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RESEARCH PAPER

Is *Hippopotamus antiquus* (Mammalia, Hippopotamidae) affected by body size variations? The contribution of the Mosbach (Germany, Middle Pleistocene) specimen

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Abstract

Hippopotamus antiquus is a well-documented species within the Hippopotamidae family, with evidence of its presence in almost all Europe during the Pleistocene. Despite its abundance in the fossiliferous record, there is still much debate surrounding the first and last appearance data of this taxon, as well as its evolutionary trend. In this work we present a well-preserved mandible recovered from Mosbach (Germany) referred to the Middle Pleistocene. The latter period is represented by less *H. antiquus* remains in comparison to the Early Pleistocene, making the description of this specimen helpful for morphometric and morphological considerations. Early Pleistocene *H. antiquus* specimens from Upper Valdarno, Collecurti and Durfort display larger dimensions in comparison to those from Middle Pleistocene localities, including Maglianella, Ortona, Ponte Molle and the specimen from Mosbach. A decrease in body size in *H. antiquus*, most likely correlated to climate fluctuations, is therefore discussed providing news insights into the biogeography, morphology and morphometry of late *H. antiquus*.

Keywords *Hippopotamus antiquus* · Morphometry · Body size · Central Europe · Quaternary

Introduction

The occurrence of hippopotamuses in the fossil record is usually considered as a good indicator of the presence of permanent bodies of water (Mazza & Bertini, 2013), and, given their tight connection to these specific environments, fossil hippopotamuses provide critical insights for paleoenvironmental reconstructions (Adams et al., 2022; Fidalgo et al., 2023; Jablonski, 2004). Among hippopotamids, *Hippopotamus antiquus* Desmarest, 1822 is arguably the most well-known fossil hippopotamus of the European mainland. This species was most likely more aquatic than the extant *H. amphibius* Linnaeus, 1758. This last assumption relies on the high δ15N values detected in the bone collagen of *H. antiquus* individuals collected from Venta Micena (Spain), which is probably linked to a diet primarily based on aquatic non-nitrogen fixing plants (Martínez-Navarro et al., 2010; Palmqvist et al., 2003, 2008a). The particularly low δ18O values also support a more aquatic lifestyle than the extant hippopotamus (Cerling et al., 2008; Martínez-Navarro et al.,, 2010; Palmqvist et al., 2003, 2008a, 2022).

Hippopotamus antiquus has been usually regarded as larger than *H. amphibius* (Caloi et al., 1980; Cuvier, 1804, 1821; Faure, 1985). According to some authors, *H. antiquus* was most likely twice (2–2.1) as large as the common hippo (Konidaris et al., 2024; Martínez-Navarro et al., 2010; Palmqvist et al., 2022). The average weight for the common hippo, as reported by Eltringham (1999), is 1536 kg for males and 1386 kg for females. In South Africa, Pienaar et al. (1966) reported a mean body mass of 1492 kg for male extant hippopotamuses and 1325 kg for female ones. Ledger (1968) reported an average of 1490 kg for males and 1277 kg for females, whereas Voysey et al. (2023), following a

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culling operation of 2994 individuals in Uganda, reported average weights of 1332 kg and 1393 kg for male and female hippopotamuses respectively. However, the maximum recorded value for the common hippopotamus is over 2000 kg (Bere, 1959; Pienaar et al., 1966). In Mazza and Bertini (2013) the Body Mass (BM) of *H. antiquus* calculated based on the measurements of teeth (upper and lower second molars), femur and fifth metatarsal using classical regression formulae (Janis, 1990), was estimated to be between 2100 kg and 2750 kg for the specimens from Upper Valdarno (Italy), 2100–2600 kg for those from Collecurti (Italy), 2200–3200 kg for the large hippopotamids from Untermaßfeld (Germany), 1700–2750 kg for *H.* ex gr. *H. antiquus* from Maglianella (MSNCC C.601, Italy), 1000–2100 kg for the specimen from Ortona (SAApal43, Italy) and 2200 kg for the hippopotamids from Colle Lepre (Italy) (Mazza & Bertini, 2013). A mean value of 3200 kg for *H. antiquus* was estimated by Palmqvist et al., (2008a, 2008b, 2022) based on measurements of humerus, radio-ulna, femur, and tibia of several large hippopotamuses specimens. A range between 3012 kg and 3699 kg based on the postcranial measurements (humerus, radius-ulna) of *H. antiquus* from Incarcal (Spain) was reported by Martínez-Navarro et al. (2010). The same authors also reported a range between 2277 kg and 4153 kg for the Untermaßfeld specimens. More recently, Romano et al. (2024) estimated a BM between 2930 kg and 3370 kg, with an average of 3200 kg, for the *H. antiquus* from Upper Valdarno (IGF1043). Konidaris et al. (2024) also estimated the BM of *H. antiquus* based on humerus, femur and tibia measurements of specimens collected from different Greek sites, obtaining values of 2366 kg (Choremi 6), 2111 kg (Kyparissia 4), 1893 kg (Kyparissia 1) and 1738 kg (Marathousa 1). The range of *H. antiquus* was reported as between 1602 kg and 4694 kg, with a mean of 3197 kg (Konidaris et al., 2024).

Hippopotamus antiquus is known to have occurred during the Early Pleistocene (Athanassiou, 2022; Bellucci et al., 2012; Blandamura & Azzaroli, 1977; Kahlke, 1997, 2001; Kostopoulos & Koufos, 1994; Martino & Pandolfi, 2022; Napoleone et al., 2003; Nesti, 1820; Pandolfi & Petronio, 2015; Reimann & Strauch, 2008), and between 1.2 Ma and the early Middle Pleistocene, it was present in almost all of Europe (Adams et al., 2022; Agostini et al., 2005; Athanassiou, 2022; Auguste, 2009; Faure, 1985; Fidalgo et al., 2023, 2024; Guérin et al., 2003; Kahlke, 1989, 1997; Koenigswald & Heinrich, 1999; Martino & Pandolfi, 2022; Martino et al., 2023, 2024b; Mazza, 1995; Mazza & Ventra, 2011; Mecozzi, 2023; van Kolfschoten & Vervoort-Kerkhoff, 1985). The last occurrence (LO) of *H. antiquus* or closely related forms is reported at around 0.4 Ma in Portugal (Fidalgo et al., 2024; Martino et al., 2023), Italy (Martino et al., 2024b), and Greece (Konidaris et al., 2023, 2024). The ancestor of *H. antiquus* is still matter of debate. Mazza (1991) and Martínez-Navarro (2010) proposed *H. antiquus* as derived from *H. gorgops* Dietrich, 1928, a peculiarly large Pleistocene African hippopotamus. In contrast, van der Made et al. (2015) highlighted that *H. antiquus* may have originated from the poorly known East African *H. kaisensis* Hopwood, 1926. As also stressed out by Fidalgo et al. (2023), there are divergent opinions among experts regarding the phylogenetic relationships of the Hippopotamidae representatives, and more studies are therefore needed in order to detangle the intricate systematics of this group.

This study reports a comprehensive description and detailed illustration of a well-preserved *H. antiquus* mandible from Mosbach (Germany). This mandible was initially discovered in the first half of the twentieth century and was subsequently described in brief by Schertz (1939) and Kuss (1957). This paleontological specimen is notably smaller than other well-known Early Pleistocene hippopotamus remains from Upper Valdarno and Collecurti. The Middle Pleistocene is characterized by less abundant and poorly preserved hippopotamid material when compared to the Early Pleistocene (Kahlke, 1997; Mazza, 1995; Mazza & Ventra, 2011). Consequently, the studied mandible provides important insights into the morphology and the morphometry of the late form of *H. antiquus*. Further, we report an estimation for the body mass of the hippopotamus from Mosbach, of several specimens from European Early and Middle Pleistocene localities, as well as of extant hippopotamuses, in order to detect possible size trends through time. Finally, the mandible from Mosbach is one of the northernmost and best-preserved occurrences of *H. antiquus* in Europe, therefore also providing significant paleobiogeographical insights.

Geological setting

Mosbach, located in the Rhineland, represents one of the most significant Pleistocene fossiliferous sites in Central Europe (Fig. 1a). This site, also known as "Mosbach sands", is characterized by deposits spanning from the Early Pleistocene to the Late Pleistocene (Brüning, 1977; Koenigswald et al., 2007). The fossil mammal fauna was investigated by Andreae (1884), Kinkelin (1892), Pohlig (1887) and Schröder (1898) among others. The first mention of hippopotamid remains from Mosbach dates back to von Meyer (1841), while Schröder (1898) reported the presence of *H. antiquus*. The latter author also mentioned the occurrence of two lower jaw fragments with incisors, canines and molars, along with several limb bones stored in the Museum of Frankfurt (Senckenberg Naturmuseum). Unfortunately, these mandibles seem to be lost, and no other information are available regarding these remains. Some limited information regarding the mandible currently stored in the Naturhistorisches Museum

