparent continuous record on both the Italian peninsula [2] and the Iberian Peninsula. As has already been proposed for other taxa (e.g., [51,52]; among others), the population mobility dynamics of hippopotamuses during the Middle Pleistocene could correspond to a push-pull mechanism, lingering in glacial intervals in these warmer peninsulas and dispersing to more northern areas during interglacial intervals (e.g., UK [5,16,47]). However, a better understanding of the Central European and British records is crucial for the evaluation of these biogeographical hypotheses. Similarly, a detailed study of the state of health of the last well-recorded populations of *H. amphibius* in Europe (e.g., Barrington [16] or Bolomor [22]) would allow us to refine the causes of the continent-wide disappearance of a group of mammals that inhabited this area for more than two million years.

In particular, the Iberian Quaternary hippopotamus records offer exceptional specimens and fossil assemblages of great importance in paleobiological studies. Localities such as Incarcas-I (ca. 0.86 Ma; MIS21 [31,53]) have anatomical elements with an extremely limited representation in fossil records. In the same locality, together with the Vallparadís Section fossil assemblage (1.2–0.86 Ma; [21,54,55]), partially complete individuals have been excavated, with most of their anatomical elements articulated (Figure 3n). At the same time, at these sites, we found individuals characterized by different ontogenetic stages and belonging to both sexes (Figure 3a–d). Another highlight of this fossil record is the presence of different skeletal pathologies (e.g., dental enamel hypoplasias, malocclusion, stress deformities, or joint problems) that are being studied in a global bioclimatic context [49].

Most of the fossil assemblages with hippopotamus presence on the Iberian Peninsula are the result of interspecific interactions (e.g., accumulation by carnivores [56]) or show evidence of this type of event (e.g., feeding by hyenas [21,57]; Figure 3m). The peculiar hippopotamus lifestyle brings a particular value to the characterization of interspecific relationships, allowing us to infer the behavior of carnivores around water bodies. In contrast, there is very little evidence of human exploitation of hippopotamuses across the European continent [58] (Figure 3l). Of this scarce evidence, only one reference is outside the Iberian Peninsula, in the Greek locality of Marathousa [58]. In particular, a limited number of cut marks identified on specimens from the sites of Barranco León [59] and Fuente Nueva-3 [20] allow us to propose human access to hippopotamus carcasses in the Early Pleistocene. More evident seems to be the accumulation of hippopotamus remains in the locality of Bolomor Cave at the end of the Middle Pleistocene [22]. Further elaboration on this topic is beyond the scope of this paper and will be dealt with in more detail in future works.

5. Conclusions

The review and detailed study of the Quaternary fossil record of hippopotamuses from the Iberian Peninsula has allowed us to highlight several biogeographical data of global importance: (a) we infer the arrival of *Hippopotamus antiquus* populations to the Iberian Peninsula later than to the rest of the European Mediterranean areas (ca. 1.7 Ma vs. 2.1–2.2 Ma);

(b) the possibility of a brief coexistence between *H. antiquus* and *Hippopotamus amphibius* on the peninsula in chronologies close to the extinction of the populations of the former taxon (ca. 0.45 Ma); and (c) the idea of a local extinction of all hippopotamus populations in this area between MIS 5 and MIS 3 is considered, mostly coinciding with the proposals published for the Italic peninsula. The biogeographical proposals considered have been evaluated in a paleoecological and paleoclimatic context, opening the possibility of new paleoenvironmental reconstructions.

