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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)

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ABSTRACT

The study of European Pleistocene *Hippopotamus* presents unresolved questions and a lack of consensus among specialists being matter of hotly debate in the last decades. The number of taxa, their geographical and chronological distribution and their palaeobiological affinities are still under evaluation. The present work presents the results of comparative analyses using descriptive anatomy, linear biometry and geometric morphometrics of *Hippopotamus* specimens found in the archaeopalaeontological outcrops of the Barranc de la Boella Section (Francolí Basin, NE Iberian Peninsula) and other coeval European sites in the context of the record of the genus *Hippopotamus* in Europe and its putative migrations from Africa. The deposits from Barranc de la Boella Section documented for the first time the presence of hominids with Acheulian technology and hippos roughly coinciding with the *Early-Middle Pleistocene Transition* (EMPT), one of the periods with strongest climate asymmetry throughout the Pleistocene. The evaluation of the studied specimens and the other European record favor the consideration of *Hippopotamus antiquus* as the only taxon of its family present in Europe from the Early Pleistocene (ca. 2.1 Ma) to the mid-Middle Pleistocene (ca. 0.4 Ma), when the extant species (*Hippopotamus amphibius*) dispersed from Africa. Even so, there is a need for a more detailed understanding of the large intraspecific variability and sexual dimorphism reported within the genus *Hippopotamus* to characterise the phenotype of individuals in its populations across different chronologies, geographic locations, and environmental conditions. The detailed review of the distribution of *H. antiquus* during the EMPT raises the possibility that the Iberian and Italic peninsulas acted as climatic refugia for its populations strongly dependents of the aquatic environment during the coldest climatic stages (e.g. MIS 22).

1. Introduction

The genus *Hippopotamus* (Artiodactyla, Hippopotamidae) include the extant terrestrial megaherbivores most ecologically associated with the continental aquatic environments. These large mammals are linked with environments that conserve permanent bodies of water, conditioning their dispersal capacity according to habitat connectivity (Stoffel et al., 2015). This ecological peculiarity brings great interest to the study of hippopotamus palaeobiology to carry out palaeoecological reconstructions of archaeopalaeontological sites (Palmqvist et al., 2022). The environmental range together with the large extent of hippopotamus distribution in chronologies with recorded dispersals in hominin evolution offers a unique potential for assessing possible pathways of

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Abbreviations

C	upper canine
P2	upper second premolar
P3	upper third premolar
P4	upper fourth premolar
M1	upper first molar
M2	upper second molar
M3	upper third molar
Botot	maximum lateral width of the occipital
BOc	length between the lateral ends of the occipital condyles
BFm	maximum lateral width of the foramen magnum
HFm	maximum dorso-ventral width of the foramen magnum
OM	length of the molar series
L	mesio-distal diameter
Wbucco-lingual diameter**Bs**	bucco-lingual diameter**Bs**minimum width of the diaphysis
DTM	mean transverse diameter
DAPM	mean anteroposterior diameter
DTCa	cranial transverse diameter of the lesser calcaneum process

connection between geographic areas with anthropological records (Boisserie and Gilbert, 2008; Martínez-Navarro, 2010; O'Regan, 2008).

Despite the great interest of studying the palaeobiology of hippopotamus, nowadays remained major gaps in our knowledge of the evolutionary history of this biological group throughout the Quaternary (Puzachenko et al., 2021). There is currently a debate between different biogeographical models of intercontinental dispersals between Africa and Eurasia (see, for example van der Made et al., 2017b; Fidalgo et al., 2021b). In this framework is common the re-evaluation of the validity and relationships between the taxa that inhabited these areas in the Pleistocene (see Faure, 1985; Mazza and Bertini, 2013; Petronio, 1995). As already remarked by Boisserie and Gilbert (2008) or more recently by Konidaris et al. (2018), there is a lack of consensus among specialists on the phylogenetic relationships, systematics and diagnostic features of the different recorded and/or erected species.

The earliest accepted occurrences of the genus *Hippopotamus* in Europe and its subaerial connection areas with Africa date back to the Early Pleistocene in the Coste San Giacomo (occurrence highly debated and based on an isolated incisor not in situ; see Pandolfi and Petronio, 2015) and Chiusi Basin sites in Italy (Bellucci et al., 2012; Martino and Pandolfi, 2021; Pandolfi and Petronio, 2015, Fig. 1), and Elis and Aetorrachi in Greece (Reimann and Strauch, 2008), with chronologies between 2.1 and 2 Ma. Some authors point to earlier occurrences in the Late Pliocene deposits of Valea Graunceanului (Romania; Bolomey, 1965) or Moldavian Roussillion (Moldova; Vangengeim et al., 1998), although the validity of the determinations and the stratigraphic position of the materials have been disputed (O'Regan, 2008). Valea Graunceanului was ascribed to Late Pliocene before the re-evaluation of the Plio-Pleistocene boundary, but now is ascribed to MNQ18a, 2–1.8 Ma (sensu Spassov, 2003). Subsequently, there are references to hippo specimens in the Turkish site of Kocakır-2 (ca. 1.9–1.6 Ma; Demirel et al., 2016), the Italian deposits around the Upper Valdarno area, Monte Riccio, Poggio ai Venti, Torrente il Crostolo, San Lorenzo, Bacino di Travernelle and Montecastrilli (ca. 1.8–1.6 Ma; Gliozzi et al., 1997; Martino and Pandolfi, 2021), the Spanish site of Mencal-9 (Spain, ca. 1.7 Ma; Arribas, pers. comm.; Pla-Pueyo et al., 2011) and the Greek localities of Livakos and Kapetanios (ca. 1.6 Ma; Koufos, 2001).

According to Mazza's (1991) proposal, all Early Pleistocene hippo occurrences in Europe stem from a single entry from Africa of forms included in *H. gorgops* that become included in the hypodigm of *H. antiquus* (=*H. major*) on the European continent. On the other hand, van der Made et al. (2017b) propose to differentiate between *H. antiquus* in sites with chronologies before 1.7 Ma and *H. tiberinus* for those with chronologies after 1.4 Ma, recovering the disputed taxon *H. tiberinus* described by Mazza (1991) from Middle Pleistocene materials from the Italian Peninsula and Germany (Mazza, 1995). According to the latter proposal, *H. antiquus* populations would come from a first dispersal of forms included in *H. kaisensis*, while *H. tiberinus* would be the result of a second input of forms more derived from *H. gorgops*, both with African origin.

The record of localities with the presence of *H. antiquus* from 1.5 Ma until its disappearance increases notably. Its geographical area expanded, from being limited to the peripheral areas of the Mediterranean Sea to occupy areas of central Europe, reaching as far as the present-day British Isles (Adams et al., 2021). With the data available so far, Epivillafranchian is the period with the greatest presence and geographical distribution of *H. antiquus* in Europe, with records from Spain (Martínez-Navarro et al., 2004a), France (Guérin et al., 2003), the United Kingdom (Adams et al., 2021), the Netherlands (Vervoort-Kerkhoff and van Kolfschoten, 1988), Germany (Kahlke, 2001), Italy (Martino and Pandolfi, 2021) and Greece (Athanassiou, 2022) (Fig. 1). Also dated to these chronologies, the species *H. georgicus* was described in Georgia from specimens from Akhalkalaki (0.9–0.8 Ma; Vekua, 1959, 1986). After re-evaluation of the materials, this species has been interpreted as a form belonging to *H. antiquus* (Faure, 1983; Kahlke, 1987).

It was precisely with materials from La Maglianella (Italy; ca. 0.6 Ma) that Mazza (1991) erected the species *H. tiberinus*, noticing morphological differences and a decrease in the size of the individuals were the result of a modification of certain populations of *H. antiquus* in Europe and accepting a temporary coexistence of these two species on the European continent. Later, Petronio (1995) re-evaluated the available evidence indicating that *H. tiberinus* does not show enough morphological differences as compared with older European specimens and can be accomodated within the intraspecific variability of *H. antiquus*. Finally, Mazza and Bertini (2013) applied the terminology of *H.* ex gr. *H. antiquus* to what they considered smaller forms of *H. antiquus*, later or coeval with the *Early-Middle Pleistocene Transition*. Even so, authors such as Athanassiou et al. (2018) take the assertion of this decrease in size with caution, questioning the nomenclature of *H.* ex gr. *H. antiquus*.

The Middle Pleistocene record of *H. antiquus* is also quite disputed. If the determination given by Mazza (1995) to the materials from Castel di Guido were confirmed, the populations would continue at least until MIS 11 (0.412 Ma ±2 ka; Marra et al., 2018; Martino and Pandolfi, 2021). This putative extirpation time is reinforced by the latest re-evaluation of hippopotamus specimens from Condeixa (Portugal; ca. 0.4 Ma; Cardoso, 1993) carried out by Martino et al. (2022). The next younger citations of *H. antiquus* would be found in Apidima Caves and Marathousa (Greece, 0.45–0.2 Ma; Konidaris et al., 2018; Tsoukala, 1999, Fig. 1) and other German (with some reservations Mauer and Mosbach; Koenigswald and Heinrich, 1999) and Italian (e.g. Via Aurelia; see Martino and Pandolfi, 2021) localities around 0.4 Ma.

Throughout this chronological span the species *H. gorgops* (described from Olduvai, Tanzania; Dietrich, 1928) stands out as the most abundant taxon of the family Hippopotamidae in Africa, with records from eastern and northern Africa and Israel (van der Made

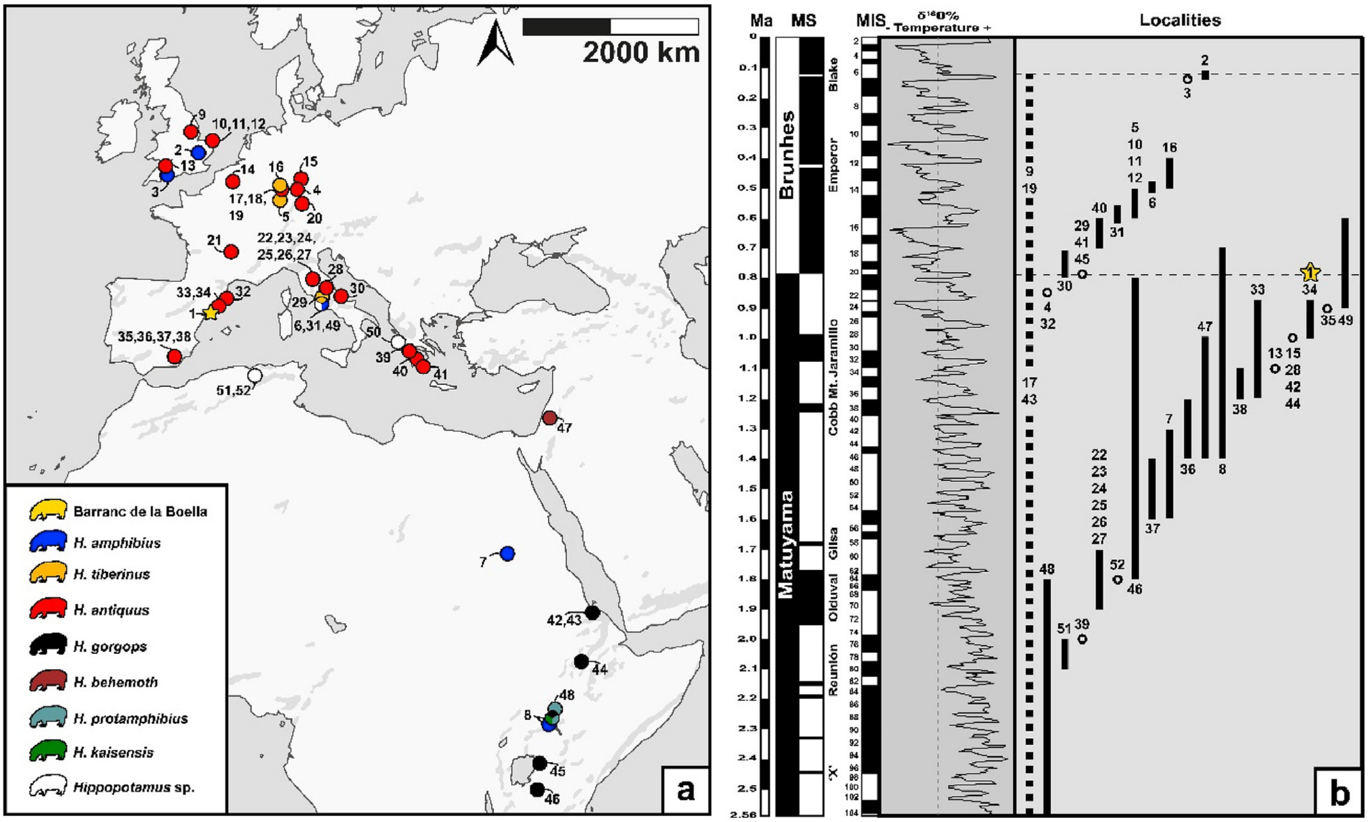


Fig. 1. Geographical and chronological location of the localities for which data have been analysed in this study. a) Geographical location of each locality and taxonomic assignment of its specimens. b) Approximate chronology of the localities against the estimated climatic evolution (Marine Isotopic Stages; MIS) in the Quaternary. 1: Barranc de la Boella; 2: Barrington; 3: Honiton River Gravels; 4: Würzburg-Schalksberg; 5: Jockgrim; 6: Cava Montanari (Tor di Quinto); 7: Kaddanarti; 8: West Turkana; 9: Beckingham; 10: Sidestrand (Norfolk); 11: Trimingham (Norkolk); 12: Norfolk; 13: Westbury Cave; 14: Grange d'Auby Binazat; 15: Untermassfeld; 16: Mosbach; 17: Leeheim; 18: Stockstadt/Rhein; 19: Gross-Rohrheim; 20: Wierstein; 21: Saint Yvoine; 22: Figline; 23: Renacci (Upp. Vald.); 24: Tasso (Upp. Vald.); 25: Upper Valdarno; 26: Cava Bacchi (Upp. Vald.); 27: Vacchereccia (Upp. Vald.); 28: Collecurti; 29: San' Oreste; 30: Ortona; 31: Maglianella; 32: Incarcal; 33: Cal Guardiola; 34: Vallparadís Estació; 35: Huescar-1; 36: Barranco León 5; 37: Venta Micena; 38: Fuente Nueva 3; 39: Elis; 40: Kyparíssia; 41: Myrtiá; 42: Buia; 43: Mulhuli-Amo; 44: Daka Member; 45: Rawe; 46: Olduvai; 47: Ubeidiya; 48: Omo; 49: Monte delle Piche; 50: Mantzavináta; 51: Ain Boucherit; 52: Ain Hanech.

et al., 2017b). At the site of Tighennif (Algeria) the species *H. sirensis* (Pomel, 1890, 1896) is described, although it seems to be accepted that it is a synonym of *H. gorgops*, the priority in taxonomic nomenclature continuing to be debated (Geraads, 1980, van der Made et al., 2017b). A similar situation is found in the case of specimens from Ubeidyia (Israel) with which *H. behemoth* was described (Faure, 1986; Martínez-Navarro et al., 2004b). More debated is the validity of the species *H. kaisensis*, accepted by several authors as a predecessor of the "*antiquus*" and "*amphibius*" lineages (Mazza and Bertini, 2013, van der Made et al., 2017b) although with a scarce anatomical and geographical record (Boisserie and Gilbert, 2008).

Within Middle Pleistocene chronologies, Tor di Quinto site (= Cava Montanari, = Cava Nera Molinario, Italy, MIS 13-MIS 11, ca. 0.524–0.474 Ma; Caloi et al., 1980; Kotsakis and Barisone, 2008, Fig. 1) is reported, with some consensus, as the earliest occurrence to *H. amphibius* in Europe. This presence is reinforced by the record of hippo materials in localities near this site with chronologies close to it (e.g. Fontana Ranuccio; Pandolfi and Petronio, 2015). According to Faure (1985), these populations correspond to the taxon *H. incognitus* described by Faure (1984), although this species has been discredited on the grounds of lack of anatomical data to support it (Petronio, 1986, 1995). The possibility of coexistence of *H. antiquus* and *H. amphibius* populations in Europe in chronologies between 0.5 and 0.4 Ma is still under debate (Martino and Pandolfi, 2021). *H. amphibius* is known in Europe (although their determinations are based on poor specimens) during the last interglacial period, disappearing with the last glacial period (Mazza, 1995). Some authors propose that its populations may have persisted in southern Europe until 20–30 Ka ago (Mazza and Bertini, 2013; Stuart and Lister, 2001). It seems unanimous to consider *H. amphibius* and *H. antiquus* as distinct taxa representing lineages with an independent evolutionary history in two different geographical areas and with different palaeobiology and environmental requirements. Even so, some authors have remained firm in considering both taxa as forms of the same species, with value at the subspecific level (Kahlke, 2000, 2001, 2006; Stuart, 1991).

The materials found at the Barranc de la Boella Section (Francolí Basin; NE Iberia; 0.99–0.78 Ma; Vallverdú et al., 2014) present a new opportunity to evaluate aspects of hippo palaeobiology at a period of strong asymmetry in the glacial cycles, such as the *Early-Middle Pleistocene Transition*. In fact, this period roughly coincides with one of the strongest and longest glaciation periods of the Pleistocene referred to as the "0.9 Ma event" (between isotopic stages MIS 24–22; Head and Gibbard, 2015; Maslin and Brierley, 2015; Strani et al., 2019) and carries associated with it a series of phenomena of modification of European faunas with inflows and outflows of taxa that characterise the Epivillafranchian period (Kahlke, 2000, 2004; Madurell-Malapeira et al., 2010, 2014, 2017). In this context, a European human settlement with sufficiently sophisticated technology to access trophic resources from large terrestrial mammals has been demonstrated (Mosquera et al., 2015).

In this paper we describe the fossil skeletal elements of hippos from the *Early-Middle Pleistocene Transition* found in the archaeopalaeontological Section of Barranc de la Boella (Francolí Basin, NE Iberian Peninsula) and compare their anatomical characteristics with the available fossil record of Quaternary hippos using different techniques (descriptive anatomy, linear biometry and geometric morphometrics). The aim of these analyses is to provide a new anatomical and quantitative perspective on the taxonomy, systematics, palaeobiology, palaeoecology and palaeobiogeography of the European Pleistocene hippo record and its relationship with the taxa present in Africa, with special interest in those specimens from the Early and Middle Pleistocene.

2. The Barranc de la Boella section

The unpublished specimens evaluated in this paper come from two localities of the stratigraphic sequence of the Barranc de la Boella (La Canonja, Francolí Basin), in the northeast of the Iberian Peninsula, 3 km from the Mediterranean coast and 50 m above sea level (Fig. B1a) (Vallverdú et al., 2008). UTM coordinates of the central point: X 346.559, Y 4.555.526.

Geologically, the Barranc de la Boella (BB) deposits are composed of sands, gravels and coarse pebbles that are poorly stratified and with lateral variations in which many fossil bones, coprolites and lithic tools corresponding to the Acheulean are included (Mode 2; Vallverdú et al., 2014). The current geomorphology of the BB is modelled by the erosion of the torrential floods that fill a ravine, leaving outcrops of the sequence for hundreds of metres.

Archaeopalaeontological excavations have been carried out at three different localities within the BB Section, although the fossils that could be included in this analysis come from only two of them, La Mina (LM) and El Forn (EF). Both localities have the same stratigraphic position (Fig. B1b; Vallverdú et al., 2014 and Mosquera et al., 2015 for further details).

The entire sequence was deposited during the Early and Middle Pleistocene. Unit II, from which the described fossils come from, is constrained within the Matuyama chron in the Early Pleistocene, due to its reversed polarity (Vallverdú et al., 2014). Geochronological and biostratigraphic data adjust the range to the late part of the chron, in the Jaramillo subchron (Fig. 1c and B.1b). Micromammal biozonation estimates an absolute age of the unit between 0.99 and 0.78 Ma (Lozano-Fernández et al., 2014). Additionally, according to Madurell-Malapeira et al. (2019) the macromammal assemblage corresponds to a typical Epivillafranchian association of the post-Jaramillo subchron, coinciding in the faunal list with geographically close deposits of similar chronology of the Vallparadís Section (layers EVT7 or CGRD7; Madurell-Malapeira et al., 2010, 2017).

The sediments that make up the BB sequence are associated with a fluvio-deltaic environment with high-density flows (Vallverdú et al., 2014). The sedimentary characteristics and the distribution of fossil elements seem to indicate a temporal regime with events of accumulation and dispersal of materials (Rosas et al., 2015). Optimal habitat analyses of the micromammals indicate an aquatic environment with abundant vegetation, alternating grasslands (Lozano-Fernández et al., 2015). The assemblage of gastropods and bivalves provides a similar environmental approximation to that obtained with micromammals, with dry terrestrial, wet terrestrial and stagnant aquatic areas (Vallverdú et al., 2008). The torrential regime and the results of the palynological analysis of the coprolites are consistent with a Mediterranean climate (Pineda et al., 2017; Rosas et al., 2015). For what hippos concerns, taphonomic data indicate the specimens were deposited in the same biotope that the individuals inhabited. This hypothesis supports the possibility of finding individuals of different ontogenetic classes and sexes in the BB geological layers.

