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Taxonomy, chronology, and dispersal patterns of Western European Quaternary hippopotamuses: New insight from Portuguese fossil material

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ABSTRACT

The taxonomy, chronology and dispersal patterns of hippopotamuses in Western Europe are still a matter of debate, despite the long history of researchers on these topics. In this framework, the Portuguese material has never been investigated or recently revised, and it can contribute to increasing our comprehension about Quaternary hippopotamuses. The material considered in this work, collected from sites dated between 1 Ma and 0.13 Ma, is compared with fossil Pleistocene hippopotamuses from the Iberian Peninsula, Italy, Germany and Greece, in order to contribute into the discussion on evolutionary and dispersal patterns of these large semi-aquatic mammals in Europe during the Pleistocene. Portugal deposits recorded the presence of *H. antiquus*, starting from 1 Ma up to 0.4 Ma, and *H.* cf. *amphibius* during the late Middle Pleistocene. In particular, the occurrence of *H. antiquus* in Condeixa, dated around 0.4 Ma, can be considered as the LAD of this species in Europe. The paleobiogeography and dispersal patterns of European hippopotamuses are further discussed.

1. Introduction

Portugal is the South-Western façade of Europe in the Iberian Peninsula, and its climate is deeply affected by the interaction between the Atlantic Ocean and the Mediterranean Sea (Mora and Vieira, 2020). Iberia possibly worked as dispersal way from Africa to Europe (Collina-Girard, 2001; O'Regan, 2008), and/or as Pleistocene "glacial refugia" within Europe (Hewitt, 1999, 2000, 2001), and therefore as source of post-glacial recolonisation by warm-temperate mammals. Within this framework then, refugia are considered as "lifeboats" (sensu Dennell et al., 2011). However, despite its interesting role for the Quaternary of Western Europe, the Pleistocene mammals from Portugal are still poorly understood (Cardoso, 1993, 1996; Brugal and Valente, 2007; Estraviz-López, 2019).

Portugal has more than 50 fossiliferous Pleistocene localities, where primates, artiodactyls, perissodactyls, proboscideans, carnivores, and cetaceans are reported since the nineteenth century (Brugal and Valente, 2007; Estraviz-López, 2019). Among the large mammals, hippopotamids are the only ones characterised by a semi-aquatic lifestyle (Boisserie et al., 2011). Hippopotamids appear first in the Afro-Arabian fossiliferous record from around 7.5 Ma ('Hippopotamine event' sensu Boisserie, 2006), probably in relation with the expansion of C4 plants (Boisserie et al., 2011). These large artiodactyls widespread outside Africa towards Europe at least three times: around 6 Ma (Boisserie, 2005, 2007; Martino et al., 2021), during the Early Pleistocene (ca. 2 Ma) (Gliozzi et al., 1997; Martínez-Navarro, 2004; Petronio et al., 2011; Palombo, 2014), and in the Middle Pleistocene (ca. 0.4 Ma) (Martino and Pandolfi, 2022). In Europe, two main continental species are generally recognised, *Hippopotamus antiquus* Desmarest, 1822, and *H. amphibius* Linnaeus, 1758. *H. major* should be considered as a younger synonym of *H. antiquus* (Mazza, 1995 and references therein). Some authors questioned the validity of *H. antiquus* and erroneously referred it as a subspecies of the extant hippopotamus, *H. amphibius antiquus* (Stuart, 1991; Kahlke, 2000, 2001, 2006). It is generally assumed that *H. antiquus* was closely related or evolved from the African species *H. gorgops* (Coryndon, 1977, 1978; Blandamura and Azzaroli, 1977; Faure, 1985). van der Made et al. (2017) hypothesized the possible synonymy of *H. antiquus* and *H. kaisensis* or that *H. kaisensis* gave rise to *H. antiquus*. Unfortunately, *H. kaisensis* is poorly understood, and new evidence is required to support this hypothesis. Two further species, *H. incognitus* (Faure, 1984) and *H. tiberinus* (Mazza, 1991), have been described in Europe during the past century, but their validity is being

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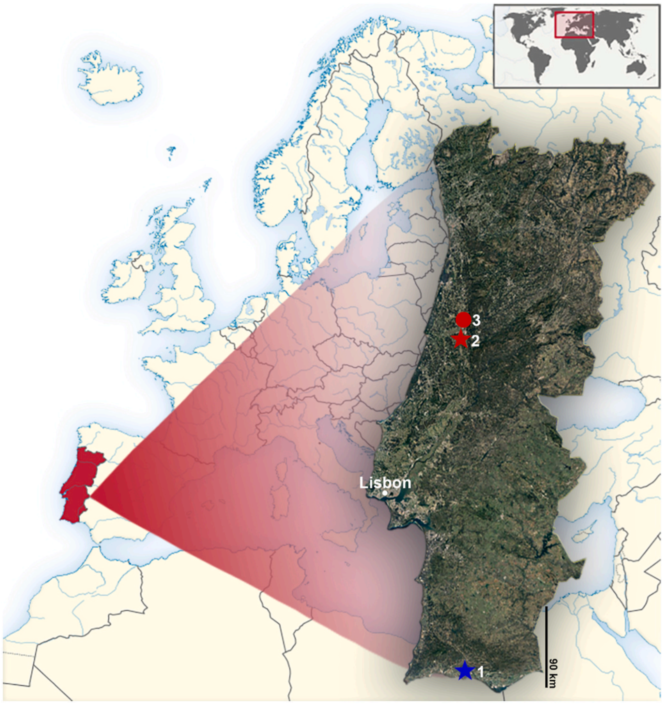

Fig. 1. Location of Portuguese localities (blue, Early Pleistocene; red, Middle Pleistocene). *H. antiquus* (star) and *H.* cf *amphibius* (dot). 1, Algoz; 2, Condeixa; 3, Mealhada. (For references see Web References). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

strongly debated (Petronio, 1995). Further, Mazza (1991) argued that *H. georgicus*, a species erected on some material collected from Akhalkalaki (Georgia) and described by Vekua (1986), probably belonged to the *gorgops-antiquus* group. Finally, van der Made et al. (2017) hypothesized the possible synonymy of *H. tiberinus*, *H. gorgops*, *H. georgicus* and *H. sirensis*, the latter collected from northern Africa, and the possible synonymy of *H. icosiensis* (Pointe Pescade and Beni Saf, Algeria) and *H. incognitus*, both species would in fact indicate an early, larger, evolutionary stage of *H. amphibius*.

In this paper, we revise and describe hippopotamid material from several Portuguese localities spanning from the Early to late Middle Pleistocene. The remains here discussed can contribute to a better knowledge of the hippopotamid record and their dispersal to the Iberian Peninsula. Further, the taxonomic, paleobiogeographic and biochronological implications of this study are discussed within the framework of the Quaternary hippopotamids of Europe.

1.1. *Portuguese deposits: mammals' assemblages, age and considerations*

In Portugal three different sites list the occurrence of hippopotamids: Algoz (civil parish of Algoz and Tunes, Municipality of Silves, District of Faro, Algarve), Condeixa (Condeixa-a-Velha, District of Coimbra) and Mealhada (District of Aveiro) (Fig. 1). Hippopotamid remains from the open-air site of Algoz were firstly mentioned by Zbyszewski (1950). A more detailed revision of the fossil assemblage was later performed by Antunes et al. (1986). This locality is marked by the presence of *H. antiquus*, *Cervus* sp. (cf. *rhenanus-perolensis*), *Eucladoceros* cf. *dicranios* (=*Praemegaceros*?) and *Oryctolagus lacosti* (Antunes et al., 1986). The age indicated for this assemblage by Antunes et al. (1986) is around 1 Ma, corresponding to MN17 to MN20 mammal unit and "Biharian mammal fauna" (Lower Pleistocene) (Pais et al., 2000). Algoz is an important Portuguese locality, because together with Santa Margarida and Morgadinho is one of the three oldest Quaternary sites known from Portugal (Estraviz-López, 2019 and references therein; Estraviz-López and Mateus, 2019). From an ecological point of view, Algoz was characterized by a warm climate, probably a marshy environment rich of vegetation near a river (Antunes et al., 1986). Choffat (1895) was the first to mention the presence of hippopotamus remains in Portugal, in association with proboscideans (*Palaeoloxodon antiquus*), in the calcareous tuffs of Condeixa. The "Tufos of Condeixa" (Condeixa Tuffs) occupy an area greater than 20 km^2 (Soares, 1999) and show an ordered succession of facies: conglomerates (Cg), yellow mud (Pa), tuffs (Ta and Tc), and grey mud with *Lymnea* (Pc). The base of Condeixa Tuffs (Cg) was ascribed by Cardoso (1993, 1996) to the Middle Pleistocene (Mindel/Riss). This attribution agreed with the age determination of the Tufos de Santiago do Cacém made by Gaida and Radtke (1983): 329 ± 70 ka (U/Th) and 383 ± 80 (ESR). Soares (1999) considering Cunha (1990), Cardoso (1993, 1996), Soares et al. (1997), and Marques (1997) also estimated an age around 0.4 Ma for the Condeixa Tuffs base. A well-known site, coeval (389–436 ka) with Condeixa, is Gruta da Aroeira (Daura et al., 2018). This locality yielded several large and small vertebrates in association with hominins (Daura et al., 2018; López-García et al., 2018; Croitor et al., 2019). The mammals' assemblage of this site pointed out that the environment around the cave was dominated by an open-woodland landscape and by the relatively mild, semi-humid conditions of MIS 11c (López-García et al., 2018). Condeixa was probably characterized by a similar environment, but with the presence of wetlands, inhabited by *H. antiquus*. The mammal assemblage of Condeixa suggests a warm and humid paleoclimate, and a dense forest environment with an important wetland, in agreement with the interglacial age of the deposit (Cardoso, 1993). Regarding Mealhada, the mammal assemblage listed in Cardoso (1993) includes: *Homotherium latidens, P. antiquus, Equus* sp., *H. incognitus, Cervus* cf. *elaphus,* cf. *Bos primigenius,* and *Oryctolagus* cf. *cuniculus.* The deposit can be divided into two sedimentary cycles: the older one essentially consists of clayey deposits, with small sandy passages, while the more modern one corresponds to a coarser detrital sedimentation, represented by sandstone to conglomeratic deposits. According to indications, the fossil material, the flint, and quartzite artefacts were all collected from the older assemblage, which is related to a fluvial environment of fine, lowland, freshwater sedimentation; if the sedimentary facies is incontrovertible, the age has been the subject of contradictory opinions during the years. Zbyszewski (1977) considered Mealhada to be contemporary with the beginning of the Würmian glaciation or an intermediate phase of it. The recognition of *Homotherium latidens* by Antunes (1986) reinforced the pre-Würmian age of the deposit. *H. latidens* has long been considered a Lower-Middle Pleistocene species, but its Middle-Late Pleistocene presence was confirmed from the "Spear Horizon" at Schöningen (Germany) dated around 0.3 Ma (Serangeli et al., 2015), and from the North Sea, were some remains were dubiously dated around 28 ka BP (Reumer et al., 2003). The study of lithic materials, particularly those whose stratigraphic position is known, a cordiform biface and a flake core (Zbyszewski, 1977; Antunes et al., 1988), pointed to the Upper Acheulean, corresponding to the Riss glaciation (Antunes et al., 1988). Teixeira (1943) mentioned leaf prints of *Salix cinerea* and *Phragmites* sp. The palynological analysis indicated an association dominated by *Pinus sylvestris* and *P. cembra, Rhododendron* and *Betula*, corresponding to a temperate-cold climate. Further, Mealhada can be correlated with the T3-T4 terraces of Vila Nova da Barquinha-Santa Cita area (Lower Tejo River basin, central Portugal): T3 is older than 300 ka while T4, ~300-160 ka (MIS 8, MIS 7 and MIS 6) (Martins et al., 2010). Terraces from T1 up to T4 display typical reddening, high clay content and swell-and-shrink structures, typical of clayey soils in mild-temperate climate, with alternating rainy and dry seasons (Martins et al., 2010). Mealhada was probably characterized by paleoclimatic conditions similar to those of Vila Nova da Barquinha-Santa Cita. The paleontological, archaeological and palynological analyses indicate that this deposit can be ascribed to the Riss glaciation (0.2–0.13 Ma), probably to an interglacial/interstadial episode (=Saalian in Antunes et al., 1988; Cunha, 1990; 1999).

