

Original Article

An enduring palaeontological riddle: how many hippopotamid species roamed Sicily? The case study of Amoroso Cave

Roberta Martino^{1,2,*}, Carolina Di Patti³, María Ríos^{1,2}, Lorenzo Rook⁴,
Mirko Di Febbraro⁵, Pasquale Raia⁶ and Luca Pandolfi^{7,*}

¹GEOBIOTEC, Department of Earth Sciences, NOVA School of Science and Technology, Universidade NOVA de Lisboa, Campus de Caparica, 2829-516 Caparica, Portugal

²Museu da Lourinhã, R. João Luís Moura, 95, 2530-158, Lourinhã, Portugal

³Museo Geologico 'G.G. Gemmellaro'- Università degli Studi di Palermo, Corso Tukory 131, 90133 Palermo, Italy

⁴Dipartimento di Scienze della Terra, Paleo[Fab]Lab, Università degli Studi di Firenze, G. La Pira 4, 50121 Firenze, Italy

⁵EnviX-Lab, Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, 86090 Pesche, Italy

⁶Dipartimento di Scienze della Terra, dell'Ambiente e delle Risorse, Università di Napoli Federico II, 80126 Napoli, Italy

⁷Dipartimento di Scienze della Terra, Università di Pisa, via S. Maria 53, 56126 Pisa, Italy

*Corresponding author: R. Martino, GEOBIOTEC, Department of Earth Sciences, NOVA School of Science and Technology, Universidade NOVA de Lisboa, Campus de Caparica, 2829-516 Caparica, Portugal. E-mail: r.martino@campus.fct.unl.pt; L. Pandolfi, Dipartimento di Scienze della Terra, Università di Pisa, via S. Maria 53, 56126 Pisa, Italy. E-mail: luca.pandolfi@unipi.it

ABSTRACT

Hippopotamus pentlandi, although lacking a comprehensive description, is regarded as one of the best known dwarfed hippopotamid species within the Mediterranean region. This study provides a detailed analysis of a hippopotamus mandible from Amoroso Cave (Palermo, Sicily). Morphological and morphometric comparisons with insular and continental species reveal a significant similarity between the Amoroso mandible and some specimens from San Ciro Cave (Palermo, Sicily), as well as with *Hippopotamus amphibius*. Conversely, material from Cannita Cave (Palermo, Sicily) attributed to *H. pentlandi* is less robust, more elongated and smaller. 3D geometric morphometric analysis performed on the symphyseal sagittal cross-section further support a closer morphological affinity of the Amoroso mandible to San Ciro Cave specimens and *H. amphibius*, suggesting an attribution to the latter. Our research reveals the presence of at least two different, potentially coeval, taxa in the Pleistocene of Sicily: the dwarfed *Hippopotamus pentlandi* primarily known from Cannita Cave, and *H. amphibius*. While Cannita Cave material has been thoroughly studied over the years, abundant remains from other localities, e.g. San Ciro Cave, require re-evaluation. A thorough analysis of Sicilian hippopotamids is crucial to improve our understanding of their systematics and to provide new insights into the palaeobiogeography, palaeobiology, and palaeoenvironment of Sicily during the Pleistocene.

Keywords: Hippopotamus; morphometry; morphology; paleobiogeography; Sicily; Pleistocene.

INTRODUCTION

Sicily, Italy's largest island, has a long palaeontological history. Fossil vertebrate remains from the island are known since the 15th century, with early interpretations attributing the bones to 'giants', who were thought to be the first inhabitants of the island (Fazello 1558, Valguarnera 1614). The fossil material was later formally recognized as belonging to fossil animals by Bivona Bernardi (1830), who, thanks to the work of Cuvier (1812), realized the true nature of the remains (Fabiani 1928, Burgio *et al.* 2002). Unfortunately, a large number of vertebrate

fossils (especially of hippopotamids) were later collected and sold, and several caves were almost completely depleted of their fossiliferous content (Bivona Bernardi 1830, Scinà 1831, Desnoyers 1845).