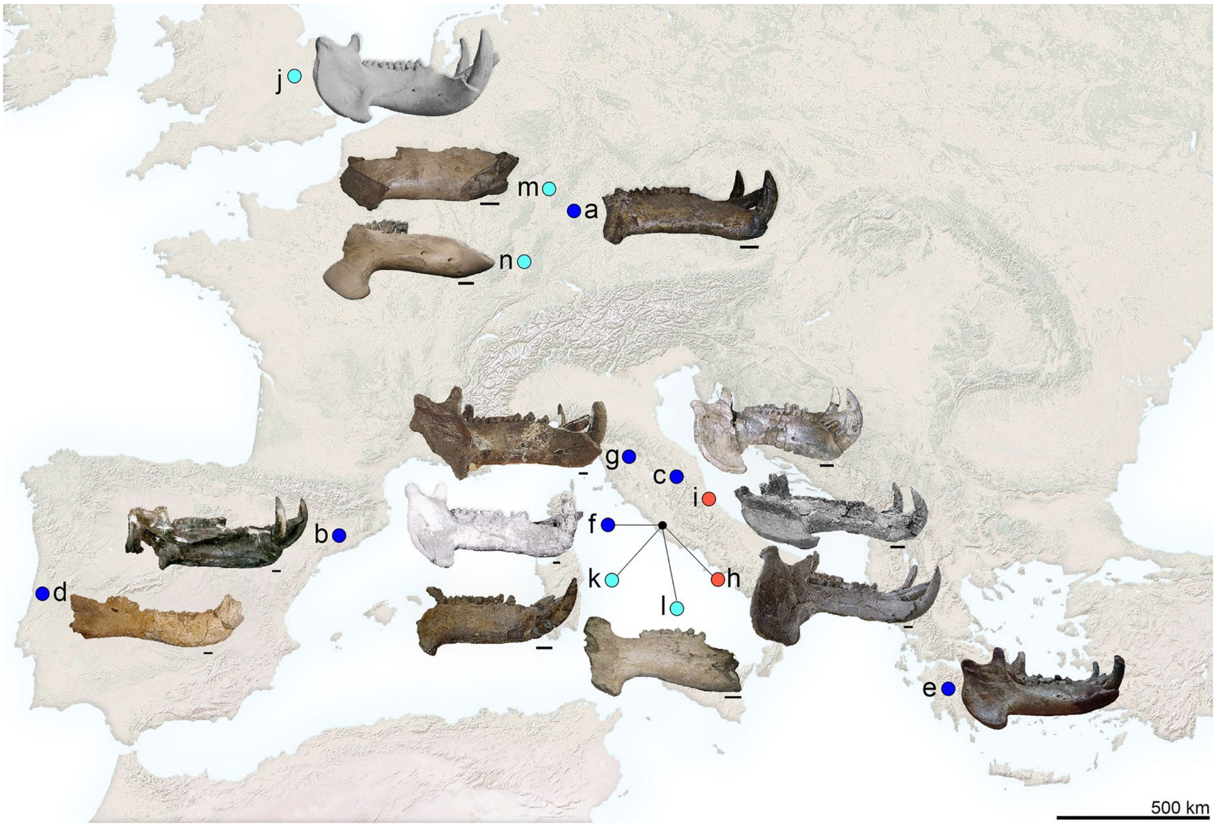

Fig. 1 Hippopotamid distribution in Europe. *Hippopotamus antiquus*: a, Mosbach 2 (NHMMZ1937.1, Middle Pleistocene); b, Cal Guardiola (IPS14513, Early Pleistocene); c, Collecurti (MNSUC52486, Early Pleistocene); d, Condeixa (MG3665, Middle Pleistocene); e, Megalopolis (Middle Pleistocene); f, Sant'Oreste (MPUR/V1950, Early Pleistocene?), g, Upper Valdarno (IGF1043, Early Pleistocene, mirrored). *Hippopotamus* ex gr. *H. antiquus*: h, Maglianella (MSNCC C.601, Middle Pleistocene); i, Ortona (SAApal43, Middle Pleistocene). *Hippopotamus amphibius*: j, Barrington (SMUC D3980, Late Pleistocene), k, Cava Montanari (MPUV/R149, Middle Pleistocene, mirrored); l, Fosso Malafede (ISPRA4449, Middle Pleistocene, mirrored); m, Gimbsheim (NHMMZ PW2013/30, Late Pleistocene); n, Rheinhansen, Osterwiesen (SMNS6717.7.6.642, Late Pleistocene). F courtesy of Prof. C. Petronio, b modified from Fidalgo et al. (2024), i modified from Agostini et al. (2005), k modified from Mecozzi et al. (2023) and j modified from Reynolds (1922). E courtesy of Prof. A. Athanassiou. Scale bars 5 cm a, g, c, k, l, i, n, m and 3 cm f, h, d, b

Mainz/Landessammlung für Naturkunde Rheinland-Pfalz was provided by Schertz (1939). According to the latter author "*[…] Zu Beginn dieser Eiszeit lagerten sich die tieferen Schichten der Mosbacher Sande ab, aus denen der Unterkiefer vom Nilpferd stammt*" that can be translated to "[…] At the beginning of this ice age, the deeper layers of the Mosbach sands, from which the lower jaw of the hippopotamus originates, were deposited". Additionally, the article documented the occurrence of a broad-fronted moose, a large beaver, elephants, and a bison from the same stratigraphic level. The indication provided by Schertz (1939) would suggest that the mandible was recovered from the older layers of Mosbach (also known as Mosbach 1 or Grobes Mosbach "Coarse Mosbach", Early Pleistocene). According to palaeomagnetic measurements, these sediments should be slightly older than 0.9 Ma (Brüning, 1977; Keller & Radtke, 2007; Koci et al., 1973). However, the fauna from Mosbach 1 is characterized by a notable depletion, which is indicative of a colder environment. Notably, the occurrence of hippopotamuses has never been reported from this association (Bohatỳ, 2018; Keller & Radtke, 2007). A second Middle Pleistocene fluvial cycle at Mosbach, known as Mosbach 2 or Graues Mosbach "Grey Mosbach", was deposited over a significant hiatus. The age of Mosbach 2 has been the subject of debate. Originally dated as slightly younger than 0.78 Ma (Keller & Radtke, 2007; Koenigswald & Tobien, 1987), it has more recently been ascribed to MIS 15 or 13 (ca. 0.6–0.5 Ma) (Hemmer et al., 2008; Kahlke et al., 2011). According to Kahlke et al. (2011), Mosbach 2 is slightly younger than the faunal assemblage of Mauer (Germany), which was correlated to MIS 15 (ca. 0.6 Ma) (Wagner et al., 2011). The fauna from Mosbach 2 is characterised by the presence of taxa that are typical of a warmer period, associated with "cold" species, such as reindeers, most likely due to the influence of subsequent depositional processes. The fossil record of Mosbach 2 is particularly rich, comprising more than 60 species, including *H. antiquus* (Hemmer et al., 2008). It seems probable that the hippopotamid mandible was therefore recovered from this richer fossiliferous level. Furthermore, in Mosbach 2 the hippopotamus is associated with elephants (*Palaeoloxodon antiquus* and *Mammuthus trogontherii)*, the broad-fronted moose (*Cervalces latifrons)*, the beaver (*Castor fiber*) and bisons (*Bison schoetensacki* and *B. priscus)* (Hemmer et al., 2008), all fauna mentioned from the same fossiliferous level of the mandible analysed in this work (Schertz, 1939).

Material and methods

The material described herein is an almost complete mandible collected from Mosbach and currently stored at the Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, Germany (Fig. 1a). The morphological terminology followed Boisserie et al. (2010) (Fig. 2). The studied specimen was compared with extant *H. amphibius* (Congo River, and other sites), fossil *H. amphibius* (Tor di Quinto, Malafede, and other sites), *H. antiquus* and closely related forms (Upper Valdarno, Chiusi, Maglianella, and other sites), *H. gorgops* (Koobi Fora), and published data (See Supplementary Material, S.1 and S.2). The measurement protocol is delineated in Fig. 2. All the measurements are reported in Supplementary Material, S.1 and S.2.

All the statistical analyses were developed in the RStudio environment (R Core Team, 2019). ANOVA and MANOVA were performed on the dataset using the R-package stats (Venables & Ripley, 2003). Scatterplots and boxplots were made using the R-package ggplot2 (Wickham et al., 2016). To test the variability of the dimensions of the third lower molars through time we sub-divided the different Pleistocene ages as follows: Early Pleistocene (early 2.58–1.5

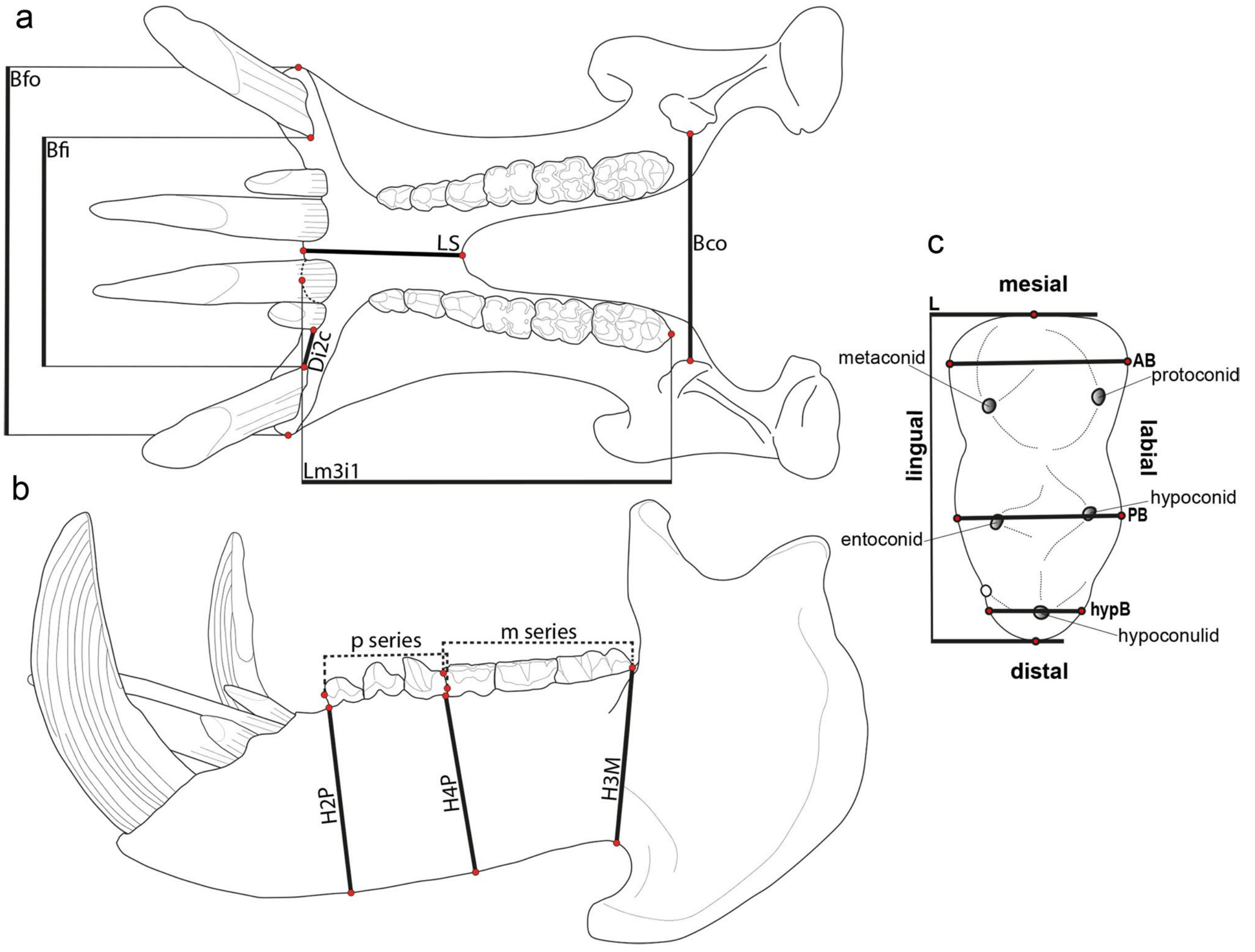

Fig. 2 Protocol followed for measurements, modified from Mazza (1995). **a**, **b**, Mandible. **c** Teeth. Nomenclature followed for molar cuspids in **c**, modified from Boisserie et al. (2010)

Ma, middle 1.5–1 Ma, late 1–0.75 Ma), Middle Pleistocene (early 0.75–0.5 Ma, middle 0.5–0.3 Ma, late 0.3–0.12 Ma) and Late Pleistocene.