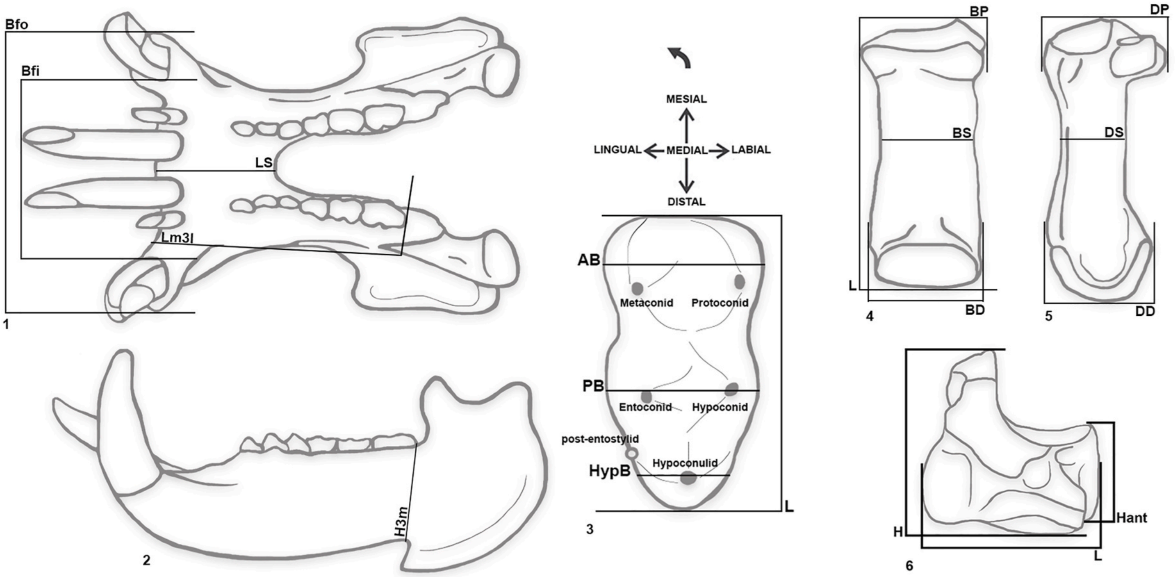

Fig. 2. Measuring points of cranial (1, dorsal view mandible; 2, lateral view mandible; 3, occlusal view m3) and post-cranial remains (4, anterior view MT; 5 lateral view MT; 6, anterior view cuboid). Modified from Mazza (1995) and Boisserie et al. (2010).

2. Material and methods

The Portuguese hippopotamid material includes cranial and post-cranial remains. The morphological terminology for the cranial remains follows Boisserie et al. (2010) and Mazza (1995) (Fig. 2), while post-cranial terminology follows Mazza (1995) (Fig. 2). All the remains were measured following the protocol reported by Caloi et al. (1980) and Mazza (1995). The Portuguese specimens were compared with remains of *H. amphibius*, *H. antiquus*, *H. tiberinus*, *H. incognitus* (=*H. amphibius*) and *H. gorgops* from direct observations (R.M. and L.P.) and published data (Reynolds, 1922; Hooijer, 1950; Accordi, 1955; Boekschoten and Sondaar, 1966; Caloi et al., 1980; Faure, 1984, 1985, 1986; Harris et al., 1988a, 1988b; Harris, 1991; Mazza, 1991, 1995; Kahlke, 1997; Galobart et al., 2003; Tsoukala and Chatzopoulou, 2005; Athanassiou et al., 2018; Georgitsis et al., 2022; Rowan et al., 2022). Character 6 in Faure (1985) is the height at the beginning of the m3, while H3m is the height of the mandible at the end of the tooth. The differences are minimal and therefore we grouped them together and indicated as H3m. The analyses were developed on RStudio Software (2022.07.1 version, R Core Team, 2019) using the packages devtools(), ggplot2() and ggExtra() (Wickham, 2016, 2022). Data were tested with ANOVA (analysis of variance) and/or MANOVA (Multivariate analysis of variance). The complete database is reported in the Supplementary Material.

Institutional abbreviations - **MG**, Museu Geológico de Lisboa, Lisbon, Portugal; **MGGC**, Museo Geologico Giovanni Capellini, Bologna, Italy; **IGF**, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Università degli Studi di Firenze, Florence, Italy; **MZUF**, Museo di Storia Naturale, collezioni della Sezione di Zoologia ''La Specola'', Università di Firenze, Florence, Italy; **MSNCC**, Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa, Italy; **MSNAF**, Museo di Storia Naturale dell'Accademia dei Fisiocritici, Siena, Italy; **MCZR**, Museo Civico di Zoologia, Rome, Italy; **MPUR**, Museo di Paleontologia, Sapienza, Università di Roma, Rome, Italy; **RMCA**, Royal Museum of Central Africa, Tervuren, Belgium; **SMUC**, Sedwick Museum of the University of Cambridge, United Kingdom.

Anatomical abbreviations - **C/c**, upper/lower canine; **I/i**, upper/lower incisor; **M/m**, upper/lower molar; **P/p**, upper/lower premolar; **MT**, metatarsal.

Measurements abbreviations - **AB**, anterior breadth; **B**, greatest breadth; **BD**, breadth of the distal epiphysis; **bFi**, inner breadth of the rostral fan; **Bfo**, outer breadth of the rostral fan; **BP**, breadth of the proximal epiphysis; **BS**, smallest breadth of the diaphysis; **DAP**, anteroposterior diameter; **DD**, depth of the distal epiphysis; **DS**, smallest depth of the diaphysis; **DT**, transverse diameter; **DP**, depth of the proximal epiphysis; **H**, height; **Hant**, height of the dorsal face of the bone; **hypB**, hypoconulid breadth; **H3m**, height of the horizontal ramus at the level of the m3 hypoconulid; **L**, greatest length; **LS**, length of the mandibular symphysis; **Lm3i**, posterior border of the m3 alveolus-incisor alveolus length; **ML**, medial length; **PB**, posterior breadth.

3. Description of the material

3.1. Algoz

3.1.1. Material

MG25769.1: femur articular head; MG25769.2: distal fragmented of right tibia; MG25769.3: fragmented right calcaneus; MG25769.4: fragmented right astragalus; MG25769.10: fragmented right cuboid missing the posterior portion; MG25769.5: fragmented right navicular, missing the posterior portion; MG25769.6: right third metatarsal slightly damaged in the proximal-posterior portion; MG25769.9: right third proximal phalanx; MG25769.8 right middle third phalanx; MG25769.7 right second middle phalanx.

3.1.2. Description

The femur articular head (MG25769.1) does not show useful morphological features due to its conservation status (Fig. 3 A) and does not provide taxonomically meaningful characters. The distal end of a right tibia (MG25769.2; Fig. 3 B–C), has a squared shape in distal view (Fig. 3 B), with the articular surfaces for the astragalus separated by a prominent saddle. The lateral articular surface is transversally crossed by a sinuous groove. The right massive calcaneus (MG25769.3) is severely damaged (Fig. 3 D and E-F). The sustentacular facet is subtriangular in shape (Fig. 3 F). The calcaneal tuberosity is well-developed (Fig. 3 D), and its proximal part shows a wide and shallow trochlea-like groove (Fig. 3 E). The distal articulation of the astragalus (MG25769.4; Fig. 3 H–M) is well-preserved and displays two facets (one for the cuboid and the other for the navicular) proximal distally convex and mediolaterally concave. In anterior view (Fig. 3 H), the articular facet for the cuboid is higher than that for the navicular. In lateral view (Fig. 3 I), the distal articular facet for the calcaneus is ogival-shaped with an almost straight antero-posterior major axis. In posterior view (Fig. 3 K), the

Fig. 3. Remains collected from Algoz. A, MG25769.1, femur head (A, proximal view). MG25769.2, right tibia (B, distal view; C, lateral view); MG25769.3, right calcaneus (D, posterior view; E, distal view; F, articular surface for the astragalus; G, medial view); MG25769.4, right astragalus (H, anterior view; I, lateral view; J, distal view; K, posterior view; L, medial view; M, proximal view); MG25769.10, right cuboid (N, anterior view; O, proximal view); MG25769.5, right navicular (P, proximal view; Q, anterior view; R, lateral view; S, distal view); MG25769.6, right MTIII (T, anterior view; U, lateral view; V, posterior view; W, medial view); right phalanxes in anterior view (X, MG25769.9, third proximal phalanx; Y, MG25769.8, third middle phalanx; Z, MG25769.7, second middle phalanx). All scale bars are 3 cm.

articular surface for the sustentaculum tali is severely damaged in the lateral side but it is transversally wide and partially delimited by a shallow groove on its distal border. In medial view (Fig. 3 L), the posterior end of the medial ridge expands posteriorly. There is also visible in medial view the articular facet for the medial malleolus, which is wide and particularly well-developed. The anterior face of the cuboid (MG25769.10) is rectangular in shape (Fig. 3 N–O). All the articular surfaces of this bone are badly preserved and cannot be deeply described. In proximal view (Fig. 3 P), the right navicular (MG25769.5) displays a wide and concave proximal articular surface, whilst in distal view (Fig. 3 S), the distal articular surface is composed by three distinct facets: a larger one for the external cuneiform, and two smaller ones for the internal cuneiform and the mid cuneiform. In the anterior view the navicular is mainly rectangular-shaped (Fig. 3 Q). In medial view (Fig. 3 R), in the anterior part of the navicular, are visible two articular facets for the cuboid. The right MTIII (MG25769.6) is quite long, with a wide distal epiphysis (Fig. 3 T–W). The proximal epiphysis, in anterior view (Fig. 3 T), bears a slightly concave articulation for the cuneiform. MG25769.6 in anterior (Fig. 3 T) and posterior views (Fig. 3 V), has a roughly clepsydra-shape, with a diaphysis narrower than the proximal and distal epiphyses. In posterior view (Fig. 3 V) there is also visible and very deep fossa, not particularly wide. The posterior portion of the proximal epiphysis is missing (Fig. 3 U, W) and it is not possible to describe the proximal articular surface of the MT. The proximal right third phalanx (MG25769.9) completely lacks the posterior prominence (Fig. 3 X). The right middle third phalanx (MG25769.8) is partially damaged on the proximal portion (Fig. 3 Y). This bone is rectangular in shape, flattened along the lateral-medial axis. The right second middle phalanx (MG25769.7) is almost complete (Fig. 3 Z), trapezoidal in shape, and with a prominent tuberosity on the medial side. However, phalanxes do not provide useful morphological characters to discriminate among the different hippopotamus species.