Several cranial and post-cranial bones coming from Benfratelli Cave (Palermo) were mentioned by Pentland (1832). These specimens were morphologically similar to *Hippopotamus amphibius*, although they were considerably smaller. In the same year, based on Pentland's work, von Meyer (1832) established the species *Hippopotamus pentlandi*. The author mentioned that

the bones, about 100 specimens, were collected in Benfratelli Cave, and later stored in the Museum des Königl, Gartens of Berlin. According to von Meyer (1832), the Sicilian hippopotamus shared morphological characters with both large fossil and extant hippopotamuses. Nonetheless, he noted that it was only a little larger than a domestic ox. However, apart from its smaller size, von Meyer (1832) did not report any additional diagnostic characters when he coined the species name *H. pentlandi*.

During the past century, several researchers considered *H. amphibius* to be the ancestor of *H. pentlandi* based on cranial and post-cranial morphological affinities (Accordi 1955, Caloi and Palombo 1983, Capasso Barbato and Petronio 1983, Faure 1983, 1984, 1985, Faure and Guérin 1989, Guérin 1996, Marra 1998, 2005). The comprehensive work by Accordi (1955) examined the abundant cranial and post-cranial material attributed to *H. pentlandi*, found in Cannita Cave (Palermo), and kept in various Italian institutions (Istituto di Geologia e Mineralogia of the University of Ferrara, Museo dell'Istituto di Geologia of the University of Padova, and the P. Leonardi collection of the Natural History Museum of Venice). Accordi (1955) described several characteristics that distinguish the Sicilian hippopotamus from *H. amphibius* and recognized a clear affinity between the two species. Similarly to Accordi (1955), Capasso Barbato and Petronio (1983) focused on the cranial and post-cranial material of *H. pentlandi* collected from Cannita Cave and stored in the Natural History Museum of Milan. The latter authors noted that bones of different size, but of similar morphology, came from the same locality, which they explained as evidence of multiple dispersals of *H. amphibius* onto the island. Caloi and Palombo (1983) provided a comprehensive revision of the Mediterranean island hippopotamids, mainly comprising *H. pentlandi*, *Hippopotamus creutzburgi*, and *Hippopotamus minor*, compared to the mainland *Hippopotamus antiquus* and *H. amphibius*. Based on both morphological and morphometric data, Caloi and Palombo (1983) emphasized that *H. pentlandi* is a species that most likely derived from *H. amphibius*. In contrast, some scholars later supported the derivation of *H. pentlandi* from *H. antiquus* (Faure 1983, 1984, 1985, Faure and Guérin 1989, Guérin 1996, Marra 1998). In a more recent paper, Marra (2005) proposed that the 'mixed characters' of *H. pentlandi* are related to a possible common ancestry between *H. antiquus* and *H. amphibius*. This hypothesis, although compelling, requires more extensive studies to support it.

Hippopotamus pentlandi was widespread throughout Sicily during the late Middle Pleistocene until MIS 4 (Bonfiglio *et al.* 2003). The occurrence of *H. pentlandi* has been reported from several fossiliferous localities such as Mazzarino, Niscemi, Mazzamuto Cave, Muletta Cave, Maccagnone Cave, Puntali Cave, Cannita Cave, Corso Vittorio Emanuele, San Ciro Cave, Santa Rosalia Cave, Olivella Cave, Billiemi, Benfratelli Cave, Malatucca Cave, Impisu Cave, Condannato Cave, Ponte Cave, Termini Imerese, Za' Minica Cave, Alcamo, San Vito lo Capo, San Teodoro Cave, Coste di Gigia, Ghiaie di Messina, Contrada Tabuna, Spinagallo Cave, Capo Peloro, Mazzarino, Niscemi, Fiume Imera, Boccadifalco, Riparo Messina, Emiliana Cave, Giovanna Cave, Rocca Scodonì, Fata Donnavilla Cave, Taormina, Contrada Fusco, Amoroso Cave, Simeto Valley, Cugno Ballarella, Alcamo, Cape Tindari, Comiso, and Perciata Cave (Fig. 1; Supporting information S1