Principal component analysis (PCA) on molar measurements was performed using the R-packages factoextra, FactoMiner, ggbiplot and ggfortify (Husson et al., 2016; Kassambara & Mundt, 2017; Lê et al., 2008; Tang et al., 2016; Vu, 2011). To further test the PCA results, it was also performed a pairwise PERMANOVA analysis followed by p-value adjustment (Holm correction) on all the available PC values, using the R-package pairwiseAdonis (Martínez Arbizu, 2020).

For the body mass (BM) estimation we considered the formulae reported in Mendoza et al. (2006) for lower teeth of ungulates, since the only available complete data in the studied specimen are represented by the dimensions of the lower premolars and molars. Seven different algorithms were reported for the lower teeth (Mendoza et al., 2006). We tested all the different algorithms using the data of NHMMZ1937.1, *H. antiquus* (MSNC n.c., MNHNP DUR500 1876-76, MGGC9416, MNHNP3866), *H.* ex gr. *H. antiquus* (MSNCC C.601, SAApal43), and *H. amphibius* (MCSNV n.c., IAF n.c., 1640, 6427, 53506, 11894, 20160745, 20160739, 20160744) (Avedik & Clauss, 2023; Mazza, 1995) (see Supplementary Material, S.2).The specimens selected for our research are adult hippopotamids exhibiting the m3 fully erupted (see Table 1). The only exception is represented by the specimen MNHNP DUR500 1876-796, that is a sub-adult with an erupting m3. Unfortunately, some of the specimens analysed are not figured nor fully described in the published literature, thereby hindering a more accurate evaluation of their age at death. Mazza (1995) described the specimen MSNC n.c. as a mature adult, based on the degree of wear of the teeth (IDAS 4–5 in Anders et al., 2011). No further data on the age of *H. antiquus* and *H. amphibius* specimens were provided in Mazza (1995). The hippopotamuses reported in Avedik and Clauss (2023) were ascribed to different age groups based on Laws (1968): 1640 (X, 17 ±3 years), 6427 (XVI, 33 ±3 years), 53506 (XIV, 33 ±3 years), 11894 (XIII 24 ±3 years), 20160745 (XVI, 33 ±3 years), 20160739 (XIV, 27 ±3 years), 20160744 (X, 17 ±3 years). Following the protocol provided by Laws (1968), MGGC9416, MSNCC C.601 and SAApal43 can be ascribed to group XVI (33 ±3 years). For the BM estimation we implemented only two algorithms from those proposed by Mendoza et al. (2006) as they yielded results that were comparable to the known body mass of *H. amphibius* (1300 kg–2000 kg). The values employed are the breadth of the fourth premolar (B p4), the length of the first molar (L m1) and the length of the molar row (L m1 − m3). The equations used are of the form $\log(\text{mass in kg}) = b1(\log X1) + b2(\log X2) + c$. The algorithms are: $2.045\ \text{L m1} + 1.073\ \text{L m1–m3} + 1.507$ and $1.213\ \text{L m1} + 1.421\ \text{m1–m3} + 0.422\ \text{B p4} + 1.380$. It should be noted that Mendoza et al. (2006) reported a range of mean percent prediction error between 21 and 23% for the chosen algorithms. We calculated the maximum error (23%) for each body mass estimation. The results obtained using the formulae of Mendoza et al. (2006) are listed in the Table 1. In order to test the results obtained using the formulae reported in Mendoza et al. (2006) we also implemented the regression model methodology described by Janis (1990). In line with the approach taken by Mazza and Bertini (2013), we selected the length of the second lower molar (L m2) for estimating the body mass. According to Janis (1990), the regression model parameters include the length of the m2, an intercept of − 0.289 and a slope of 0.280. The L m2 values used to estimate the BM are listed in the Supplementary Material (S.2). The results obtained applying the formula of Janis (1990) are also reported in the Table 1. *Institutional abbreviations*—IGF, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Università degli Studi di Firenze, Florence, Italy; ISPRA, Istituto Superiore per la Protezione e la Ricerca Ambientale, Rome, Italy; MG, Museu Geológico de Lisboa, Lisbon, Portugal; MGGC, Museo Geologico Giovanni Capellini, Bologna, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNSUC, Museo di Scienze Naturali dell'Università di Camerino, Camerino, Italy; MUST, Museo Universitario di Scienze della Terra, Dipartimento di Scienze della Terra, Sapienza Università di Roma, Rome, Italy (including the former MPUR, Museo di Paleontologia, Sapienza, Università di Roma, Rome, Italy); MSNAF, Museo Scienze Naturali Accademia dei Fisiocritici, Siena, Italy; MSNCC, Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa, Italy; NHMMZ, Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany; SAApal, Museo Geopaleontologico Alto Aventino, Palena, Italy; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SMUC, Sedwick Museum of the University of Cambridge, Cambridge, United Kingdom.

Anatomical abbreviations—c, lower canine; i, lower incisor; M/m, upper/lower molar; p, lower premolar.

Measurements abbreviations—AB, anterior breadth; B, greatest breadth; Bco, breadth of the two rami across the coronoid process; BFi, inner breadth of the rostral fan; Bfo, outer breadth of the rostral fan; capD, antero-posterior diameter of the c; cmLD, mesio-lateral diameter of the c; Di2c, length of the diastema between the i2 and c; Hm3, height of the horizontal ramus or corpus at the level of the m3 hypoconulid; Hp2, height of the horizontal ramus at the level of the p2; Hp4, height of the horizontal ramus at the level of the p4; hypB, hypoconulid breadth; i1/i2apD, antero-posterior diameter of the i1/i2; i1/i2 mlD, mesio-lateral diameter of

Table 1 Body mass estimations for different extinct and extant hippopotamid specimens applying the formulae reported in Mendoza et al. (2006) and Janis (1990)

Species	Specimen	Locality	Formula 7.6 following Mendoza et al., (2006)	± error (kg)	Formula 7.7 following Mendoza et al., (2006)	± error (kg)	Following Janis (1990)	References	Sex	Age
H. antiquus	NHMMZ1937.1	Mosbach	1.969 kg	453	2.140 kg	526	1.245,16 kg	NHMMZ		17–20 ± 3 years
H. antiquus	MSNC n.c	Collecurti	2.493,575 kg	574	3.260,611 kg	750	2.503,35 kg	Mazza, 1995		Adult
H. antiquus	MNHNP DUR500 1876-796	Durfort	2.495,222 kg	574	2.558,381 kg	588	2.125,53 kg	Mazza, 1995		Sub-adult
H. antiquus	MGGC9416	Upper Valdarno	1.789,589 kg	412	2.154,383 kg	496	1.170,17 kg	MGGC		33 ± 3 years
H. ex gr. *H. antiquus*	SAApal43	Ortona	1.782,616 kg	410	1.913,048 kg	440	1.224,3 kg	SAApal		33 ± 3 years
H. antiquus	MNHNP3866	Upper Valdarno	2.088,486 kg	480	2.367,829 kg	545	1.790,62 kg	Mazza, 1995		Adult
H. ex gr. *H. antiquus*	MSNCC C.601	Maglianella	1.695,13 kg	390	1.633,82 kg	376	1.012,53 kg	MSNCC; Mazza, 1995		33 ± 3 years
H. amphibius	MCSNV n.c	Congo	1.210,772 kg	278	1.329,706 kg	306	653,5 kg	Mazza, 1995	F?	Adult
H. amphibius	IAF n.c	Somalia	1.615,482 kg	372	1.589,016 kg	365	944,7 kg	Mazza, 1995	M?	Adult
H. amphibius	1640	Sudan	1.530,092 kg	352	1.560,948 kg	359	944,7 kg	Avedik & Clauss, 2023	F	17 ± 3 years
H. amphibius	6427	Chad	1.292,345 kg	297	1.598,903 kg	368	1.319,33 kg	Avedik & Clauss, 2023	M	33 ± 3 years
H. amphibius	53506	Captivity	1.954,243 kg	449	2.038,561 kg	469	1.897,69 kg	Avedik & Clauss, 2023	M	33 ± 3 years
H. amphibius	11894	Captivity	1.038,608 kg	239	1.186,521 kg	273	819 kg	Avedik & Clauss, 2023	M	24 ± 3 years
H. amphibius	20160745	Unknown	1.084,474 kg	249	1.495,141 kg	336	558 kg	Avedik & Clauss, 2023	F?	33 ± 3 years
H. amphibius	20160739	Africa, locality not specified	2.205,979 kg	507	2.247,213 kg	517	1.237,1 kg	Avedik & Clauss, 2023	F?	27 ± 3 years
H. amphibius	20160744	Congo	1.488,22 kg	342	1.481,183 kg	341	1.158,63 kg	Avedik & Clauss, 2023	M?	17 ± 3 years

the i1/i2; Lm3i1, length between the distal border of the m3 alveolus and the most ventral point of first incisor alveolus; LS, length of the mandibular symphysis; m1–m3, length of the molar series; p2–m3, length of the teeth series; p2–p4, length of the premolar series; L, greatest length; PB, posterior breadth.

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758
Order **Artiodactyla** Owen, 1848
Suborder **Cetancodonta** Arnason, Gullberg, Solweig Ursing & Janke, 2000.
Superfamily **Hippopotamoidea** sensu Gentry & Hooker, 1988
Family **Hippopotamidae** Gray, 1821.

Genus ***Hippopotamus*** Linnaeus, 1758

Type species. Hippopotamus amphibius Linnaeus, 1758

Important diagnostic features. The cranium of *H. antiquus* is slenderer and more elongated than that of *H. amphibius*. The zygomatic arches are transversally shorter than the transverse diameter between the external borders of the canine, and the sagittal crest is rather short. The mandible of *H. antiquus* usually exhibits a concave ventral profile of the mandibular corpus. The general aspect of the mandible is slenderer than in *H. amphibius*, with the ramus less developed than the mandibular corpus.