3.2. *Condeixa*

3.2.1. *Material*

MG3665: mandible fragment with right mandibular corpus and portion of the incisor corpus, preserving the right m3, proximal part of a right c, a right i1, a right i2, a left i1, and a left i2; MG3677: left complete c; MG25174: left fragmented nasal bone; MG25170: fragmented right

Fig. 4. Remains collected from Condeixa. MG3665, right mandible fragment (A, dorsal view; B, m3 occlusal view; C, left lateral view; D, anterior view; E, right lateral view); MG3677, left canine (F, lateral view; G, mesial view); MG25172, left I2 (H, lateral view; I, ventral view); MG25170, right M1/M2 (J, occlusal view; K, labial view); MG25175, left m3 (L, labial view; M, occlusal view; N, lingual view); MG25171 thoracic vertebra (O, anterior view). All scale bars are 3 cm.

M1/M2; MG25172: left I2; MG25175: isolated left m3; MG25171: fragmented thoracic vertebra with the vertebral spine that does not provide taxonomically meaningful characters.

3.2.2. *Description*

The material collected from Condeixa is poorly preserved. The right mandibular corpus (MG3665) is partially crushed (Fig. 4 A–E). In lateral view, it is relatively long and slender (Fig. 4 C). The ventral profile of the mandible below the molars is concave. The ventral profile of the mandibular symphysis, in the anterior view, looks slightly concave (Fig. 4 D), whilst the rostral fan, in dorsal view, is relatively broad (Fig. 4 A). The two lower canines (MG3665 and MG3677) from Condeixa belong to a single individual and have a similar morphology: the right one (MG3665, Fig. 4 A, C, D) is still in its anatomical position, while the left one (MG3677, Fig. 4 F–G) is isolated and partially embedded in the alveolus. MG3677 is complete and its enamel surface displays marked spaced ridges on the lateral side (Fig. 4 F), and less developed ridges and a well-visible groove in the mesial side (Fig. 4 G). The ridges on the lateral side are parallel and marked along the entire length of the canine (Fig. 4 F), whilst the groove on the mesial side tapers apically (Fig. 4 G). The cross-section is triangular. All the lower incisors collected from Condeixa are in their anatomical position. In dorsal view, a small diastema is present between the right and left i1, whilst the i1-i2 diastema is almost absent, and between the right i2 and the right c is very short (Fig. 4 A). The i1s are massive, with thin finely grooved enamel, three times larger than the i2s, procumbent, and slightly divergent in dorsal view (Fig. 4 A). The cross-section of the i1s is mainly rounded (Fig. 4 D), and both are slightly curved lingually. The i2s are elliptical-shaped in cross-section, elongated along the mesial-lateral axis and slightly aligned in anterior view (Fig. 4 A, D). An isolated incisor, probably an I2 (MG25172, Fig. 4 H–I) displays some finely enamel grooves (Fig. 4 H) and it is partially twisted on the apical part in ventral view (Fig. 4 I). A slightly worn wear surface is barely visible on the ventral view of the tooth. The isolated M1/M2 (MG25170; Fig. 4 J–K) is fragmented and highly worn and the only detectable feature is the high and crenulated cingulid in labial view (Fig. 4 K). The two m3s (MG25175, MG3665) display thick and rough enamel, with five prominent cuspids, a comma-shaped entoconid, and a marked post-entostylid on the MG3665 (Fig. 4 B), and a poorly developed post-entostylid on MG25175 (Fig. 4 M). Both m3s show a similar stage of wear and probably belong to the same individual. The transverse valleys are V-shaped in both specimens in lingual view. The cingulid on MG25175 is particularly high on the mesial side, better visible on the lingual side than on the labial one (Fig. 4 L, N). There is a pillar at the end of the posterior-lingual valley on MG3665 (Fig. 4 B). The wear pattern of the hypoconulid on MG25175 is trefoiled (Fig. 4 M), while on MG3665 seems to be comma-shaped (Fig. 4 B). MG2517 is a partially preserved vertebra; with a high spine, and a developed right processus transversus which forms an angle of 90° with the vertebral corpus (Fig. 4 O).

3.3. *Mealhada*

3.3.1. *Material*

MG8040: left cuboid; MG8041: fourth proximal juvenile phalanx.

3.3.2. *Description*

MG8040 is an almost complete left cuboid (Fig. 5). In proximal view (Fig. 5 A), the calcaneal facet (Fig. 5 A1) is small and anterior-posteriorly concave, whilst the astragalar facet (Fig. 5 A2) displays an indentation on the medial edge (Fig. 5 A3). In anterior view (Fig. 5 B), it is rectangular in shape. On the medial side of the bone (Fig. 5 C), two articular surfaces are visible: the cuneiform facet (Fig. 5 C4) is posteriorly

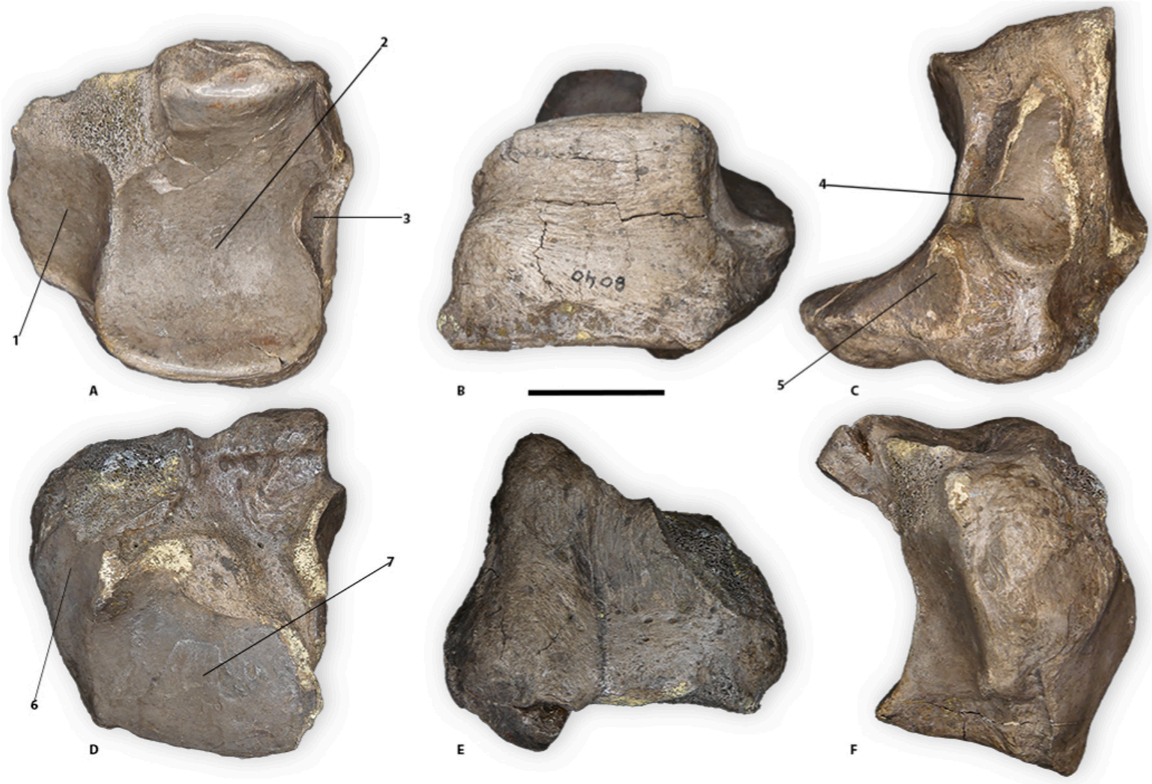

Fig. 5. Remains collected from Mealhada. MG8040, left cuboid. A, proximal view; B, anterior view; C, medial view; D, distal view; E, posterior view; F, lateral view. 1, articular surface for the calcaneum; 2, articular surface for the astragalus; 3, indentation on the medial edge; 4, articular surface for the cuneiform; 5, articular surface for the navicular; 6, articular surface for the MTV; 7, articular surface for the MTIV. Scale bar 3 cm.

Fig. 6. Mandibles in right lateral view. A, MG3665, mandible fragment from Condeixa. *H. tiberinus*. B, C.601, from La Maglianella; C MPUR/V 1950, from Sant'Oreste (rotated); *H. antiquus*. D, IGF689, from Valdarno; E, IGF1043, from Valdarno (rotated); F, IGF771, from Valdarno; G, MSNAF, (without catalogue number, NC) from Chiusi. *H. amphibius*. H, MCZRM1, recent; I, RMCA20854, recent (rotated); J, RMCA18652, recent (rotated); K, D3980, from Barrington. All scale bars 3 cm, D and K 5 cm. C, redrawn from Caloi et al. (1980); K, redrawn from Reynolds (1922).

elongated while the navicular facet (Fig. 5 C5) projects towards the anterior side of the bone. In distal view (Fig. 5 D), the cuboid is squared, and the articular surfaces for the MTIV and MTV (Fig. 5 D6, D7) are well-developed. These two facets are separated by a groove that deepens posteriorly. In posterior view (Fig. 5 E), the facet for the calcaneus is partially missing. On the lateral side (Fig. 5 F), the calcaneal facet is concave and well-developed. The phalanx (MG8041) depicted in Zbyszewski (1977, p. 17, est. IV, fig. 55) and Antunes et al. (1988, p. 168, fig.2), clearly belongs to a juvenile individual due to the unfused proximal epiphysis.

4. Morphological comparison

4.1. Mandible

The development of the ventral profile of the corpus in the mandible of Condeixa is relatively concave (Fig. 6 A). Caloi et al. (1980) listed this character as diagnostic for *H. antiquus* (Fig. 6 D–G), mainly because the ventral profile of the corpus is convex in adult individuals of *H. amphibius* and almost straight in young and sub-adult individuals (Fig. 6 H–K). Petronio (1995) also used this single character to attribute the specimen collected from Campo di Merlo (early Middle Pleistocene, central Italy, Rome) to *H. antiquus*. Nevertheless, Mazza (1995), claimed that the ventral profile of the mandible in *H. antiquus* is variable, from slightly convex to flat to slightly concave, and therefore it cannot be solely used as a diagnostic character. *H. antiquus* specimens figured in Fig. 6 (D, IGF689, E, IGF1043, F, IGF771) share a convex ventral profile. This feature is also partially visible in MSNAF NC (Fig. 6 G). Caloi et al. (1980), Mazza (1995), and Faure (1985) agreed that the mandibles of *H. antiquus* are usually slenderer than those of *H. amphibius*, and therefore the ratio between the corpus of the mandible and the ascending rami is higher in *H. antiquus* rather than in *H. amphibius*. The greater slenderness of the mandible of *H. antiquus* compared to *H. amphibius* can be detected by comparing the different specimens depicted in Fig. 6. In the mandible from Condeixa the ascending ramus is not preserved, but the corpus is quite elongated and slender (Fig. 6 A). A similar morphology is observable in the specimen MPUR/V 1950, ascribed to *H. tiberinus* (*H.* cf *antiquus*) and collected from Sant'Oreste (early Middle Pleistocene, central Italy, Rome) (Fig. 6 C). The latter mandible is slender, with the corpus particularly long and poorly developed in height. The morphology of the mandible from Condeixa partially resembles the specimen MSNCC C. 601 from La Maglianella (Middle Pleistocene, central Italy, Rome) assigned to *H. tiberinus* (Fig. 6 B). Nevertheless, in MSNCC C. 601, incisors and canines are smaller than in the mandible from Condeixa; a character that may be related to sexual dimorphism. In the mandible collected from Condeixa the rostral fan is not particularly wide. Usually, the rostral fan is wider in *H. amphibius* and proportionally narrower in *H. antiquus*. Nevertheless, it should be also mentioned that usually rostral fan widens with age and therefore it is affected by ontogeny (Mazza, 1995).