Together with these data, the potential of the Iberian record for the progress of paleozoological and paleoecological studies of the European Quaternary, including aspects related to human evolution, has been highlighted: (a) the abundance of records, the presence of poorly-known anatomical elements and the occurrence of partially complete individuals displaying articulated body segments; (b) a good representation of intraspecific diversity, with individuals of different ontogenetic stages and assignable to both sexes; (c) the existence of specimens with paleopathologies particularly relevant for paleoecological reconstructions; (d) the exceptional presence of at least three events of hippopotamus exploitation by humans, scarcely documented on the whole European continent.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/quat7010004/s1>, Table S1: Quaternary hippopotamus fossil record from the Iberian Peninsula. References [60–85] are cited in the Supplementary Materials

Author Contributions: Conceptualization, D.F.; methodology, D.F. and J.M.-M.; software, D.F.; validation, D.F., J.M.-M., R.M. and L.P.; formal analysis, D.F.; investigation, D.F. and R.M.; resources, D.F., J.M.-M. and R.M.; data curation, D.F.; writing—original draft preparation, D.F.; writing—review and editing, D.F., J.M.-M., R.M., L.P. and A.R.; visualization, D.F.; supervision, J.M.-M., L.P. and A.R.; project administration, D.F.; funding acquisition, D.F., J.M.-M., R.M. and A.R. All authors have read and agreed to the published version of the manuscript.

Funding: The research activity of D.F. and A.R. was funded by Ministerio de Ciencia e Innovación, PID2021-122356NB-I00. D.F. was supported by the Ayuda del Programa de Formación de Profesorado Universitario (FPU20/03389) and is a Ph.D. student at the Programade Doctorado en Biología at the Universidad Complutense de Madrid. R.M. benefited from a GeoBioTec NOVA grant UIDB/04035/2020 and a Ph.D. fellowship 2021.08458.BD provided by the Fundação para a Ciência e Tecnologia.

Data Availability Statement: All data included in this paper are available in the Supplementary Materials.

Acknowledgments: We would especially like to thank the editors and the three anonymous reviewers for their helpful comments, which significantly improved this paper. We would also like to thank all of the curators of the assessed collections included in this review for facilitating the work of collecting information and consulting the specimens: Susana Fraile (Museo Nacional de Ciencias Naturales), Silvia Menéndez (Museo Geominero (IGME)), Cesar Laplana (Museo Arqueológico y Paleontológico de la Comunidad de Madrid), Eduardo Galán (Museo Arqueológico Nacional), Alberto González (Museo de San Isidro), personal del Museo de la Catedral de Astorga, personal del Museo de la Rinconada, Núria Ibáñez (Institut Català de Paleoeologia Humana i Evolució Social), Josep M. Robles (Institut Català de Paleontologia), Andrea Ferrer (Museu Arqueològic Comarcal de Banyoles), Isidro Toro and Bienvenido Martínez-Navarro (Museo Arqueológico y Etnológico de Granada), and José Antonio Moita and Ruben Dias (Museu Geológico de Lisboa). Likewise, this work would not have been possible without the information provided by the researchers who dedicated personal communications to us: Guiomar Garrido (Universidad Internacional de la Rioja), Alfonso Arribas (Instituto Geológico y Minero de España), Ruth Blasco (Institut Català de Paleoeologia Humana i Evolució Social), Josep Fernández Peris (Museu de Prehistòria de València), and Michael Walker (Universidad de Murcia).

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Fidalgo, D.; Galli, E.; Madurell-Malapeira, J.; Rosas, A. Earliest Pleistocene European hippos: A review. *Comun. Geol.* **2021**, *108*, 69–73.
2. Martino, R.; Pandolfi, L. The Quaternary Hippopotamus records from Italy. *Hist. Biol.* **2022**, *34*, 1146–1156. [[CrossRef](#)]
3. Iannucci, A.; Mecozzi, B.; Sardella, R. Beware of the “Wolf event”—Remarks on large mammal dispersals in Europe and the late Villafranchian faunal turnover. *Alp. Mediterr. Quat.* **2023**, *36*, 75–90.
4. Mazza, P. Interrelations between pleistocene hippopotami of Europe and Africa. *Bollet. Soc. Paleont. Ital.* **1991**, *30*, 153–186.
5. Stuart, A.J.; Gibbard, P.L. Pleistocene occurrence of *Hippopotamus* in Britain. *Quartärpaläontologie* **1986**, *6*, 209–218.
6. Pandolfi, L.; Petronio, C. A brief review of the occurrences of Pleistocene *Hippopotamus* (Mammalia, Hippopotamidae) in Italy. *Geol. Croat.* **2015**, *68*, 313–319. [[CrossRef](#)]
7. Athanassiou, A. The fossil record of continental hippopotamids (Mammalia: Artiodactyla: Hippopotamidae) in Greece. In *Fossil Vertebrates of Greece Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics*; Vlachos, E., Ed.; Springer: Cham Switzerland, 2022; pp. 281–299.