modified from Martino and Pandolfi 2022) (Bivona Bernardi 1830, Alessi 1833, Anca 1867, Falconer 1868, Battaglia and Ciofalo 1883, Ciofalo and Battaglia 1888, De Gregorio 1924, 1925, Fabiani 1928, 1931, Accordi 1955, Bonfiglio and Berdar 1969, Bonfiglio 1983, Bonfiglio and Violanti 1983, Burgio *et al.* 1983, Caloi and Palombo 1983, 1986, Burgio *et al.* 2002, Capasso Barbato and Petronio 1983, Burgio and Di Patti 1990, Mannino and Zava 1994, Bonfiglio *et al.* 2002, Marziano and Chilardi 2002, Di Patti and Calandra 2004, Di Patti and Piccione 2004, Abbate *et al.* 2006, Mannino 2008, Petruso and Taschetta 2011, Chilardi *et al.* 2012, Martino and Pandolfi 2022). In addition to *H. pentlandi*, other hippopotamus material not identified to the species level (and therefore reported as *Hippopotamus* sp.) occurs in other localities (see Martino and Pandolfi 2022 and references therein) (Fig. 1; Supporting information S1 modified from Martino and Pandolfi 2022).

In this paper, we present an unpublished mandible collected from Amoroso Cave. This fossiliferous locality has already been reported in the literature (Burgio *et al.* 2002, Di Patti and Calandra 2004), but its fossil hippopotamid content has never been studied. The material reported here will provide more data on the morphology and morphometry of Sicilian hippopotamids, which despite their abundance have not been extensively studied. In addition, we will apply 3D geometric morphometrics methods to better analyse morphological features such as the symphyseal sagittal cross section, a character that has never been studied in *H. pentlandi*. In general, this study aims to assess two main hypotheses: (i) the material found in Amoroso Cave can be ascribed to *H. pentlandi*, as its occurrence is extensively recorded throughout Sicily during the Middle and Late Pleistocene; (ii) the mandible discovered in Amoroso Cave exhibits greater similarity to *H. amphibius*, suggesting the occurrence of two hippopotamid taxa in Sicily. The possible coexistence of two different taxa would imply multiple entries of *H. amphibius* from the mainland to Sicily.

Amoroso Cave

The geological information regarding Amoroso Cave (38°09'04.6"N 13°09'20.1"E) is rather scarce. The site is located in the Puntali Cave Natural Reserve, in the municipality of Carini (Palermo) (Fig. 2). Amoroso is a karstic cave that opens into the limestone cliff of Monte Lungo, along the northwest coast of Sicily (Fig. 2A, B). Unfortunately, the cave is located inside a private property. Over the years, various masonry artefacts have been built, completely covering the fossil layers. Burgio *et al.* (2002) reported the presence of a cavity containing various elephant bones, which was covered by human artefacts sometime after 1986. The cave is therefore no longer accessible, and no further studies can be carried out. The presence of fossils in the Amoroso Cave, hereafter referred to as Amoroso, has been known since the 19th century. The known fauna of Amoroso includes *H. pentlandi*, elephants, and doubtfully bears (Anca F., personal communication in Gemmellaro 1866) (Burgio *et al.* 2002).

Sicilian faunal assemblages: biochronology and endemism in the Middle to Late Pleistocene

The faunal assemblages recovered from the Sicilian fossil sites usually contain similar groups of mammals, with more or less taxa represented, depending on the richness of each different



Figure 1. Distribution of *Hippopotamus pentlandi* (in red), *Hippopotamus amphibius* or *H. amphibius* ssp. (in orange), and *Hippopotamus* sp. (in blue) in Sicily during the Middle–Late Pleistocene. List of occurrences modified from Martino and Pandolfi (2022) (see Supporting information S1).