4.2. Anterior teeth

4.2.1. Upper incisor

The upper incisor MG25172, probably an I2 (Fig. 4 H–I), is useless for specific determination, as already pointed out by Mazza (1995).

4.2.2. Lower incisors

The enamel of these teeth is slightly grooved, and they have no characters useful to uniquely assigned them to a species. Regarding incisors arrangement we agree with Mazza (1995) that observations on lower incisors are not useful for species discrimination. The only character fairly significant is the diastema between the i2 and c: in *H. antiquus* this diastema is shorter than in *H. amphibius* (Mazza, 1995). In that regard, the mandible from Condeixa shows a short diastema between the right i2 and the c. Similarly, the mandible MPUR/V 1950 from Sant'Oreste, displays i1 larger than i2, a short diastema between i1 and i2 and a barely visible diastema between i2 and c.

4.2.3. Lower canines

One of the most important characters displayed by MG3677 is the well-developed parallel longitudinal enamel ridges on the lateral side of the tooth. Caloi et al. (1980) recognised this character as one of the "characters that are diagnostic if concomitant" with other observations. According to Caloi et al. (1980) and Petronio (1995), these enamel ridges are usually parallel and shallow in *H. antiquus* and deeper and anteriorly convergent in *H. amphibius*. Unfortunately, the other two concomitant characters, i.e., the development of dental arches and of the posterior profile of the ascending arch, cannot be observed in the mandible from Condeixa. It should be highlighted that the morphology and development of the canine ridges in *Hippopotamus* is particularly high, and Mazza (1995) claimed that ridges and grooves on the lower canines cannot be used for discrimination purposes. The latter author also underlined that, in general, all characters shared by canines are not suitable for species attribution. In that regard, the isolated canine of *H. antiquus* from Upper Valdarno shows both well-developed and parallel (IGF786 and IGF812) or anteriorly convergent (IGF771 and IGF807) enamel ridges (Blandamura and Azzaroli, 1977).

4.3. Upper cheek teeth

4.3.1. First/second molar

According to Mazza (1995), a strong crenulated cingulum is a character quite common in *H. amphibius*, *H. antiquus* and *H. gorgops*. According to the same author, the only diagnostic character for specific attribution of isolated molars is their breadth. Unfortunately, it is not possible to consider this character on the studied specimen MG25170 due to the absence of the lingual side of the tooth.

4.4. Lower cheek teeth

4.4.1. Third molars

H. antiquus and *H. amphibius* display similar morphological characters of the lower molars: five main cuspids and trefoil wear-pattern. Mazza (1995) claimed that the entoconid usually displays a comma-shaped wear pattern in fossil species, while this character is poorly represented in *H. amphibius*. The comma-shaped entoconid is shared in both specimens from Condeixa. Mazza (1995) highlighted the high variability of the hypoconulid in *Hippopotamus*, but in most cases, it appears trefoiled, as in the specimen from Condeixa. The outlets of the transverse valleys are V-shaped, a character that is shared by fossil and extant *H. amphibius*, but also by other hippopotamuses' species, that can show V-shaped or U-shaped morphology.

4.5. Postcranial remains

4.5.1. Calcaneus

The calcaneal tuberosity of the Algoz specimen is quite similar to KYP4-332 from Kyparíssia, described by Athanassiou et al. (2018) and assigned to *H. antiquus*. The morphology of the sustentaculum tali is subtriangular in shape, similar to the Greek specimen (Athanassiou et al., 2018) and to *H. tiberinus* (MSNCC).

4.5.2. Astragalus

Following Mazza (1995), the astragali of *H. amphibius* differs from those of *H. antiquus* and *H. gorgops* by having a trochlea with a narrower and deeper groove, and by having a narrower distal end of the medial lip of the trochlea in distal view. Further, the medial lip fans out medially and anteriorly, and in anterior view, the lips of the proximal trochlea are in contact with the proximal margin of the distal articular surface, whilst in *H. antiquus* and *H. gorgops* both lips are separated from the distal articular facet. Unfortunately, these characters are not fully observable on the specimen from Algoz because it is partially fragmented and eroded. However, the astragali of *H. amphibius* and *H. antiquus* also display different general proportions (Faure, 1985; Mazza, 1995), which point to a similarity of the Algoz specimen to *H. antiquus* (See Morphometric Comparison).

4.5.3. Cuboid

In anterior view, MG8040 from Mealhada is more squared than

Table 1
Mandible measurements in mm (N, number of specimens; min-max; mean).

	Portugal specimen				*H. amphibius*				*H. antiquus*				*H. gorgops*				*H. tiberinus*			
Character	N	min	max	M	N	min	max	M	N	min	max	M	N	min	max	M	N	min	max	M
LS	1			220	80	135	213	178.73	10	160	234	197.81	5	119	205	169.5	2	176	204	190
Lm3i	1			390	26	332	451	382.53	8	380	495	428.78					2	386	449	417.5
Bfo	1			430	81	235	466	349.51	11	278	470	382.16					1			408
Bfi	1			250	64	180	298	236.53	10	209	281	246.9					2	245	268	256.5
H3m	1			110	44	117	197	146.88	19	126	185	155.05					2	128	149	138.5

H. gorgops: Harris (1991). *H. antiquus*: Caloi et al. (1980); Mazza (1991), 1995; direct observations. *H. tiberinus*: Mazza (1991), 1995. *H. amphibius*: Reynolds (1922); Hooijer (1950); Boekschoten and Sondaar (1966); direct observations.

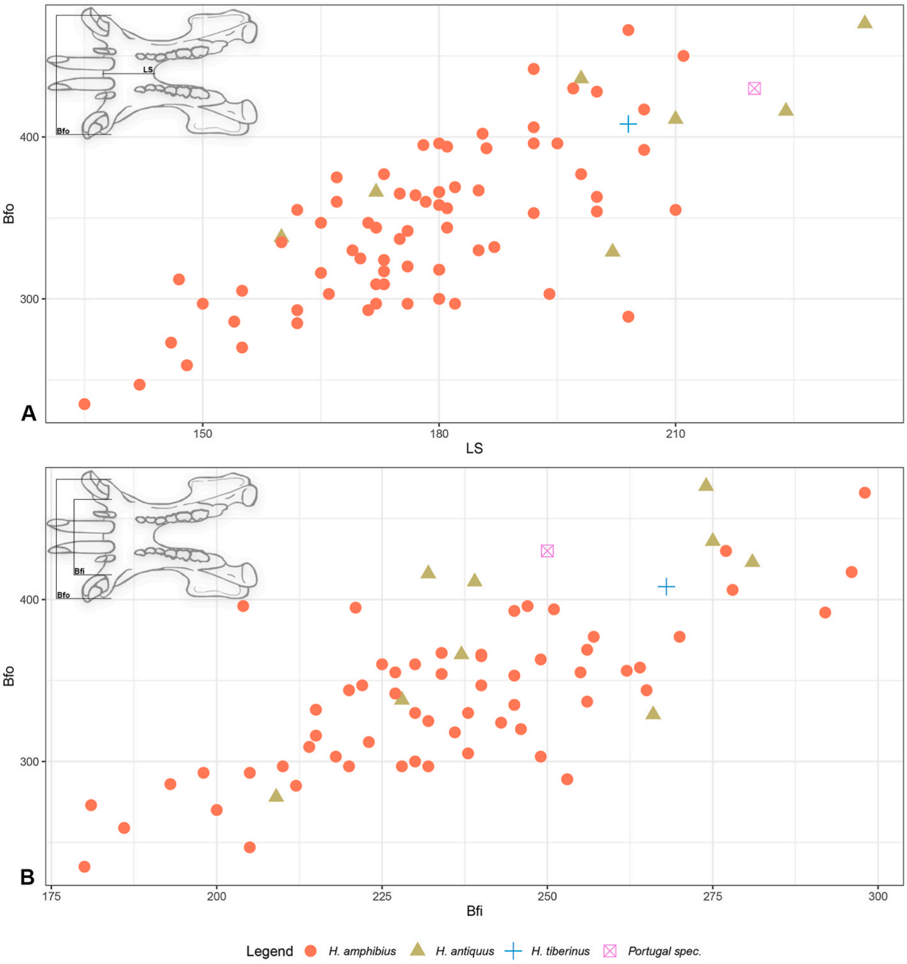

Fig. 7. Mandible dispersion plots (in mm). A, length of the mandibular symphysis (LS) vs outer breadth of the rostral fan (Bfo) and B, inner breadth of the rostral fan (Bfi) vs outer breadth of the rostral fan Bfo. (*H. gorgops*: Harris, 1991. *H. antiquus*: Caloi et al., 1980; Mazza, 1991, 1995; direct observations. *H. amphibius*: Reynolds, 1922; Hooijer, 1950; Boekschoten and Sondaar, 1966; direct observations).

MG25769.10 from Algoz. In proximal view, the astragalar facet is antero-posteriorly concave and more developed than the calcaneal one; the latter being particularly narrow as in *H. amphibius* (Faure, 1985). These two facets are divided by a longitudinal keel. Proximally, as already noticed by Cardoso (1993), an indentation is present on the medial border of the cuboid. Cardoso (1993), in agreement with Faure (1985), considered this indentation poorly developed on *H. antiquus*. Nevertheless, the specimen KYP1-786 collected from Kyparíssia, Greece, and ascribed to *H. antiquus*, clearly displays this feature (Athanassiou et al., 2018). This indentation is also well-recognizable in two cuboids collected from La Maglianella and ascribed to *H. tiberinus*. On the medial side, the inferior facet for the cuneiform is less elongated on MG8040 than in *H. antiquus*, where this facet can be as long as the medial side (Faure, 1985). This feature is also well-visible on KYP1-786. According to Faure (1985), *H. antiquus* displays a posterosuperior facet that corresponds with the navicular. This facet is present in KYP1-786 and in the specimen from La Maglianella but is absent in MG8040 from Mealhada. However, this character seems to be relatively variable within the extant species (Hooijer, 1950: pl. XXI, figs. 3-4).

4.5.4. *Navicular*

In distal view, the articular surface for external cuneiform on MG25769.5 from Algoz extends towards the medial part of the bone; this character is usually absent in *H. amphibius*. The medial view of the bone from Algoz presents an oblique posterior facet contiguous with the distal articulation, a typical feature reported in *H. antiquus* (Faure, 1985).

Table 2
Lower third molar measurements in mm (N, number of specimens; min-max; mean).