8. Martino, R.; Ríos, M.I.; Mateus, O.; Pandolfi, L. Taxonomy, chronology, and dispersal patterns of Western European Quaternary hippopotamuses: New insight from Portuguese fossil material. *Quat. Int.* **2023**, *674–675*, 121–137. [[CrossRef](#)]
9. Petronio, C. Note on the taxonomy of Pleistocene hippopotamuses. *Ibex* **1995**, *3*, 53–55.
10. Fidalgo, D.; Rosas, A.; Madurell-Malapeira, J.; Pineda, A.; Huguet, R.; García-Taberner, A.; Cáceres, I.; Ollé, A.; Vallverdú, J.; Saladie, P. A review on the Pleistocene occurrences and palaeobiology of *Hippopotamus antiquus* based on the record from the Barranc de la Boella Section (Francolí Basin, NE Iberia). *Quat. Sci. Rev.* **2023**, *307*, 108034. [[CrossRef](#)]
11. Mazza, P. New evidence on the Pleistocene hippopotamuses of western Europe. *Geol. Rom.* **1995**, *31*, 61–241.
12. Vekua, A.K. The lower Pleistocene mammalian fauna of Ahkalkalaki (southern Georgia, USSR). *Palaeontogr. Ital.* **1986**, *74*, 63–96.
13. Mazza, P.; Bertini, A. Were Pleistocene hippopotamuses exposed to climate driven body size changes? *Boreas* **2013**, *42*, 194–209. [[CrossRef](#)]
14. van der Made, J.; Sahnouni, M.; Boulaghrayef, K. *Hippopotamus gorgops* from El Kherba (Algeria) and the Context of its Biogeography. In Proceedings of the II MAP, Burgos, Spain, 15–16 April 2015; pp. 135–169.
15. Caloi, L.; Palombo, M.R.; Petronio, C. Resti cranici di *Hippopotamus antiquus* (= *H. major*) e *Hippopotamus amphibius* conservati nel Museo di Paleontologia dell’Università di Roma. *Geol. Rom.* **1980**, *19*, 91–119.
16. Reynolds, S.H. A Monograph on the British Pleistocene Mammalia VOL. III, Part I. Hippopotamus. Pages 1–38; plates I–VI. *Monogr. Palaeontogr. Soc.* **1922**, *74*, 1–38. [[CrossRef](#)]
17. Mecozzi, B.; Iannucci, A.; Mancini, M.; Tentori, D.; Cavasinni, C.; Conti, J.; Yuri Messina, M.; Sarra, A.; Sardella, R. Reinforcing the idea of an early dispersal of *Hippopotamus amphibius* in Europe: Restoration and multidisciplinary study of the skull from the Middle Pleistocene of Cava Montanari (Rome, central Italy). *PLoS ONE* **2023**, *18*, e0293405. [[CrossRef](#)] [[PubMed](#)]
18. Bytinski-Salz, H. Recent findings of *Hippopotamus* in Israel. *Isr. J. Zool.* **1965**, *14*, 38–48.
19. Silva, P.G.; Bardají, T.; Roquero García-Casal, E.; Baena Preysler, J.; Cearreta, A.; Rodríguez Pascua, M.A.; Rosas, A.; Zazo, C.; Goy, J.L. El periodo cuaternario: La historia geológica de la Prehistoria. *Cuat. Geomorf.* **2017**, *31*, 113–154.
20. Espigares, M.P. Análisis y Modelización del Contexto Sedimentario y los Atributos Tafonómicos de los Yacimientos Pleistocénicos del Borde Nororiental de la Cuenca de Guadix-Baza. Ph.D. Thesis, Universidad de Granada, Granada, Spain, 2010.