site. Five different biochronological faunal complexes (FCs) have so far been identified (Bonfiglio *et al.* 2002). The two oldest faunal complexes (Monte Pellegrino FC and *Palaeoloxodon falconeri* FC) refer to lower Middle Pleistocene marine sediments characterized by fauna with different degrees of endemism. In the *Palaeoloxodon falconeri* FC, besides the peculiar dwarf elephant, only *Vulpes* sp. is mentioned among the largest mammal fauna. The most recent faunal complexes include the *Palaeoloxodon* sp. (originally *Palaeoloxodon mnaidriensis*) FC, Grotta S. Teodoro–Contrada Pianetti FC, and Castello FC (Mangano *et al.* 2020). The *Palaeoloxodon* sp. FC has more recently also been referred to as the Maccagnone FC by Bonfiglio *et al.* (2022). These faunal complexes are more similar to those found in southern Italy at this age, suggesting a link between the mainland and Sicily. *Hippopotamus pentlandi* is recorded exclusively in the *Palaeoloxodon* sp. FC (following Mangano *et al.* 2020), a well-balanced faunal assemblage that includes *Palaeoloxodon* sp., *H. pentlandi*, *Cervus elaphus siciliae*, *Canis lupus*, *Dama carburangelensis*, *Ursus* cf. *arctos*, *Crocota crocuta spelaea*, *Bos primigenius siciliae*, *Sus scrofa*, and *Vulpes vulpes* (Bonfiglio *et al.* 2002, Larramendi *et al.* 2020, Mangano *et al.* 2020). The Grotta S. Teodoro–Contrada Pianetti FC lists several carnivores, including *U.* cf. *arctos*. However, this faunal list does not include the occurrence of *Hippopotamus pentlandi* or a different hippopotamus species (Bonfiglio *et al.* 2002). The

Castello FC does not record the occurrence of bears, hippopotamuses, nor elephants (Bonfiglio *et al.* 2002).

The list provided by Mangano *et al.* (2020) for the *Palaeoloxodon* sp. FC is consistent with the poor mammalian fauna reported from Amoroso (remains of elephant, bear, and hippopotamus). These three taxa have been reported exclusively from the *Palaeoloxodon* sp. FC, while older and younger faunal units do not include the co-occurrence of these species. In the light of the previously discussed information, we can ascribe the fossil material from Amoroso to the *Palaeoloxodon* sp. FC. The remains from Sicily are peculiarly abundant and the fauna retrieved from each fossiliferous locality has been extensively reported in the literature, therefore the attribution of the material from Amoroso to the *Palaeoloxodon* sp. FC is well supported. Different ages were provided for the *Palaeoloxodon* sp. FC. Electron spin resonance (ESR) dating of *Palaeoloxodon* sp. and *H. pentlandi* enamel from Contrada Fusco gave ages ranging from 146.8 ± 28.7 kya to 88.2 ± 19.5 kya (Rhodes 1996). However, the analysis of *Dama carburangelensis* from Cape Tindari suggested an age of 200 ± 40 kya (Bada *et al.* 1991). Bonfiglio *et al.* (2008) reported an age between MIS 10 and MIS 4 for the *Palaeoloxodon* sp. FC *sensu* Mangano *et al.* (2020). In Mangano *et al.* (2020) the hippopotamid material from San Teodoro Cave is reported under a phosphatic crust dated 120 kya. The exact age of the *Palaeoloxodon* sp. FC is therefore controversial, although it