Hippopotamus antiquus Desmarest, 1822
Figure 3

1939 *Hippopotamus antiquus* Desmarest–Schertz: p. 87.
1957 *Hippopotamus antiquus* Desmarest–Kuss: p. 301.

Remarks. *Hippopotamus antiquus* Desmarest, 1822 is a large extinct hippopotamid. This species is distinguished from *H. amphibius* by its larger overall size, and by several cranial features, including a more slender cranium and mandible, as well as a shorter sagittal crest and a mandible corpus with a concave ventral profile (Caloi et al., 1980; Leonardi, 1948 and references therein). The lectotype for *H. antiquus* (IGF1043) was collected from Figline (Upper Valdarno) and is currently stored at the IGF (Blandamura & Azzaroli, 1977). This species exhibits a broad geographical distribution, encompassing a significant portion of Europe and potentially extending into the Levant (see Martino & Pandolfi, 2022 and references therein). The chronological distribution of this species spans from the Early Pleistocene (around 2 Ma) up to 0.4 Ma (Martino & Pandolfi, 2022 and references therein; Fidalgo et al., 2024; Konidaris et al., 2024; Martino et al., 2023). The occurrence of this species is usually correlated with fluvial or lacustrine environments, and more generally, with the presence of water bodies (Mazza & Bertini, 2013).

Referred material. NHMMZ1937.1 is an almost complete mandible. The vertical rami are both fragmented and p2 s and p3 s are missing. Incisors, canines and the p4–m3 series are complete.

Description

In lateral view the mandible is rather long and slender, and the development of the ventral profile is concave. The gonial angle (Fig. 3a, b) is preserved on the left side while fragmented on the right one. The preserved gonial angle joins the lower profile of the mandible with an almost right angle. The left hemimandible is slightly deformed, probably due to diagenetic processes (Fig. 3b, c). The right hemimandible shows a well-developed mental foramen close to the canine process (Fig. 3a). In dorsal view the rostral fan is fairly wide, with the canine processes well-developed (Fig. 3c). The mandibular corpus is fairly straight, posteriorly diverging. The diastema between the i2 and the c is marked, while the diastema between the i1 and i2 and between the two i1s is less prominent (Fig. 3c, h). The mandibular symphysis is not particularly thick. In anterior view the ventral profile of the rostral fan is concave (Fig. 3h). In ventral view the corpora are quite diverging (Fig. 3i). The broken portion of the ascending ramus is peculiarly thin. The cross section of the mandibular symphysis is bean shaped (Fig. 3f). Despite being currently fragmented, in Schertz (1939) the mandible NHMMZ1937.1 is depicted as complete and partially figured (Fig. 3g). From the figure it is visible that the right ramus was complete, as well as both premolar series. The ramus was not particularly high, and it was fairly inclined outwards (Fig. 3g). There was most likely also a diastema between the p2 and the p3.

The canines are complete, and not particularly large (Fig. 3a, b). The enamel exhibits ridges that run parallel to the tooth's length until reaching the tip. The enamel is slightly wrinkled. A well-developed groove runs in the mesial side of the canines. The mandible NHMMZ1937.1 displays all incisors in anatomical position (Fig. 3c, h). The diastema between i1–i2 and i2–c is not particularly large. The i1 s are straight, procumbent, and larger than the i2 s. The enamel is not well-preserved however some minor grooves are partially visible. The cross section of the left i1 is mainly elliptical, with the mesial-lateral length greater than the lingual-labial one. The right i1 has a mostly rounded cross-section. It displays a wear surface more developed than

Fig. 3 Mandible NHMMZ1937.1 from Mosbach 2: **a** right lateral view; **b** left lateral view; **c** dorsal view; **d** left dental series (p4, m1, m2, m3); **e** right dental series (p4, m1, m2, m3); **f** sagittal cross section; **g** mandible depicted in Schertz (1939); **h** anterior view; **i** ventral view. Scale bars 5 cm **a**, **b**, **c**, **h** and **i**, 3 cm **d** and **e**, 20 cm g

the left i1, extending in almost all the lingual-distal side of the tooth. The i2 s are considerably smaller and shorter compared to the i1 s and they show a perfectly rounded cross-section. The wear surface of both i2 s is on the labial side of the teeth. The enamel of the i2 s is badly preserved and not investigable.

The development of the teeth series in dorsal view is almost straight. The premolar series is not complete, the p4 is the only tooth preserved (Fig. 3d, e). The p4 is almost triangular with a single large cuspid. It shows a thick crenulated and pustulated enamel with a robust distal cingulid which forms a strong distostylid. The cingulid is well developed disto-labially and disto-lingually, while it is less strong mesially. Anteriorly the cingulid develops a strong mesiostylid. The wear surface is slightly cruciform.

The molar series are complete (Fig. 3d, e). Both m1s are fairly worn, exhibiting a thick enamel. In labial view the cingulid is distally strong while in lingual view it is well-developed. The cingulid is also strong distally and mesially, forming a mesiostylid and a distostylid respectively. The second lower molars are characterized by four cuspids, all displaying a trefoiled wear pattern except the entoconid, which shows a comma-shaped pattern (Fig. 3d, e). The distostylid is particularly strong and partially worn out. The cingulid is also well-developed mesially, while less stressed lingually and labially. The m3 s is characterized by five cuspids almost unworn, with just the anterior cuspids partially worn-out (Fig. 3d, e). The enamel is finely wrinkled. The protoconid, the metaconid and the hypoconid are large cuspids while the entoconid is fairly smaller. The hypoconulid is strong and placed in the distal part of the m3. The metaconid is connected with the hypoconid through the postmetacristid and the prehypocristid. The cingulid is strong mesially, while in other views is not visible. Since the m3 s of NHMMZ1937.1 are still partially in the mandible some characters are not clearly detectable. The valleys between the anterior and medial cuspids are deep, with the labial ones more developed than the lingual valleys. The wear pattern on the occlusal surface of the teeth of NHMMZ1937.1 indicates that the individual was most likely a member of group X-XI of Laws (1968). Therefore, the estimated age of the Mosbach hippopotamus at the time of its death was approximately 18 years old, with a margin of error of plus or minus four years.

Morphological, morphometric and body size comparison

Morphological comparison

In specimens ascribed to *H. antiquus*, namely IGF1043 from Upper Valdarno (Fig. 1g, Early Pleistocene, Italy) and MNSUC52486 from Collecurti (Fig. 1c, latest Early Pleistocene, Italy) the ventral profile of the mandibular corpus is concave, and the mandible is slender (Mazza & Ventra, 2011), exhibiting a similar morphology to that observed in the Mosbach specimen. In MNSUC52486, the mandible exhibits prominent canines, whereas in IGF1043 and NHMMZ1937.1, the canines are less pronounced. Additionally, the canines are also notably large in the specimens MGGC9416, MNHN.F.ITL40 and MNHN.F.ITL41, all collected from the area of Upper Valdarno. The *H. antiquus* mandible IPS14513 collected from Cal Guardiola (Fig. 1b, Early Pleistocene, Spain), which was figured in Fidalgo et al. (2024), also exhibits a slender and long mandibular corpus, as observed in the mandible from Mosbach. However, the ventral profile of the latter is straight whereas that of the German specimen is concave. An almost complete individual (MPUR/V1950), dubiously ascribed to late Early Pleistocene, was also found in Sant'Oreste (Fig. 1 f, Rome, Italy) and ascribed to *H. antiquus* (Caloi et al., 1980). Mazza (1991) designated this specimen as the paratype of *H. tiberinus*. However, MPUR/V1950 was subsequently identified as *H.* ex gr. *H. antiquus* (Palombo, 2004). The mandible belonging to this individual is slender, the ventral profile of the mandibular corpus is concave, the ramus is not robust, the diastema between i2-c is modest, all characters also detectable in the mandible from Mosbach. The mandible of *H. antiquus* from the Middle Pleistocene of Condeixa (Portugal, MG3665) exhibits similarities to the specimen from Mosbach, including a slender horizontal ramus, a low mandibular corpus, a concave ventral profile and a small diastema between i2-c (Fig. 1d). The ventral profile of the mandibular corpus exhibits a great variability during the ontogenetic growth (Martino et al., 2024c). However, in adult *H. antiquus*, it is usually concave, while in adult *H. amphibius* it is convex (Caloi et al., 1980; Martino et al., 2023; Mazza, 1995). Additionally, a concave ventral profile and a slender ramus can be observed in more fragmented remains attributed to *H. antiquus*, including MGGC9412 (Upper Valdarno, Early Pleistocene, Italy), MSNAF4726 and MSNAF n.c. (Chiusi, Early Pleistocene?, Italy). Another character visible in *H. antiquus* mandibles is the development of the mandibular corpi in dorsal view. In MNHN.F.ITL41, IGF1043 and MPUR/V1950 the mandibular corpi are almost straight, with a sub-parallel development. In *H. amphibius* the mandibular corpi in dorsal view show a more divergent trend (Caloi et al., 1980). Unfortunately, this character is not fully investigable in the mandible from Mosbach since the mandibular corpi are slightly deformed.

MSNCC C.601, which was initially erected the holotype of *H. tiberinus* (Mazza, 1991, 1995), and SAApal43, respectively collected from Maglianella (Middle Pleistocene, Italy, Fig. 1h) and Ortona (late Early-early Middle Pleistocene, Italy Fig. 1i) are currently ascribed to *H.* ex gr. *H. antiquus* (Agostini et al., 2005; Mazza & Bertini, 2013). Similarly to the specimen from Mosbach, the previous specimens also exhibit an overall slender mandible, a low mandibular corpus, a straight-concave ventral profile of the corpus, a short teeth series, a rostral fan that is not particularly wide, and canine processes that are not robust. Additionally, the canines are not particularly large, as observed in the Mosbach specimen.