	Portugal specimen				*H. amphibius*				*H. antiquus*				*H. gorgops*				*H. tiberinus*			
Character	N	min	max	M	N	min	max	M	N	min	max	M	N	min	max	M	N	min	max	M
L	2	73.61	74.52	74.07	53	58	86	71.73	45	72	93	83.21	14	73.3	90.3	78.86	11	68	80	74
AB	2	44.72	45.4	45.06	28	35	49	40.81	37	40	49	44.82	14	39	48.7	42.67	9	38.6	54	48
PB	2	37	38	37.5	27	35	45	38.9	36	38	48	43.58	12	40	48	42.8	10	40.2	47	43.25
hypB	1			29.2	28	15	33	20	35	18	34	25.65	7	20	44.4	25.83	9	18.9	25.1	21

H. gorgops: Harris (1991); Mazza (1991), 1995. *H. antiquus*: Mazza (1991), 1995; Galobart et al. (2003); Mazza and Bertini (2013); direct observations. *H. tiberinus*: Mazza (1991), 1995. *H. amphibius*: Hooijer (1950); direct observations.

4.5.5. Metatarsal III

According to Mazza (1995), MTIII in *H. antiquus* is characterized by wider latero-medially and narrower antero-posterior epiphyses in comparison to *H. amphibius*, and by a latero-medially narrow and antero-posterior thick diaphysis. In *H. amphibius*, the MTIII is more rectangular-shaped, with a smaller distal trochlea and particularly slender if compared with *H. antiquus*. The general shape of the MT from Algoz resembles the specimen KYPT-865 figured by Athanassiou et al. (2018: p. 190, fig. 9 G) and the specimen IGF1043 from Upper Valdarno, and it is morphologically different from *H. amphibius* (see the specimen R.G.13194, in Georgitsis et al., 2022: p. 23, fig 14.2).

5. Morphometric comparison

5.1. Mandible

The mandible is one of few better-preserved specimens that are suitable for analysis. The measurements available for the mandible from Condeixa are the outer breadth of the rostral fan (Bfo), the inner breadth of the rostral fan (Bfi), the length of the mandibular symphysis (LS), the height of the horizontal ramus at the level of the m3 hypoconulid (Hm3), and the length between the posterior border of the m3 alveolus and the incisor alveolus (Lm3i), reported in Table 1. The values of LS, Bfi and Bfo (Fig. 7) fall within the variability of *H. antiquus*. The H3m of the mandible from Condeixa is lower than that of *H. amphibius* and *H. antiquus*. However, this character can be affected by a possible dorso-ventral deformation of the specimen. The value of Lm3i falls within the variability of largest *H. amphibius* and smallest *H. antiquus* specimens. The fossil from Condeixa displays a lower value for the H3m compared to the values of both *H. antiquus* (min-max by Faure, 1985: 140–164 mm) and *H. amphibius* (min-max by Faure, 1985: 113–156 mm). In Mazza (1995) Lm3i resulted as a diagnostic character to discriminate *H. amphibius* from *H. antiquus*. However, the ANOVA tests performed show that all the differences of the characters here analysed are not statistically significant: Bfo (df = 3, Fvalue = 2.622, p = 0.0554) Bfi (df = 3, Fvalue = 0.809, p = 0.493), LS (df = 3, Fvalue = 5.079, p = 0.0027), Lm3i (df = 3, Fvalue = 4.77, p = 0.00701) and Hm3(df = 3, Fvalue = 3.564, p = 0.0191).

5.2. Lower cheek teeth

H. antiquus molars are usually longer and larger than in *H. amphibius*. Both third lower molars from Condeixa (MG25175, MG3665) fall better within the variability of *H. antiquus* (Caloi et al., 1980; Faure, 1985; Mazza, 1995) (Table 2). As already pointed out by Blandamura and Azzaroli (1977), and Caloi et al. (1980), the distinction between *H. antiquus* and *H. amphibius* cannot be solely based on size differences. Faure (1985) claimed that the differences between *H. antiquus*, *H. amphibius* and *H. incognitus* (=*H. amphibius*) can be seen in the L-AB dispersion plot. Nevertheless, such clear division is not detectable in our graphic, which merely points out that *H. antiquus* has greater proportions than *H. amphibius*, while *H. antiquus*, *H. tiberinus* and *H. gorgops* share similar dimensions (Fig. 8). Portuguese m3s are characterized by greater AB values, similarly to the specimens belonging to *H. antiquus*. ANOVA testing on L (df = 4, Fvalue = 21.57, p = 3.18e-12), and AB (df = 4, Fvalue = 7.928, p = 1.84e-05), reveals that the differences are statistically consistent ($p < 0.001$), in agreement with Faure (1985). The greatest statistical differences regarding L are observed between *H. antiquus-H. amphibius*, *H. amphibius-H. gorgops* and *H. tiberinus-H. antiquus*, while for AB in *H. amphibius-H. antiquus*.

The lower canines collected from Condeixa are particularly massive. Size differences in lower canines are mainly attributable to sexual dimorphism (Blandamura and Azzaroli, 1977). For that reason, a comparative morphometric analysis is not possible without taking into accounts the sex of each investigated specimens. In agreement with this statement, Mazza (1995) claimed that ANOVA revealed that all

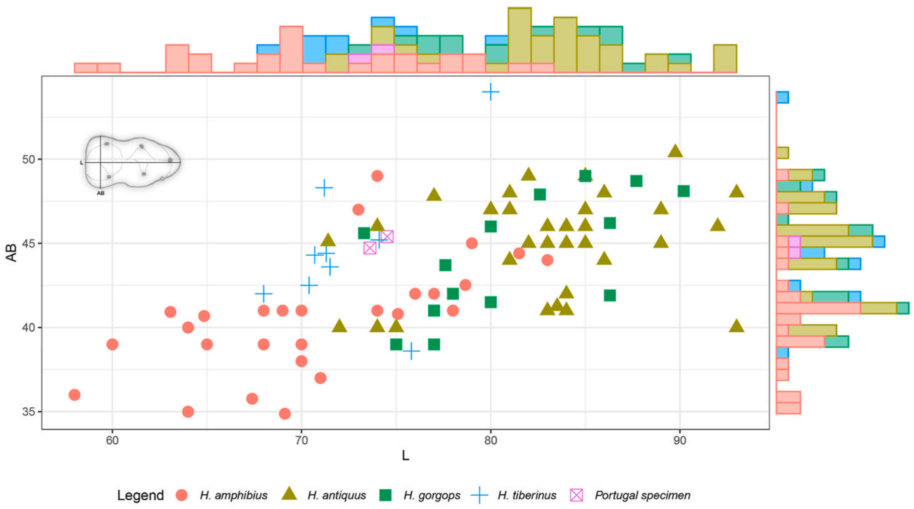

Fig. 8. Lower third molars dispersion plot (in mm). Greatest length (L) vs anterior breadth (AB). (*H. gorgops*: Harris, 1991; Mazza, 1991, 1995. *H. antiquus*: Mazza, 1991, 1995; Galobart et al., 2003; Mazza and Bertini, 2013; direct observations. *H. tiberinus*: Mazza, 1991, 1995. *H. amphibius*: Hooijer, 1950; direct observations).

characters of the lower tusks (canines and incisors) are inadequate for specific discrimination.

5.3. Postcranial remains

5.3.1. Astragalus

MG25769.4 dispersion plot (BD vs ML) shows that the specimen collected from Algoz clearly falls within the variability of *H. antiquus-H. gorgops* (Fig. 8 A, Table 3). ANOVA testing reveals that BD (df = 4, Fvalue = 23.23, p = 4.87e-13) and ML (df = 4, Fvalue = 11.64, p = 1.34e-07) are useful for species discrimination, in particular for *H. antiquus-H. amphibius* and *H. gorgops-H. amphibius*. The same results were also obtained by Mazza (1995). MANOVA (BD-LM) results are also highly significant (df = 4, Fvalue = 8, p = 1,02e-04). The variability of the astragali reported by Faure (1985) for *H. amphibius* is BD (min-max: 69–106 mm), and ML (min-max: 72–103 mm) while for *H. antiquus* is BD (min-max: 92.5–120 mm), and ML (min-max: 90–110 mm). The specimen from Algoz (BD, 104.76 mm; ML, 96.23 mm) is closer to *H. antiquus* rather than to *H. amphibius*.

5.3.2. Cuboid

Unfortunately, the cuboid collected from Algoz is too damaged for a detailed morphometric comparison. The one collected from Mealhada is complete and, in our sample, is closer to *H. antiquus* rather than *H. amphibius* (Fig. 9 B, Table 3). However, the sample here analysed is scant, and only three cuboids of *H. amphibius* were included. The specimen from Mealhada, L (86 mm), H (74.51 mm), H ant (44.24 mm), and l ant face (56.29 mm), are closer to the values of *H. amphibius* reported by Faure (1985). The ANOVA test highlights that L (df = 3, Fvalue = 10.41, p = 9.01e-05), and H (df = 3, Fvalue = 14.29, p = 2.19e-05) results are statistically valid to discriminate *H. amphibius* from *H. antiquus*. supporting the ANOVA results, MANOVA on L and H values is also significant (df = 3, Fvalue = 4.98, p = 0.0005762).

5.3.3. Navicular

The value of B (63.86 mm) measured on MG25769.5 is dimensionally close to *H. antiquus* (Table 3). The variability reported by Faure (1985) in *H. amphibius* (*H. incognitus* included) (min-max: 39–60 mm) and *H. antiquus* (min-max: 58–71 mm) confirms that the Algoz specimen falls within the variability of *H. antiquus*. ANOVA confirms that the differences for B (df = 2, Fvalue = 16.06, p = 0.000121) are significant.

5.3.4. Metatarsal III

MG25769.6 is the best-preserved specimen from Algoz. All the measurements (L, 137.3 mm; BD, 55.13 mm; DD, 45.96 mm; BS, 48.92 mm; DS, 31.75 mm; BP, >47.27 mm) fall within the variability range of *H. antiquus* (Table 3). In particular BD, DD and BS (Fig. 9 C) show that *H. amphibius* and *H. antiquus* have different proportions, as already pointed out in the morphological comparison. Faure (1985) reported the measurements of the MTIII of the extant hippo and *H. antiquus* (Tab. 28, p. 50), and the specimen from Algoz falls better within the variability of *H. antiquus* (min-max: L, 127–155 mm; BD, 49–60 mm; DD, 41–50 mm; BS, 47–56 mm; DS, 27.5–37.5 mm; BP, 46–57 mm) rather than *H. amphibius* (min-max: L, 112–144 mm; BD, 35–46 mm; DD, 31–38 mm; BS, 33–46 mm; DS, 19–30 mm; BP, 37–46 mm). ANOVA confirms that the differences in each character are statistically significant: BD (df = 4, Fvalue = 27.79, p = 3.74e-10), DD (df = 4, Fvalue = 13.92, p = 9.37e-07), BS (df = 4, Fvalue = 34.15, p = 2.66e-11), DS (df = 4, Fvalue = 14.43, p = 6.52e-07), BP (df = 4, Fvalue = 13.84, p = 7.27e-07) and L (df = 4, Fvalue = 6.931, p = 0.000364). The same results were also highlighted by Mazza (1995). MANOVA analyses on BD-BS (df = 4, Fvalue = 8.60, p = 1.02e-04), DS-DD (df = 4, Fvalue = 5.52, p = 3.064e-05), and L-BD (df = 4, Fvalue = 7.22, p = 1.165e-06) are also significant. The PCA on the MTIII (Fig. 10) shows that the specimen from Algoz falls within the variability of the *H. antiquus-H. gorgops* group (positive values of PC1), while *H. amphibius* plots in a well separated morphospace (negative values of PC1 and PC2). PC1 explains the 87.1% of the variability while PC2 only the 6.41% (tot>93%). The variable with the highest absolute correlation to the first and second axis is BD. There are three specimens ascribed to *H. antiquus* that do not fall within the variability of *H. antiquus*. The above-mentioned specimens are the third metatarsals (KLT221, KLT69, KLT131) collected from Kyparíssia, Greece, and dated 1.2–1.1 Ma (Tsoukala and Chatzopoulou, 2005). These remains are characterized by a larger size compared with other specimens of *H. antiquus*, in particular by greater L, BP and BD (See Supplementary Material).