For more information of the geographical, geological and palaeoecological context, see Appendix A.1.

3. Material and methods

3.1. Material

The fossil specimens studied in this work were unearthed during the 2008–2020 field surveys of the BB Section. These former specimens correspond to fossils of hippo skeletal elements that are temporarily housed in the Palaeoanthropology Laboratory of the Museo Nacional de Ciencias Naturales (MNCN, CSIC) for study.

Referred specimens—Partial skull preserving two fragments of the maxilla with P2 to M3 (BB'09C2IIS.1515 + BB'09C2IIS.1526, BB'09C2IIS.1522 + BB'10C2II3S.1502 + BB'08C2IIP.1419; Fig. 2) and posterior part of the neurocranium (BB'09C2IIR.1403 + BB'09C2IIS.1407; Fig. 3); a fragment of right maxilla with M2 and M3 (BB'11EFIIK.1407; Fig. 4); right M2 (BB'11EFIIP.1411; Fig. 5a–e); right P3 (BB'11EF2K.1408 1408; Fig. 5g–k); fragment of left C1 (BB'09EF3O.1101; Fig. 5f); 5 cervical vertebrae (C2: BB'15C2IIQ.1506, C3: BB'09C2IIR.1518, C4: BB'16C2II3Q.1507, C5: BB'15C2IIQ.1505, C7: BB'09C2IIS.1533; Fig. 6); 3 thoracic vertebrae (BB'13EF4P.1203, BB'15C2IIR.1602, BB'20C2IIS.1709; Fig. B2); proximal half of a right ulna (BB'13EFIIP.1105; Fig. B3c-e); humeral diaphysis (BB'09C2IIQ.1521; Fig. B3a,b); distal half of a left femur (BB'12EFIIO.1102; Fig. B3f-h); fragmented calcaneus (BB'08EFIIH.1301; Fig. B3i-k).

In addition to the unpublished specimens, comparative data and the study of other materials have been used. The authors also studied the collections of the Incarcal Complex, Bòbila Ordis, Vallparadís Estació, Cal Guardiola, Orce sites, Upper Valdarno and Collecurti respectively housed at the Museu Arqueològic Comarcal de Banyoles, Institut Català de Paleontologia, Museo Arqueológico de Granada, Dipartimento di Science della Terra, Università di Firenze and Museo Archeologico di Camerino. Additionally, the authors studied extant specimens from the Museo de Ciencias Naturales de Madrid, Museu de Ciències Naturals de Barcelona and Royal Museum for Central Africa at Tervuren (Belgium) (See Tables C1-C.5).

The taxa for which information has been included in the anatomical and biometric analyses are the common hippo (*Hippopotamus amphibius*) and fossils of the taxa *H. amphibius*, *H. antiquus*, *H. tiberinus*, *H. behemoth*, *H. gorgops*, *H. sirensis*, *H. protamphibius* and *H. kaisensis*. The taxonomic attribution of the specimens by the institutions in charge of the material or by the authors of the last publication in which the specimens have been re-evaluated has been maintained. The list of specimens and sample size used in each analysis is detailed in Tables C1-C.5. The geographical location and chronological range of the localities from which the specimens included in the analyses originate are detailed in Fig. 1.

3.2. Systematic and descriptive anatomical analysis

For anatomical terminology, the nomenclature used in the works of Zorić et al. (2018) and Lucy et al. (2018) for the cranium and mandible (Fig. B4), in Rakotovao et al. (2014) and Mazza (1995) for the dentition (Fig. B5) and Faure (1985) for the postcranial has been modified. The descriptive anatomical comparisons of the specimens has been carried out through photographs in most cases,

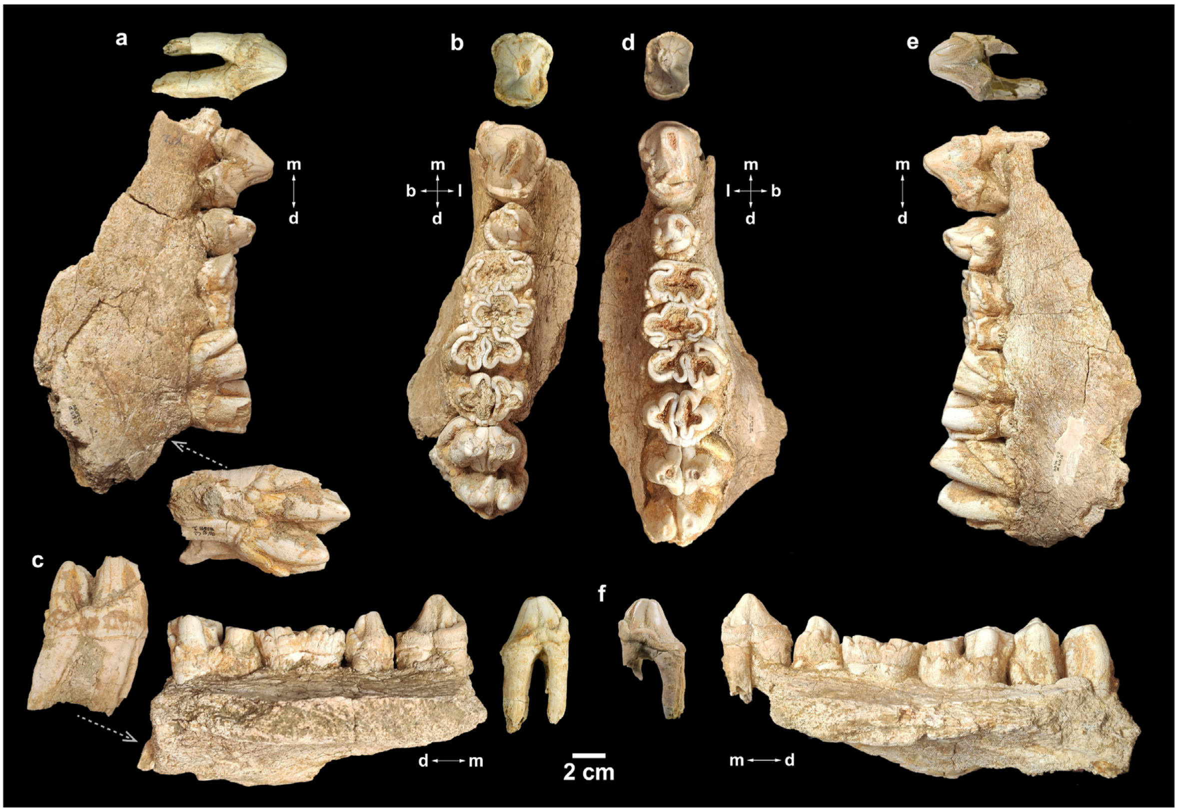


Fig. 2. *Hippopotamus* maxilla fragments (with dentition from P2 to M3) from the site of La Mina (Barranc de la Boella). a-c) Right laterality, specimen BB'09C2IIS.1522 + BB'10C2II3S.1502 + BB'08C2IIP.1419; f-h) left laterality, specimen BB'09C2IIS.1515 + BB'09C2IIS.1526. a and e) buccal view; c and f) lingual view; b and d) occlusal view.

although it has been possible to access physically or through 3D models to specimens of living and fossil hippos preserved in several Spanish and Italian institutions, as well as to models disseminated collaboratively in repository websites.

3.3. Linear biometric analysis

Linear biometric data were taken according to Fig. B4 (for cranial elements), Fig. B5 (for dentition) and Fig. B7 (for postcranial), following the protocol outlined by Faure (1985), Harris (1991), Mazza (1991) and Kahlke (1997). The data of the specimens included in the analyses are detailed in Supplementary information.

To assess the biometry of the specimens, graphs have been generated using Past 4.03 (Hammer et al., 2001). The set of cranial measurements has been included in a dimensionality reduction analysis by Principal Component Analysis (PCA) that includes the loadings of each measurement in the first two Principal Components (PC); the variance collected by each principal component is detailed in brackets in the title of the axis.

To test statistically the differences between the taxa evaluated, analysis of variance tests were carried out on the cranial and dental data. The generality of the data did not correspond to normal and homoscedastic samples and small samples were included in the assessment, so non-parametric tests were used. For analyses of a sample with a single dependent variable, Kruskal-Wallis test was applied, together with Mann-Whitney pairwise post hoc test. In cases with more than one dependent variable, one-way ANOSIM test was used. Those taxa with sufficient data to be compared statistically in each analysis are indicated in the post hoc test results. For these analyses the BB specimens have been considered within the *H. antiquus* hypodigm, coinciding with the results of the systematic evaluation discussed below. The test results are specified in Table C7.

3.4. Analysis with geometric morphometrics

A quantitative comparison of the shape of the hippo teeth included in this study was carried out using two-dimensional analysis with geometric morphometrics. The landmark placement template used in this work was developed in-house and is shown in Fig. B6. The proposed landmarks and their description are presented in Table C6. The positioning of landmarks and semilandmarks followed the tooth contour and the basic structure of the internal elements of the occlusal face.

To ensure mathematical homology between the semilandmarks measured on the different specimens, a sliding process has been carried out (Bookstein, 1991, 1997; Gunz et al., 2005, 2009, 2013; Mitteroecker and Gunz, 2009). This methodology is based on the application of algorithms that optimise as much as possible the mathematical correspondence between the points that define two lines or two surfaces. The algorithm used in this case is the bending energy minimisation algorithm, based on thin-plate spline deformation (Bookstein, 1996, 1997; Bookstein et al., 2002; Green, 1996; Gunz and Mitteroecker, 2013; Perez et al., 2006).

For these analyses, we used: 1) photographs taken by the authors; 2) photographs provided by other research groups; 3) photographs of specimens included in specific bibliography. The impossibility of physically taking photographs of all the comparison specimens for this study using the same protocol has made it

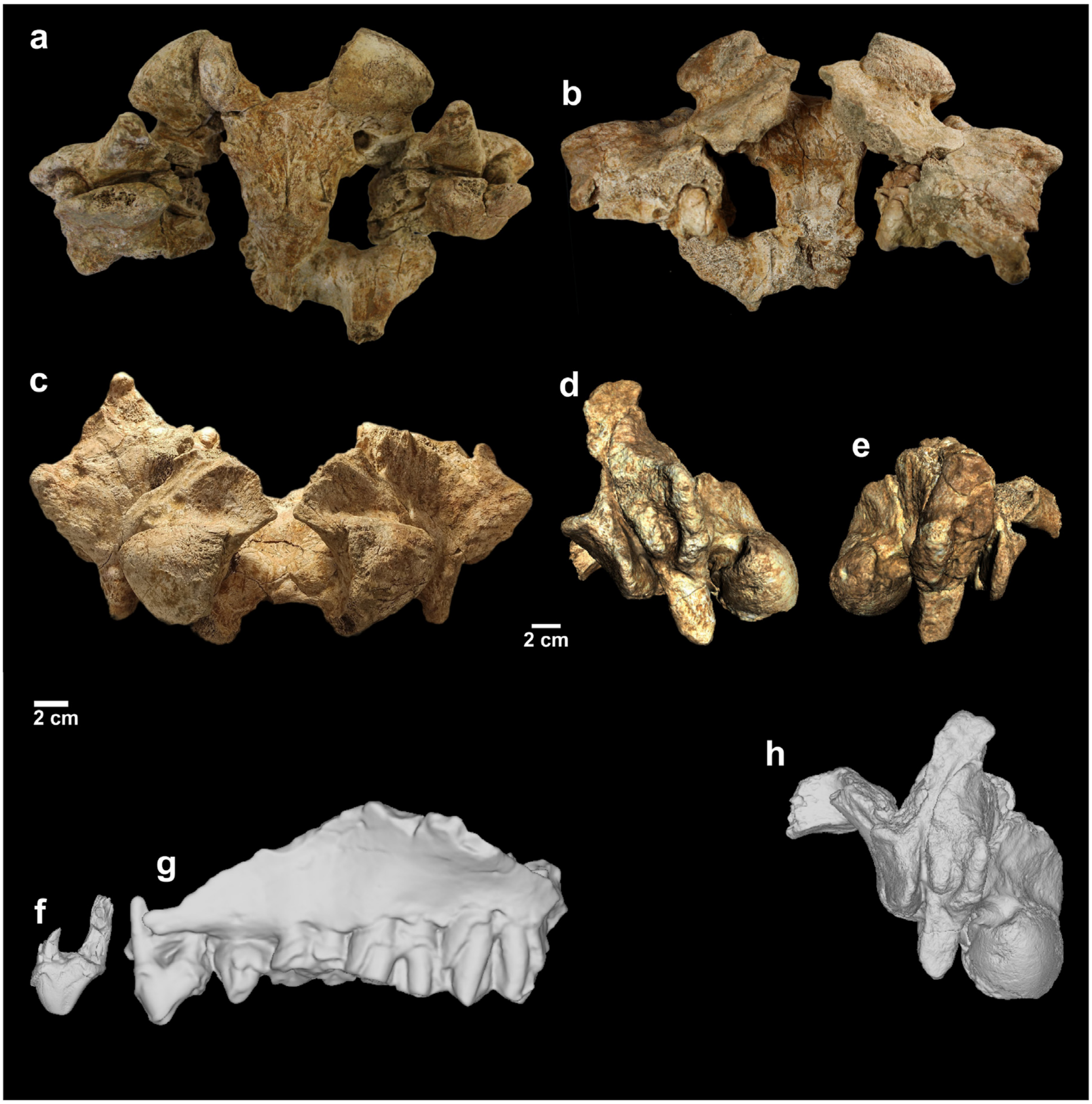


Fig. 3. *Hippopotamus* cranial fragments recovered from the site of La Mina (Barranc de la Boella). a-e) Fragment of basicranium (BB'09C2IIR.1403 + BB'09C2IIS.1407); f-h) 3D reconstruction of the relative position of the neurocranium, maxilla and P2 of individual "a". a) basilar view, b) parietal view, c) occipital view, d) left lateral view, e) right lateral view, f-g) BB'09C2IIS.1515 + BB'09C2IIS.1526 left lateral view, h) lateral view.

necessary to select only suitable photographs, thus reducing the size of the sample. The absence of a suitable scale in most of the available images has made it necessary to dispense with the incorporation of size (centroid size) in the analyses.

The inclusion of premolars in the evaluation with geometric morphometrics has been ruled out. These teeth are scarcely represented in the scientific literature and the available figures do not usually present an occlusal view suitable for analysis. M3 is also not included in the analysis due to the state of emersion of these teeth in the specimens, as part of their structures generally remain hidden in the alveolar cavities, making it impossible to locate significant anatomical points.

For the evaluation of the M1, only its outline was taken into account. The high intensity of wear on these teeth makes it impossible to locate internal anatomical points on the occlusal surface. The M2s were evaluated both at the level of the contour and the internal elements of the occlusal surface. The selection of valid photographs for analysis was based on the following points: a) absence of fractures that would have altered the morphology of the crown contour; b) presence of all the cingulae, which form the most mesial, distal, lingual and buccal points of the element. Concealment of anatomical contour structures by cusps was avoided due to a non-standardised view at the time of photography.

The measurement of the different landmarks and semilandmarks on all specimens has been carried out in Viewbox 4 software (dHAL software, Kifissia, Greece; Bastir et al., 2019). The sliding of the semilandmarks has been carried out with the specific tools provided by the same software. The original coordinates have been extracted and organised for the subsequent statistical analysis. To ensure that the intra-observer measurement error has not significantly affected the results, a permutation test has been carried out following the proposal of Klingenberg (2011). The intra-observer error was accepted after testing that the largest Procrustes distance within 5 measurements of the same individual was smaller

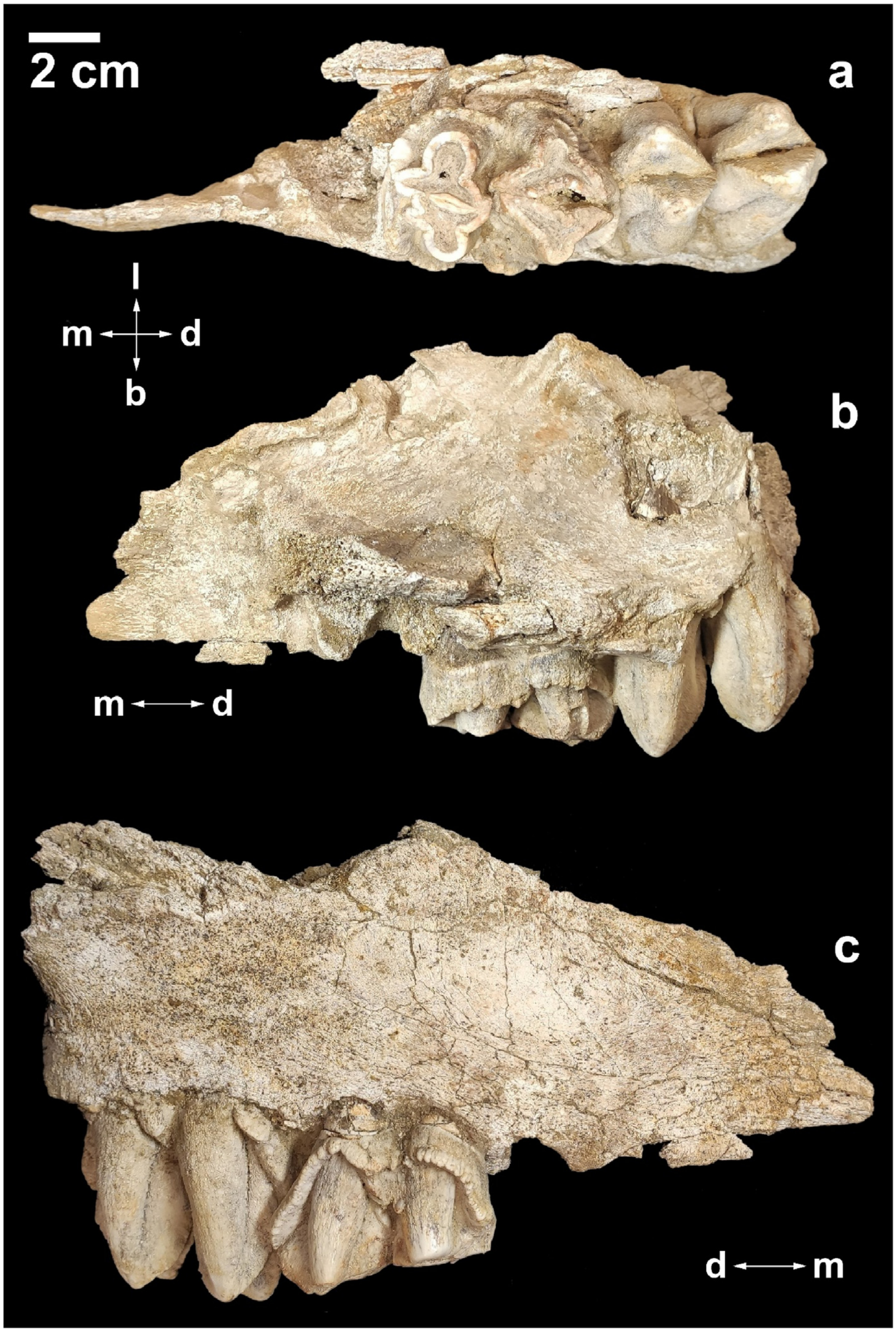


Fig. 4. Fragment of *Hippopotamus* right maxilla (preserved M2 and M3; BB'11EFIIK.147) from the site of El Forn (Barranc de la Boella). a) occlusal view, b) lingual view, c) buccal view.

than the smallest Procrustes distance between 10 specimens of different individuals. Data processing and analysis and the production of graphical results were implemented in the software Morphologika2 v2.5 (O'Higgins and Jones, 2006), MorphoJ 1.07a (Klingenberg, 2011), Past 4.03 and RStudio. To assess differences in tooth element morphology between taxa and sites, independent PCA dimensionality reduction analyses were performed for M1 and M2, detailing the variability picked up by the first three PCs in brackets in the title of the axes. The analyses include the graphical expression of the shape change associated with their axes.

To test statistically the differences between taxa assessed based on procrustes distances, the distance-based test procrustes ANOVA was used. Due to the paucity of data, only the taxa *H. antiquus* and *H. amphivius* (living) could be statistically evaluated, so a post hoc test was not necessary. For these analyses the BB specimens have been considered within the *H. antiquus* hypodigm, coinciding with the results of the systematic evaluation discussed below. The test results are specified in Table C7.