21. Madurell-Malapeira, J.; Alba, D.M.; Espigares, M.P.; Vinuesa, V.; Palmqvist, P.; Martínez-Navarro, B.; Moya-Sola, S. Were large carnivores and great climatic shifts limiting factors for hominin dispersals? Evidence of the activity of *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Vallparadís Section (Vallès-Penedès Basin, Iberian Peninsula). *Quat. Int.* **2017**, *431*, 42–52. [[CrossRef](#)]
22. Blasco, R.; Peris, J.F. From tortoises to elephants: The impact of elephants in the broad spectrum diet at Bolomor Cave (MIS 9–5 Spain). In *Contributions in Paleoanthropology Band 1: Human-Elephant Interactions: From Past to Present*; Konidaris, G.E., Barkai, R., Tourloukis, V., Harvati, K., Eds.; Tuebingen Paleoanthropology Book Series: Tuebingen, Germany, 2021; pp. 363–385.
23. Pla-Pueyo, S.; Viseras, C.; Soria, J.M.; Tent-Manclús, J.E.; Arribas, A. A stratigraphic framework for the pliocene-pleistocene continental sediments of the Guadix basin (Betic Cordillera, S. Spain). *Quat. Int.* **2011**, *243*, 16–32. [[CrossRef](#)]
24. Alberdi, M.T.; Ruiz Bustos, A. Descripción y significado biostratigráfico y climático del *Equus* e *Hippopotamus*. en el yacimiento de Venta Micena (Granada). *Estud. Geol.* **1985**, *41*, 251–261. [[CrossRef](#)]
25. Reimann, C.K.; Strauch, F. Ein Hippopotamus-Schädel aus dem Pliozän von Elis (Peloponnes, Griechenland). *Neues Jahrbuch Geol. Palaontol.-Abhandlungen* **2008**, *249*, 203–222. [[CrossRef](#)]
26. Bellucci, L.; Bona, F.; Corrado, P.; Magri, D.; Mazzini, I.; Parenti, F.; Scardia, G.; Sardella, R. Evidence of late Gelasian dispersal of African fauna at Coste San Giacomo (Anagni Basin, central Italy): Early Pleistocene environments and the background of early human occupation in Europe. *Quat. Sci. Rev.* **2014**, *96*, 72–85. [[CrossRef](#)]
27. Mazza, P.; Rustioni, M. The fossil bear from Senèze (Southern France). *Rend. Lincei.* **1994**, *5*, 17–26. [[CrossRef](#)]
28. Martínez-Navarro, B.; Palmqvist, P.; Madurell-Malapeira, J.; Ros-Montoya, S.; Espigares, M.P.; Torregrosa, V.; Pérez-Claros, J.A. La fauna de grandes mamíferos de Fuente Nueva-3 y Barranco León-5: Estado de la cuestión. In *Ocupaciones Humanas en el Pleistoceno Inferior y Medio de la Cuenca de Guadix-Baza*; Toro, I., Martínez-Navarro, B., Agustí, J., Eds.; Junta de Andalucía, Consejería de Cultura: Sevilla, Spain, 2010; pp. 197–236.

29. Madurell-Malapeira, J.; Ros-Montoya, S.; Espigares, M.P.; Alba, D.M.; Aurell-Garrido, J. Villafranchian large mammals from the Iberian Peninsula: Paleobiogeography, paleoecology and dispersal events. *J. Iber. Geol.* **2014**, *40*, 167–178. [[CrossRef](#)]
30. Antunes, M.T.; Azzaroli, A.; Faure, M.; Guérin, C.; Mein, P. Mammifères pleistocènes de Algos, en Algarve: Une révision. *Ciênc. Terra.* **1986**, *8*, 73–86.
31. Galobart, À.; Ros, X.; Maroto, J.; Vila, B. Descripción del material de hipopótamo (*Hippopotamus antiquus* Desmarest, 1822) de los yacimientos del Pleistoceno inferior de Incarcal (Girona, NE de la Península Ibérica). *Paleont. Evol.* **2003**, *34*, 153–173.