6. Discussion

6.1. Specific attribution of Portuguese material

The Portuguese material is quite scarce and fragmented; however, it adds new paleobiogeographic and bio-chronological implications on the dispersal of the Hippopotamidae within the European continent.

The specimens from Algoz are represented by an almost complete

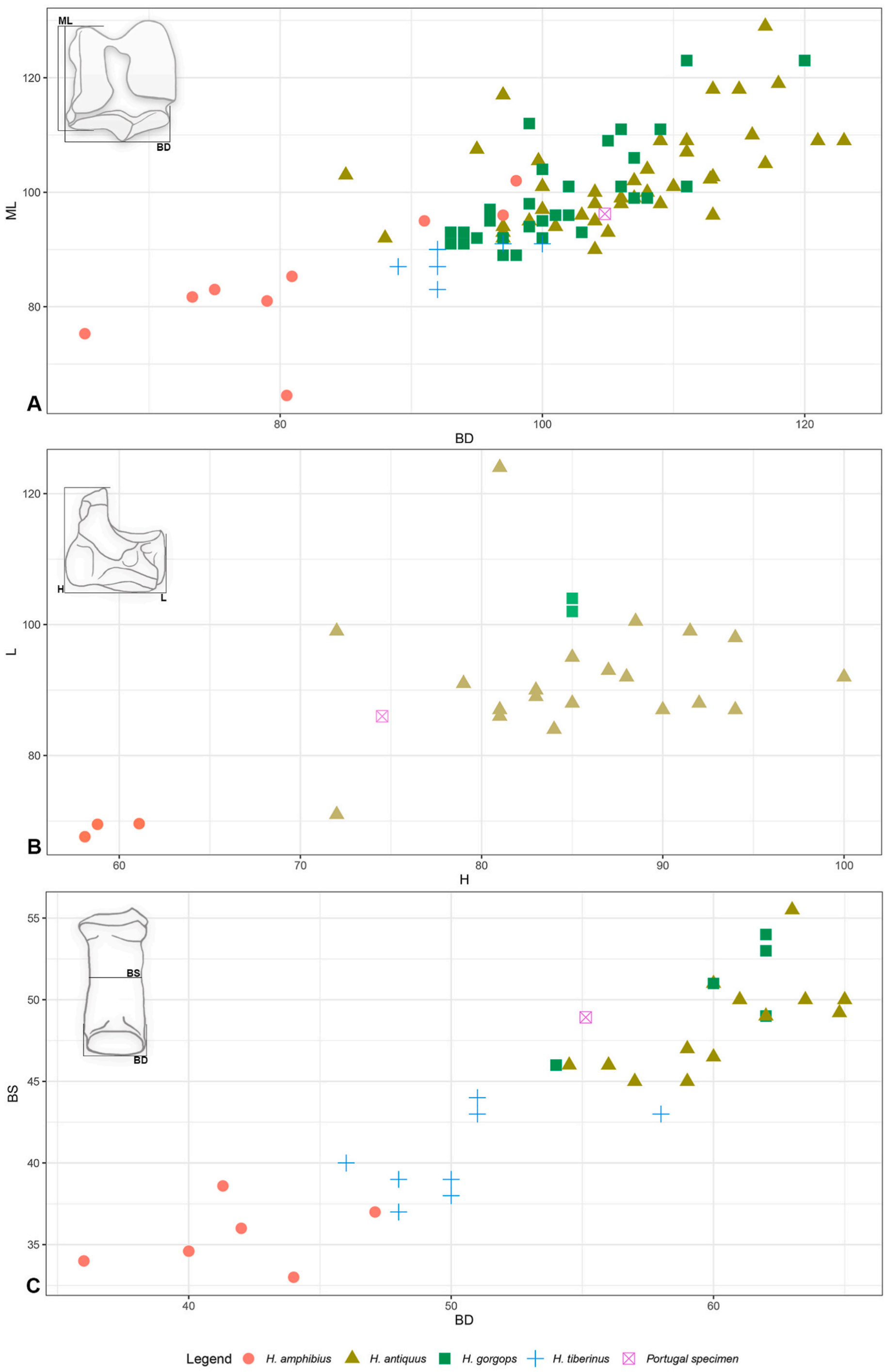

Fig. 9. Postcranial remains dispersion plots (in mm). A, astragalus, breadth of the distal epiphysis (BD) vs median length (ML); B, cuboid, height (H) vs greatest length (L); C, MTIII breadth of the distal epiphysis (BD) vs smallest breadth of the diaphysis (BS). (*H. gorgops*: Mazza, 1991, 1995; Harris et al., 1988a, 1988b. *H. antiquus*: Mazza, 1991, 1995; Kahlke, 1997; Galobart et al., 2003; Tsoukala and Chatzopoulou, 2005; Athanassiou et al., 2018; Georgitsis et al., 2022. *H. tiberinus*: Mazza, 1991, 1995. *H. amphibius*: Reynolds, 1922; Hooijer, 1950; Boekschoten and Sondaar, 1966; Mazza, 1995; Georgitsis et al., 2022).

forelimb, probably belonging to the same individual. Only a few characters are useful for a taxonomic identification because of the conservation status of the material. On the calcaneus (MG25769.3), the morphology of the calcaneal tuberosity and the shape of the sustentaculum astragali are similar to those ascribed to *H. antiquus* by Athanassiou et al. (2018: p. 187, fig. 7 J). The navicular (MG25769.5) displays a surface for the external cuneiform with a protrusion towards the medial part of the bone, that is usually absent in *H. amphibius*. On the same bone, in medial view, it is possible to detect an oblique posterior facet contiguous with the distal articulation, similarly to *H. antiquus* (Faure, 1985). The MTIII from Algoz has wide proximal and distal epiphyses, similarly to *H. antiquus*. In agreement with Mazza (1995), *H. antiquus* MTIII epiphyses are usually wider latero-medially and narrower antero-posteriorly in comparison with *H. amphibius*. The dimensions of the MTIII from Algoz are closer to those of hippopotamid specimens collected from localities chronologically close to the Jaramillo subchrone, such as Kalamotó (Mygdonia basin, Macedonia), Untermaβfeld (Thuringia, Germany) and Colle Curti (Macerata, Italy), than the specimens from post-Jaramillo localities, such as Mosbach (Germany) (Mazza, 1995; Kahlke, 1997; Tsoukala and Chatzopoulou, 2005). All the analyses here performed, suggest that the specimens from Algoz are morphometrically closer to *H. antiquus* rather than *H. amphibius*. ANOVA test on different postcranial elements (astragalus, calcaneus, navicular, cuboid, MTIII) produces almost all statistically significant results. PCA on MTIII underlines that the specimen from Algoz is closer to the variability of *H. antiquus* rather than *H. amphibius*,

Table 3
Post-cranial measurements in mm (N, number of specimens; min-max; mean).

		Portugal specimen				*H. amphibius*				*H. antiquus*				*H. gorgops*				*H. tiberinus*			
	Character	N	min	max	M	N	min	max	M	N	min	max	M	N	min	max	M	N	min	max	M
CUBOID	**H**	1			74.51	3	58.1	61.1	59.33	20	72	100	85.06	2	85	85	85				
	L	1			86	6	67.6	78	75.67	23	71	124	91.95	2	102	104	103				
	H ant	2	44.24	45.6	44.92					17	37	61	52.12								
NAVICULAR	**L**	1			63.86	5	41.9	52	45.66	14	53	81	64.33								
ASTRAGALUS	**BD**	1			104.76	11	65.1	97	86.43	42	85	123	106.51	30	94	120	101.6				
	ML	1			96.23	10	64.5	102	89.67	43	90	129	103.05	30	89	123	99.5				
MTIII	**L**	1			137.3	6	120	144.7	123.33	16	134	170	143.58	8	138	160	148.63	7	122	131	129.29
	BP	1			>47.27	6	39	43	41.5	17	42	66	53	8	49	58	53	8	41	46	44.13
	BD	1			55.13	6	36	47.1	42.1	16	54.5	64.8	59.69	7	48	62	57.57	8	46	58	50.25
	DD	1			45.96	6	22.7	38	34.2	15	42	56	47.33	8	38	53	47	8	35	43	38.63
	BS	1			48.92	6	33	38.6	35.33	16	45	51	47.69	6	46	54	49.83	9	38	44	40.22
	DS	1			31.75	6	20.5	22.5	21.25	17	23	33	29.46	5	28	37	34	9	23	31	25.67

H. gorgops: Harris (1991); Mazza (1991), 1995. *H. antiquus*: Mazza (1991), 1995; Kahlke (1997); Tsoukala and Chatzopoulou (2005); Athanassiou et al. (2018). *H. tiberinus*: Mazza (1991), 1995. *H. amphibius*: Reynolds (1922); Boekschoten and Sondaar (1966); Mazza (1995); Georgitsis et al. (2022).

in agreement with the observations on morphological characters. Accordingly, all the specimens from Algoz are referred to *H. antiquus*.

The remains from Condeixa, as well as the cuboid collected from Mealhada, were ascribed to *H. incognitus* by Antunes et al. (1988) and Cardoso (1993, 1996). *H. incognitus* was established by Faure (1984), based on a complete skull (SMUC D3980) and a composite skeleton figured by Reynolds (1922), both collected from an Upper Pleistocene locality of Barrington (UK). According to Faure (1984), the distinctive features of *H. incognitus* are: a fairly large size, a cranium relatively long with a post-orbital constriction, a nuchal face relatively low but very wide at the mastoid processes, a tetraprotodont mandible with a low and wide horizontal ramus, a zeugopodium (radius-ulna and tibia) strongly elongated and fourth metapodials almost long as the third ones. Following Faure (1984), *H. incognitus* differs from *H. amphibius* by overall larger size and wider breadth of m3, whilst it differs from *H. antiquus* by overall smaller size, shorter muzzle, less exaggerated periscope position of the orbits, shorter stylopodium, and longer metapodials. According to Mazza (1995) and Petronio (1995), the diagnostic characters listed for *H. incognitus* by Faure (1984) fall within the intra-specific variability of the extant *H. amphibius*. Accordingly, Petronio (1995) and Mazza (1995) considered *H. incognitus* as a junior synonym of the extant hippopotamus, and Mazza and Bertini (2013) considered the specimen from Barrington as the first well-documented occurrence of *H. amphibius* in Europe. Recently, van der Made et al. (2017) claimed that *H. incognitus* could be recognised as a larger *H. amphibius* subspecies, i.e. *H. amphibius incognitus*. Further, according to van der Made et al. (2017), *H. incognitus* is morphologically and morphometrically similar to the North African *H. icosiensis* established by Pomel (1896). However, looking at the morphological characters of *H. amphibius* and its great morphometrically variability, we agree with Petronio (1995) and Mazza (1995) in considering *H. incognitus* as a junior synonym of *H. amphibius*. Therefore, the material from Condeixa and Mellhada cannot be referred as *H. incognitus*.