4. Results

4.1. Description

According to the anatomical representation and the estimated age of the individual to which each specimen belongs, the hippopotamus materials found at BB can be assigned to at least three

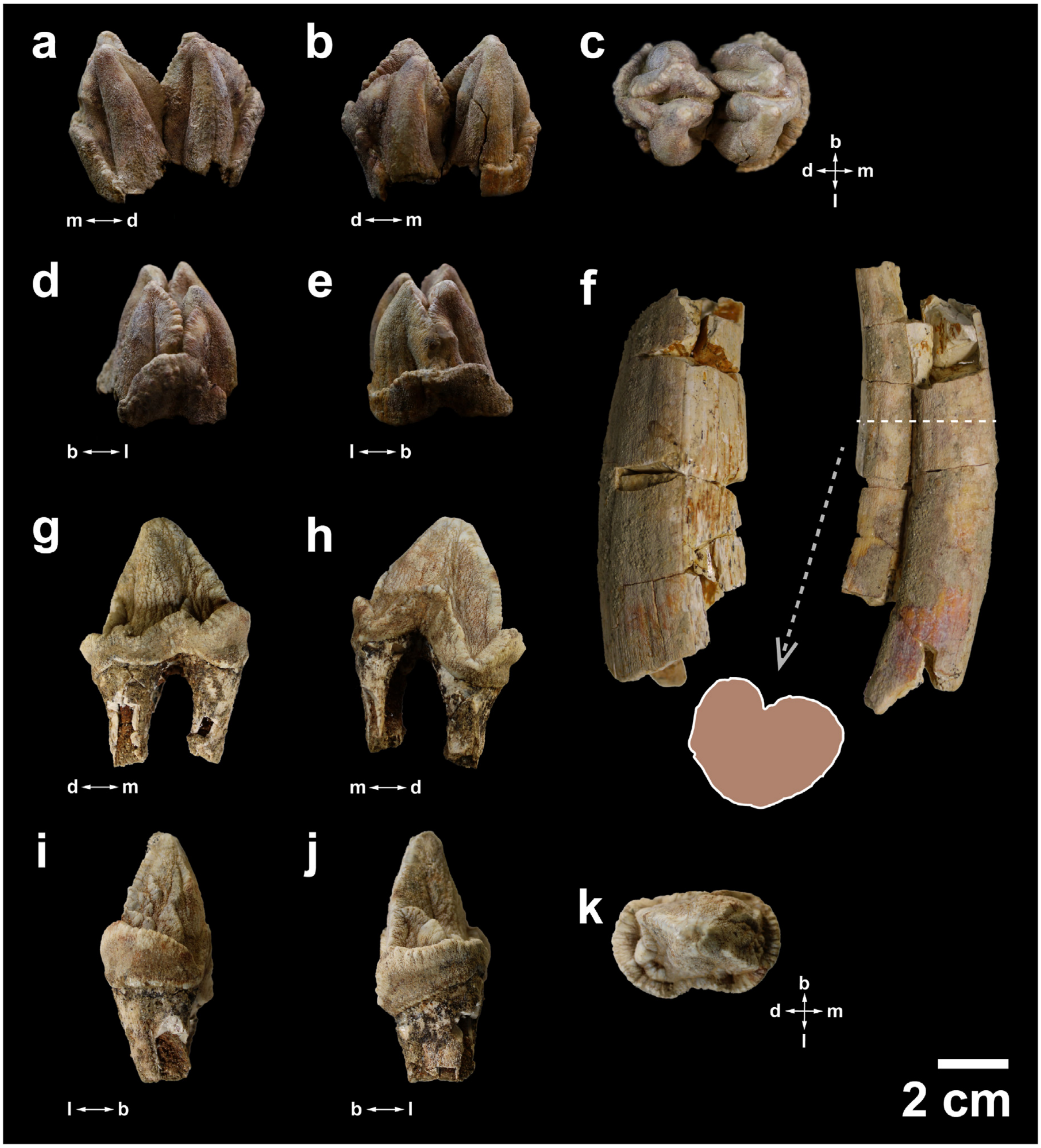


Fig. 5. Isolated dental elements of *Hippopotamus* from the Barranc de la Boella sites. a-e) right M2 (BB'11EFIIP.1411); f) fragment of left C1 (BB'09EF3O.1101); g-k) right P3 (BB'11EF2K.1408 1408). a,h) lingual view, b,g) buccal view, c,k) occlusal view, d,j) distal view; e,i) mesial view; f) buccal, lingual and transversal section view.

individuals. These individuals will be referred with the nomenclature “individual a, b and c" hereafter.

4.1.1. *Dentognathic specimens*

A partial skull, including the posterior and lower part of the neurocranium and both sides of the maxilla of the same individual, has been recovered (individual “a"; Figs. 2 and 3). The two maxillars are fragmented at the most mesial point of the root of P3, behind the most distal point of M3, a few centimetres from the palate and inferior to the infraorbital foramen and the zygomatic process of the maxilla (Fig. 2). Both P2 (Fig. 2 a-f) and the right M3 (Fig. 2a,c) were located separately from the maxilla, but were easily associated due to the proximity of the specimens and the state of occlusal wear. The occipital margins are markedly angulate and the paracondylar processes do not extend beyond the limit of the occipital condyles (Fig. 3c). These condyles are proportionally highly extended laterally, delimiting a broad foramen magnum (Fig. 3a–c). On the basis occipitalis the tuberculum musculare is very marked (Fig. 3a). The basisphenoid and zygomatic processes are fragmented, and the petrous bones are absent (Fig. 3a).

The specimen BB'11EFIIK.1407 (individual “b"; Fig. 4) shows M2 and M3 included in a fragment of maxillar. The isolated molar BB'11EFIIP.1411 (individual “c"; Fig. 5a–e) corresponds to the crown of a possible right M2 which is fragmented at its midpoint.

The preserved canine fragment (Fig. 5f) shows the typical curved section of the upper canines. This canine is fragmented at both ends and probably belongs to a young individual (BB'09EF3O.1101; Fig. 5f).

P2 and P3 (Figs. 2 & Fig. 5g–k) have a large trihedral paracone perimetered on the lingual side by a wide cingulum, which extends towards the distal and mesial sides forming a precingulum and a postcingulum including the endostyle/protocone and distostyle. The buccal cingulum is poorly developed, unlike the endoparafossa. All cingulae have a crenulate-crenate margin surface. The few differences between P2 and P3 are found at the level of the post-cusps, more noticeable in P3, and the curvature of the cusps, more pronounced in P2. The isolated P3 from El Forn (BB'11EF2K.1408; Fig. 5g–k) does not show any type of wear and the crests of its crown maintain all the roughness of the enamel, which may correspond to a tooth that has not yet emerged or is in the process of emerging. The morphology of the P4 (Fig. 2) is composed of a conical paracone with enamel folds that generate pits on its surface. The paracone base is bordered almost entirely by a wide cingulum. The cingulum has a crenulated-crenated surface.

The first of the upper molars (M1; Fig. 2) presents the classic morphology with four trilobed cusps common in the genus *Hippopotamus*. The twelve pits that determine the trefoil shape of each of the four cusps are well distinguished. The development of the cingulae is very pronounced, with the presence of accessory structures such as mesiostyles, distostyles, mesostyles and cingulae on all faces. These cingulae have a markedly crenulated-crenated surface. The distostyle has the mesiostyle of M2 (Figs. 2, 4 & 5a-e) superimposed on its most buccal part. In the M2 the mesiostyle overlaps the distostyle of the M1s and their distostyle overlaps the mesiostyle of the M3s (Figs. 2 and 4). The buccal cingulum of individual “a" are less developed than in its M1. The mesostyle of individual “b" is very well developed (Fig. 4). The M2 of individual “c" is very similar in the development of its structures to that of individual “b" and allows us to observe the presence of crenulations in the most distal part of the cusp ridges (Fig. 5a–e). The M3 cusps of individual “a" (Fig. 2) are more globular than those of individual “b" (Fig. 4), which has crenulations in the most distal part of the cusp ridges. In individual “a" a distinctly greater width is observed on the more mesial cusps than on the more distal ones. The pits of M3 are less distinct than those observed in M1 and M2. In neither of the two individuals the eruption of these teeth is complete and only in the case of individual “a" has the wear of the paracone and protocone begun. The mesiostyles are not visible as they are under the M2 distostyles (Fig. 2).

4.1.2. *Axial specimens*

Nine specimens have been determined as vertebrae or vertebral fragments. Seven of these specimens have been extracted at La Mina and could correspond to part of the cervical (Fig. 6 & B2a-e) and first thoracic series (Fig. B2f) of individual “a". The cervical vertebrae from La Mina have been located in the series as a C2 to C7 (Fig. 6). The thoracic vertebrae from La Mina correspond to the middle part of the thoracic series, one of them being relatively complete (Fig. B2f).

C2 (Fig. 6a & B.2a) does not preserve the spinous process and has a fragmented left anterior articular process and right transverse process. The axis is highly developed cranially and dorso-ventrally. The anterior articular surfaces are very flat and with a slightly inclined orientation with respect to the perpendicular of the axis tooth. The posterior articular processes are relatively narrow and caudally elongated. C3 (Fig. 6b & B2b) has a fragmented end of the spinous process and lacks the tubercles of the transverse processes. C4 (Fig. 6c & B2c) is also fragmented at the level of the spinous and transverse processes. C5 (Fig. 6d & B2d) is the most complete vertebra, with some fracture of the tubercles of the transverse process and the right posterior articular process. From C3 to C5 (Fig. 6b–d & B2b-d) there are very narrow and caudally elongated posterior articular processes. The vertebral bodies, on the other hand, are remarkably short antero-posteriorly, with a marked ventral ridge and the anterior articular processes slightly cranially inclined. The C7 (Fig. 6f and B.2f) has fractures at the level of the vertebral body, the spinous process and the transverse processes. The spinous process of C7 is very wide antero-posteriorly and its anterior articular processes relatively narrow.

All thoracic vertebrae are strongly fragmented. Specimen BB'20C2IIS.1709 (Fig. B2f) stands out as the best preserved. This vertebra lacks the most dorsal part of the spinal process and the transverse processes. The vertebral body is very wide laterally and its spinous process very robust from its junction with the posterior articular processes. The costal facets are very marked, especially the anterior one. The anterior articular processes are very well developed, with a wide incision at the base of the spinous process.

4.1.3. *Appendicular specimens*

The fragment of left humerus (Fig. B3a-b) displays the lateral supracondylar ridge marked, although the general morphology is gracile. No ridge is visible above the coronoid fossa. The proximal fragment of right ulna (Fig. B3c-e): the 10.5 cm of diaphysis distal to the lateral coronoid process and the trochlear notch with its two articular facets are preserved (although compressed medio-laterally). Despite the large size of the element, there is no evidence of fusion (ankylosis) with the radius. The two articular facets of the trochlear notch are widely separated. The fragment of left femur (Fig. B3f-h): preserves the distal half of the diaphysis without deformation and the distal epiphysis with great fragmentation. The section of the diaphysis is approximately circular. The supracondylar fossa does not show a great proximal-distal development, but a marked depth and medio-lateral extension. Finally, the fragment of right calcaneus (Fig. B3i-k) shows from the middle of the posterior talar facet to the middle of the calcaneal tuberosity. The only articular facet that is partially preserved is the medial talar facet.

4.2. *Age classes*

Following the proposal of Laws (1968) and the extrapolation for upper dentition by Martínez-Navarro et al. (2022) on the ontogenetic development of dentition in hippos, the maxillar specimens from Barranc de la Boella are assigned to two individuals of age class XI-XII. These classes correspond to an age range between 20 and 24 years. The isolated molar and premolar correspond to an age class prior to stage VII (younger than 11 years). Accepting the correlation of dental age classes with bone fusion times proposed by Weston (1997) for *H. amphibius*, the unfused ulna with the radius would correspond to an individual younger than 11 years.

4.3. *Anatomical comparisons*

With the current analysis of the cranial fragments of individual “a" of the BB, it is not possible to reconstruct their relative position in an exact way to obtain the original dimensions and anatomy of the cranium, so the characteristics that depend on the relative position between the neurocranium and the splacnocranium have not been considered. Even so, Fig. 3f,g,h shows the set of elements of the same cranium found so far and their approximate position, estimated on the 3D model of the skull of IGF1043 of *H. antiquus* from Figline. At the level of the neurocranium, the occipital condyles protrude slightly caudally from the limit of the occipital laterals (Fig. 3d,e,h), as in specimens from Cal Guardiola (Madurell-Malapeira, 2006; Madurell-Malapeira et al., 2010), Elis (Reimann and Strauch, 2008), Collecurti (Mazza, 1995), Figline (Blandamura and Azzaroli, 1977) or other Upper Valdarno sites (various specimens hosted in Museo di Storia Naturale della Università di Firenze

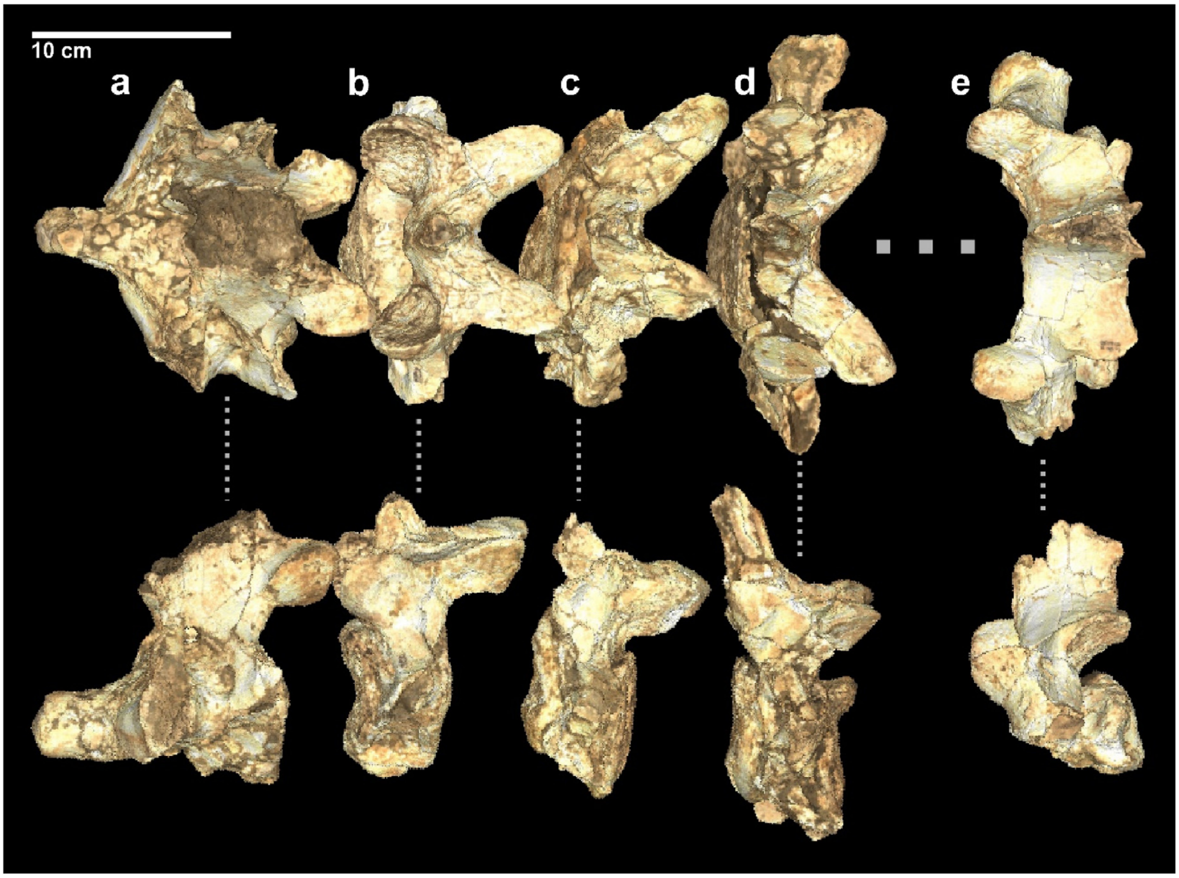


Fig. 6. 3D models of *Hippopotamus* cervical vertebrae (C) recovered from the La Mina site (Barranc de la Boella), placed in anatomical order in dorsal and left lateral view. a) C2 (axis, BB'15C2IIQ.1506); b) C3 (BB'09C2IIR.1518); c) C4 (BB'16C2II3Q.1507); d) C5 (BB'15C2IIQ.1505); e) C7 (BB'09C2IIS.1533).

and Museum National d'Histoire Naturelle); with extremes in specimens from Tor di Quinto (Pandolfi and Petronio, 2015) and Barrington (Reynolds, 1922; Mazza, 1995), or in living *H. amphibius*. In contrast, in specimens from Untermassfeld (Kahlke, 2001), S. Oreste (Mazza, 1995) or Maglianella (Mazza, 1991, 1995) the occipital condyles are markedly projected caudally. This projection of the condyles is extreme in the specimen apparently more derived from *H. gorgops* from Rawe (Mazza, 1995), El Kherba (van der Made et al., 2017b) or the holotype from Oduvai Gorge (van der Made et al., 2017b), but more similar to the BB material in the specimen of *H. gorgops* from Olduvai Gorge figured by Mazza (1991) or the juvenile from Buia published by Martínez-Navarro et al. (2022). In occipital view, the angularity of the occipital sides of the BB specimen is remarkable (Fig. 3c). Only the juvenile specimen of *H. gorgops* found in Buia (Martinez-Navarro et al., 2022) shows this character more marked. The lateral development of the occipital condyles is also remarkable in relation to the width of the occipital, surpassing the specimens from Upper Valdarno (various) or Figline (Blandamura and Azzaroli, 1977), and resembling the skulls from Collecurti (Mazza, 1995), Elis (Reimann and Strauch, 2008) or Cal Guardiola (Madurell-Malapeira, 2006).

Comparing the dentition specimens from BB with other dental series in the fossil record, the large overlapping of M2 over M1 and the development of P3 stand out. The BB P2s are rectangular (Fig. 2), with the same development of both ends of the teeth. If we compare these materials with some of the specimens of *H. gorgops* from Olduvai (holotype figured e.g. van der Made et al., 2017b), we find a more angular morphology in those from BB, although the development of the cingulum is similar. The morphology of this dental element does not seem to vary much in *H. antiquus* and agrees in the absence of distal cingulum with the specimens from sites such as Cal Guardiola, although their size is highly variable. In all the present individuals, a larger buccolingual diameter has been observed at the level of the postparacrista, in the most distal part of P3 (Figs. 2 & 5g-k). In contrast, the BB specimens show this widening at the level of the preparacrista (although it is not very marked in specimen BB'11EF2K.1408), in the most mesial part of the tooth. Within *H. antiquus*, the Cal Guardiola (Madurell-Malapeira, 2006) and Upper Valdarno (various specimens hosted in Firenze and Madrid) specimens coincide with the morphology of the P3 from BB. However, the P3 from Maglianella (Mazza, 1991), Venta Micena (Alberdi and Ruiz Bustos, 1985) and Barranco León (Espigares, 2010) have the flaring in the same position as the current *H. amphibius*, as do the specimens of *H. gorgops* from Olduvai (Mazza, 1991, van der Made et al., 2017b). Apparently the positions of the P3 flaring are variable in Early Pleistocene hippos and do not seem to have a strong phylogenetic signal. In the P4 of the BB specimens (Fig. 2) a clear lateral asymmetry has been detected, both in their position with respect to the maxilla and in their relationship between the paracone and the cingulum, which responds to the twisting of the topological axes of one of the teeth while maintaining the same plane of the base of the crown. This torsion phenomenon also seems to be observed in specimens from Barranco León (Espigares, 2010), together with an asymmetry of the diastemas between P4 and M1. Asymmetry at the diastemas level is also found in some current zooreared specimens. Despite the differences detected in the premolars, these dental elements are highly variable in the current *H. amphibius* sample observed, both in terms of the morphology of the teeth and their orientation with respect to the maxilla and position with respect to the other teeth (size of the diastemata). On the other hand, the size of these teeth does seem to show a certain constant relationship in the taxa and its value at a systematic level will be discussed in future sections.

It seems clear that there is less robustness and a greater tortuosity in the enamel folds at the level of pits, cingulum and crenulations in the BB molars (Figs. 2 and 4) than in most sites with *H. amphibius* (e.g. Barrington; Reynolds, 1922), *H. antiquus* (e.g. Cal Guardiola; Madurell-Malapeira, 2006), *H. gorgops* (e.g. Olduvai; Mazza, 1991) or *H. sirensis* (e.g. Tighenif; van der Made, pers. Comm.). Some of the pieces from Cal Guardiola (e.g. IPS13557b; Madurell-Malapeira, 2006) could be close to this morphology with wide cingulum and crenulate-crenate ridges. The possible distortion of these observations must be taken into account due to the great wear and tear of some of the specimens, reaching extremes of total or partial loss of teeth, as in some particulary old individuals from Cal Guardiola (e.g. IPS14960 or IPS14993; Madurell-Malapeira, 2006).

The axial skeleton of Pleistocene hippos is poorly known and there is a lack of literature showing most of these elements. It is particularly interesting to note that compared to the living *H. amphibius* specimens that are accessible, all cervical vertebrae of the BB (Fig. 6 & B2) have much more developed facets and articular processes with respect to the craniocaudal length of the vertebral bodies. This characteristic is mainly evident in the axis tooth and the posterior articular processes. In contrast, in the only thoracic vertebra evaluated (Fig. B2f) the vertebral body is very wide laterally and its spinous process very robust from the beginning of its development.