32. Agustí, J.; Leroy, S.A.; Lozano-Fernández, I.; Julià, R. Joint vegetation and mammalian records at the early Pleistocene sequence of Bòbila Ordis (Banyoles-Besalú Basin, NE Spain) and their bearing on early hominin occupation in Europe. *Paleobiodivers. Paleoenviron.* **2018**, *98*, 653–662. [[CrossRef](#)]
33. Mazza, P.P.A.; Ventra, D. Pleistocene debris-flow deposition of the hippopotamus-bearing Collocurto bonebed (Macerata, Central Italy): Taphonomic and paleoenvironmental analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2011**, *310*, 296–314. [[CrossRef](#)]
34. van der Made, J.; Rosell, J.; Blasco, R. Faunas from Atapuerca at the Early- Middle Pleistocene limit: The ungulates from level TD8 in the context of climatic change. *Quat. Int.* **2017**, *433*, 296–346. [[CrossRef](#)]
35. Álvarez-Posada, C.; Parés, J.M.; Sala, R.; Viseras, C.; Pla-Pueyo, S. New magnetostratigraphic evidence for the age of Acheulean tools at the archaeo-palaeontological site “Solana del Zamborino” (Guadix-Baza Basin, S Spain). *Sci. Rep.* **2017**, *7*, 13495. [[CrossRef](#)]
36. Baena, R.; Cunha, P.P.; Guerrero, I.C.; Fernández, J.J.; Cortés, M.; Silva, P.G.; Simón, M.; Murray, A.S.; Buylaert, J.P. El pleistoceno medio y superior en la secuencia general de las terrazas del Guadalquivir (sgtg): Nuevas dataciones por luminiscencia de la t12 y t13 en la Rinconada (SW de España). In Proceedings of the XV Reunión Nacional Cuaternario, Bilbao, Spain, 1–5 July 2019; pp. 369–372.
37. Gómez-Alba, J. Catálogo razonado de los vertebrados fósiles de España del Museo de Geología de Barcelona (1882–1982). In *Treballs del Museu de Geologia de Barcelona*; Ajuntament de Barcelona: Museu de Geologia: Barcelona, Spain, 1997; pp. 1–296.
38. Blain, H.A.; Santonja, M.; Pérez-González, A.; Panera, J.; Rubio-Jara, S. Climate and environments during Marine Isotope Stage 11 in the central Iberian Peninsula: The herpetofaunal assemblage from the Acheulean site of Áridos-1, Madrid. *Quat. Sci. Rev.* **2014**, *94*, 7–21. [[CrossRef](#)]
39. Sese, C.; Soto, E. Vertebrados del Pleistoceno de Madrid. *Flora Fauna* **2000**, *6*, 216–243.
40. Blasco, R.; Rosell, J.; Peris, J.F.; Cáceres, I.; Vergès, J.M. A new element of trampling: An experimental application on the Level XII faunal record of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* **2008**, *35*, 1605–1618. [[CrossRef](#)]
41. Faure, M. *Hippopotamus incognitus* nov. sp., un hippopotame (Mammalia, Artiodactyla) du Pléistocène d’Europe occidentale. *Geobios* **1984**, *17*, 427–437. [[CrossRef](#)]
42. Donner, J.J.; Kurtén, B. The floral and faunal succession of “Cueva del Toll”, Spain. *E G Quat. Sci. J.* **1958**, *9*, 72–82. [[CrossRef](#)]
43. Trinkaus, E.; Walker, M. *The People of Palomas: Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern Spain*; Texas A&M University Press: College Station, TX, USA, 2017; p. 320.
44. Pieruccini, P.; Forti, L.; Mecozzi, B.; Iannucci, A.; Yu, T.L.; Shen, C.C.; Bona, F.; Lembo, G.; Muttillio, B.; Sardella, R.; et al. Stratigraphic reassessment of Grotta Romanelli sheds light on Middle-Late Pleistocene palaeoenvironments and human settling in the Mediterranean. *Sci. Rep.* **2022**, *12*, 13530. [[CrossRef](#)]
45. Palmqvist, P.; Rodríguez-Gomez, G.; Figueirido, B.; García-Aguilar, J.M.; Perez-Claros, J.A. On the ecological scenario of the first hominin dispersal out of Africa. *Anthropologie* **2022**, *126*, 102998. [[CrossRef](#)]
46. Kierdorf, U.; Kahlke, R.D. Pathological findings on remains of hippopotamids from the Early Pleistocene site of Untermassfeld. In *The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany). Part 4*; Kahlke, R.D., Ed.; Senckenberg: Frankfurt, Germany, 2020; Volume 40, pp. 1251–1272.