In lateral view the specimen NHMMZ1937.1 differs from *H. amphibius* in having a long and slender mandible, a concave ventral profile of the mandibular corpus, and a gonial angle connected with the ventral profile through a right angle (Caloi et al., 1980; Mazza, 1995). The *H. amphibius* mandibles MPUR/V149 (Fig. 1k) from Cava Montanari (Mecozzi et al., 2023) and the specimens from Barrington SMUC D3980 figured in Reynolds (1922, pl. II, figs. 1–2, pl. iii, figs. 1–2, pl. iv figs. 1–2) are more robust and shorter in lateral view than NHMMZ1937.1. Furthermore, the ventral profile of the mandibular corpus is more straight in MPUR/V149 and more convex in SMUC D3980 than in the mandible from Mosbach. Additionally, in contrast to the specimens from Mosbach, these specimens exhibit an angular process connecting the mandibular corpus and the ramus with an anteriorly arched angle, as well as a process of the gonial angle that is strongly protruding mesially. The rostral fan exhibits a greater width in all the specimens from Barrington when compared to NHMMZ1937.1. ISPRA4449 (Fig. 1l) recently described in Martino et al. (2024a) and ascribed to *H. amphibius* also exhibits a mandible of notable robustness, a thick sagittal cross-section of the mandibular symphysis and a convex ventral profile of the mandibular corpus. The fragmented mandibles NHMMZ PW2013/30 from Gimbsheim (Fig. 1m) and SMNS6717.7.6.64.2 (Fig. 1n) from Rheinhausen (Late Pleistocene, Germany) both ascribed to *H. amphibius*, also exhibit a robust mandibular corpus with a convex ventral profile in lateral view. In the extant *H. amphibius* specimen SMNS17526 the mandible is robust, the gonial angle is anteriorly arched, the ramus is high, and the ventral profile of the mandibular corpus is convex.

The ridges on the canines are parallel, a character common to, but not exclusive to, *H. antiquus* (Blandamura & Azzaroli, 1977; Caloi et al., 1980). A recent study attested a prevalence of the parallel ridges in *H. antiquus*, claiming that hippopotamid canines began to exhibit convergent patterns with a greater frequency after 0.5 Ma (Mecozzi et al., 2024). Parallel ridges are also visible in the specimens from Ortona and Maglianella. However, Mazza (1995) underlined how this character in question can be variable and may not be diagnostic at the species level within the genus *Hippopotamus*. The straight development of the teeth series is a character listed as "diagnostic if concomitant" for *H. antiquus*, together with parallel ridges in the canines and the development of the ramus (Caloi et al., 1980). Although the latter structure is not preserved, the parallel ridges on the canines and the straight development of the teeth series are both present in the Mosbach specimen. The diastema between the p2 and p3 visible in Schertz (1939), is a common feature in *H. antiquus* (Mazza, 1995). The p4s display considerable morphological variation. However, in general, these teeth are more robust in *H. amphibius* rather than in *H. antiquus* (Mazza, 1995). It is typical for premolars to display considerable variability, rendering them of limited utility for attributions at species level. The m1 is too worn-out to recognize any diagnostic character. In the m2 of *H. antiquus* the entoconid is typically comma-shaped (Mazza, 1995), as observed in NHMMZ1937.1, whereas in *H. amphibius* is usually trefoiled. Mazza (1995) also reported that usually the distostylid in *H. amphibius* is typically trefoiled or triangular-shaped, whereas in *H. antiquus* it is usually roundish or irregular roundish or irregular-shaped in *H. antiquus*. In the Mosbach specimen a roundish distostylid is clearly visible, as in *H. antiquus*. The m3s of NHMMZ1937.1 are unworn and the entoconid is the smaller cuspid, as in both *H. amphibius* and *H. antiquus*. The m3 MGGC7567 from Upper Valdarno has a similar morphology to the Mosbach specimen. The Table 2 resumes all the characters above discussed for *H. antiquus*, *H. amphibius* and the mandible here analysed. Moreover, the Fig. 4 points out all the diagnostic characters recognized in the Mosbach mandible.

Morphometric comparison

All the available measurements of the mandible (LS, Bfi, Bfo, Bco, Lm3i1, Hm3, Hp2 and Hp4) fall within the variability observed in *H. amphibius* (See Supplementary Material, S.1). However, these values are also closer to the measurements of smaller specimens of *H. antiquus* and *H.* ex gr. *H. antiquus*. As illustrated in Fig. 5a, the variability of the common hippopotamus is notably extensive, indicating that characters such as the length of the symphysis and the outer breadth of the rostral fan exhibit pronounced intraspecific variability. Regarding the measurements of the lower anterior teeth (Supplementary Material, S.1), Mazza (1995) argued that no statistical differences can be recognized among the different hippopotamid taxa. The mean value reported by Mazza (1995) for the i1apD and i1 mlD is respectively 50.89 mm and 45.16 mm for *H. antiquus* and 52.03 mm and 45.91 mm for *H. amphibius*. The sample of *H. amphibius* reported by Avedik and Clauss (2023) has a mean value for i1 mlD of 38.99 mm (See Supplementary Material, S.1). The values for Mosbach are (37.43–47.43) mm for i1apD and (37.42–37.55) mm for i1 mlD. The mean measurements for the i2 are 27.73 mm (i2apD) and 23.73 mm (i2 mlD) for *H. antiquus* and 27.5 mm (i2apD) and 24.36 mm (i2 mlD) for *H. amphibius* (Mazza, 1995). The sample of *H.*

Table 2 List of diagnostic characters and their respective state in the mandible from Mosbach compared with *H. antiquus* and *H. amphibius*

Character	Mosbach	*H. antiquus*	*H. amphibius*
Overall aspect of the mandible	Slender	Slender	Robust
Ventral profile of the mandibular corpus	Concave	Concave	Convex
Angle between the gonial angle and the mandibular corpus	Right angle	Right angle	Arched angle
Mandibular symphysis	Rather slender	Slenderer than in *H. amphibius*	Robust
Rostral fan	Moderate	Narrow	Wide
Teeth series	Straight	Straight	Double curvature
Ridges on canines	Parallel	Usually parallel	Usually convergent
Diastema p2-p3	Present	Present	Usually absent
m2 entoconid	Comma-shaped	Comma-shaped	Trefoil-shaped
m2 dystostylid	Roundish	Roundish	More complex than in *H. antiquus*
Diastema i2-c	Moderate	Small	Large

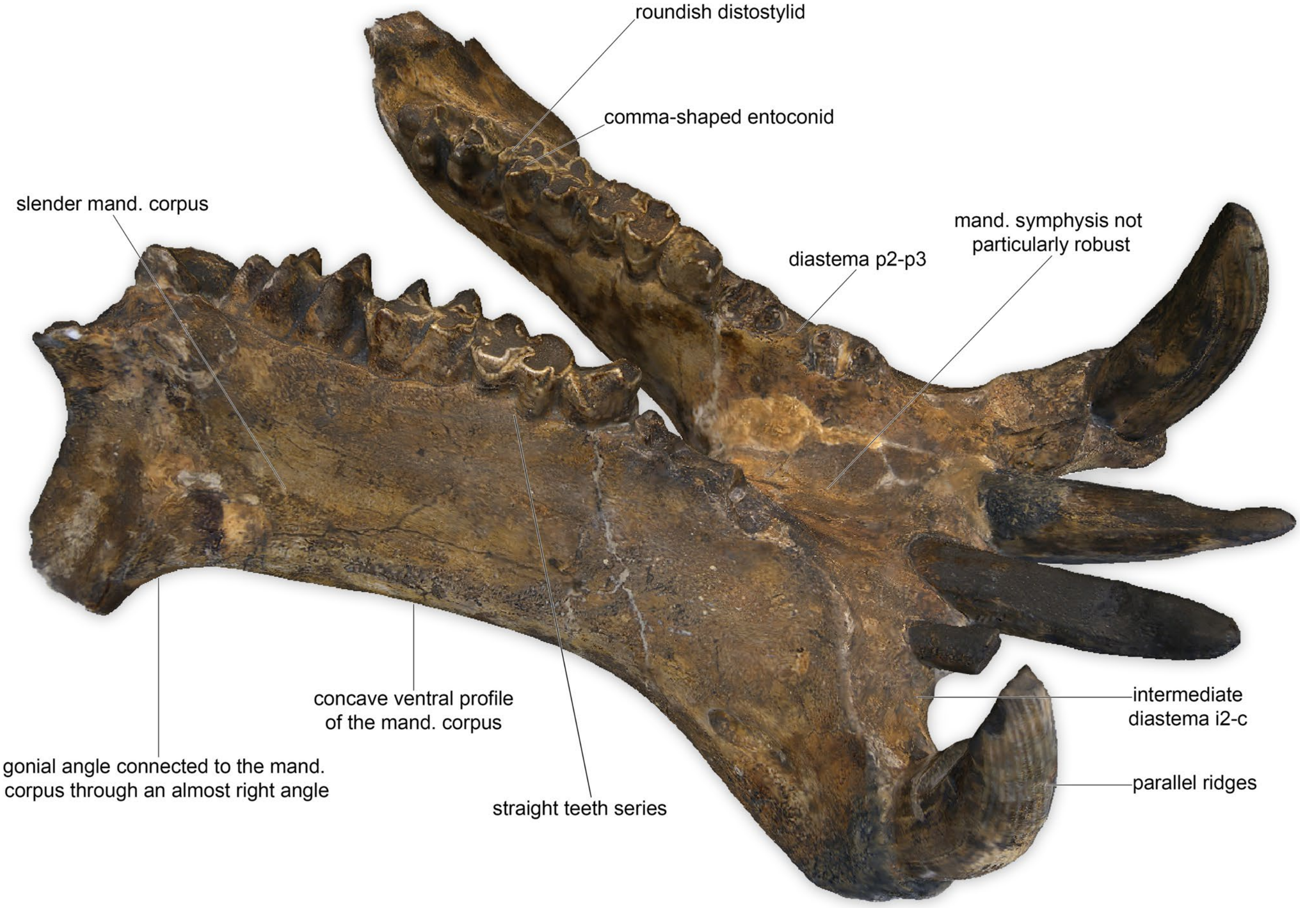

Fig. 4 Diagnostic characters recognised in the specimen NHMMZ1937.1

amphibius reported by Avedik and Clauss (2023) has a mean value for i2 mlD of 23.05 mm (See Supplementary Material, S.1). The measurements for Mosbach are respectively 22.23–23.56 mm and 20.9–22.95 mm. No big differences between *H. antiquus* and *H. amphibius* are detectable in the measurements of lower incisors. Regarding lower canines the values of Mosbach are 52.28–54.26 mm for capD and 34.04–39.89 mm for cmlD. The mean values reported by Mazza (1995) for capD and cmlD are 73.70 mm and 44.53 mm for *H. antiquus* and 69.54 mm and 43.05 mm for *H. amphibius*. The canines of the Mosbach specimen are, in comparison to the mean value of both hippopotamid species, relatively diminutive. Mazza (1995) emphasised that the sole significant difference between the three species is in the length of the diastema between the i2 and the c (Di2c). Mazza (1995) reported a mean Di2c of 34.89 mm for *H. antiquus*, 51 mm for *H.* ex gr. *H. antiquus* and 47.47 mm for *H. amphibius*. The sample of *H. amphibius* reported by Avedik and Clauss (2023) has a mean value for Di2c of 47.08 mm (See Supplementary Material, S.1). The mean value for the mandible of Mosbach is 39.1 mm, closer to *H. antiquus* rather than *H. amphibius*.