The appendicular elements of the BB (Fig. B3) are strongly fragmented and most of the anatomical characters previously described for *H. antiquus* are not visible. In the humerus (Fig. B3a,b) the absence of the ridge above the coronoid fossa, described for *H. antiquus* by Faure (1985), is notable. The ulna (Fig. B3c-e) lacks fusion marks and structures with the radius. Although it is somewhat smaller than the ulnae figured from Incarcal-I (Galobart et al., 2003), Cal Guardiola (Madurell-Malapeira, 2006) and Megalopolis (Kyparíssia; Athanassiou et al., 2018), this state of fusion would be expected in individuals at ontogenetic stages corresponding to smaller sizes. The femur (Fig. B3f-h), despite being strongly fragmented, shows a development of the supracondylar fossa that coincides with that described by Mazza (1995) for *H. antiquus*. Unlike *H. amphibius*, the size is much larger, especially at the distal epiphysis, and the supracondylar fossa is very distal and deep, but with little proximal-distal development. The morphology of the preserved part coincides with that figured and described in the specimens from Cal Guardiola (Madurell-Malapeira, 2006), Figline (Mazza, 1995) or Untermassfeld (Kahlke, 1997); and differs from the morphology of the Barrington specimen figured by Reynolds (1922).

4.4. *Linear biometrical comparisons*

See Table 1 for original measurements.

4.4.1. *Skull*

The results of the multivariate analysis including the measurements of the development of the molar series and the measurements of the posterior part of the occipital together with the occipital condyles are highly representative. The first principal component (PC1) captures 80.5% of the variance, the second principal component (PC2) captures 9% and the third principal component (PC3) captures 6.5% for the *H. amphibius* data set (living and fossil) together with those of *H. antiquus* (and *H. tiberinus* from S. Oreste), *H. gorgops* and the BB specimens (Fig. 7). The set of specimens assigned to *H. antiquus* is characterised by high values for cranial dimensions and especially the high relative proportion of occipital condyles, contrasting with the average values of *H. amphibius*. In PC1 the BB specimen is located in the most positive part of the variability of *H. amphibius*, while in PC2 and the PC1-2 set it is closer to the values of the *H. tiberinus* specimen of S. Oreste (MPUR V1950; Mazza, 1995). This similarity is centred on relatively high values for the second component, with the development of the occipital condyles standing out. *H. gorgops* shows a great difference between the two available samples. The Olduvai Gorge skull (M 14957; Mazza, 1995) is placed at the most positive value for PC1, close to most specimens of *H. antiquus* and together with PC2 is closest to one of the Barrington specimens (SMC D13938 and SMC D3980 a&b; Mazza, 1995); in contrast, the value in PC1 from Rawe (M 15162; Mazza, 1995) is close to the values of S. Oreste (MPUR V1950; Mazza, 1995), the BB and some specimens of *H. amphibius*. European *H. amphibius* fossils overlap with the variability of living *H. amphibius*, with one of the Barrington specimens (SMC D13938; Mazza, 1995) exceeding its PC1 values.

Table 1
Linear measurements in millimetres of the hippo specimens found in the Barranc de la Boella sites (Francolí Basin, NE Iberia). Only the standardised measurements that could be taken are indicated. a) BB'09C2IIS.1515 + BB'09C2IIS.1526; b) BB'09C2IIS.1522 + BB'10C2II3S.1502 + BB'08C2IIP.1419; c) BB'11EF2K.1408; d) BB'11EFIIK.1407; e) BB'11EFIIP.1411.

Element	Measure					
Skull	BFm	65.6	—	—	—	—
	BOc	167.4	—	—	—	—
	Botot	283.5	—	—	—	—
	HFm	55.9	—	—	—	—
	OM left	151.56	—	—	—	—
	OM right	152	—	—	—	—
		A	**b**	**c**	**d**	**e**
P2	L	40.0	~40.0	–	–	–
	W	28.7	~28.7	–	–	–
P3	L	40.4	38.5	45.8	–	–
	W	35.9	38.9	30.8	–	–
P4	L	31.4	26.2	–	–	–
	W	28.0	29.3	–	–	–
M1	L	48.0	48.4	–	–	–
	W	43.3	42.3	–	–	–
M2	L	56.2	56.4	–	60.0	54.0
	W	51.9	51.2	–	44.6	43.0
M3	L	60.0	58.7	–	63.1	–
	W	51.6	54.7	–	48.9	–
Femur	Bs	73.0	–	–	–	–
Calcaneus	DTCa	–	73.0	–	–	–
	DTM	–	37.0	–	–	–
	DAPM	–	60.0	–	–	–

In general, the BB skull seems to be closer to the variability of *H. antiquus-H. tiberinus* although it has a relatively small occipital dimension, coinciding with the S. Oreste specimen (MPUR V1950; Mazza, 1995). The results of the one-way ANOSIM statistical test show the presence of significant differences between the taxa evaluated. The post hoc test performed highlights the presence of significant differences between living *H. amphibius* and the other taxa considered (fossil *H. amphibius*, *H. antiquus* and *H. gorgops*). No statistically significant differences are detected between any other taxa (see Table C7).

4.4.2. *Upper dentition*

Comparison of the BB L, W and L/W values with the average for each taxon shows a similar biometric pattern and largely overlapping variability in fossil *H. amphibius*, *H. antiquus*, *H. tiberinus*,

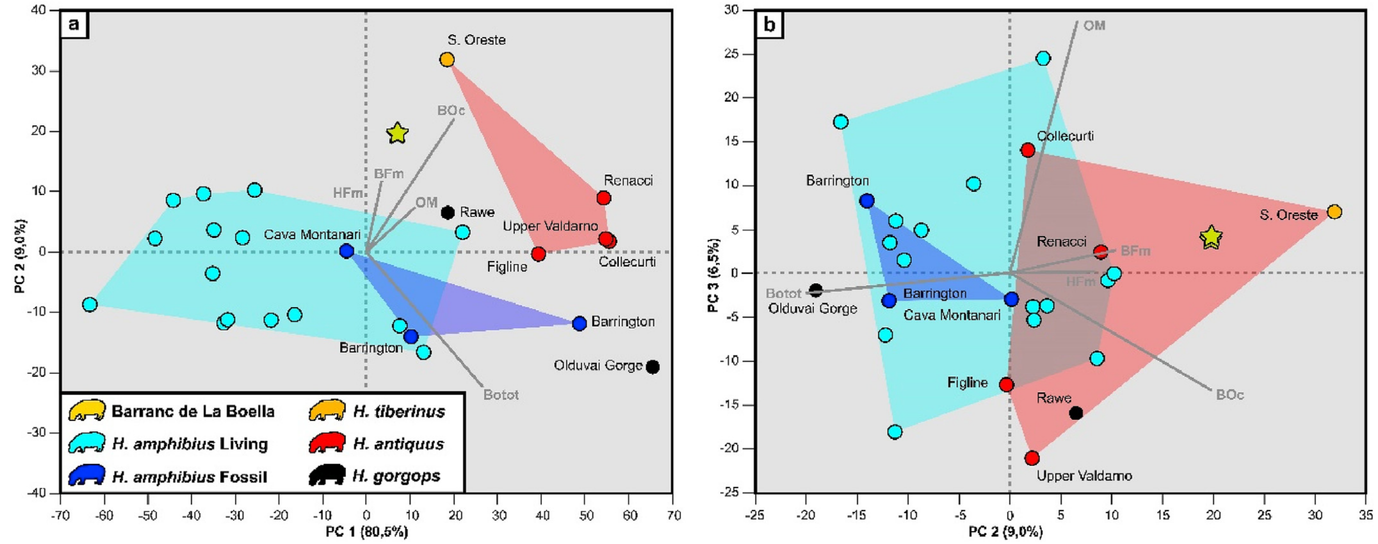


Fig. 7. Principal component analysis of the cranial measurements of the specimens of the genus *Hippopotamus* included in this study, highlighting the skull found at the site of La Mina (Barranc de la Boella). a) Principal Component (PC) 1 versus PC 2; b) PC2 versus PC3. The percentage of variance collected by each PC is indicated in brackets next to its name. Species has been used as a graphic grouping factor. In this analysis we have included the variables maximum lateral width of the occipital (Botot), length between the lateral ends of the occipital condyles (BOc), maximum lateral width of the foramen magnum (BFm), maximum dorso-ventral width of the foramen magnum (HFm) and length of the molar series (OM).

H. behemoth, *H. gorgops* and the BB specimens (Fig. 8; Table C5). The small size of the teeth in *H. protamphibius* contrasts, although the pattern of variation in the series is maintained. Despite the small sample size in this biometric comparison, the measurements of *H. antiquus*, *H. gorgops* and *H. amphibius* (fossil) seem to coincide in most elements. It is interesting the larger mesio-distal diameter proportions for the molars of *H. behemoth*. In general, the parameters of BB are close to the average of *H. antiquus*, although it presents particularly high values for the buccolingual diameter of P3, which changes the proportions of this tooth. Specimens of *H. tiberinus* are of similar size and proportions to those of *H. antiquus*, with the exception of the dimensions of P2, which appear to be slightly larger.

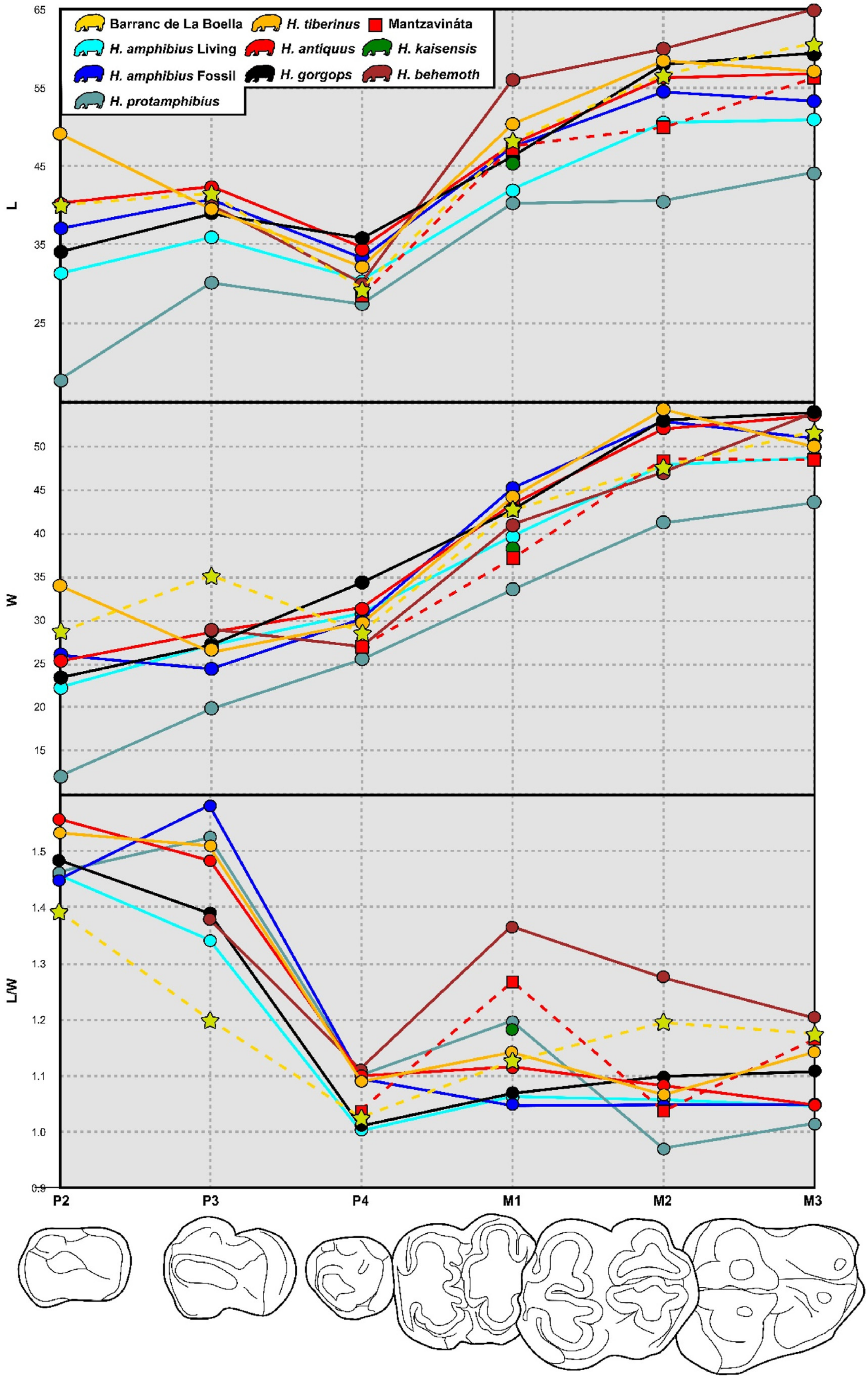
Evaluating together the measurements of each dental element (Fig. 9), a lower proportion for all teeth seems clear for the species *H. protamphibius* than for the rest of the Quaternary extinct taxa considered. The average measurements of living *H. amphibius* individuals show a markedly lower mean than those observed in fossil *H. amphibius*, *H. antiquus*, *H. tiberinus* and *H. gorgops*, especially for P3, M2 and M3. The ability to discriminate fossil *H. amphibius* from *H. antiquus* and *H. gorgops* with the measurements of isolated teeth is practically inexistent. The great intraspecific variability in both *H. antiquus* and *H. gorgops* is striking, with disparate data even among specimens from the same locality, as in the case of Cal Guardiola. In general, the measurements of the BB specimens fit within the known proportions of *H. antiquus*, although with a particularly high relative bucco-lingual diameter of the P3 only comparable to the values of Venta Micena or S. Oreste, considering the striking differences between individuals and laterality within the same individual (Fig. 9b). The dimensions of P2 are similar to those of specimens from Collecurti, Cal Guardiola or the Incarcal Complex (Fig. 9a). The twisting processes we have observed in the BB specimens (Fig. 9c) may alter the measurements of P4.

The BB data for M1 are especially close to those of some of the Cal Guardiola and Stockstadt/Rhein specimens (Fig. 9d). In M2, the BB pieces show biometric differences between individuals, with individual “a" approximating the data from Buia, Olduvai Gorge or Leeheim and individual “b" approximating the data from Cal Guardiola or Ubeidiya (Fig. 9e). In the results obtained for M3, the BB specimens not only show differences between individuals, but also asymmetry between the two laterals of the same individual (Fig. 9f). Broadly speaking, the M3 from BB are similar in their measurements to those from Figline, Olduvai Gorge, Húescar-1 or Mulhuli-Amo, although in their range of variation they include the data from Maglianella.

Results of the Kruskal-Wallis and one-way ANOSIM statistical tests show significant differences between the taxa evaluated in all measures. Post hoc tests of the dentition dimensions (except in P4 W) of *H. antiquus* and living *H. amphibius* display significant differences. No significant differences were found in any case (except in M3 W) between *H. antiquus* and *H. tiberinus*. The data set of *H. antiquus* and *H. gorgops* shows very few variables with significant differences (see Table C7).

The results of the multivariate analysis including the measurements of the premolar series (P2—P4) account for 52% of the variance in PC1, 18.59% in PC2 and 10.9% in PC3 (Fig. 10a,a'). BB specimens are included in the variability recorded for *H. antiquus*, with values close to those of Cal Guardiola in the first two components. PC3 highlights the variability between both laterals of the same individual. *H. antiquus* presents mean values notably different from those of living *H. amphibius*, more positive in PC1 and negative in PC2. In contrast, the three specimens for which data are available for *H. gorgops* are closer to the average of *H. amphibius*, especially the Olduvai Gorge specimen and the Turkana specimen for PC2. The fossil specimens of *H. amphibius* show a large variation for PC2, placing Cava Montanari (Tor di Quinto) outside its current variability and Barrington close to its average.

The PCA of the molar series (M1-M3) show a 71% representation of the variance by PC1, 12.5% for PC2 and 7.1% for PC3 (Fig. 10b,b'). The distribution of values in PC1 reinforces the observation of a trend towards lower proportions in the molars of *H. amphibius* compared to *H. antiquus* and *H. gorgops*. The fossil specimens of *H. amphibius* are closer to the variability ranges of *H. antiquus*, without falling within the variability of *H. gorgops*. If we focus on the BB specimens, the set of their measurements places them close


Barranc de La Boella
H. tiberinus
Mantzavináta
H. amphibius Living
H. antiquus
H. kaisensis
H. amphibius Fossil
H. gorgops
H. behemoth
H. protamphibius
L
65
55
45
35
25
W
50
45
40
35
30
25
20
15
L/W
1.5
1.4
1.3
1.2
1.1
1.0
0.9
P2
P3
P4
M1
M2
M3

to the data taken at Untermassfeld, Barranco León-5 or Barrington, within the range of variability of *H. antiquus* and outside the range of *H. gorgops*. This position is found in positive CP1 values, close to Maglianella, Olduvai Gorge or Turkana West, and in negative CP2 values that coincide with data from Figline, Cava Bachi, Collecurti or Ubeidiya. The arrangement of the two Cal Guardiola specimens at opposite ends of CP2 and the position of the Ubeidiya specimen far from the variability of *H. gorgops* stand out. In this analysis, it is also not possible to differentiate a pattern of distribution of the proportions of the dental elements directed by the chronology of the deposits, nor to adequately separate the range of anatomical variability of *H. antiquus* and *H. gorgops*.

In the joint assessment of the entire upper jugal series (P2-M3) by means of a PCA, 59.7% of the variance is collected in PC1, 9.4% in PC2 and 6.7% in PC3 (Fig. 10c,c'). The values of the BB specimens are within the expected range for *H. antiquus* and especially close to those of Cal Guardiola. The average for *H. antiquus* is more positive for PC1 and more negative for PC2 than for *H. amphibius*. On the contrary, the specimens of *H. gorgops* show very positive values for PC2, although in PC1 they are between the values of *H. antiquus*. Again, the fossil specimen of *H. amphibius* from Cava Montanari (Tor di Quinto) departs from the variability of living *H. amphibius* with more negative PC2 values. PC3 highlights the variability between individuals from the same site (Cal Guardiola) or lateralities of the same individual (case of BB).

Analyses of variance one-way ANOSIM of the P2—P4, M1-M3 and P2-M3 samples show significant differences between the taxa analysed. Post hoc test results show significant differences between *H. antiquus* and living *H. amphibius* in all three analyses. In the molar series data, no significant differences are observed between *H. antiquus* and *H. tiberinus*. While in the premolar and molar series separately no significant differences are observed between *H. antiquus* and *H. gorgops*, in the total series (P2-M3) these differences do stand out. The fossils of *H. amphibius* do not differ significantly from the assemblages of any of the other taxa (see Table C7).

4.4.3. Appendicular skeleton

The dimensions of the BB appendicular elements are particularly small. The minimum width of the femoral diaphysis (Bs) is below the range of variation of *H. antiquus* given by Faure (1985), although it agrees with some specimens from Untermassfeld, Cal Guardiola, Monte delle Piche and Kyparíssia (Fig. B7a). As in the Cal Guardiola specimens, the cranial transverse diameter of the lesser calcaneal process (DTCa) deviates from the measurements reported for *H. antiquus* and overlaps with the biometric ranges given for *H. amphibius* by Faure (1985; Fig. B7b). Analysis of the mean transverse diameter (DTM) versus mean anteroposterior diameter (DAPM) of the calcaneus places the BB specimen within the range of variability of *H. amphibius* proposed by Faure (1985) and departs from the measurements of *H. antiquus* (Fig. B7c).

4.5. Geometric morphometrics comparisons

First upper molar—The geometric morphometrics analysis of the outline of M1 captures 55.42% of the variability in morphology with the first three principal components (Fig. 11). PC1 accounts for 26.83% of the variance, associated in its positive values with an “8″ morphology with a higher ratio of mesiodistal to buccolingual diameter and a more flattened morphology on the mesial and distal side in the negative values. PC2 accounts for 14.98% of the variance, with morphologies with a greater development of the protocone and metacone with respect to the paracone and hypocone in their positive values and inversely in their negative values (Fig. 11a). PC3 accounts for 13.61% of the variance and is associated with greater mesiostyle and distostyle development in its positive values and lesser in its negative values (Fig. 11b).

The outline morphology of the M1s markedly overlaps between living *H. amphibius* and *H. antiquus*. The individual from BB shows some lateral asymmetry, as can be observed in the other individuals for which teeth from both laterals have been counted. Both teeth from BB have positive PC1 and negative PC2 values close to the mean of the current *H. amphibius*, as do the specimens from Cal Guardiola. Those of the BB specimens are negative for PC3, close to the values of one of the Upper Valdarno specimens. Procrustes ANOVA statistical test does not show any significant difference between the set of values of both *H. antiquus* and *H. amphibius* specimens (see Table C7).

Second upper molar—The results of the M2 evaluation with geometric morphometrics capture 50.57% of the morphological variability among the specimens with the first three principal components (Fig. 12). PC1 represents 24.01% of the variance, being associated in its positive values to a morphology with little development in its distal end and with the lingual crests of the protocone and hypocone oriented distally, while in its negative values it presents morphologies with a great development of the distostyle and a morphology of the cusps close to rectangular triangles. PC2 accounts for 14.12% of the variance, with “8″ morphologies with a higher ratio of mesio-distal to bucco-lingual diameter for its positive values and mesio-distally flattened with the protocone and hypocone forming acute angles in its lingual crests for its negative values (Fig. 12a). PC3 accounts for 12.44% of the variance and is associated with morphologies that generate a space between the innermost parts of the protocone and hypocone with respect to the paracone and metacone, while in its negative values the preprotocrest approaches the preparacrest, the porstrotocrest approaches the postparacrest, the prehypocrest approaches the premetacrest and the posthipocrest approaches the postmetacrest (Fig. 12b).