47. Adams, N.F.; Candy, I.; Schreve, D.C. An Early Pleistocene hippopotamus from Westbury Cave, Somerset, England: Support for a previously unrecognized temperate interval in the British Quaternary record. *J. Quat. Sci.* **2022**, *37*, 28–41. [[CrossRef](#)]
48. Head, M.J.; Gibbard, P.L. Early–Middle Pleistocene transitions: Linking terrestrial and marine realms. *Quat. Int.* **2015**, *389*, 7–46. [[CrossRef](#)]
49. Fidalgo, D.; Rosas, A.; Bartolini-Lucenti, S.; Boisserie, J.-R.; Pandolfi, L.; Martínez-Navarro, B.; Palmqvist, P.; Rook, L.; Madurell Malapeira, J. Increase on environmental seasonality through the European Early Pleistocene inferred from dental enamel hypoplasia. *Sci. Rep.* **2023**, *13*, 16941. [[CrossRef](#)]
50. Berends, C.J.; Köhler, P.; Lourens, L.J.; Van de Wal, R.S.W. On the cause of the Mid-Pleistocene transition. *Rev. Geophys.* **2021**, *59*, e2020RG000727. [[CrossRef](#)]
51. Fidalgo, D.; Rosas, A.; Estalrich, A.; García-Taberner, A.; Pastor, F.J.; Pineda, A.; Huguet, R.; Cáceres, I.; Ollé, A.; Vallverdú, J.; et al. First presence of *Macaca sylvanus* at the late early Pleistocene of barranc de la Boella (La Mina locality, Francolí basin, NE Iberia). *J. Hum. Evol.* **2023**, *179*, 103368. [[CrossRef](#)] [[PubMed](#)]
52. Boscaini, A.; Madurell-Malapeira, J.; Llenas, M.; Martínez-Navarro, B. The origin of the critically endangered Iberian lynx: Speciation, diet and adaptive changes. *Quat. Sci. Rev.* **2015**, *123*, 247–253. [[CrossRef](#)]
53. Duval, M.; Martínez-Navarro, B.; Oms, O.; Rufí, I.; Sorbelli, I.; Prat-Vericat, M.; Madurell-Malapeira, J. The Early Pleistocene fossil assemblage from Incarcal-I: First numerical dating results. In Proceedings of the XXI Inqua Congress, Rome, Italy, 13–20 July 2023.
54. Madurell-Malapeira, J. Estudi de les Restes d’*Hippopotamus antiquus* (Hippopotamidae, Mammalia) del Jaciment del Pleistocè Inferior de Cal Guardiola (Terrassa). Master’s Thesis, Universidad Autònoma de Barcelona, Barcelona, Spain, 2006.

55. Madurell-Malapeira, J.; Minwer-Barakat, R.; Alba, D.M.; Garcés, M.; Gómez, M.; Aurell-Garrido, J.; Ros-Montoya, S.; Moyà-Solà, S.; Berástegui, X. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quat. Sci. Rev.* **2010**, *29*, 3972–3982. [[CrossRef](#)]
56. Espigares, M.P.; Palmqvist, P.; Rodríguez-Ruiz, M.D.; Ros-Montoya, S.; Pérez-Ramos, A.; Rodríguez-Gómez, G.; Guerra-Merchán, A.; García-Aguilar, J.M.; Granados, A.; Campaña, I.; et al. Sharing food with hyenas: A latrine of *Pachycrocuta brevirostris* in the Early Pleistocene assemblage of Fuente Nueva-3 (Orce, Baza Basin, SE Spain). *Archaeol. Anthropol. Sci.* **2023**, *15*, 1–29. [[CrossRef](#)]
57. Pineda, A.; Saladié, P.; Huguet, R.; Cáceres, I.; Rosas, A.; García-Tabernero, A.; Estalrich, A.; Mosquera, M.; Ollé, A.; Vallverdú, J. Coexistence among large predators during the Lower Paleolithic at the site of La Mina (Barranc de la Boella, Tarragona, Spain). *Quat. Int.* **2015**, *388*, 177–187. [[CrossRef](#)]
58. Konidaris, G.; Tourloukis, V.; Boni, G.; Athanassiou, A.; Giusti, D.; Thompson, N.; Syrides, G.; Panagopoulou, E.; Karkanis, P.; Harvati, K. Marathousa 2: A New Middle Pleistocene Locality in the Megalopolis Basin (Greece) with Evidence of Hominin Exploitation of Megafauna (*Hippopotamus*). *PaleoAnthropology* **2023**, *2023*, 34–55.