The premolar measurements are dimensionally closer to *H. antiquus* and *H.* ex gr. *H. antiquus*, with the exception of the p3, which is closer to *H. amphibius* variability (see Supplementary Material, S.2). The p4 measurements fall within the variability of *H. antiquus* (See Supplementary Material, S.2). The ANOVA on L p4 values revealed that the differences between *H. antiquus* and *H. amphibius* are statistically significant. The same analysis on the B p4 values highlighted that the differences between *H. antiquus* and *H. amphibius, H. gorgops* and *H. amphibius,* and the specimens from Mosbach and *H. amphibius* are all statistically significant (See Supplementary Material, S.2). The MANOVA performed on the p4 measurements is also statistically significant (see Supplementary Material, S.2). The m1 measurements of NHMMZ1937.1 fall within the variability of both the extant and the fossil hippopotamids. In the plot L m1 vs AB m1 (Fig. 5b) the dimensions of the m1 from Mosbach fall within the variability of *H. antiquus, H. gorgops* and *H. amphibius*. The results of both ANOVA and MANOVA tests on L, PB and AB m1 showed that the differences between *H. amphibius* and *H. antiquus*

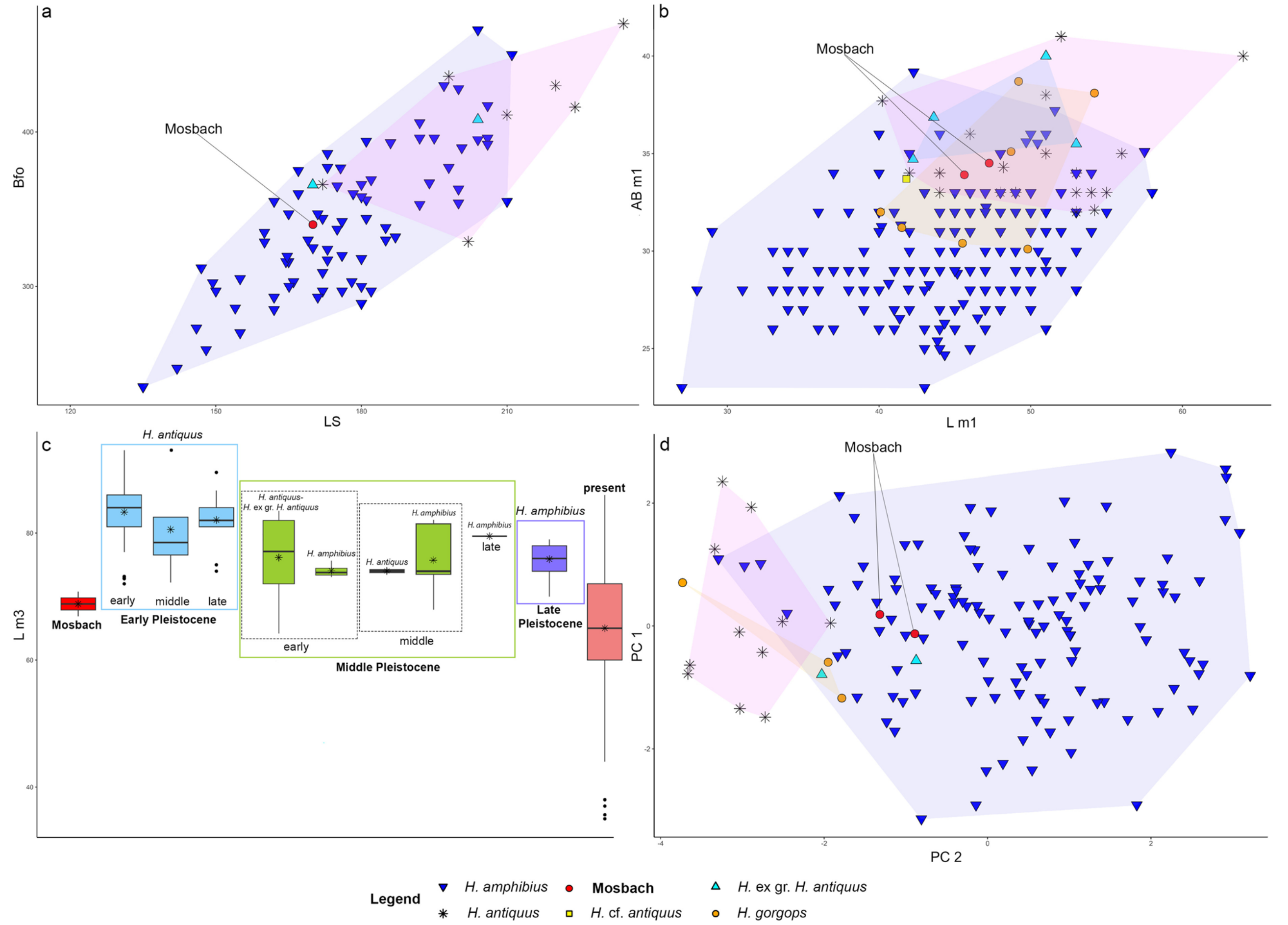

Fig. 5 Scatter and bar plots. **a** Scatter plot length of the symphysis (LS) vs outer breadth of the fan (Bfo) (in mm). **b** Scatter plot greatest length (L) m1 vs anterior breadth (AB) m1 (in mm). **c** Bar plot of greatest length (L) m3 (in mm) for different time periods. Asterisks indicate mean values. The time periods considered are the following: Early Pleistocene (early 2.58–1.5 Ma, middle 1.5–1 Ma, late 1–0.75 Ma), Middle Pleistocene (early 0.75–0.5 Ma, middle 0.5–0.3 Ma, late 0.3–0.12 Ma), Late Pleistocene, present. The following localities were considered for each time period: Chiusi, Durfort, Incarcal and Upper Valdarno (early Early Pleistocene, *H. antiquus*); Colle Lepre, Collecurti and la Cuenca de Guadix-Baza (middle Early Pleistocene, *H. antiquus*); Cava Redicicoli, Durfort, Overstrand and Würzburg-Schalksberg (late Early Pleistocene, *H. antiquus*); Bussi, Cava Montanari, Isernia La Pineta, Kyparissia, Maglianella, Monte Antenne, Mosbach, Ortona, Sidestrand, Terranera, Trentagioli and Vallinfreda (early Middle Pleistocene, *H. antiquus*-*H.* ex gr. *H. antiquus* and *H. amphibius*); Condeixa and Ponte Molle (middle Middle Pleistocene, *H. antiquus* and *H. amphibius* respectively); Malafede (late Middle Pleistocene, *H. amphibius*); Barrington, Casal de' Pazzi, Rohrheim (Late Pleistocene, *H. amphibius*); present (*H. amphibius*). The complete list with all the specimens used is provided in the Supplementary Material (S.2). **d** Scatter plot of the PCA results using teeth values reported in the Supplementary Material (S.2)

are always statistically significant (see Supplementary Material, S.2). More in particular, the ANOVA on the AB m1 values showed statistical differences between *H.* ex gr. *H. antiquus* and *H. amphibius,* and *H. gorgops* and *H. amphibius*. For the PB m1 values also the differences between *H.* ex gr. *H. antiquus* and *H. amphibius* are significant. The m2 and the m3 have measurements close to both *H. antiquus, H.* ex gr. *H. antiquus* and *H. amphibius*. The ANOVA and the MANOVA tests on the AB and PB m2 values are all statistically significant for *H. amphibius* and *H. antiquus, H.* ex gr. *H. antiquus* and *H. amphibius*, and *H. gorgops* and *H. amphibius* (see Supplementary Material, S.2). Regarding the L m2 the only statistically significant differences are between *H. antiquus* and *H. amphibius, H.* cf. *amphibius* and *H. antiquus,* and *H. gorgops* and *H. amphibius*. The ANOVA and MANOVA performed on the m3 measurements are meaningful for L, AB and PB, with the differences between *H. amphibius* and *H. antiquus, H.* cf. *antiquus* and *H. amphibius*, and *H. gorgops* and *H. amphibius* statistically significant (See Supplementary Material, S.2). Based on the recorded values for AB m3, *H.* cf. *amphibius* and *H. amphibius* are also recovered as statistically different. In addition, also the differences between the values of PB and AB m3 are statistically significant for *H.* ex gr. *H. antiquus* and *H. amphibius*. In general, the values of the molars of the Mosbach specimen fall within larger *H. amphibius* and smaller *H. antiquus* (see Supplementary Material, S.2). In the boxplot in Fig. 5c the values of the greatest length of the m3 were divided by time slices. For *H. antiquus* larger values of m3 are associated with Early Pleistocene, especially with the early (e.g., Upper Valdarno), the middle Early Pleistocene (e.g., Collecurti) and the late Early Pleistocene (e.g., Durfort). Starting from the beginning of the Middle Pleistocene there is a reduction in the m3 dimensions. The values observed in the Mosbach sample are similar to those typically seen in European hippopotamids from the Middle Pleistocene. Numerically, the only statistically differences ($p < 0.05$) are between the Early Pleistocene time periods and the present period, the early Middle Pleistocene and the present period and the Late Pleistocene and the present period (see Supplementary Material, S.2). A trend similar to the m3, with Early Pleistocene specimens larger than Middle Pleistocene ones, is also visible using the greatest length of the m1 (see Supplementary Material, S.3) and m2 (see Supplementary Material, S.4). Nonetheless, due to the morphological similarities between these two teeth, their individual classification can be challenging when these fossil remains are found isolated. Due to its unique morphology, characterized by five cusps, the m3 is easily distinguishable. This unique structure leads to a greater number of teeth being classified as m3, thereby contributing to a more comprehensive dataset for the measurements associated with this tooth. The molar series more closely aligned with the values observed in *H. amphibius* and *H.* ex gr. *H. antiquus* than with those of *H. antiquus* (see Supplementary Material, S.2). A principal component analysis (PCA) was also conducted using the variables L m1, L m2, L m3, AB m3 and PB m3. The PC1 accounts for 54.26% of the variance, while the PC2 explains the 27.22% of the remaining variation (> 80%). The specimens from the Mosbach sands exhibit a degree of variability that falls between the variability of *H. amphibius*, but also closer to the variability of *H. antiquus* (Fig. 5d). The specimens from Mosbach also plot close to the sample ascribed to *H.* ex gr. *H. antiquus* (Maglianella and Ortona). Three specimens of *H. amphibius* fall within the range of variability exhibited by *H. antiquus*, an exceptional large extant common hippo and the fossils from Cava Montanari (Mecozzi et al., 2023). The PERMANOVA performed on all the PCs revealed statistically significant differences between *H. amphibius* and *H. antiquus,* as well as between *H. amphibius* and *H. gorgops*.