Despite the small sample size, a tendency of the extinct taxa towards mesiostyle and distostyle morphologies can be seen, with forms closer to an “8″ with a large relative proportion of mesiodistal to bucco-lingual diameter. The Procrustes ANOVA statistical test highlights the presence of significant differences between the set of values of *H. antiquus* and *H. amphibius* specimens (see Table C7). Even so, it is not possible to clearly discriminate between *H. antiquus*, *H. gorgops* and *H. amphibius*. The values of the BB specimens have great variability, occupying an area in the morphospace almost as wide as that occupied by the totality of *H. antiquus* specimens for components 1 and 2. In CP1 these values range from the negative extreme to the first positive values, comprising the values of the specimens from all the sites with *H. antiquus*, *H. gorgops* and *H. protamphibius* except for Vallparadís Estació, including the specimens without specific determination from Aboucherit and Ain Hanech. In CP2 the variability is lower, presenting positive values and overlapping only with the values from Cal Guardiola or Würzburg-Schalksberg (Fig. 12a). In CP3 variability increases again, although it increases to a greater extent within *H. antiquus*. For CP3 the BB specimens take both negative and positive values and overlap with the values of specimens from

Fig. 8. Ratio diagrams of the dental series (P2-M3) of the specimens of the genus *Hippopotamus* included in this study, highlighting the materials from the Barranc de la Boella sites (Francolí Basin, NE Iberia). L) mesio-distal diameter; W) bucco-lingual diameter; L/W) ratio mesio-distal diameter to bucco-lingual diameter. The basic morphology of each tooth is schematically represented in the lower part of the figure.

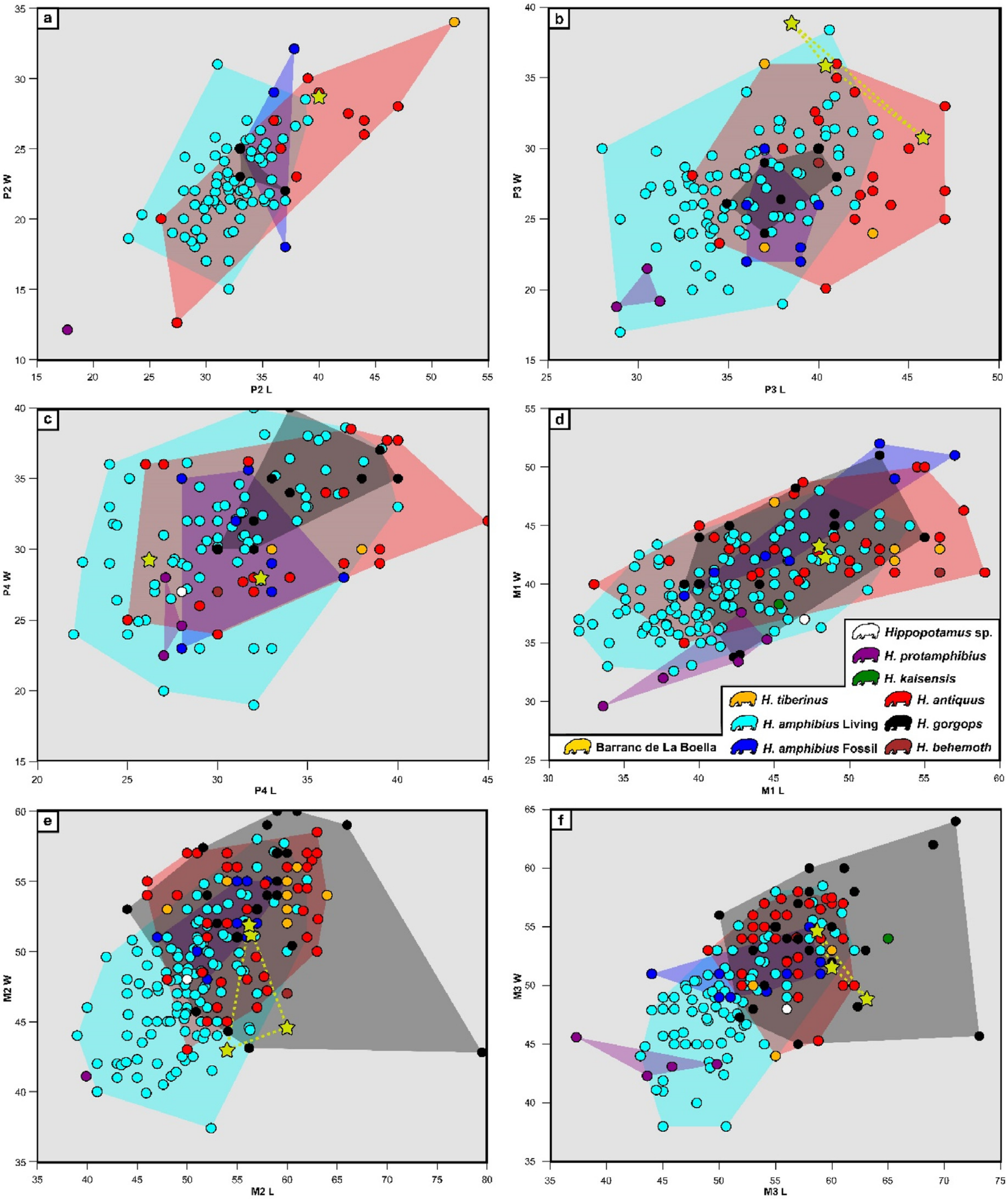


Fig. 9. Scatterplot of mesio-distal diameter (L) versus the bucco-lingual diameter (W) of each dental element (P2-M3) of the specimens of the genus *Hippopotamus* included in this study, highlighting those found in the Barranc de la Boella sites. a) P2, b) P3, c) P4, d) M1, e) M2, f) M3.

all sites with *H. antiquus*, *H. gorgops* and *H. protamphibius* with the exception of Vallparadís Estació and Venta Micena, including the specimens without specific determination from Aboucherit (Fig. 12b).

5. Discussion

5.1. Taxonomic determination

Considering the chronological and geographical overlap of the possible recorded taxa, *H. antiquus* (=*H. major*; =*H. georgicus* sensu Mazza, 1991), *H. tiberinus* (= *H.* ex gr. *H. antiquus*/*H. georgicus*; sensu van der Made et al., 2017b) and *H. amphibius* (=*H. incognitus*) in the European Quaternary and the lack of consensus among authors (Faure, 1985, van der Made et al., 2017b; Mazza, 1991; Mazza and Bertini, 2013; Petronio, 1995), in this paper we consider the most parsimonious systematic hypothesis. This hypothesis is supported by the data that will be presented in the following sections, close to the proposed by Petronio (1995) except for the origin of these taxa from the species *H. protamphibius*. Certainly, the anatomical

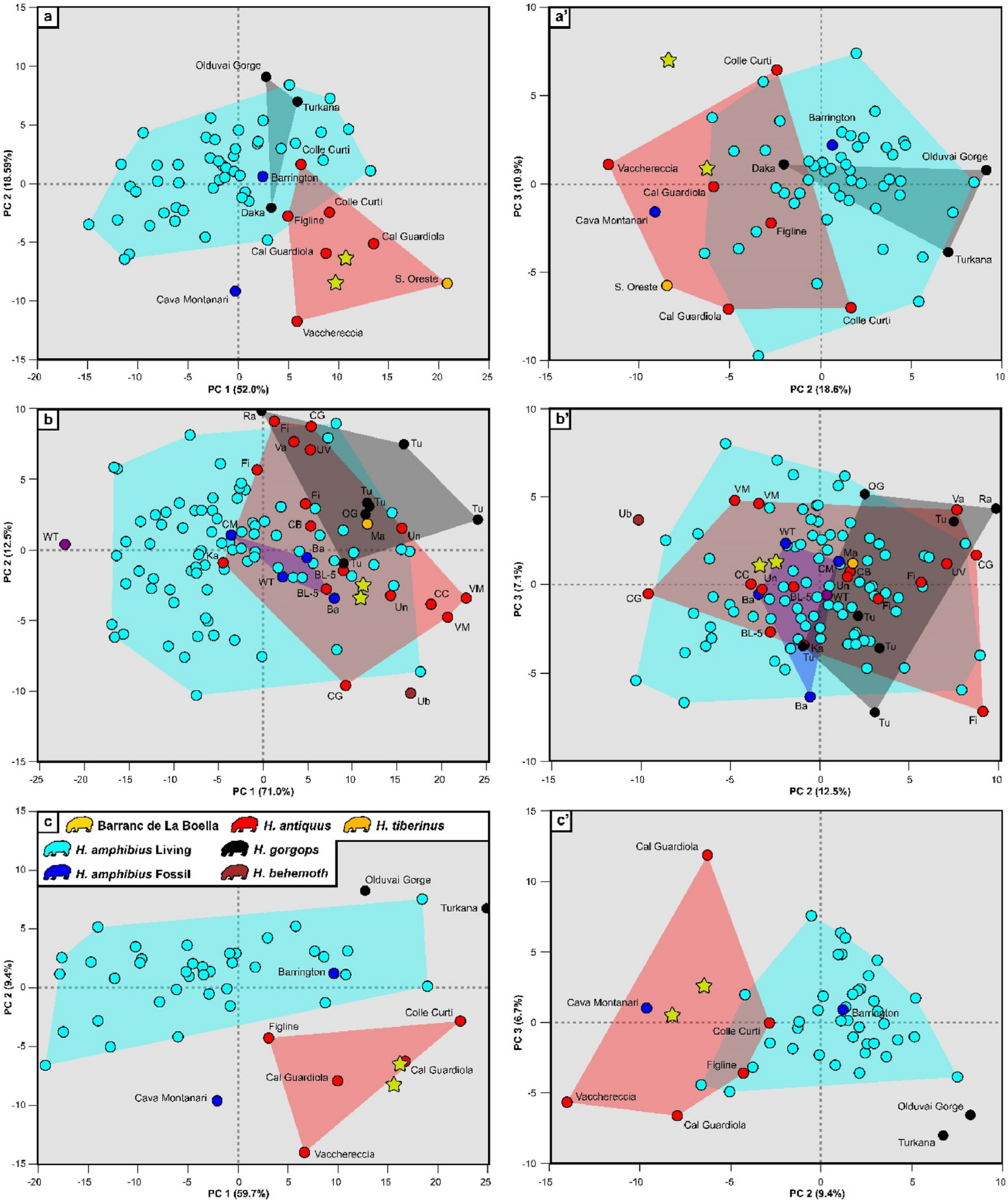


Fig. 10. Principal component analysis of the dentition of the specimens of the genus *Hippopotamus* included in this study, highlighting the materials from the Barranc de la Boella sites (Francolí Basin, NE Iberia). The mesio-distal and bucco-lingual diameters of the premolar (P2–P4; a-a'), molar (M1-M3; b-b') and complete series (P2-M3; c-c') are included. a,b,c) Principal Component (PC) 1 versus PC 2; a',b',c') PC2 versus PC3. The percentage of variance collected by each PC is indicated in brackets next to its name. The species has been used as a graphical grouping factor. The site where the specimen were found is indicated next to each specimen. Ba: Barrington; BL-5: Barranco León-5; CB: Cava Bacchi; CC: Collecurti; CG: Cal Guardiola; CM: Cava Montanari (Tor di Quinto); Fi: Figline; Ka: Kaddanarti; Ma: Maglianella; OG: Olduvai George; Ra: Rawe; Tu: Turkana; Ub: Ubeidiya; Un: Untermassfeld; UV: Upper Valdarno; Va: Vaccherecia; VM: Venta Micena; WT: West Turkana.

characteristics of the specimens bring the BB hippos closer to the less derived forms of *H. antiquus* from the Early Pleistocene, although the intraspecific variability of this taxon and the validity of the consideration of these characteristics as derived/ancestral is not fully known. With current knowledge the presence of *H. amphibius* (=*H. incognitus*) in Europe is significantly younger than the chronological range of BB (Caloi et al., 1980; Kotsakis and Barisone, 2008) and its anatomical and biometric characteristics differ from those present in the described specimens (see previous sections), thus ruling out the determination of the specimens within this taxon. Biometric data and adequate figures of the upper dentition of *H. sirensis* and *H. kaisensis* are lacking (see further discussion in Weston and Boisserie, 2010; van der Made et al., 2017b). The chronological data of the unpublished specimens

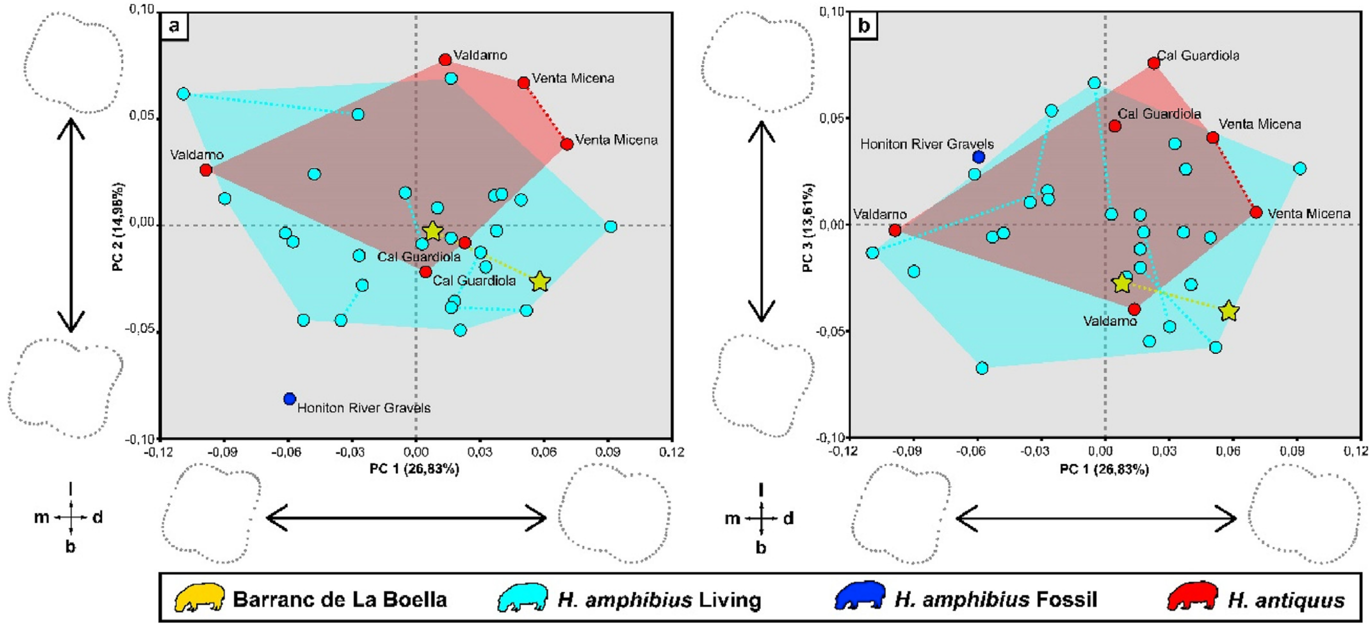


Fig. 11. Principal component analysis of the procrustes values of the landmarks and semilandmarks evaluated in the M1 contour of the specimens of the genus *Hippopotamus* included in this study, highlighting those found in the Barranc de la Boella sites (Francolí Basin, NE Iberia). a) Principal Component (PC) 1 versus PC 2; b) PC2 versus PC3. The percentage of variance collected by each PC is indicated in brackets next to its name. The species has been used as a graphical grouping factor. The shape change is represented associated with the extreme of each PC.

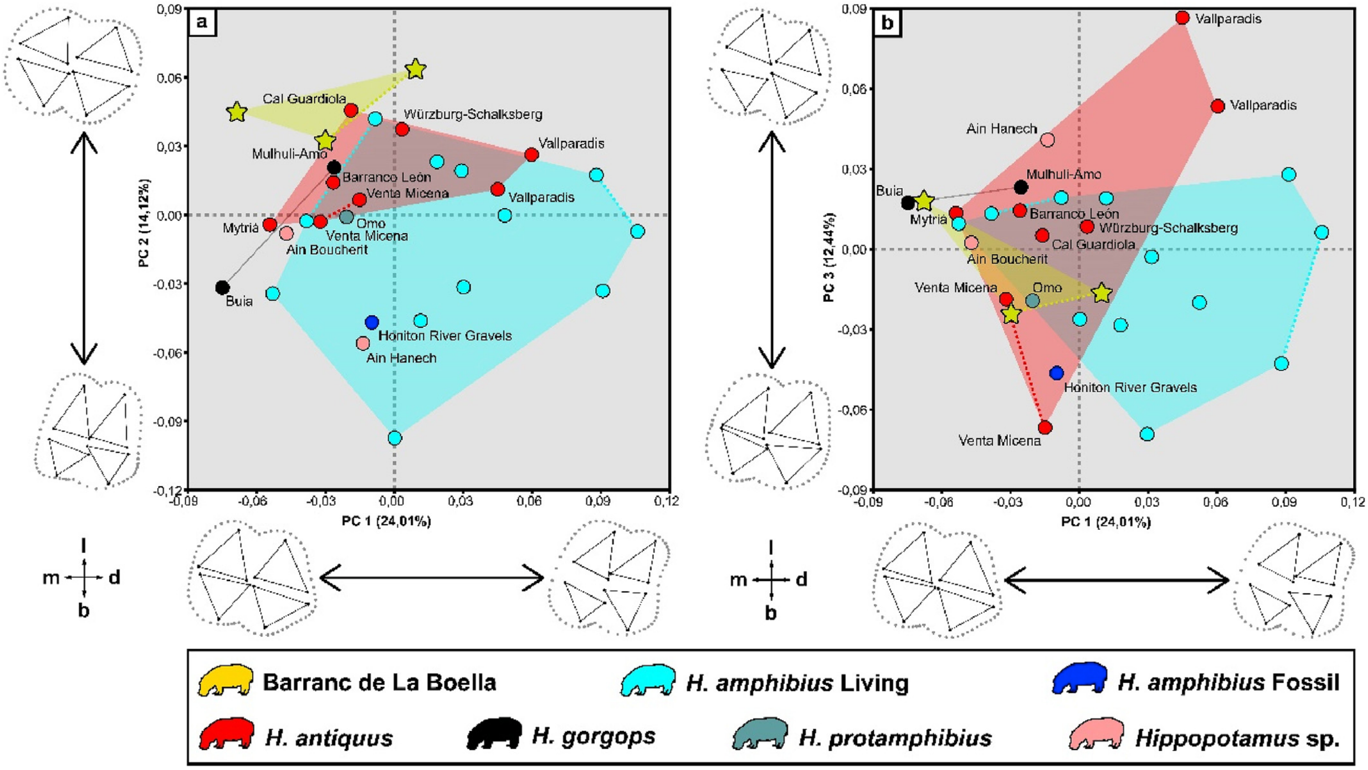


Fig. 12. Principal component analysis of the procrustes values of the landmarks and semilandmarks evaluated in the M2 contour of the specimens of the genus *Hippopotamus* included in this study, highlighting those found in the Barranc de la Boella sites (Francolí Basin, NE Iberia). a) Principal Component (PC) 1 versus PC 2; b) PC2 versus PC3. The percentage of variance collected by each PC is indicated in brackets next to its name. The species has been used as a graphical grouping factor. The shape change is represented associated with the extreme of each PC.

studied, their geographic location, anatomy and biometry are in good agreement with *H. antiquus*, and therefore their identification within this species is proposed. The data on geographical distribution, chronological distribution, descriptive anatomy, linear biometry and geometric morphometrics are discussed in more detail in the following sections.

5.2. Systematic and chrono-corological considerations

From the Neogene to the present day, only two to three genera of representatives belonging to the family Hippopotamidae have been described from the European continent, all belonging to the subfamily Hippopotaminae (Boisserie et al., 2010; Martino et al., 2021). According to the review by Boisserie (2007), the genus *Hippopotamus* as well as the genera *Hexaprotodon* and *Archaeopotamus* are characterised by bunodont molars different from those of tayassuids and P4 with a single main cusp. Differences between *Hippopotamus* and the other two genera are found at the level of dental formula in the number of incisors, in the morphology of the canines, in the development of the orbits and in the robustness of the mandibular symphysis and limbs. Accepting the assessment of Martino et al. (2021), the genera *Hexaprotodon* (*Hexaprotodon*? following Martino et al., 2021) and *Archaeopotamus* are only present in Europe for a short period in the Mio-Pliocene transition, after the Messinian Salinity Crisis. According to the measurements compiled in Martino et al. (2021), both genera have notably smaller tooth dimensions than those observed in the BB specimens. In this case, the morphology of the canines, the measurements of the dental elements, the robustness of the appendicular elements and their geographical and chronological distribution allow us to assign the specimens studied here to the genus *Hippopotamus*.