59. Yravedra, J.; Solano, J.A.; Herranz-Rodrigo, D.; Linares-Matás, G.J.; Saarinen, J.; Rodríguez-Alba, J.J.; Tilton, S.; Serrano-Ramos, A.; Courtenay, L.A.; Mielgo, C.; et al. Unravelling hominin activities in the zooarchaeological assemblage of Barranco León (Orce, Granada, Spain). *J. Paleolit. Archaeol.* **2022**, *5*, 6. [[CrossRef](#)]
60. Alonso Herrero, E.; Fernández-Martínez, E.; Rodríguez-Fernández, L.R.; Matías Rodríguez, R. *Guía Geológica Visual de León*; Editorial Celarayn: León, Spain, 2004; p. 274.
61. Rosas, A.; Huguet, R.; Pérez-González, A.; Carbonell, E.; Bermúdez de Castro, J.M.; Vallverdú, J.; van der Made, J.; Allue, E.; García, N.; Martínez-Pérez, R.; et al. The “Sima del Elefante” cave site at Atapuerca (Spain). *Estud. Geol.* **2006**, *62*, 327–348. [[CrossRef](#)]
62. Rodríguez, J.; Burjachs, F.; Cuenca-Bescós, G.; García, N.; van der Made, J.; Pérez González, A.P.; Blain, H.-A.; Expósito, I.; López-García, J.M.; García Antón, M.; et al. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). *Quat. Sci. Rev.* **2011**, *30*, 1396–1412. [[CrossRef](#)]
63. Van der Made, J. Ungulados de Gran Dolina, Atapuerca: Nuevos datos e interpretaciones. *Atapuerca Evol. Hum.* **1998**, 97–110.
64. Aguirre, E. Remarques sur la stratigraphie et la paléontologie du bassin de Granada (Espagne). *Comptes Rendus Hebd. Seances L Acad. Des Sci.* **1958**, *246*, 2140–2142.
65. Sánchez, B.; Pesquero, M.D.; Fraile, S.; Salesa, M.J. Las colecciones de Vertebrados fósiles del Museo Nacional de Ciencias Naturales (CSIC): Aportación del Profesor Emiliano Aguirre a la Paleontología española. *Zona Arqueol.* **2004**, *4*, 527.
66. Crusafont, M. El cuaternario español y su fauna de mamíferos: Ensayo de síntesis. *Rev. Fac. Cienc.* **1960**, *2*, 181–199.
67. Bech, J. Nuevo hallazgo de *Hippopotamus amphibius major* en Banyoles (Gerona). *Acta Geológica Hispánica* **1970**, *5*, 51–53.
68. Julià, R. Nuevos datos sobre la posición cronoestratigráfica de los materiales cuaternarios de la cuenca lacustre de Banyoles-Besalú (Girona). *Acta Geol. Hisp.* **1977**, *12*, 55–59.
69. Faure, M. Les hippopotamidés du Pléistocène ancien d’Oubeidiyeh (Israël). *Mem. Travaux Cent. Rech. Fr. Jerus.* **1986**, *5*, 107–142.
70. Ruiz-Bustos, A.; Fernández, J.; Morales, J.; Rodríguez-Fernández, J.; Vera, J.A. Bioestratigrafía de los materiales Plio-Cuaternarios del borde norte de la Depresión de Granada. *Estud. Geol.* **1990**, *46*, 277–290. [[CrossRef](#)]
71. Cardoso, J.L. *Contribuição Para o Conhecimento dos Grandes Mamíferos do Plistocénico Superior de Portugal*; OEIRAS: Oeiras, Portugal, 1993; pp. 171–567.