Taxonomic attribution

The mandible from Mosbach is characterized by a concave ventral profile of the mandibular corpus, a long and slender mandibular body, and a gonial angle connected with the ventral profile through a right angle. In the figure reported in Schertz (1939) is also visible a diastema between the p2 and p3. The entoconids of the m2 are comma-shaped and the distostylid is roundish. The mandible from Mosbach exhibits diagnostic characteristics that align with those observed in *H. antiquus* from a morphological perspective. However, the morphology exhibits by the German mandible is also similar to the specimens from Maglianella and Ortona ascribed to *H.* ex gr. *H. antiquus*. The mandibular measurements are largely consistent with those observed in *H. amphibius* and are similar to those reported for specimens ascribed to *H.* ex gr. *H. antiquus*. However, the latter measurements demonstrate a considerable degree of intraspecific variability for the common hippopotamus. The available data for *H. antiquus* is limited, and therefore the full range of variation observed in the fossil European hippo is unknown. The dental measurements indicate that the hippopotamid from Mosbach exhibited typical characteristics of large *H. amphibius* or small *H. antiquus* specimens. The values of the teeth are notably similar to those of specimens gathered from Ortona and Maglianella and attributed to *H.* ex gr. *H. antiquus*. *Hippopotamus* ex gr. *H. antiquus*, used by Mazza and Bertini (2013), encompasses late advanced *H. antiquus* specimens. Following Sigovini et al. (2016) the term *ex grege* is defined as 'of the group including' and indicates affinity to a certain species. However, this term is misleading and the specimens from Sant'Oreste, Maglianella and Ortona should be revised (Agostini et al., 2005; Mazza, 1991, 1995; Mecozzi et al., 2024). In light of the aforementioned evidence, it can be concluded that the mandible from Mosbach is consistent with the species *H. antiquus*.

Body mass estimation

Several attempts were made by scholars to estimate the body mass (BM) of extinct hippopotamuses during the past decades, resulting in partially contradictory estimations with limits in their applications (Martínez-Navarro et al.,, 2010; Mazza & Bertini, 2013; Palmqvist et al., 2008a, 2008b; Romano et al., 2024). In order to allow a more reliable comparison between BMs and to investigate the possible presence of a trend, we decided to use the regression formulae by Mendoza et al. (2006) to estimate BMs of several hippopotamus specimens (Table 1), including fossil and extant representatives.

The BM of the specimen from Mosbach is estimated between 1969 ± 453 kg and 2140 ± 492 kg. The regression formulae by Mendoza et al. (2006) also provides an average between 2125 ±489 kg and 2287 ±526 kg for IGF1043, with a maximum value closes to that reported by Mazza and Bertini (2013). We also obtained an average BM between 1790 ±412 kg and 2368 ±545 kg for two specimens, MNHNP3866 and MGGC9416, from Upper Valdarno (Table 1). The specimen from Collecurti has an estimated BM between 2494 ±574 kg and 3261 ±750 kg, while that from Durfort has an estimated BM between 2495 ±574 kg and 2558 ±588 kg (Table 1). A small BM is calculated for MSNCC C.601, between 1634 ±376 kg and 1695 ±390 kg, and for SAApal43, between 1783 ±410 kg and 1913 ±440 kg. The BM was also calculated using the regression formula reported by Janis (1990). The values for *H. antiquus* (range between 1170–2503 kg) and *H.* ex gr. *H. antiquus* (SAApal43 1224 kg and MSNCC C.601 1013 kg) are more or less close to those obtained using the formulae of Mendoza et al. (2006). However, the values obtained for some *H. amphibius* (MCSNV n.c., 654 kg and 20160739, 558 kg) are peculiarly smaller than the average known BM of the extant hippopotamus. The BM variability of the different specimens analysed is figured in Fig. 6.

The BM of *H. amphibius* specimens, including female and male individuals (Table 1), suggests that males are usually larger than females. The minimum and maximum BM values for males are between 1292 ±297 kg and 2039 ±469 kg, while for females are between 1084 ±249 kg and 1561 ±359 kg (Avedik & Clauss, 2023; Mazza, 1995). As reported in Table 1, some BM values are higher than the ones presented above, but the sex of these larger specimens is uncertain, and therefore, we cannot rule out a gender misattribution. However, considering the size of the canines of the specimen from Collecurti, it is possible to assume that this mandible belongs to a large adult male. The Upper Valdarno specimens were larger than the specimens ascribed to *H.* ex gr. *H. antiquus* from Maglianella and Ortona, but

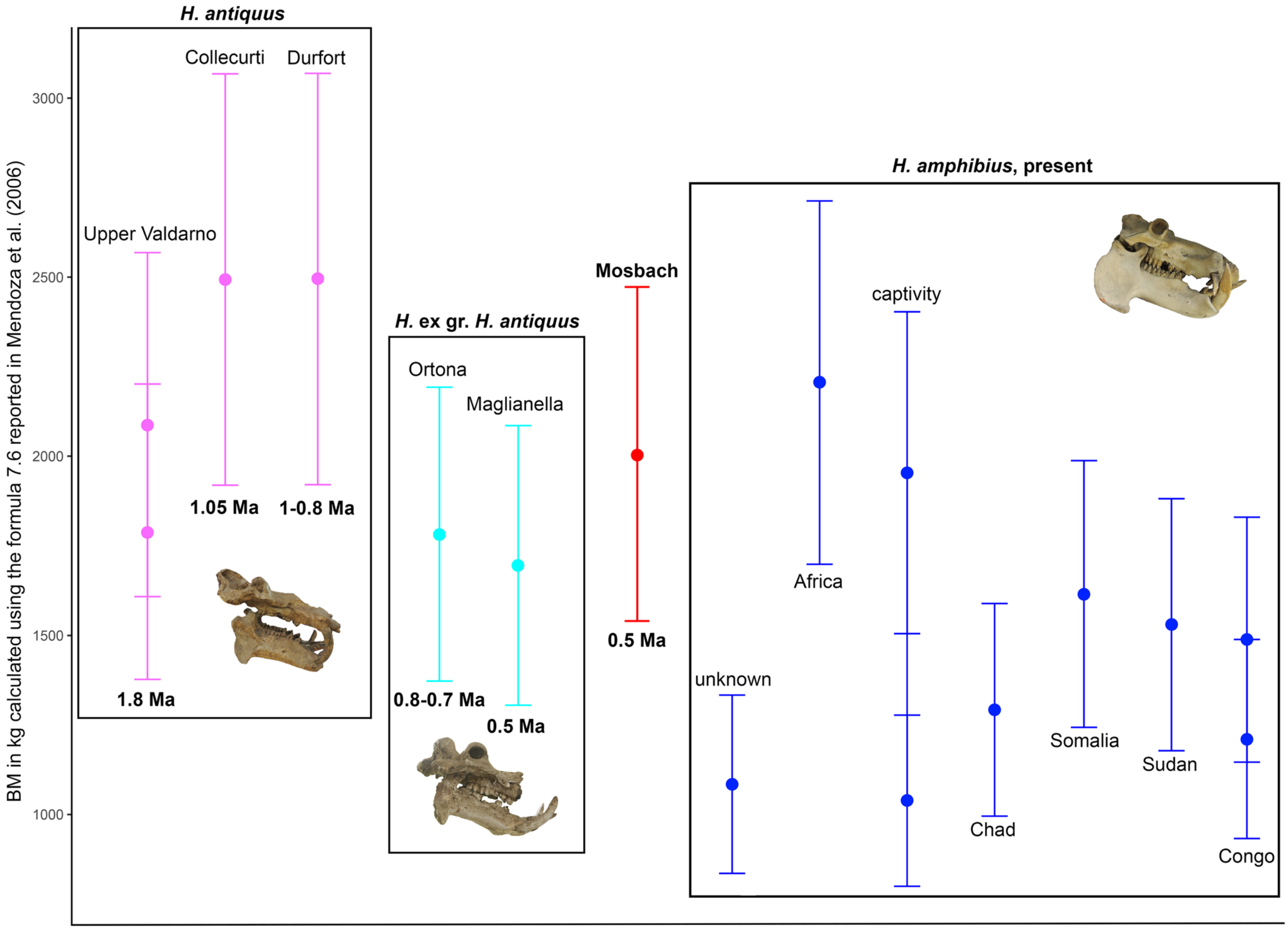

Fig. 6 Body mass (BM) in kg calculated using the formula 7.6 reported in Mendoza et al. (2006). In pink *H. antiquus* from Early Pleistocene sites (Upper Valdarno, Collecurti, Durfort), in light blue *H.* ex gr. *H. antiquus* from Early and Middle Pleistocene localities (Ortona, Maglianella) and in blue extant *H. amphibius* specimens (Africa, Chad, Somalia, Sudan Congo). The BM of Mosbach is reported in red. More information is reported in the Table 1

smaller than *H. antiquus* from Collecurti. The specimen from Mosbach has a BM smaller than that from Upper Valdarno, Collecurti and Durfort. The BM calculated for the specimen from Mosbach is closer to the specimen from Ortona, while the one from Maglianella has the smallest BM value among the fossil hippopotamids.