Considering the specimens from Chiusi Basin, Coste San Giacomo (Bellucci et al., 2012; Pandolfi and Petronio, 2015), Elis and Aetorráchi (Athanassiou, 2022; Reimann and Strauch, 2008) as the earliest known representatives so far of the genus *Hippopotamus* in Europe, and accepting its determination within the species *H. antiquus*, this species would have a presence on the continent since 2.1 Ma ago and extending to about 0.4 Ma in the most conservative estimates (Konidaris et al., 2018; Martino et al., 2022; Tsoukala, 1999). Geographically this taxon has records from the south-westernmost tip of the Iberian Peninsula (Algoz, Portugal, Antunes et al., 1986) to the Caucasus (Akhalkalaki, Georgia, Vekua, 1959), bordering directly with the higher latitude records of *H. behemoth* and *H. gorgops* in the Levant (Ubeidyiah, Israel, Faure, 1986; Latamne, Syria, Guérin et al., 1993). Specimens of the species *H. sirensis*, *H. gorgops* and *H. kaisensis* have been identified near the Strait of Gibraltar, along the African border (van der Made et al., 2017b). Both the chronological range and geographic distribution of *H. antiquus* coincide with the BB data.

Petronio (1995) questioned the validity of *H. tiberinus* meanwhile Mazza (1991) and van der Made et al. (2017b) advocated for its validity. Petronio (1995) indicate that the cranial characteristics that allow it to be differentiated from *H. antiquus* are part of the intraspecific variability known for members of Hippopotamidae. Kahlke (2001), accordingly, points out the low probability that two closely related species coincide in the same chronology and geographic areas, as is the case of Ortona (assigned to *H. antiquus*; Mazza and Bertini, 2013) and S. Oreste (with the characteristics defined by Mazza for *H. tiberinus*; Mazza, 1991, 1995). According to the analysis performed here, there is no characteristic in the anatomical elements evaluated that justifies the separation of two species or chronospecies, neither in the classical sense of *H. tiberinus* (Mazza, 1991) nor in the one proposed by van der Made et al. (2017b). Qualitative anatomical characteristics such as linear biometrics and geometric morphometrics show similar diversity in the set of specimens found in sites with chronologies ranging from the earliest records of *H. antiquus* in the Early Pleistocene to its disappearance in the Middle Pleistocene. Moreover, the large differences between specimens from the same site seem to indicate a large intraspecific variability and sexual dimorphism that could justify the reported differences between sites. This phenomenon has been previously reported by Madurell-Malapeira (2006) at the Cal Guardiola site specifically in canines, astragalus and patella. The former sexual dimorphism and large intraspecific variability displayed by Cal Guardiola and Vallparadís Estació *H. antiquus* specimens contrast with the extant species on where is quite difficult to observe or characterise the sexual dimorphism in isolated anatomical elements (Madurell-Malapeira, 2006; J.M.-M. unpublished data).

Recent revisions of the geographic and temporal distribution of the known record support the hypothesis of a single hippo dispersal into Europe through the Early Pleistocene as the most plausible scenario (Fidalgo et al., 2021a, 2021b), contrasting with van der Made et al. (2017b). The record of hippos between 2.1 Ma and 1.6 Ma in Europe is sparse but seems to be more or less distributed with specimens from Greece (Elis, Athanassiou, 2022; Reimann and Strauch, 2008) to Spain (Mencal-9, Arribas, pers. comm.). The occurrence of specimens in Turkey (Kocakır-2, Demirel et al., 2016) in chronologies that overlap with the first occurrences in the Levantine corridor of the forms considered by van der Made et al. (2017b) as *H. gorgops*/*sirensis* reinforce this geographical and chronological continuity of European hippos from the Early Pleistocene (for a more detailed discussion see Fidalgo et al., 2021b).

In their work, Mazza and Bertini (2013) consider the taxon *H.* ex gr. *H. antiquus* as a more appropriate synonym of the species *H. tiberinus*, describing a trend towards a decrease in the average size of the individuals over time. This taxon would group populations of small-sized individuals assigned to *H. antiquus* from 1 Ma onwards and would last until the end of the Middle Pleistocene. Although several authors (Faure, 1985; Mazo, 1989; Galobart et al., 2003) have previously proposed this downsizing trend, the measurements of the dental elements evaluated here do not seem to show any clear anatomical trend in relation to the chronology. The Upper Valdarno materials alternate in their dimensions with specimens from Middle Pleistocene sites such as Maglianella, and the BB specimens show a variability ranging from values close to those obtained at Mosbach (0.4–0.5 Ma) to values close to Cal Guardiola or Collecurti (ca. 1 Ma). Athanassiou et al. (2018) have also remarked this absence of a decrease in size. Although, according to Mazza (1991), the dental elements seem to have a more conservative morphology and dimensions in relation to the rest of the anatomical elements when discriminating between *H. antiquus* and *H.* ex gr. *H. antiquus*. Certainly, the appendicular elements of the BB are remarkably small. Even so, some of the specimens analysed by Madurell-Malapeira (2006) from the Cal Guardiola levels dated at 1.2 Ma already present these small proportions.

Some authors such as Petronio (1995), Madurell-Malapeira (2006), Martínez-Navarro et al. (2015) or Pandolfi et al. (2020) have highlighted the anatomical similarities between *H. antiquus* (in a broad sense) and *H. gorgops*, raising the possibility of considering *H. gorgops* a junior synonym of *H. antiquus*. The data presented in this paper maintain certain doubts in the consideration of this synonymy: while it is true that the average values of the upper dental series are very similar between taxa and the anatomical variability of their molars is overlapping and does not exceed the variability known in the current common hippo, the set of measurements of the neurocranium and upper premolars suggest a morphology with certain differences for the few specimens of *H. gorgops* for which data were available. More detailed analyses are still needed to resolve this problem.

Faure (1986) describes the species *H. behemoth* as a separate taxon from Ubeidyia (Israel; ca. 1.4 Ma), to which Guérin et al. (1993) ascribe specimens from the Latamne site (Syria; ca. 0.6 Ma). Authors such as Martínez-Navarro et al. (2004b) or Martínez-Navarro and Rabinovich (2010), who assimilate the specimens to forms derived from *H. gorgops*, have questioned this species. Certainly, the anatomical parameters of the upper dentition specimens of Ubeidyia show slightly different values, especially at the level of the proportions of each dental element in the series. Particularly noteworthy are the PCA results of the molar series, which bring the Ubeidyia specimens closer to *H. antiquus* individuals than to the known data of *H. gorgops*.

In Europe we find several sites from the Epivillafranchian (Early-Middle Pleistocene Transition) with records of hippos. These localities range from the Iberian Peninsula to Greece, through France, Italy, Hungary, Germany and the Netherlands (Fig. B8). Among the specimens for which we have been able to compare data in this work are those from the sites of S. Oreste, Collecurti, Renacci (Mazza, 1995), Myrtiá (Athanassiou and Bouzas, 2010), Untermassfeld (Kahlke, 2001), Húescar-1 (Mazo, 1989), Cal Guardiola (Madurell-Malapeira, 2006), Barranco León 5 and Vallaparadís Estació (J.M.-M. and D.F. unpublished data). The biometric values of the neurocranium and upper dentition of these specimens are widely distributed throughout the morphospace, occupying practically all the variability of *H. antiquus*. In general, the BB materials present morphologies and measurements intermediate between the more "advanced" forms (according to the term used by Kahlke (2001) for morphologies similar to S. Oreste specimens) and those more typical of *H. antiquus* (such as the Collecurti specimens). Their small dimensions (especially in the appendicular elements) and the general morphology of M1 and M2 resemble some of the Cal Guardiola specimens, although multivariate analyses of molar measurements bring them closer to the data from Barranco León-5 or Untermassfeld. In any case, the BB hippo specimens studied in this work coincide within the morphological and biometric margins of *H. antiquus* from the Epivillafranchian.

It is interesting to mention the position in morphospace of the specimens without specific determination from Aboucherit (MNHN 195—13·94; van der Made, Pers. Comm.) and Ain Hanech (CNRPAH-A J21 12; van der Made, Pers. Comm.). Some of the Aboucherit material has been determined with doubts as *H. kaisensis*, while in Ain Hanech the presence of *H. gorgops* has been reported (van der Made et al., 2017b). Paradoxically, in the evaluation with geometric morphometrics of one specimen from each site, the Aboucherit specimen most closely matches the range of variability of *H. gorgops* from Buia and Mulhuli-Amo, while the Ain Hanech specimen is more distant in morphospace (Fig. 12). Unfortunately, no specimens assigned to *H. kaisensis* could be found in the geometric morphometric analyses, but the M1 from West Turkana (Harris et al., 1988) for which linear biometric data were available appears to be within the variability of *H. gorgops* and *H. amphibius*.

Although the geographic distribution of *H. amphibius* in the Pleistocene has been remarkably extensive and most of the biometric parameters of its fossil representatives overlap with those obtained for *H. antiquus*, its chronological range in Europe is much younger than the BB estimated chronological range (Pandolfi and Petronio, 2015). With the present data, it is unlikely that this taxon was present in the Iberian Peninsula in the chronology recorded in the BB. Even so, the results of the multivariate analyses of the skull and upper dentition seem to rule out more reliably the assignment of the BB specimens to *H. amphibius*. It is worth mentioning that the specific determination of a large number of specimens discovered in Europe, Anatolia and the Levant is still unknown, and the presence of this species in Africa predates these chronologies, so there is a possibility of future re-evaluations of its chronological and geographical range in Europe.

5.3. Palaeoecological considerations

The Epivillafranchian record of *H. antiquus* is attested at least at 42 sites with a chronological span from 1.1 to 1 Ma to 0.86 Ma (Fig. B8). It is precisely in these chronologies that the greatest geographical range has been reported for this species, with records from the Caucasus (Akhalkalaki; Vekua, 1959) to the Iberian Peninsula (maximum longitude in Algoz; Martino et al., 2022) and from latitudes as low as the southernmost tip of Greece (Megalopolis; Koufos, 2001) to the North Sea (Het Gat and Noordzee II; van Kolfschoten, 2001), the Netherlands (Maasvlakte; Vervoort-Kerkhoff and van Kolfschoten, 1988) or the United Kingdom (Westbury Cave; Adams et al., 2021). Following the latest revisions of the occurrence of *Hippopotamus* in northwestern Europe by Adams et al. (2021), a large dispersal of its populations seems likely in chronologies just prior to the BB record. This putative dispersal event coincides with the onset of the 'Early-Middle Pleistocene Transition' and the transition to the more arid and open-environments characteristic of the Late Villafranchian to the starts of the asymmetry on glacial cycles and an increase in seasonality which in the Mediterranean area means more wet and wooded environments (Madurell-Malapeira et al., 2014 and references therein). Interestingly, this abundance on the *Hippopotamus* record roughly coincides with the first record of acheulian tools precisely at the Barranc de la Boella section (Vallverdú et al., 2014) pointing a possible related climatic constraint for both species.

During the Early-Middle Pleistocene Transition (EMPT; Berends et al., 2021; Head and Gibbard, 2015; Maslin and Brierley, 2015; Strani et al., 2019) the alternation between warm and humid periods and colder and drier phases becomes more acute especially in MIS 22 to MIS 21 (Head and Gibbard, 2015). These changes in the climate generated a response in the composition of faunas in Europe in the form of progressive faunal replacement (Epivillafranchian; Kahlke, 2000; 2004) and in the biological strategies of the populations that remain (e.g. Sorbelli et al., 2021). Interestingly, the composition of faunas in the Iberian Peninsula and other lower latitudes does not seem to alter significantly until MIS 21 (Madurell-Malapeira et al., 2017, 2021). Precisely, the presence of hippo specimens from these chronologies until the mid-Middle Pleistocene is apparently continuous in the Italic and Iberian peninsulas (Fig. 1 & B.8; Martino and Pandolfi, 2021; Pandolfi and Petronio, 2015). In the Iberian Peninsula we find records in several layers of the sequence of Vallparadís Estació (Madurell-Malapeira et al., 2010), Fuensanta del Júcar (Mazo et al., 1990; Sánchez et al., 2004), Barranco León 5 (Espigares, 2010; Gibert et al., 1998; Ribot et al., 2015), Cal Guardiola (Madurell-Malapeira, 2006; Madurell-Malapeira et al., 2010), Pontón de la Oliva (Sesé and Soto, 2000); Incarcal I and II (Galobart et al., 2003), Valverde de Calatraba (Crusafont, 1960), Húescar 1 (Mazo, 1989; Alberdi et al., 1989), Atapuerca-TD8 (Carbonell et al., 1999, van der Made, 1998, van der Made et al., 2017a) and Algoz (Martino et al., 2022). In contrast, the presence of *H. antiquus* in northwestern Europe is more discontinuous, with an apparent absence from post-Jaramillo chronologies (Untermassfeld; Kahlke, 1997; 2001) to MIS 17—15 collected in Abbeville (France; Antoine et al., 2016) or Pakefield/Kessingland (UK; Stuart and Lister, 2001).

Despite their apparent characteristic niche parameters, the palaeoecological plasticity of *Hippopotamus* species populations remains unclear. The climatic range of these species during the Pleistocene and Holocene includes climates ranging from humid Mediterranean areas to areas with warm and humid climates in Africa or the Arabian Peninsula (van der Made et al., 2017b; Stewart et al., 2019; among others). The presence of hippos in areas such as the banks of the Nile (in Egypt) until recent times makes it clear that ethological thermal control strategies allow them to withstand low overall humidity at high temperatures, as long as sufficient water bodies are present (Manlius, 2000). It is difficult to infer the lower limit of temperatures included in the climatic range of hippos. A climate with thermal phases leading to freezing of the surface of water bodies is not acceptable, as it would preclude much of their natural habits. Even so, hippos have occasionally been seen at high altitudes (1500–2000 m above sea level) and withstanding extremely low temperatures in zoos (Walzer and Stalder, 2015). While it is true, assessments of the response of captive hippos to water temperature point to a lower use of water bodies at lower temperatures and condition a drastic change in their behaviour (Fernandez et al., 2020). In general and coinciding with Candy et al. (2010) and Mazza and Bertini (2013), the abundance of permanent water bodies seems to be the most limiting environmental factor for the maintenance of hippo populations in an area.

Following the palaeoecological inferences made for *H. antiquus* by authors such as Mazza (1995), Martínez-Navarro et al. (2010), van der Made et al. (2017b) or Palmqvist et al. (2022), this species presented an ecomorphotype more closely linked to the aquatic environment than the current species of common hippo. This hypothesis is based on the stable isotope data of the Venta Micena specimens (Palmqvist et al., 2003, 2008, 2022), the estimates of body mass of individuals from different localities (Mazza and Bertini, 2013; Palmqvist et al., 2022), the cranial anatomy characteristic of the species (Martínez-Navarro et al., 2010; Mazza, 1995, van der Made et al., 2017b) and the anatomy and proportions of the limb bones (Kahlke, 1997; Martínez-Navarro, 2010; Mazza, 1995). On the other hand, other stable isotope data in dentition of specimens of *H. gorgops* (closely related to *H. antiquus*, as mentioned above) from African sites (Harris et al., 2008) or the presence of characteristic locomotor palaeopathologies (Kierdorf and Kahlke, 2020) point to a palaeoecology of *H. antiquus* populations like that of current *H. amphibius* populations. A possible conciliatory view might consider that the set of anatomical characteristics of *H. antiquus* indicates a more aquatic behaviour than that of the current common hippo, although maintaining the same basic live style and subject to possible changes in the life history of this species. However, this approach is beyond the scope of this paper.

Taking into account the estimates of the ecological ranges to which this species would be subject and the hardening of the cold and arid climatic phases in Europe from the chronologies represented in the BB (Fig. 13), it seems reasonable that areas with greater Mediterranean influence, a milder climate and the availability of permanent bodies of water (such as the Iberian Peninsula, the Italian Peninsula or Greece) acted as climatic refugia for hippo populations. Even so, the data obtained from the stratigraphic sequences of the Quibas site (Piñero et al., 2020) and Valparadís Estació (Madurell-Malapeira et al., 2017; Sorbelli et al., 2021) report arid phases in the Jaramillo subchron and sparse record of hippos which in contrast are very abundant at the post-Jaramillo times of Vallparadís Section layers CGRD7 and EVT7 (MIS 21) on where wet and milder temperatures were inferred (Strani et al., 2019). The study and comparison of more complete time series with hippo records in these chronologies, such as those represented in the Vallparadís Section (Madurell-Malapeira et al., 2010), and their comparison with the European record may help to find an explanation for the apparent maintenance in Europe of populations of a mammal so associated with humid and warm climates in times of strong climatic change.

The favourable environmental conditions for hippo populations do not seem to be very different from those estimated for early hominin populations in Europe (Saarinen et al., 2021). These environmental conditions (e.g. permanent watercourses or milder winters) may have equally driven the distribution of both taxa during the Early Pleistocene. Indeed, some of the hypotheses for the distribution of human populations at the end of the Early Pleistocene point to large dispersals across the European continent that would overlap with those proposed by Adams et al. (2021) for

Fig. 13. Palaeoartistic reconstruction of the environment of Barranc de la Boella (Francolí Basin, NE Iberia) in the Early Pleistocene by the illustrator Domingo López González, according to the version of the author of this paper A.R.

hippos (Kahlke et al., 2011; Michel et al., 2017; Muttoni et al., 2010, 2018). Consumption of hippos by hominins with the technological capacity present at Barranc de la Boella is amply demonstrated in the African record (Altamura et al., 2020; Clark and Kurashina, 1979; Hill, 1983). In contrast, evidence for hippo consumption in Europe during the Early and Middle Pleistocene is very limited. Only the controversial finds from Vallparadís Estació and Untermassfeld (Garcia et al., 2013; see Madurell-Malapeira et al., 2012), which have been quarantined by the scientific community (Roebroeks et al., 2018), and a single specimen with cut mark found in Barranco León (Espigares, 2010) have been reported with chronologies relating to the Early Pleistocene. Bolomor Cave is the only site where this type of consumption has been reported in the Middle Pleistocene (Blasco et al., 2013). Despite the large overlap in the climatic optimum between the two mammals, it does not appear that they had a very close direct trophic relationship in Europe. This phenomenon is compatible with the great danger of accessing carcasses of animals that live, and die, within groups with high density of individuals and pose a threat to other mammals due to their known aggressiveness and territorial behaviour when in water (Eltringham, 1999). However, future findings or re-evaluations of this topic may shed light on the causes of these differences between the apparent relationships between hippopotamuses and hominins in Africa and Europe.

Specifically, the palaeoenvironment estimated for the BB is consistent with what would be expected for the optimal environmental range of hippos. The palaeoecological reconstructions inferred from micromammals (Lozano-Fernández et al., 2015), malacofauna (Vallverdú et al., 2008) and palynological analyses (Pineda et al., 2017) are qualified by the presence of this large amphibious mammals, suggesting that in this habitat of patchy vegetation and seasonal rainfall (Rosas et al., 2015; Vallverdú et al., 2014) there is a constant presence of sufficient bodies of water to allow the subsistence of its populations. The evidence of human presence in the same archaeological levels where hippo fossils appear raises the possibility in future work of paying special attention to the ecological relationship between two mammals that underwent major changes in their spatial distribution in a period of great climatic change coinciding with the end of the Early Pleistocene.

6. Conclusions

According to the data and analysis presented here, we can conclude that the studied *Hippopotamus* specimens, from the Barranc de la Boella Section, fit within the characteristics considered for the species *Hippopotamus antiquus*. The biometric values and anatomical characteristics of these specimens are consistent with the morphological variability found in the hippopotamuses previously recorded in the Epivillafranchian of Europe. Even so, the great overlap in the phenotypic characteristics of *H. antiquus* specimens dated with different chronologies reinforces the idea of considering a single species of hippo in the Early Pleistocene and part of the Middle Pleistocene in Europe, when the extant *H. amphibius* is first reported from this continent. Likewise, data from the fossil record (chronological and geographic distribution), together with anatomical assessment, point to a single entry of hippos into Europe during the Early Pleistocene. In addition, knowledge of intraspecific variability in *H. antiquus* has been expanded, highlighting the importance of an adequate understanding of its sexual dimorphism, ontogeny and phenotypic response to environmental changes. With the available data, it has not been possible to reach a conclusion on the synonymy between *H. antiquus* and *H. gorgops*, so this debate remains pending for future work more focused on this issue.

The presence of this taxon in the archaeopalaeontological Section of Barranc de la Boella and other Epivillafranchian sites from northeast Iberia highlights the great importance of permanent water bodies in the ecosystems represented, raising the debate as to whether the fossil associations of these sites correspond to interglacial periods of great expansion of hippo populations or whether it is possible that these areas acted as climatic refugia in colder stages. The co-occurrence of hominids and hippos at these sites and their similarities in terms of geographic distribution in the Early Pleistocene highlight the importance of delving deeper into the palaeoecology and biogeography of European hippos as an approach to the biotic and abiotic parameters that shaped the ecosystems in which hominid populations were found. Finally, the increase of relative abundance of *Hippopotamus* record during the Epivillafranchian in lower latitudes, associated at Barranc de la Boella Section with the first European Acheulian tools, suggest a putative climatic constraint for these species probably related with the abundance of water bodies and mild temperatures.