The material from Condeixa is abundant but poorly preserved and severely fragmented. The mandible displays some useful morphological features such as a concave ventral profile, incisors without a diastema between i1-i2 and with a poorly developed diastema between i2-c, a rostral fan not particularly wide in ventral view, a horizontal ramus elongated and slender, and a left canine with parallel grooves on the enamel. Caloi et al. (1980) considered the ventral profile of the mandible as a diagnostic character to distinguish between the extant species and *H. antiquus*, but Mazza (1995) gave scarce credit to it. Considering the morphological variability observed in *H. amphibius*, we agree with the statement reported by Mazza and focus our comparison on other characters. Caloi et al. (1980), Faure (1985), and Mazza (1995) stated that, in general, the mandible of *H. antiquus* is usually slenderer and longer than that of *H. amphibius*, and it is characterised by a narrower rostral fan, as observed on the mandible from Condeixa. In addition, according to Mazza (1995), in *H. antiquus* the diastema between i2 and c is usually narrower than in *H. amphibius*: a feature displayed by the mandible from Condeixa. Concerning the lower canines, the presence and development of enamel grooves and ridges on the surface has been used alternatively as diagnostic (Caloi et al., 1980) or useless for specific discrimination (Blandamura and Azzaroli, 1977; Mazza, 1995). Considering the direct observations on living hippopotamuses and *H. antiquus* specimens, we consider this feature as poorly diagnostic for taxonomic purposes. Considering the morphometric characters, Bfo vs Bfi plot (Fig. 7 B) shows that the specimen from Condeixa is morphometrically close to *H. antiquus*, whilst L vs AB plot of m3s (Fig. 8) shows that most of the specimens of *H. antiquus* and *H. amphibius* plot in two different areas, and the remains from Condeixa fall within the variability of *H. antiquus*. ANOVA results performed on m3 (L, AB, PB, hypB) are fairly significant. The lower molars of *H. antiquus* are usually more elongated and slenderer than in *H. amphibius*. Faure (1985) highlighted that the greatest length (L) - anterior breadth (AB) proportion in lower teeth is usually quite useful

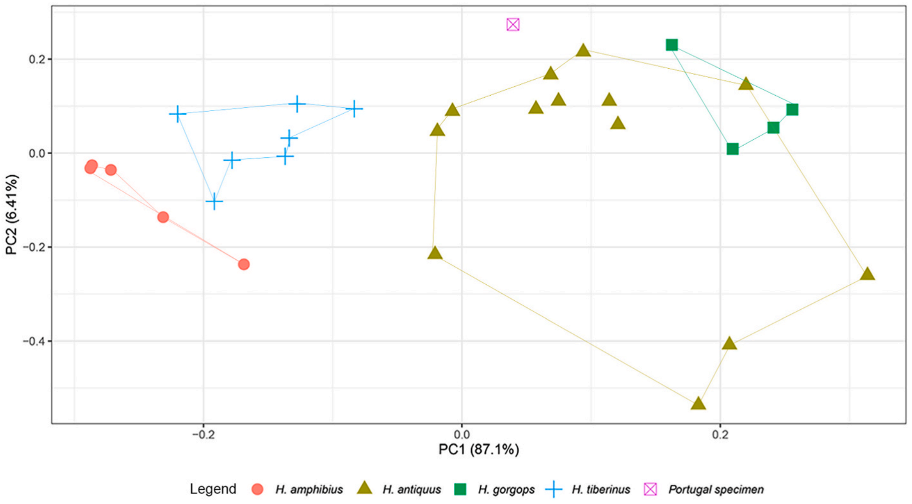

Fig. 10. PCA performed on the MTIII. PC1(87.1%) on x-axis plane and PC2 (6.41%) on y-axis plane. (*H. gorgops*: Harris, 1991; Mazza, 1991, 1995. *H. antiquus*: Mazza, 1991, 1995; Kahlke, 1997; Tsoukala and Chatzopoulou, 2005; Athanassiou et al., 2018. *H. tiberinus*: Mazza, 1991, 1995. *H. amphibius*: Reynolds, 1922; Boekschoten and Sondaar, 1966; Mazza, 1995; Georgitsis et al., 2022).

for specific determination. We agree with this observation, at least for *H. amphibius-H. antiquus* discrimination. Accordingly, all the specimens from Condeixa can be re-ascribed to *H. antiquus*.

The material collected from Mealhada is too scant for a specific attribution. However, some morphological characters, such as a short inferior facet for the cuneiform and the absence of a postero-superior facet, usually well-visible in *H. antiquus*, suggest a closer affinity to *H. amphibius*. In addition to the morphological characters, also the dimensions of the cuboid from Mealhada are closer to *H. amphibius* rather than *H. antiquus*. Accordingly, we refer the material from Mealhada as *Hippopotamus* cf. *amphibius*.

6.2. *Paleobiogeographical and paleoenvironmental implications*

A map with some of the hippopotamids occurrences during the Quaternary in Europe is provided in Fig. 11. Algoz, dated around 1 Ma, is one of the oldest fossil assemblages of Portugal and, so far, the only Early Pleistocene locality where *H. antiquus* is recorded in this region. The species probably dispersed from East to West in southern Europe, reaching the westernmost area of the Iberian Peninsula only during the latest Early Pleistocene. Time and mode of this pattern is still partially debated, mainly because the first occurrence of this species in Europe has been questioned several times. Vangengeim et al. (1998) cited an hippopotamid occurrence in a Late Pliocene Moldovan locality, Roussillon. The Late Pliocene faunas from Moldova are historically called "Bessarabian Roussillon" since they were roughly correlated with French Roussillon. Actually, the age of "Bessarabian Roussillon" (Late Pliocene) does not correspond to the age of French Roussillon fauna (Early Pliocene), therefore it is better to omit this outdated term ("Bessarabian Roussillon"). Nevertheless, the validity of the specific attribution and the stratigraphic position of this locality is still questionable (O'Regan, 2008). Bolomey (1965) cited the presence of hippopotamid in Valea Graunceanului (Romania), a site ascribable to MNQ18a, around 2–1.8 Ma (sensu Spassov, 2003). However, the occurrence of hippopotamids in this site has not been confirmed in more recent articles (Radulesco and Samson, 1990, 2001; Terhune et al., 2020). *H. antiquus* is reported from several localities of the Valdarno area (Tuscany, Italy) referred to a time span between ca. 1.9 Ma and 1.7 Ma (Fidolini et al., 2013) and from Elis (NW Peloponnesus, Greece) ascribed to the earliest Pleistocene (Athanassiou, 2022) (Fig. 11). Several hippopotamid remains were also collected from Chiusi basin (Tuscany, central Italy), where the faunal assemblage (*H. antiquus, Gazella* sp., *Axis* cf. *A. nestii* and *Eucladoceros* sp.) suggests an age similar to that of Coste San Giacomo (Cuscani Politi, 1966, 1971; Pandolfi and Petronio, 2015) (Fig. 11, 53). In Turkey *Hippopotamus* sp. is described from Kocakır-2 (Burdur, Fig. 11, 99), a site placed chronologically between Gerakarou (Greece, ca. 1.9 Ma) and Livakos (Greece, ca 1.6 Ma) (Demirel et al., 2016). In France the presence of *Hippopotamus* ex gr. *H. antiquus* (sensu Palombo and Valli, 2003), is testified from different late Early-Middle Pleistocene localities (Auguste, 2009 and references therein), whilst in Spain *H. antiquus* is known starting from 1.5 to 1.6 Ma (Madurell-Malapeira et al., 2014 and references therein). According to Petronio (1995), *H. antiquus* also occurred in two different Algerian localities, Ain Hanech (Fig. 11, 103) dated around 1.78 Ma (Sahnouni et al., 2013) and Ternifine (or Tighennif, Fig. 11, 104) ascribed to late Calabrian, around 1 Ma (Geraads, 2016). Hippopotamids from Ternifine were first erroneously ascribed by Pomel (1890) to *H. sirensis*, a junior synonym of *H. gorgops* (Geraads, 1980). Further, Petronio (1995) suggested that *H. antiquus* and *H. gorgops* should probably be assigned to the same species (*H. antiquus*) and Martínez-Navarro (2004) and Martínez-Navarro et al. (2022) highlighted some similarities between the cranial features of *H. gorgops* and *H. antiquus*. An origin of *H. antiquus* from *H. gorgops* cannot be ruled out and a dispersal pattern of latter taxon trough the Levantine Corridor seems to be a plausible hypothesis (see also O'Regan et al., 2005; Croitor, 2018). A better comparison between the earliest *H. antiquus* and the late *H. gorgops* would probably clarify this point. Hippopotamids post-cranial material from Algoz are also quite interesting because, according to Mazza and Bertini (2013), hippopotamids chronologically close to 1 Ma were generally larger than the pre-Jaramillo and post-Jaramillo representatives. According to the abovementioned authors, these large semi-aquatic mammals were relatively larger during warmer and humid stages, whilst under non-ideal environmental conditions they became smaller. In this framework, the material from Algoz would confirm this trend, being the specimens closer to those from Kalamotó (Mygdonia basin, Macedonia), Untermaβfeld (Thuringia, Germany) and Colle Curti (Marche, Italy), all of them dated around 1 Ma. Accordingly, a general increase in size of European hippopotamids can be detected throughout Europe, and this can represent a useful bio-chronological and paleoenvironmental tool.