Discussion

The occurrence of *H. antiquus* is well documented in Europe, with several evidences along the entire Italian Peninsula, from the North (e.g., Leffe and Asolo di Forabosco) to the South (e.g., Saticula and Calorie) (Martino & Pandolfi, 2022), and from all the Iberian Peninsula, with records from southern Portugal (Algoz), Atapuerca (north Spain), Venta Micena (south Spain), Huescar I (south Spain) and Incarcal (east Spain) (Fidalgo et al., 2024). Furthermore, the presence of *H. antiquus* in Greece is also well documented, as evidenced by findings in the Megalópolis Basin (Marathoúsa and Kyparíssia), Apollonía, Elis and Kalamotó (Athanassiou, 2022 and references therein; Konidaris et al., 2024). *Hippopotamus antiquus* has been also documented in Slovenia (Postojnska Caves) and Hungary (Budapest and Budakalász) (Jánossy, 1986; Rakovec, 1954, 1967). The occurrence of the large European hippopotamus in Germany has been reported from Kärlich, Mauer, Jockgrim and Untermaßfeld (Kahlke, 1997; Kahlke et al., 2011; Koenigswald & Tobien, 1987; Mazza, 1995). However, only the latter locality yielded a considerable amount of cranial and post-cranial bones, while comparatively limited data is available from other German sites. Accordingly, the detailed description, the morphometric data, and the proper illustrations of the mandible from Mosbach are useful to fill a gap in our knowledge of hippopotamus from central-northern Europe. The mandible described herein provides valuable insights into the paleobiogeographical distribution and the morphological variability of the hippopotamids in Germany, and more broadly in Europe, during the Middle Pleistocene.

Climate fluctuations and body size variations in hippopotamids: a revaluation of Middle Pleistocene specimens

Hippopotamids, have historically been associated with the presence of water bodies due to their unique semi-aquatic lifestyle (Lewison & Pluháček, 2017). Accordingly, past and present climate fluctuations affected hippopotamid occurrences and their body characteristics (Mazza & Bertini, 2013; Stoffel et al., 2015; Utete, 2020). The impact of climate fluctuations on body size has been extensively examined in a range of herbivorous taxa (Huang et al., 2022; Pandolfi et al., 2015; Saarinen et al., 2014, 2016; Samartzidou et al., 2021; Wright & Viner-Daniels, 2015). An important contribution related to body size variation in hippopotamids was published by Mazza and Bertini (2013). The latter authors focused their research on Pleistocene species, including *H. antiquus*, *H.* ex gr. *H. antiquus* and *H. amphibius*. In recent years, the redescription and re-evaluation of hippopotamid material have provided a valuable opportunity to re-examine the body size variations observed in hippopotamids. A number of intriguing mandibles attributed to *H. antiquus* have been documented from various locations in Europe, including Portugal, Spain, Italy and Greece (Agostini et al., 2005; Athanassiou, 2022; Fidalgo et al., 2024; Martino et al., 2023; Mazza, 1995; Melentis, 1965). Differently from the mandibles collected from Upper Valdarno and Collecurti and ascribed to *H. antiquus*, the specimens from Maglianella and Ortona, dated approximately 0.5 Ma and 0.8–0.7 Ma respectively and attributed to *H.* ex gr. *H. antiquus*, exhibit a distinctive slender morphology and a small size, similarly to the mandible from Condeixa (Portugal) (Fidalgo et al., 2024; Martino et al., 2023). The mandible from Mosbach exhibits intermediate characteristics between the two taxa reported above, displaying a degree of slenderness that is less pronounced than that observed in the *H.* ex gr. *H. antiquus*, yet less robust than that seen in *H. antiquus* mandibles from the Early Pleistocene. Additionally, the size of the mandible from Mosbach is comparable in size to that of *H.* ex gr. *H. antiquus*. The dental measurements of NHMMZ1937.1 are also comparable to those of the specimens from Ortona and Maglianella. The former represents, following Mazza and Bertini (2013), one of the smallest specimens of *H.* ex. gr. *H. antiquus*. The remains from Ortona have been ascribed to an interval between MIS 19 and 17 (Agostini et al., 2005). During that period, the glacial and interglacial cycles became progressively drier and colder, while concurrently the distribution of vegetation in the Mediterranean shifted from 'warm' steppes to ‘cold’ steppes (Bertini, 2003, 2010; Bertini et al., 2015; Suc et al., 1995). As previously highlighted by Mazza and Bertini (2013) hippopotamuses from the Early Pleistocene pre-Jaramillo were larger than those from the post-Jaramillo period. A decreasing trend is indeed discernible in Fig. 6C, which illustrates overall larger measurements of hippopotamid m3 length during the Early Pleistocene while in Middle Pleistocene the dimensions were smaller.

It is worthy to note that shape and size in hippopotamid mandibles are rather variable, and influenced by different variables (Martino et al., 2024c). Heller (1914) defined the subspecies *H. amphibius kibobo* based on hippopotamid population of East Africa. The author observed that the population exhibited a smaller body size and canines than in the Nile *H. amphibius*. Despite the recognition of several subspecies including *H. a. kibobo*, *H. a. tschadensis*, *H. a. constrictus,* and *H. a. capensis*, the validity of these has been questioned (Grubb, 1993; Stoffel et al., 2015). To further discuss the dissimilarities in size and shape, RMCA18561 and RMCA5454 (Fig. 7), both adult hippopotamuses with the m3 erupted and worn out, show different levels of robustness of mandible and canines. The latter teeth are sexually dimorphic in hippopotamuses, with canines notably larger and heavier in males (Shannon et al., 2021). However, the mass of the jaw and the size of the canines are the only structures that exhibit pronounced sexual dimorphism in hippopotamids (Shannon et al., 2021). Subsequently, larger and more robust mandibles are typically observed in male individuals.

The available data on the dimensions of the m3 of *H. amphibius* from the Late Pleistocene also indicate that the European *H. amphibius* was slightly larger than the extant population, but not as large as *H. antiquus* from the Early Pleistocene. In a recent study Mecozzi et al. (2024) investigated the hippopotamid tooth size (L M1, L M2, L M3, L m1, L m2, and L m3) in Middle Pleistocene individuals from Italy. The authors observed a reduction in overall dimensions in specimens dated around 0.6–0.5 Ma (Isernia La Pineta, Maglianella, Terranera) in comparison to hippopotamids dated to 0.7 Ma deposits (Bussi, Vallinfreda). However, it should be noted that some specimens do not align with the aforementioned pattern, potentially indicating the influence of unique local conditions or individual variability. Remains from Maglianella, Ortona and Mosbach corroborate the findings of Mazza and Bertini (2013), that hippopotamids post-Jaramillo were smaller than specimens dated before 1 Ma, including the Upper Valdarno, Collecurti, Durfort, and Untermaßfeld specimens.

Body mass estimation in different hippopotamid taxa

A small body mass in a hippopotamus can be linked to different variables, among them, the age and sex of the animal, local variability, and unfavourable living conditions (e.g., scarce

Fig. 7 Lateral view of *H. amphibius* mandibles. **a** RMCA18561 (Africa); **b** RMCA5454 (Africa, mirrored). Scale bars 3 cm

food) (Mazza & Bertini, 2013; Shannon et al., 2021; Voysey et al., 2023). The Mosbach hippopotamus was an adult, as indicated by the wear surface of its teeth, and most likely a female, based on the size of both the mandible and the lower canines. Similarly, Mazza (1991) ascribed NHMMZ1937.1 to a female individual. The specimens from Maglianella and Ortona were also deemed to be most likely females, since their mandibles exhibit a really slender mandibular corpus and small canines. In order to support the attribution of the specimen from Maglianella to a female individual it should be noted that the MSNCC holds a mandible from the same locality with canines that are twice as large of those observed in MSNCC C.601 (unpublished data). It can be thus concluded that the second mandible should be attributed to a male individual.

Considering the aforementioned evidence, the relatively modest BM calculated for the specimen from Mosbach, Maglianella and Ortona lends support to either a reduction in the size of late *H. antiquus* specimens or sexual dimorphism between male and female individuals. The BM here calculated for different extant hippos, both males and females, show that the intrasexual variability is rather relevant, with some females heavier than some male individuals. This result is also in agreement with what was highlighted by Shannon et al. (2021). In the latter work the male hippos were shown to be just 5% heavier than females, amounting to a small weight difference of approximately 60 kg. In light of that, sexual dimorphism cannot be the only variable explaining difference in BM between different hippopotamus individuals. Even though the specimens from Mosbach, Maglianella and Ortona are most likely females, it would be challenging to demonstrate that the observed differences between Early Pleistocene and Middle Pleistocene specimens can be attributed exclusively to sexual dimorphism. Most likely, different parameters such as the temperature, precipitation and food availability caused a fluctuation in hippopotamid body size (Mazza & Bertini, 2013). Nevertheless, further research on the body size variability of these large mammals is required to enhance comprehension and provide a more accurate quantification of this phenomenon.

Conclusions

The mandible from Mosbach described in this work represents one of the best specimens of hippopotamid from the Early-Middle Pleistocene of Central Europe. The concave ventral profile of the mandibular corpus, the long and slender body of the mandible, the gonial angle connected with the ventral profile through a right angle, together with the comma-shaped m2 entoconids and the roundish distostylid, provide evidence that the specimen can be attributed to *H. antiquus*. Nevertheless, the results of the morphometric analysis indicated that this mandible is of a notably small size, with values more closely aligned with those observed in *H. amphibius*. These relative dimensions are also comparable to those of *H.* ex gr. *H. antiquus*, in particular to a mandible recovered from Maglianella (Italy, 0.6 Ma). The mandible morphology observed in the Mosbach specimen shows a significant similarity to that of *H.* ex gr. *H. antiquus*, as evidenced by comparisons with specimens from Ortona and Maglianella. However, the specimens ascribed to *H.* ex gr. *H. antiquus* require a comprehensive reassessment, as their taxonomic attribution is inadequate and potentially misleading. The body mass calculated for different hippopotamid specimens highlighted that *H. antiquus* was probably larger during the Early Pleistocene than in the Middle Pleistocene. The body mass of the specimen from Mosbach is comparable to the values obtained for Maglianella and Ortona. The German mandible described in this study adds significant morphometrical data to the understanding of *H. antiquus,* and offers new insights into the early Middle Pleistocene large European hippopotamus. The data from Mosbach further supports the hypothesis that the latest *H. antiquus* exhibited a smaller size-related trend.

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Data availability statement The authors declare that all the data are accessible in supplementary material and all the specimens are stored incited Museums and Institutions.

Declarations

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

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