72. Estraviz, Q. Quaternary Fossil Vertebrates from Continental Portugal: Paleobiodiversity, Revision of Specimens and New Localities. Master Thesis, Universidade Nova de Lisboa, Lisboa, Portugal, May 2019.
73. Mazo, A.V.; Pérez-González, A.; Aguirre, E. Las faunas pleistocenas de Fuensanta del Júcar y El Provencio y su significado en la evolución del Cuaternario de la Llanura manchega. *Bol. Geol. Min.* **1990**, *101*, 404–418.
74. Mazo, A.V. Los hipopótamos del Pleistoceno medio de Huescar-1 (Granada). *Trab. Neog. Cuatern.* **1989**, *1*, 317–325.
75. Alberdi, M.T.; Alcalá, L.; Azanza, B.; Cerdeño, E.; Mazo, A.V.; Morales, J.; Sesé, C. *Consideraciones Bioestratigráficas Sobre la Fauna de Vertebrados Fósiles de la Cuenca de Guadix-Baza (Granada, España)*; CSIC—Museo Nacional de Ciencias Naturales (MNCN): Madrid, Spain, 1989; Volume 11, pp. 347–355.
76. Domingo, M.S.; Alberdi, M.T.; Sánchez Chillón, B.; Cerdeño, E. La fauna cuaternaria de la Cornisa Cantábrica en las colecciones del Museo Nacional de Ciencias Naturales. *MUNIBE* **2005**, *57*, 5–30.
77. Mariezkurrena-Gastearrena, K. Hallazgos de macromamíferos poco frecuentes en yacimientos arqueológicos y paleontológicos del Pleistoceno de la región cantábrica. *Kobie Ser. Paleoanthropol.* **2011**, *30*, 83–110.
78. Baena Escudero, R.; Fernández Caro, J.J.; Guerrero Amador, I.; Posada Simeón, J.C. La Terraza compleja del río Gualdaquivir en “Las Jarillas” (La Rinconada, Sevilla. SW de España): Cronoestratigrafía, industria lítica y macro-fauna asociada. *Cuat. Geomorf.* **2014**, *28*, 107–125.
79. Soto, E. Estudio paleontológico. In *El yacimiento Achelense de Pinedo (Toledo)*; Querol, M.A., Santonja, M., Eds.; Ministerio de Cultura: Madrid, Spain, 1979; pp. 39–42.
80. López-Recio, M.; Silva, P.G.; Roquero, E.; Cunha, P.P.; Tapias, F.; Alcaraz-Castaño, M.; Baena, J.; Cuartero, F.; Morín, J.; Torres, T.; et al. Geocronología de los yacimientos achelenses de Pinedo y Cien Fanegas (Valle del Tajo) e implicaciones en la evolución fluvial en el entorno de Toledo (España). *Estud. Geol.* **2015**, *71*, e029. [[CrossRef](#)]
81. Nolte, E. Miscelánea Arqueológica. *Kobie* **1977**, *7*, 9–27.

82. Vilaseca, S. *Reus y su Entorno en la Prehistoria*; Asociación de Estudios Reusenses: Reus, Spain, 1973; pp. 1–282.
83. Jiménez-Arenas, J.M.; Santonja, M.; Botella, M.; Palmqvist, P. The oldest handaxes in Europe: Fact or artefact? *J. Archaeol. Sci.* **2011**, *38*, 3340–3349. [[CrossRef](#)]
84. Pineda, A.; Saladié, P. The Middle Pleistocene site of Torralba (Soria, Spain): A taphonomic view of the Marquis of Cerralbo and Howell faunal collections. *Archaeol. Anthropol. Sci.* **2019**, *11*, 2539–2556. [[CrossRef](#)]
85. Bonadonna, F.P.; Alberdi, M.T. *Equus stenorhis* Cocchi as a biostratigraphical marker in the Neogene-Quaternary of the Western Mediterranean basin: Consequence on Galerian-Villafranchian chronostratigraphy. *Quat. Sci. Rev.* **1987**, *6*, 55–66. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.