The fossil specimens collected from Condeixa (Fig. 11, 2), dated around 0.4 Ma, are the best-preserved late Middle Pleistocene (ca 0.45 Ma) hippopotamid material collected from the European area so far. The attribution of these remains to *H. antiquus* is remarkably relevant because the LAD of this large mammal in Europe was still strongly debated due to the scarcity of chronologically constrained and well-preserved and taxonomical useful specimens. In Greece the presence

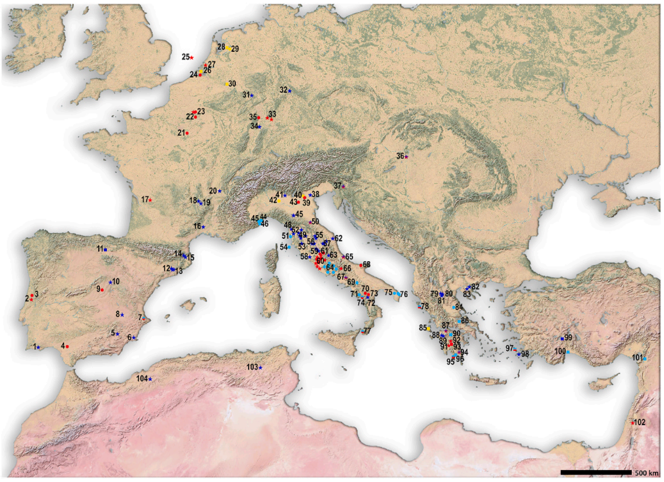

Fig. 11. Hippopotamidae distribution in Europe. *H. antiquus* (star), *H. amphibius* (dot), *Hippopotamus* sp. (square). In dark-blue, Early Pleistocene, in red Middle Pleistocene in light-blue Late Pleistocene, in yellow Pleistocene (age unknown). *H. antiquus* occurrences: Portugal (1, Algoz; 2 Condeixa); Spain (5, Venta Micena; 6, Cueva Victoria; 8, Fuente Nueva 3; 10, Pontón de la Oliva; 12, Vallparadís Estació Middle Unit (layers EVT6, EVT7 and EVT8); Vallparadís Estació Lower Unit (layers EVT10, EVT11 and EVT12); 13, Cal Guardiola Upper Unit (layers D4, D5, D6, D7); 14, Bòvila Ordis; 15, Incarcal); France (16, Durfort; 17, Nautiere; 18, Soleilhac; 19, Sainzelles; 20, Saint Pres; 23, Abbeville); Netherlands (25, Noordzee II; 27, Maasvlakte); Germany (31, Karlich; 32, Untermaβfeld; 33, Mauer; Mosbach II; 34, Jockgrim); Hungary (36, Budapest; Budakalász); Slovenia (37, Postojnska Jama Caves); Italy (38, Asolo di Forabosco; 41, Leffe; 45, Torrente Il Crostolo; 48, Poggio ai Venti; 49, Valdarno localities; 50, La Salita Cave-Oriolo; 52, Lari; 53, Chiusi; 55, Perugia; 56, Terni; 57, Aquila basin localities; 58, Ponte Galeria; 59, Rieti localities; 60, Rome localities; 62, Colle Curti; 63, Monte Riccio; 65, Chieti; 66, Isernia La Pineta; 67, Saticula; 72, Calorie-Potenza); Greece (79, Kapetánios; 80, Q-Profil; 81, Libákos; 82, Kalamotó 1, 2; 83, Ravin Voulgarákis; 87, Káto Salmeníko; 88, Aetorráchi; 89, Elis; 91, Marathoúsa 1, 2; 92, Kyparíssia 1, 3, 4, T; 94, Myrtiá; 98, Antimáchia); Israel (102, 'Ubeidiya); Algeria (103, Aïn Hanech, 104, Tighennif). *H. amphibius* occurrences: Portugal (3, Mealhada); Spain (4, Guadalquivir en La Rinconada; 7, Bolomor Cave; 9, Áridos I de Arganda); France (21, Levallois; 22, Moru; 23, Somme); Netherlands (24, Westerschelde; 29, Haerst); Germany (35, Eich); Italy (39, Serbaro di Romagnano; 40, Romagnano; 42, Pavia; 43, Zoppega I; 44, Barma Grande Cave; 45, Madonna dell'Arma Cave; 46, Balzi Rossi di Grimaldi; 51, Monte Tignoso; 54, Reale Cave; 61, Roma-Rieti localities; 64, Latina-Frosinone localities; 68, Ingarano; 69, Valle del Sele; 70, Laino di Borgo; 71, Taddeo Cave; 73, Mercure Valley localities; 74, Grande Cave of Scario; 75, Melpignano; 76, Lecce localities; 77, Bovetto); Greece (84, Peniós Valley; 96, Dyrós Cave). *Hippopotamus* sp. occurrences: Spain (11, Sima del Elefante (TE9)); Netherlands (26, Oosterschelde; 28, Mastenbroekerpolder; 30, Maastricht); Greece (78, Paliávlako; 85, Mantzavináta; 86, Tíchos; 90, Limnón Cave; 93, Chorémi; 95, Apídima A, B; 97, Kálymnos); Turkey (99, Burdur; 100, Antalya; 101, Hatay). For more complete lists: Spain, see Madurell-Malapeira et al. (2014) and references therein; Italy, see Martino and Pandolfi (2022) and references therein; France, see Auguste (2009) and Palombo and Valli (2003); Netherlands, see van Kolfschoten and Vervoort-Kerkhoff (1985) and Auguste (2009); Germany, see Mazza (1995), Van Kolfschoten and Turner (1986), von Koenigswald (2007), Kahlke et al. (2011) and references therein; Slovenia, see Jánossy (1986); Greece, see Athanassiou (2022); Turkey, see Ozansoy (1957) and Demirel et al. (2016); Algeria see Sahnouni et al. (2013) and Geraads (2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of *H. antiquus* around 0.5–0.4 Ma is documented by a dp2 and a third metacarpal collected from Marathoúsa 1 (Konidaris et al., 2018, Fig. 11., 91) and vertebrae, ribs and isolated dental remains from Marathoúsa 2 (Konidaris et al., 2019), while the well-documented record from Kyparíssia (Megalopolis basin, Fig. 11, 92) has a long age interval, between 0.7 and 0.4 Ma (Athanassiou et al., 2018). *H. tiberinus*, a controversial species erected by Mazza (1991), is mainly based on abundant remains dated around 0.6 Ma collected from La Maglianella (Rome, Fig. 11, 60). *H. tiberinus* was referred as a junior synonym of *H. antiquus* by Petronio (1995), but its morphological and morphometric characters, as also highlighted in this article, are quite peculiar and therefore its validity should be better investigated. *H. antiquus* (*H.* ex gr. *H. antiquus* in Mazza and Bertini, 2013) occurrence is also documented at Castel Guido (Rome, Italy, Fig. 11., 60), recently assigned by Marra et al. (2018) to MIS 11 (0.412 Ma ±2 ka). However, this locality just yielded some juvenile teeth, a canine, a juvenile metacarpal and the diaphysis of a tibia, and therefore a clear specific attribution is difficult to assess. The occurrence of *H. antiquus* from Condeixa, can be therefore considered as the LAD of *H. antiquus* in Europe.

The remains from Mealhada (Fig. 11, 3) are here assigned to *H.* cf. *amphibius*. The presence of this taxon in Portugal testifies that the extant hippo, or closely related forms, widely dispersed in the European Mediterranean basin. However, the fragmentary nature of most of the hippopotamid remains collected from the late Middle Pleistocene of Europe don't allow a sure specific attribution, and therefore the FOD of *H. amphibius* in Europe is still debated. *H.* cf. *amphibius* was reported from Via Aurelia km 18.9 (Rome, Latium, Fig. 11, 61), between 0.516 and 0.496 Ma (Anzidei et al., 1993; Marra et al., 2018), but the paucity of the remains collected from this locality prevent any specific attribution (Martino and Pandolfi, 2022). The presence of *H. amphibius* in Italy during MIS 13-MIS 11 is still debated and, at present, not supported by strong evidence (Martino and Pandolfi, 2022). In France the occurrence of *Hippopotamus* ex gr. *H. amphibius* is reported from the MNQ 24 (301-242 ka) locality of Levallois (Paris, Fig. 11, 21) (Guérin, 1980; Palombo and Valli, 2003), and from Celle-sur-Seine (upper Seine valley), ascribed to MIS 11 (Auguste, 2009 and references therein; Limondin-Lozouet et al., 2010). The presence of *H. amphibius* in Spain has been reported from the TD8a level, 602 ± 92 ka (Falguères et al., 1999), of the Gran Dolina deposit (van der Made, 1998, Fig. 11, 11), but this attribution is based on an isolated incisor and should be considered with caution. In Spain, *H. amphibius* is also reported from the level T12 of Guadalquivir en La Rinconada (Sevilla, Fig. 11, 4) dated around 380–490 ka (Escudero et al., 2013) and from Áridos I de Arganda (Madrid, Fig. 11, 9) chronologically correlated with MIS 11 (Soto Rodríguez, 1980; Blain et al., 2014). In the former case the attribution is based on an isolated incisor, while in the latter on an isolated canine: the taxonomic attribution of these specimens is therefore highly questionable. The presence of *H. amphibius* in Europe seems to be established at the Middle-Late Pleistocene transition and during the earliest Late Pleistocene. Hippopotamid' occurrences are reported from Turkey (*Hippopotamus* sp., in Ozansoy, 1957 and references therein), Slovenia (*H. amphibius*?, in Malez, 1986), Germany (*H. amphibius*, in van Kolfschoten, 2000), Netherlands (*H. incognitus* = *H. amphibius*, in van Kolfschoten and Vervoort-Kerkhoff, 1985), Italy (*H. amphibius*, in Martino and Pandolfi, 2022 and references therein), France (*H. incognitus* = *H. amphibius*, in Auguste, 2009 and references therein), and in Spain (*H. amphibius*, Blasco, 2008; Blasco and Peris, 2012).

7. Conclusions

Three different Portuguese localities, Algoz (ca. 1 Ma), Condeixa (ca. 0.4 Ma) and Mealhada (ca. 0.2–0.13 Ma), yielded remains of *Hippopotamus*. The material from these localities is here re-analysed and assigned to *H. antiquus* (Algoz and Condeixa) and to *H.* cf *amphibius* (Mealhada). *H. incognitus* is therefore not reported to Portugal. Algoz remains are represented by a partially complete forelimb that is morphometrically close to other specimens collected from 1 Ma localities, the latter usually larger than hippopotamids collected from pre-Jaramillo and post-Jaramillo sites. The material from Condeixa, dated around 0.4 Ma, is mainly represented by cranial remains. The mandible from this site shares a concave ventral profile, incisors without a diastema between i1-i2, a poorly developed diastema between i2-c, a rostral fan not particularly wide in ventral view, a horizontal ramus elongated and slender, and a canine with parallel grooves on the enamel. The concurrent presence of all these characters permits to clearly assign the hippopotamid material from Condeixa to *H. antiquus*. The presence of *H. antiquus* in the Tuffs of Condeixa is particularly relevant because it can be considered one of the last occurrences of *H. antiquus* in Europe, being the other late Middle Pleistocene European remains fragmentary and scarce. Algoz and Condeixa material testifies that *H. antiquus* was widely present in Europe during the Quaternary, from Greece up to Portugal. *H. amphibius* arrived in Europe during the late Middle Pleistocene. The scarce remains from Mealhada, here ascribed to *H.* cf *amphibius*, suggest that hippopotamuses reached the westernmost European area at least twice during the Pleistocene. *H. amphibius*, similarly to *H. antiquus*, probably dispersed from Africa via the Levantine corridor in Europe, reaching Portugal as the final step of this dispersal pattern.

Author contributions

Conceptualization, LP and RM; methodology, LP and RM; comparative data acquisition, LP and RM; collection of data on Portuguese specimens, RM; analysis, LP and RM; discussion, LP and RM; first writing, LP and RM; geological and paleontological settings, all the authors; discussion of the final version, all the authors. All the authors approved and improved the final version of the manuscript.

Data availability

All the specimens described in this paper are available in the selected Museums and Institutions. The collection number is reported for all the mentioned specimens.

Web references

Fig. 1 Image modified from Google Earth and Wikimedia commons. {{published|author = TUBS|date = 12 April 2011|url = https://commons.wikimedia.org/wiki/File:Portugal_in_Europe_extended_special_marker.svg|title=Portugal in Europe (extended) (special marker). svg|org = commons.wikimedia.org/}}

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quaint.2022.12.010.

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