Author statement

D. Fidalgo: research design, data analysis, writing, review and editing, **A. Rosas** and **J. Madurell-Malapeira**: experimental design, data analysis, discussion and review, **A. Pineda**, **R. Huguet**, **A. García-Tabernero**, **I. Cáceres**, **A. Ollé**, **J. Vallverdú** and **P. Saladie**: fieldwork, result discussion and review.

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

I have shared most of my data at the Attach File

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Appendix A. Supplementary data

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References

Adams, N.F., Candy, I., Schreve, D.C., 2021. An early pleistocene hippopotamus from Westbury Cave, Somerset, England: support for a previously unrecognized temperate interval in the British Quaternary record. J. Quat. Sci. https://doi.org/10.1002/jqs.3375. October.

Alberdi, M.T., Ruiz Bustos, A., 1985. Descripción y significado bioestratigráfico y climático del *Equus e Hippopotamus*, en el yacimiento de Venta Micena (Granada). Estud. Geol. 41 (c), 251–261. https://doi.org/10.3989/egeol.85413-4708.

Alberdi, M.T., Alcalá, L., Azanza, B., Cerdeño, E., Mazo, A.V., Morales, J., Sesé, C., 1989. Consideraciones bioestratigráficas sobre la fauna de vertebrados fósiles de la cuenca de Guadix-Baza (Granada, España). Geol. Paleontol. Cuenca Guadix-Baza 11 (l), 347–355.

Altamura, F., Gaudzinski-Windheuser, S., Melis, R.T., Mussi, M., 2020. Reassessing hominin skills at an early middle pleistocene hippo butchery site: Gombore II-2 (Melka Kunture, upper Awash valley, Ethiopia). J. Paleolithic Archaeol. 3, 1–32. https://doi.org/10.1007/s41982-019-00046-0.

Antoine, P., Moncel, M.H., Limondin-Lozouet, N., Locht, J.L., Bahain, J.J., Moreno, D., Voinchet, P., Auguste, P., Stoetzel, E., Dabkowski, J., Bello, S.M., Parfitthi, S.A., Tombret, O., Hardy, B., 2016. Palaeoenvironment and dating of the early Acheulean localities from the Somme river basin (northern France): new discoveries from the high terrace at Abbeville-Carrière Carpentier. Quat. Sci. Rev. 149, 338–371. https://doi.org/10.1016/j.quascirev.2016.07.035.

Antunes, M., Azzaroli, A., Favre, M., Guérin, C., Mein, P., 1986. Mammifères pléistocènes d'Algoz, en Algarve: une révision. Cien. Terra 8, 73–85.

Athanassiou, A., 2022. Fossil vertebrates of Greece. Fossil Vertebrates Greece 2. https://doi.org/10.1007/978-3-030-68442-6, 2, October.

Athanassiou, A., Bouzas, D., 2010. New hippopotamid finds in Eurotas valley (Laconia, Greece). Proc. XIX CBGA 99, 57–62.

Athanassiou, A., Michailidis, D., Vlachos, E., Tourloukis, V., Thompson, N., Harvati, K., 2018. Pleistocene vertebrates from the Kyparíssia lignite mine, Megalopolis basin, S. Greece: Testudines, Aves, Suiformes. Quat. Int. 497 (February), 178–197. https://doi.org/10.1016/j.quaint.2018.06.030.

Bastir, M., García-Martínez, D., Torres-Tamayo, N., Palancar, C., Fernández-Pérez, F.J., Riesco-López, A., Osborne-Márquez, P., Ávila, M., López-Gallo, P., 2019. Workflows in a virtual morphology lab: 3D scanning, measuring, and printing. J. Anthropol. Sci. 97, 107–134. https://doi.org/10.4436/JASS.97003.

Bellucci, L., Mazzini, I., Scardia, G., Bruni, L., Parenti, F., Segre, A.G., Naldini, E.S., Sardella, R., 2012. The site of Coste san Giacomo (early pleistocene, central Italy): palaeoenvironmental analysis and biochronological overview. Quat. Int. 267, 30–39. https://doi.org/10.1016/j.quaint.2011.04.006.

Berends, C.J., Köhler, P., Lourens, L.J., van de Wal, R.S.W., 2021. On the cause of the mid-pleistocene transition. Rev. Geophys. 59 (2). https://doi.org/10.1029/2020RG000727.

Blandamura, F., Azzaroli, A., 1977. L'"Ippopotamo Maggiore" di Filippo Nesti. Accademia nazionale dei Lincei. Atti della Accad. Naz. Lincei 14 (8), 169–188.

Blasco, R., Rosell, J., Domínguez-Rodrigo, M., Lozano, S., Pastó, I., Riba, D., Vaquero, M., Fernández Peris, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. Learning by heart: cultural patterns in the faunal processing sequence during the Middle Pleistocene. PLoS One 8 (2), e55863. https://doi.org/10.1371/journal.pone.0055863.

Boisserie, J.-R., 2007. Family Hippopotamidae. In: Prothero, D.R., Foss, S.E. (Eds.), The Evolution of Artiodactyls. Johns Hopkins University Press, Baltimore, pp. 106–119.

Boisserie, J.-R., Gilbert, W.H., 2008. Hippopotamidae. In: Gilbert, W.H., Asfaw, W. (Eds.), Homo Erectus: Pleistocene Evidence from the Middle Awash, Ethiopia. University of California Press, California, pp. 179–191.

Boisserie, J.-R., Lihoreau, F., Orliac, M., Fisher, R.E., Weston, E.M., Ducrocq, S., 2010. Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). Zool. J. Linn. Soc. 158 (2), 325–366. https://doi.org/10.1111/j.1096-3642.2009.00548.x.

Bolomey, A., 1965. Die fauna zweier villafrankischer Fundstellen in Rumänien, Vorläufige Mitteilung. Ber. Geol. Ges. DDR 10 (1), 77–88.

Bookstein, F.L., 1991. Morphometric Tools for Landmark Data. Cambridge University Press, Cambridge.

Bookstein, F.L., 1996. Combining the tools of geometric morphometrics. In: Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P., Slice, D.E. (Eds.), Advances in Morphometrics. Plenum Press, New York, pp. 131–151.

Bookstein, F.L., 1997. Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. Med. Image Anal. 1 (3), 225–243. https://doi.org/10.1016/S1361-8415(97)85012-8.

Bookstein, F.L., Streissguth, A.P., Sampson, P.D., Connor, P.D., Barr, H.M., 2002. Corpus callosum shape and neuropsychological deficits in adult males with heavy fetal alcohol exposure. Neuroimagen 15, 233–251. https://doi.org/10.1006/nimg.2001.0977.

Caloi, L., Palombo, M.R., Petronio, C., 1980. Resti cranici di *Hippopotamus antiquus* (=*H. major*) e *Hippopotamus amphibius* conservati nel Museo di Paleontologia dell'universita di Roma. Geol. Rom. 19, 91–119.

Candy, I., Coope, G.R., Lee, J.R., Parfitt, S.A., Preece, R.C., Rose, J., Schreve, D.C., 2010. Pronounced warmth during early Middle Pleistocene interglacials: investigating the Mid- Brunhes Event in the British terrestrial sequence. Earth Sci. Rev. 103, 183–196. https://doi.org/10.1016/j.earscirev.2010.09.007.

Carbonell, E., Esteban, M., Martín, A., Mosquera, M., Rodríguez-Álvarez, X.P., Ollé, A., Sala, R., Vergés, J.M., Bermúdez de Castro, J.M., Ortega, A.I., 1999. The Pleistocene site of Gran Dolina, Sierra de Atapuerca, Spain: a history of the archaeological investigations. J. Hum. Evol. 37, 313–324. https://doi.org/10.1006/jhev.1999.0282.

Cardoso, J.L., 1993. Contribuição para o conhecimento dos grandes mamíferos do Plistocénico superior de Portugal. Oeiras.

Clark, J.D., Kurashina, H., 1979. Hominid occupation of the east-central highlands of Ethiopia in the plio-pleistocene. Nature 282 (5734), 33–39. https://doi.org/10.1038/282033a0.

Crusafont, M., 1960. Le Quaternaire Espagnol et sa faune de Mammiferes. Essai de synthèse. Anthropos 1, 55–64.

Demirel, F.A., Mayda, S., Alçiçek, M.C., Kaya, T.T., Aytek, A.I., 2016. Kocakir-2: first record of early pleistocene *Canis* and *Hippopotamus* from Burdur basin (SW Turkey). XIV EAVP 39.

Dietrich, W.O., 1928. Pleistocäne deutschostafrikanische *hippopotamus*-reste. Wissensch. Ergebnisse Oldoway Exped. Herausgeben 3, 1–41.

Eltringham, S.K., 1999. In: N. J (Ed.), The Hippos: Natural History and Conservation. Princeton University Press, Princeton.

Espigares, M.P., 2010. Análisis y modelización del contexto sedimentario y los atributos tafonómicos de los yacimientos pleistocénicos del borde nororiental de la cuenca de Guadix-Baza. Universidad de Granada, Granada.

Faure, M., 1983. Les Hippopotamidae (Mammalia, Artiodactyla) d'Europe Occidentale. Université Claude-Bernard, Lyon.

Faure, M., 1984. *Hippopotamus incognitus* Nov. Sp., un hippopotame (Mammalia, Artiodactyla) du Pléistocène d'Europe occidentale. Geobios 17 (4), 427–434.

Faure, M., 1985. Les Hippopotames quaternaires non-insulaires d'Europe occidentale. Nouv. Arch. Mus. Hist. Nat. Lyon 23, 13–79.

Faure, M., 1986. Les hippopotamidés du Pléistocène ancien d'Oubeidiyeh (Israël). Mem. Travaux Cent. Rech. Fr. Jerus. 5, 107–142.

Fernandez, E.J., Ramirez, M., Hawkes, N.C., 2020. Activity and pool use in relation to temperature and water changes in zoo hippopotamuses (*Hippopotamus amphibious*). Animals 10 (6), 1–11. https://doi.org/10.3390/ani10061022.

Fidalgo, D., Galli, E., Madurell-Malapeira, J., Rosas, A., 2021a. The First Quaternary Hippos in Europe. XIX EJIP, p. 46.

Fidalgo, D., Galli, E., Madurell-Malapeira, J., Rosas, A., 2021b. Earliest Pleistocene European hippos: a review. Comun. Geol. 1098, 65–69. https://doi.org/10.34637/06rg-c937. Especial I.

Galobart, À., Ros, X., Maroto, J., Vila, B., 2003. Descripción del material de ipopótamo (*Hippopotamus antiquus* Desmarest, 1822) de los yacimientos del Pleistoceno Inferior de Incarcal (Girona, NE de la Península Ibérica). Paleontol. Evol. 34, 153–173.

Garcia, J., Landeck, G., Martínez, K., Carbonell, E., 2013. Hominin dispersals from the Jaramillo subchron in central and south-western Europe: Untermassfeld (Germany) and Vallparadís (Spain). Quat. Int. 316, 73–93. https://doi.org/10.1016/j.quaint.2013.03.005.

Geraads, D., 1980. La faune des sites à *Homo erectus* des carrières Thomas (Casablanca, Maroc). Quaternaria 22, 65–94.

Gibert, J., Gibert, L., Iglesias, A., Maestro, E., 1998. Two “Oldowan” assemblages in the Plio-Pleistocene deposits of the Orce region, southeast Spain. Antiquity 72 (275), 17–25. https://doi.org/10.1017/S0003598X00086233.

Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E., Torre, D., 1997. Biochronology of selected mammals, molluscs and ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. Riv. Ital. Paleontol. Stratigr. 103 (3), 369–388. https://doi.org/10.13130/2039-4942/5299.

Green, W.D.K., 1996. The thin-plate spline and images with curving features. In: Mardia, K.V., Gill, C.A., Dryden, I.L. (Eds.), Image Fusion and Shape Variability. University of Leeds Press, Leeds, pp. 79–87.

Guérin, C., Dewolf, Y., Lautridou, J.-P., 2003. Révision d'un site paléontologique célèbre: Saint-Prest (Chartres, France). Geobios 36 (1), 55–82. https://doi.org/10.1016/S0016-6995(02)00106-7.

Guerin, C., Eisenmann, V., Faure, M., 1993. Les grands mammifères du gisement Pléistocène Moyen de Latamné (Vallée de l'Oeonte, Syrie). In: Sanlaville, P., Bensaçon, J.U., Copeland, L., Muhesen, S. (Eds.), Le Paléolithique de la Valée Moyenne de l'Oronte (Syrie), British Archaeological Reports. International Series, Oxford, pp. 169–178.

Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and surfaces. Hystrix 24 (1), 103–109. https://doi.org/10.4404/hystrix-24.1-6292.

Gunz, P., Mitteroecker, P., Bookstein, F.L., 2005. Modern Morphometrics in Physical Anthropology: Semilandmarks in 3D. Kluwer/Plenum, Nueva York.

Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G.W., Bookstein, F.L., 2009. Principles for the virtual reconstruction of hominin crania. J. Hum. Evol. 57 (1), 48–62. https://doi.org/10.1016/j.jhevol.2009.04.004.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1), 1–9.

Harris, J.M., 1991. Family Hippopotamidae. In: Harris, J.M. (Ed.), Koobi for a Research Project, Volume 3. The Fossil Ungulates: Geology. Fossil Artiodactyls, and Palaeoenvironments. Clarendon Press, Oxford, pp. 31–85.

Harris, J.M., Brown, F.H., Leakey, M.G., 1988. Stratigraphy and paleontology of Pliocene and pleistocene localities west of lake Turkana, Kenya. Contribut. Sci. Nat. Hist. Mus. Los Angeles County 399, 1–128.

Harris, J.M., Cerling, T.E., Leakey, M.G., Passey, B.H., 2008. Stable isotope ecology of fossil hippopotamids from the lake Turkana basin of east Africa. J. Zool. 275 (3), 323–331. https://doi.org/10.1111/j.1469-7998.2008.00444.x.

Head, M.J., Gibbard, P.L., 2015. Early-Middle Pleistocene transitions: linking terrestrial and marine realm. Quat. Int. 389, 7–46. https://doi.org/10.1016/j.quaint.2015.09.042.

Hill, A., 1983. Hippopotamus butchery by Homo erectus at Olduvai. J. Archaeol. Sci. 10 (2), 135–137. https://doi.org/10.1016/0305-4403(83)90047-X.

Kahlke, R.-D., 1987. On the occurrence of *Hippopotamus* (Mammalia, Artiodactyla) in the pleistocene of Achalkalaki (Gruzinian SSR, Soviet union) and on the distribution of the genus in South-east Europe. Z. Geol. Wiss. 15, 407–414.

Kahlke, R.-D., 1997. Die Hippopotamus-reste aus dem unterpleistozän von Untermassdeld. Das Pleistozän Untermassfeld Meiningen (Thüringen), Teil 1, 277–374.

Kahlke, R.-D., 2000. The early pleistocene (Epivillafranchian) faunal site of Untermassfeld (Thuringia, Central Germany). Synthesis of new results. In: Lordkipanidze, D., Bar-Yosef, O., Otte, M. (Eds.), Early Humans at the Gates of Europe. Etudes et Recherches Archéologiques de l'Université de Liège, Liège, pp. 123–138.

Kahlke, R.-D., 2001. Schädelreste von *Hippopotamus* aus dem Unterpleistozän von Untermassfeld. Das Pleistozän Unterma?feld bei Meiningen (Th?ringen), Teil 2 40 (2), 483–500.

Kahlke, R.-D., 2004. Late early pleistocene European large mammals: a mixture of Villafranchian and Galerian (Cromerian) elements? In: Maul, L.C., Kahlke, R.-D. (Eds.), *Late Neogene And Quaternary Biodiversity and Evolution: Regional Developments and Interregional Correlations* Conference. Terra Nostra, Schriften der Alfred-Wegener-Stiftung, Berlin, pp. 125–127.

Kahlke, R.-D., 2006. Untermassfeld-A late Early Pleistocene (Epivillafranchian) fossil site near Meiningen (Thuringia, Germany) and its position in the development of the European mammal fauna. Brit. Archaeol. Rep. Ltd. Brit. Archaeol. Rep. Int. Ser. 1578, 1–144.

Kahlke, R.D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quat. Sci. Rev. 30 (11–12), 1368–1395. https://doi.org/10.1016/j.quascirev.2010.07.020.

Kierdorf, U., Kahlke, R.D., 2020. Pathological findings on remains of hippopotamids from the early pleistocene site of Untermassfeld. *The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany)*. Part 4. Monogr. RGZM Band 40 (4), 1251–1272.

Klingenberg, C.P., 2011. MorphoJ: an integrated software package for geometric morphometrics. Mol. Ecol. Resourc. 11, 353–357. https://doi.org/10.1111/j.1755-0998.2010.02924.x.

Koenigswald, W., Heinrich, W.D., 1999. Mittelpleistozäne Säugetierfaunen aus Mitteleu- ropa - der Versuch einer biostratigraphischen Zuordnung. Kaupia 9, 53–112.

Konidaris, G.E., Athanassiou, A., Tourloukis, V., Thompson, N., Giusti, D., Panagopoulou, E., Harvati, K., 2018. The skeleton of a straight-tusked elephant (*Palaeoloxodon antiquus*) and other large mammals from the Middle Pleistocenebutchering locality Marathousa 1 (Megalopolis Basin, Greece): preliminary results. Quat. Int. 497, 65–84. https://doi.org/10.1016/j.quaint.2017.12.001.

Kotsakis, T., Barisone, G., 2008. A short account on fossil vertebrates of Rome. Geol. Roma Dal Centro Stor. Alla Periferia 80 (1), 115–143.

Koufos, G.D., 2001. The Villafranchian mammalian faunas and biochronology of Greece. Boll. Soc. Paleontol. Ital. 40 (2), 217–223.

Laws, R.M., 1968. Dentition and ageing of the hippopotamus. Afr. J. Ecol. 6 (1), 19–52. https://doi.org/10.1111/j.1365-2028.1968.tb00899.x.

Lozano-Fernández, I., Bañuls-Cardona, S., Blain, H.A., López-García, J.M., Vallverdú, J., Agustí, J., Cuenca-Bescós, G., 2014. Biochronological data inferred from the Early Pleistocene small mammals of the Barranc de la Boella site (Tarragona, northeastern Spain). J. Quat. Sci. 29 (7), 722–728. https://doi.org/10.1002/jqs.2744.

Lozano-Fernández, I., Vallverdú, J., Saladié, P., Rosas, A., Agustí, J., 2015. Datos paleoambientales inferidos a partir de los micromamíferos del Pleistoceno Inferior del yacimiento del Barranc de la Boella (Tarragona, España). XIII EJIP, pp. 180–182.

Lucy, K.M., Indu, V.R., Leena, C., Fathima, R., George, C., Patki, H.S., Surjith, S., Anneth, A.J., 2018. Gross anatomy of the skull of hippopotamus (*Hippopotamus amphibius*). Indian J. Anim. Res. 52 (5), 793–795. https://doi.org/10.18805/ijar.v0iOF.7659.

Madurell-Malapeira, J., 2006. Estudi de les restes d'Hippopotamus antiquus (Hippopotamidae, Mammalia) del jaciment del Pleistocè Inferior de Cal Guardiola (Terrassa). Universidad Autònoma de Barcelona, Barcelona.

Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X., 2010. The Vallparadís section (Terrassa, Iberian peninsula) and the latest Villafranchian faunas of Europe. Quat. Sci. Rev. 29 (27–28), 3972–3982. https://doi.org/10.1016/j.quascirev.2010.09.020.

Madurell-Malapeira, J., Alba, D.M., Minwer-Barakat, R., Aurell-Garrido, J., Moyà-Solà, S., 2012. Early human dispersals into the Iberian Peninsula: a comment on Martínez et al. (2010) and Garcia et al. (2011). J. Hum. Evol. 62 (1), 169–173. https://doi.org/10.1016/j.jhevol.2011.10.005.

Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Alba, D.M., Aurell-Garrido, J., 2014. Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. J. Iber. Geol. 40 (1), 167–178. https://doi.org/10.5209/rev_JIGE.2014.v40.n1.44093.

Madurell-Malapeira, J., Alba, D.M., Espigares, M.P., Vinuesa, V., Palmqvist, P., Martínez-Navarro, B., Moyà-Solà, S., 2017. Were large carnivorans 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. 431, 42–52. https://doi.org/10.1016/j.quaint.2015.07.040.

Madurell-Malapeira, J., Sorbelli, L., Ros-Montoya, S., Martínez-Navarro, B., Vallverdú, J., Pineda, A., Rosas, A., Huguet, R., Cáceres, I., García-Tabernero, A., López-Polín, L., Ollé, A., Saladié, P., 2019. Acheulian tools and Villafranchian taxa: The latest Early Pleistocene large mammal assemblage from Barranc de la Boella (NE Iberian Peninsula). *XXXV Jornadas de Paleontología*. Sociedad Española de Paleontología, pp. 161–166. DL GR-1191-2019.

Madurell-Malapeira, J., Sorbelli, L., Prat-Vericat, M., Rufí, I., Bartolini, S., 2021. The Iberian Epivillafranchian Large Mammal Assemblages, vol. 110. VIII Conference of the European Association of Vertebrate Palaeontologists.

Manlius, N., 2000. Biogeographie et Ecologie historique de l'hippopotame en Egypte. Belg. J. Zool. 130 (1), 59–66.

Marra, F., Nomade, S., Pereira, A., Petronio, C., Salari, L., Sottili, G., Bahain, J.J., Boschian, G., Di Stefano, G., Falguères, C., Florindo, F., Gaeta, M., Giaccio, B., Masotta, M., 2018. A review of the geologic sections and the faunal assemblages of Aurelian Mammal Age of Latium (Italy) in the light of a new chronostratigraphic framework. Quat. Sci. Rev. 181, 173–199. https://doi.org/10.1016/j.quascirev.2017.12.007.

Martínez-Navarro, B., 2010. Early Pleistocene faunas of Eurasia and hominin dispersals. In: Fleagle, J.G., Shea, J.J., Grine, F.E., Baden, A.L., Leakey, R.E. (Eds.), Out of Africa I. Springer, Dordrecht, pp. 207–224. https://doi.org/10.1007/978-90-481-9036-2_13.

Martínez-Navarro, B., Rabinovich, R., 2010. The fossil Bovidae (Artiodactyla, Mammalia) from Gesher Benot Ya'aqov, Israel: out of Africa during the early-middle pleistocene transition. J. Hum. Evol. 60, 375–386. https://doi.org/10.1016/j.jhevol.2010.03.012.

Martínez-Navarro, B., Palmqvilst, P., Madurell, J., Pérez-Claros, J.A., 2004a. El registro de *Hippopotamus antiquus* en el Pleistoceno inferior de Europa: implicaciones paleoambientales e inferencias paleobiológicas. XX Jornados de Paleontologia, pp. 121–122.

Martínez-Navarro, B., Rook, L., Segid, A., Yosief, D., Ferretti, M.P., Shoshani, J., Tecle, T.M., Libsekal, Y., 2004b. The large fossil mammals from Buia (Eritrea): systematics, biochronology and paleoenvironments. Riv. Ital. Paleontol. Stratigr. 110, 61–88. https://doi.org/10.13130/2039-4942/5765.

Martínez-Navarro, B., Palmqvist, P., Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Torregrosa, V., Pérez-Claros, J.A., 2010. La fauna de grandes mamíferos de Fuente Nueva-3 y Barranco León-5: estado de la cuestión. In: Toro, I., Martínez-Navarro, B., Agustí, J. (Eds.), Ocupaciones humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza.

Martínez-Navarro, B., Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Figueirido, B., Guerra-Merchán, A., Palmqvist, P., 2015. Sobre la paleobiología de *Hippopotamus antiquus* Desmarest, 1822: ¿Un megaherbívoro acuático sin análogos vivientes? *XXXI Jornadas de Paleontología*. Sociedad Española de Paleontología, pp. 180–182.

Martinez-Navarro, B., Pandolfi, L., Medin, T., Libsekal, Y., Ghinassi, M., Papini, M., Rook, L., 2022. The ontogenetic pattern of Hippopotamus gorgops Dietrich, 1928 revealed by a juvenile cranium from the one-million-years-old paleoanthropological site of Buia (Eritrea). Comptes Rendus Palevol 21 (7), 157–173. https://doi.org/10.5852/crpalevol2022v21a7.

Martino, R., Pandolfi, L., 2021. The Quaternary *Hippopotamus* records from Italy. Hist. Biol. 1–11. https://doi.org/10.1080/08912963.2021.1965138.

Martino, R., Pignatti, J., Rook, L., Pandolfi, L., 2021. Hippopotamid dispersal across the Mediterranean in the latest Miocene: a re-evaluation of the Gravitelli record from Sicily, Italy. Acta Palaeontol. Pol. 66 (3), 67–78. https://doi.org/10.4202/app.00838.2020.

Martino, R., Ríos, M.I., Mateus, O., Pandolfi, L., 2022. Taxonomy, chronology, and dispersal patterns of Western European Quaternary hippopotamuses: new insight from Portuguese fossil material. Quat. Int. xxx (xxxx). https://doi.org/10.1016/j.quaint.2022.12.010.

Maslin, M.A., Brierley, C.M., 2015. The role of orbital forcing in the Early Middle Pleistocene Transition. Quat. Int. 389, 47–55. https://doi.org/10.1016/j.quaint.2015.01.047.

Mazo, A.V., 1989. Los hipopótamos del Pleistoceno medio de Huéscar-1 (Granada). Considerac. Biostratigr. Sobre Fauna Vertebrados Fósiles Cuenca Guadix-Baza (Granada, España) 1, 317–325.

Mazo, A.V., Perez-Gonzalez, A., Aguirre, E., 1990. Las faunas pleistocenas de Fuensanta del Jucar y El Provencio y su significado en la evolucion del Cuaternario de la Llanura manchega. Bol. Geol. Min. 101 (3), 404–418.

Mazza, P., 1991. Interrelations between pleistocene hippopotami of Europe and Africa. Bollet. Soc. Paleont. Ital. 30 (2), 153–186.

Mazza, P., 1995. New evidence on the Pleistocene hippopotamuses of western Europe. Geol. Rom. 31, 61–241.

Mazza, P., Bertini, A., 2013. Were Pleistocene hippopotamuses exposed to climate-driven body size changes? Boreas 42 (1), 194–209. https://doi.org/10.1111/j.1502-3885.2012.00285.x.

Michel, V., Shen, C.C., Woodhead, J., Hu, H.M., Wu, C.C., Moullé, P.É., Khatib, S., Cauche, D., Moncel, M.H., Valensi, P., Chou, Y.M., Gallet, S., Echassoux, A., Orange, F., De Lumley, H., 2017. New dating evidence of the early presence of hominins in Southern Europe. Sci. Rep. 7 (1), 1–8. https://doi.org/10.1038/s41598-017-10178-4.

Mitteroecker, P., Gunz, P., 2009. Advances in geometric morphometrics. Evol. Biol. 36 (2), 235–247. https://doi.org/10.1007/s11692-009-9055-x.

Mosquera, M., Saladié, P., Ollé, A., Cáceres, I., Huguet, R., Villalaín, J.J., Carrancho, A., Bourlès, D., Braucher, R., Vallverdú, J., 2015. Barranc de la Boella (Catalonia, Spain): an Acheulean elephant butchering site from the European late early pleistocene. J. Quat. Sci. 30, 651–666. https://doi.org/10.1002/jqs.2800.

Muttoni, G., Scardia, G., Kent, D.V., 2010. Human migration into Europe during the late Early Pleistocene climate transition. Palaeogeogr. Palaeoclimatol. Palaeoecol. 296 (1–2), 79–93. https://doi.org/10.1016/j.palaeo.2010.06.016.

Muttoni, G., Scardia, G., Kent, D.V., 2018. Early hominins in Europe: the Galerian migration hypothesis. Quat. Sci. Rev. 180, 1–29. https://doi.org/10.1016/j.quascirev.2017.10.031.

O'Higgins, P., Jones, N., 2006. Tools for Statistical Shape Analysis. Hull York Medical School.

O'Regan, H.J., 2008. The Iberian Peninsula e corridor or cul-de-sac? Mammalian faunal change and possible routes of dispersal in the last 2 million years. Quat. Sci. Rev. 27, 2136–2144. https://doi.org/10.1016/j.quascirev.2008.08.007.

Palmqvist, P., Gröcke, D.R., Arribas, A., Fariña, R.A., 2003. Paleoecological reconstruction of a lower Pleistocene large mammal community using biogeochemical (δ13C, δ15N, δ18O, Sr:Zn) and ecomorphological approaches. Paleobiology 29 (2), 205–229. https://doi.org/10.1666/0094-8373(2003)029<0205:PROALP>2.0.CO.

Palmqvist, P., Pérez-Claros, J.A., Janis, C.M., Figueirido, B., Torregrosa, V., Gröcke, D.R., 2008. Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an early Pleistocene community. Palaios 23 (11–12), 724–737. https://doi.org/10.2110/palo.2007.P07-073r.

Palmqvist, P., Rodríguez-Gómez, G., Figueirido, B., García-Aguilar, J.M., Pérez-Claros, J.A., 2022. On the ecological scenario of the first hominin dispersal out of Africa. Anthropologie 126 (1). https://doi.org/10.1016/j.anthro.2022.102998.

Pandolfi, L., Petronio, C., 2015. A brief review of the occurrences of Pleistocene *Hippopotamus* (Mammalia, Hippopotamidae) in Italy. Geol. Croat. 68 (3), 313–319. https://doi.org/10.4154/GC.2015.24.

Pandolfi, L., Martino, R., Rook, L., Piras, P., 2020. Investigating ecological and phylogenetic constraints in Hippopotamidae skull shape. Riv. Ital. Paleontol. Stratigr. 126 (1), 37–49. https://doi.org/10.13130/2039-4942/12730.

Perez, S.I., Bernal, V., Gonzalez, P.N., 2006. Differences between sliding semilandmark methods in geometric morphometrics, with an application to human craniofacial and dental variation. J. Anat. 208, 769–784. https://doi.org/10.1111/j.1469-7580.2006.00576.x.

Petronio, C., 1986. New hippopotamus remains from the middle Lower Pleistocene sedimentary formation in Rome and associated phylogenetic and taxonomic problems. Geol. Rom. 25, 63–71.

Petronio, C., 1995. Note on the taxonomy of Pleistocene hippopotamuses. Ibex 3, 53–55.

Pineda, A., Saladié, P., Expósito, I., Rodríguez-Hidalgo, A., Cáceres, I., Huguet, R., Rosas, A., López-Polín, L., Estalrrich, A., García-Tabernero, A., Vallverdú, J., 2017. Characterizing hyena coprolites from two latrines of the Iberian peninsula during the early pleistocene: Gran Dolina (Sierra de Atapuerca, Burgos) and la Mina (barranc de la Boella, Tarragona). Palaeogeogr. Palaeoclimatol. Palaeoecol. 480, 1–17. https://doi.org/10.1016/j.palaeo.2017.04.021.

Piñero, P., Agustí, J., Oms, O., Blain, H.A., Furió, M., Laplana, C., Sevilla, P., Rosas, A., Vallverdú, J., 2020. First continuous pre-Jaramillo to Jaramillo terrestrial vertebrate succession from Europe. Sci. Rep. 10 (1), 1–11. https://doi.org/10.1038/s41598-020-58404-w.

Pla-Pueyo, S., Viseras, C., Soria, J.M., Tent-Manclús, J.E., Arribas, A., 2011. A stratigraphic framework for the pliocene-pleistocene continental sediments of the Guadix basin (betic Cordillera, S. Spain). Quat. Int. 243 (1), 16–32. https://doi.org/10.1016/j.quaint.2011.01.028.

Pomel, A., 1890. Sur les Hippopotames fossiles de l'Algerie. C. R. Acad. Sci. 110, 1112–1116.

Pomel, A., 1896. Sur les Hippopotames fossiles de l'Algerie. C. R. Acad. Sci. 123, 1241–1242.

Puzachenko, A.Y., Titov, V.V., Kosintsev, P.A., 2021. Evolution of the European regional large mammals assemblages in the end of the Middle Pleistocene - the first half of the Late Pleistocene (MIS 6-MIS 4). Quat. Int. 605–606, 155–191. https://doi.org/10.1016/j.quaint.2020.08.038.

Rakotovao, M., Lignereux, Y., Orliac, M.J., Duranthon, F., Antoine, P.O., 2014. *Hippopotamus lemerlei* Grandidier, 1868 et *Hippopotamus madagascariensis* Guldberg, 1883 (Mammalia, Hippopotamidae): Anatomie crânio-dentaire et révision systématique. Geodiversitas 36 (1), 117–161. https://doi.org/10.5252/g2014n1a3.

Reimann, C.K., Strauch, F., 2008. Ein Hippopotamus-Schädel aus dem Pliozän von Elis (Peloponnes, Griechenland). Neues Jahrbuch Geol. Palaontol. - Abhandlungen 249 (2), 203–222. https://doi.org/10.1127/0077-7749/2008/0249-0203.

Reynolds, S.H., 1922. A Monograph on the British pleistocene Mammalia VOL. III, Part I. *Hippopotamus*. Pages 1-38; plates I-VI. Monogr. Palaeontogr. Soc. 74 (351), 1–38. https://doi.org/10.1080/02693445.1922.12035586.

Ribot, F., Gibert, L., Ferràndez-Cañadell, C., Olivares, E.G., Sánchez, F., Lería, M., 2015. Two deciduous human molars from the early pleistocene deposits of Barranco León (Orce, Spain). Curr. Anthropol. 56 (1), 134–142. https://doi.org/10.1086/679615.

Roebroeks, W., Gaudzinski-Windheuser, S., Baales, M., Kahlke, R.D., 2018. Uneven data quality and the earliest occupation of Europe—the case of Untermassfeld (Germany). J. Paleolithic Archaeol. 1 (1), 5–31. https://doi.org/10.1007/s41982-017-0003-5.

Rosas, A., Saladié, P., Huguet, R., Cáceres, I., Pineda, A., Ollé, A., Mosquera, M., García-Tabernero, A., Estalrrich, A., Pérez-Criado, L., Rodríguez-Pérez, F., Lozano-Fernández, I., López-Polín, L., Moreno, E., Vergés, J.M., Expósito, I., Agustí, J., Carbonell, E., Capdevila, R., Vallverdú, J., 2015. Estudio preliminar de las tafofacies del Pleistoceno Inferior del yacimiento de El Forn (Barranc de La Boella, Tarragona).

Saarinen, J., Oksanen, O., Žliobaitė, I., Fortelius, M., DeMiguel, D., Azanza, B., Bocherens, H., Luzón, C., Solano-García, J., Yravedra, J., Courtenay, L.A., Blain, H.A., Sánchez-Bandera, C., Serrano-Ramos, A., Rodriguez-Alba, J.J., Viranta, S., Barsky, D., Tallavaara, M., Oms, O., Agustí, J., Ochando, J., Carrión, J.S., Jiménez-Arenas, J.M., 2021. Pliocene to Middle Pleistocene climate history in the Guadix-Baza Basin, and the environmental conditions of early *Homo* dispersal in Europe. Quat. Sci. Rev. 268. https://doi.org/10.1016/j.quascirev.2021.107132.

Sánchez, B., Pesquero, M.D., Fraile, S., Salesa, M.J., 2004. Las colecciones de Vertebrados fósiles del Museo Nacional de Ciencias Naturales (CSIC): aportación del Profesor Emiliano Aguirre a la Paleontología española. Miscelánea Homenaje Emiliano Aguirre. Volumen II 527–540.

Sesé, C., Soto, E., 2000. Vertebrados del Pleistoceno de Madrid. Flora Fauna 216–243.

Spassov, N., 2003. The Plio-Pleistocene vertebrate fauna in South-Eastern Europe and the megafaunal migratory waves from the east to Europe. Rev. Paléobiol. 22 (1), 197–229.

Sorbelli, L., Alba, D.M., Cherin, M., Moullé, P.É., Brugal, J.P., Madurell-Malapeira, J., 2021. A review on *Bison schoetensacki* and its closest relatives through the early-Middle Pleistocene transition: Insights from the Vallparadís Section (NE Iberian Peninsula) and other European localities. Quat. Sci. Rev. 261, 106933. https://doi.org/10.1016/j.quascirev.2021.106933.

Stewart, M., Louys, J., Price, G.J., Drake, N.A., Groucutt, H.S., Petraglia, M.D., 2019. Middle and Late Pleistocene mammal fossils of Arabia and surrounding regions: implications for biogeography and hominin dispersals. Quat. Int. 515, 12–29. https://doi.org/10.1016/j.quaint.2017.11.052.

Stoffel, C., Dufresnes, C., Okello, J.B.A., Noirard, C., Joly, P., Nyakaana, S., Muwanika, V.B., Alcala, N., Vuilleumier, S., Siegismund, H.R., Fumagalli, L., 2015. Genetic consequences of population expansions and contractions in the common hippopotamus (*Hippopotamus amphibius*) since the Late Pleistocene. Mol. Ecol. 24 (10), 2507–2520. https://doi.org/10.1111/mec.13179.

Strani, F., DeMiguel, D., Alba, D.M., Moyà-Solà, S., Bellucci, L., Sardella, R., Madurell-Malapeira, J., 2019. The effects of the "0.9 Ma event" on the Mediterranean ecosystems during the Early-Middle Pleistocene transition as revealed by dental wear patterns of fossil ungulates. Quat. Sci. Rev. 210, 80–89. https://doi.org/10.1016/j.quascirev.2019.02.027.

Stuart, A.J., 1991. Mammalian extinctions in the late pleistocene of northern Eurasia and North America. Biol. Rev. Camb. Phil. Soc. 66 (4), 453–562. https://doi.org/10.1111/j.1469-185x.1991.tb01149.x.

Stuart, A.J., Lister, A.M., 2001. The mammalian faunas of Pakefield/Kessingland and Corton, Suffolk, UK: evidence for a new temperate episode in the British early Middle Pleistocene. Quat. Sci. Rev. 20 (16–17), 1677–1692. https://doi.org/10.1016/S0277-3791(01)00034-8.

Tsoukala, E., 1999. Quaternary large mammals from the Apidima Caves (Lakonia, S. Peloponnese, Greece). Beiträge Paläontol. 24, 207–229.

Vallverdú, J., Saladié, P., Bennàsar, M.L., Cabanes, D., Mancha, E., Menéndez, L., Blain, H.A., Ollé, A., Vilalta, J., Mosquera, M., Cáceres, I., Expósito, I., Esteban, M., Huguet, R., Rosas, A., Solé, A., López-Polín, L., Martinell, J., García-Barbo, A.B., Martínez-Navarro, B., Agustí, J., Ros-Montoya, S., Carbonell, E., Capdevila, R., 2008. El barranc de la Boella de la Canonja (Tarragonès) revisitat en la intervenció arqueològica preventiva de l'any 2007. Tribuna d'Arqueol. 7–28.

Vallverdú, J., Saladié, P., Bennàsar, M.L., Cabanes, D., Mancha, E., Menéndez, L., Blain, H.A., Ollé, A., Vilalta, J., Mosquera, M., Cáceres, I., Expósito, I., Esteban, M., Huguet, R., Rosas, A., Solé, A., López-Polín, L., Martinell, J., García-Barbo, A.B., Martínez-Navarro, B., Agustí, J., Ros-Montoya, S., Carbonell, E., Capdevila, R., 2014. Los Cazadores Recolectores Del Pleistoceno y Del Holoceno En Iberia y El Estrecho de Gibraltar: Estado Actual Del Conocimiento Del Registro Arqueológico. El Barranc de la Boella (La Canonja, Tarragona, Catalonia, Spain), pp. 287–295.

van der Made, J., 1998. Ungulados de Gran Dolina, Atapuerca: nuevos datos e interpretaciones. Atapuerca y La Evolución Humana, pp. 97–109.

van der Made, J., Rosell, J., Blasco, R., 2017a. Faunas from Atapuerca at the Early-Middle Pleistocene limit: the ungulates from level TD8 in the context of climatic change. Quat. Int. 433, 296–346. https://doi.org/10.1016/j.quaint.2015.09.009.

van der Made, J., Sahnouni, M., Boulaghraief, K., 2017b. *Hippopotamus Gorgops* from

El Kherba (Algeria) and the Context of its Biogeography. II MAP, pp. 135–169.

van Kolfschoten, T., 2001. Pleistocene mammals from The Netherlands. Boll. Soc. Paleontol. Ital. 40, 209–215.

Vangengeim, E.A., Vislobokova, I.A., Sotnikova, M.V., 1998. Large Ruscinian mammals on the territory of former USSR. Stratigr. Geol. Correl. 6 (4), 52–66.

Vekua, A.K., 1959. O gippopotame iz nizneplejstocenovyh otlozenij Gruzii-Soobs. Akad. Nauk. Gruz. SSR (Geol. Inst. Tr. Tiflis.) 23 (5), 561–566.

Vekua, A.K., 1986. The lower pleistocene mammalian fauna of Ahkalkalaki (southern Georgia, USSR). Palaeontogr. Ital. 74, 63–96.

Vervoort-Kerkhoff, Y., van Kolfschoten, T., 1988. Pleistocene and Holocene mammalian faunas from the Maasvlakte near Rotterdam (The Netherlands). Mededel. Werkgroep Tertiaire en Kwartaire Geol. 25 (1), 87–98.

Walzer, C., Stalder, G., 2015. Hippopotamidae (*Hippopotamus*). In: Fowler's Zoo and Wild Animal Medicine, ume 8. Elsevier Inc. https://doi.org/10.1016/b978-1-4557-7397-8.00059-1.

Weston, E.M., 1997. *A Biometrical Analysis of Evolutionary Change within the Hippopotamidae* (Issue October). Sidney Sussex College.

Weston, E., Boisserie, J., 2010. Hippopotamidae. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, California, pp. 861–879.

Zorić, Z., Lozanče, O., Marinković, D., Blagojević, M., Nešić, I., Demus, N., Đorđević, M., 2018. Skull bone anatomy of the young common hippopotamus (*Hippopotamus amphibius*). Acta Vet. 68 (3), 361–372. https://doi.org/10.2478/acve-2018-0030.