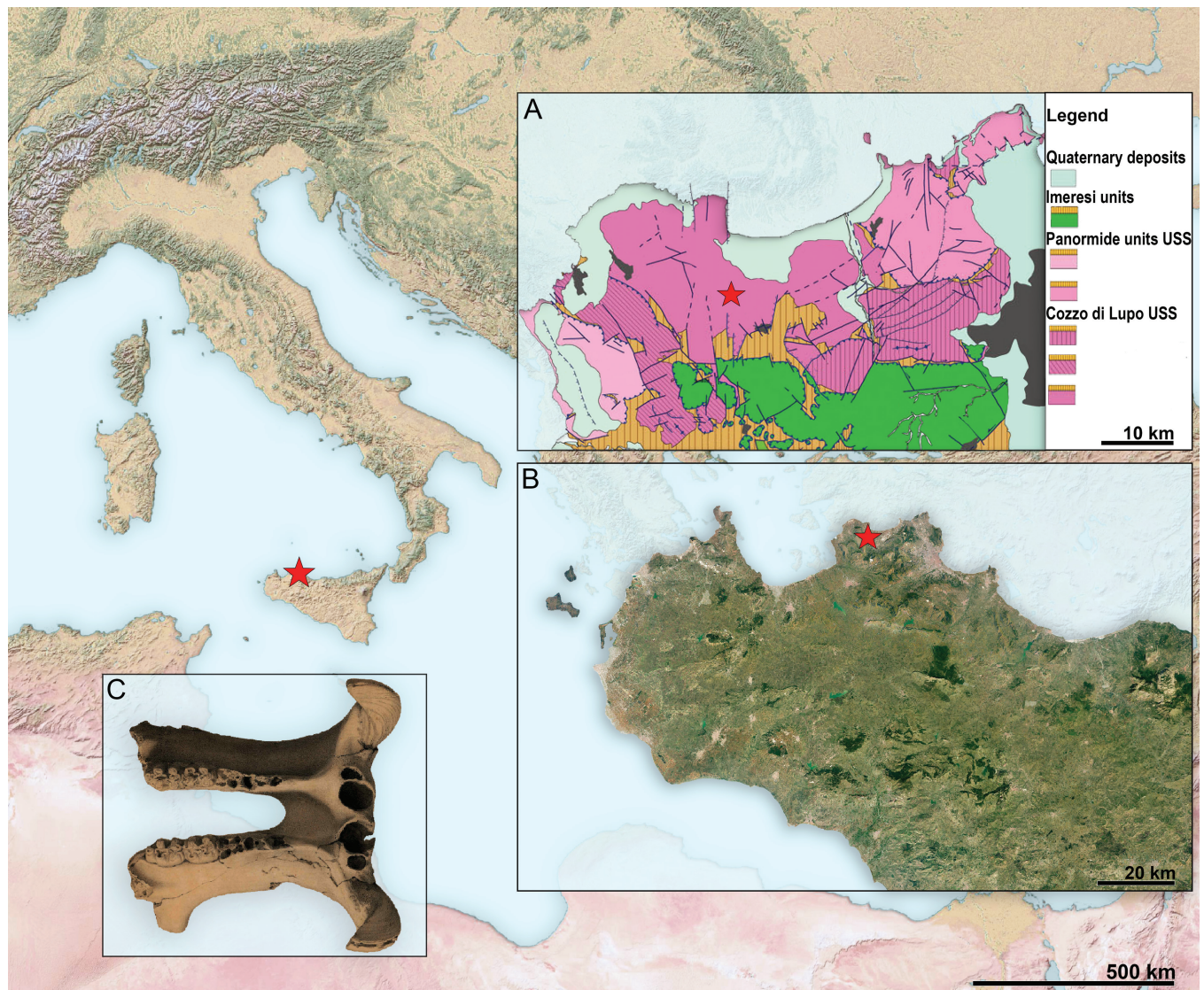


Figure 2. Location of Amoroso Cave. A, geological map following [Basilone and Di Maggio \(2016\)](#). B, close-up of Sicily and Amoroso locality. C, mandible from Amoroso in dorsal view as depicted by [Fabiani \(1928\)](#).

can be safely placed between the late Middle Pleistocene and the early Late Pleistocene.

MATERIAL AND METHODS

The mandible MGUP GA1 described in this paper is stored in the Museo di Geologia Gaetano Giorgio Gemmellaro (MGUP) in Palermo (Sicily, Italy). The mandible was collected in 1863 and has been part of the palaeontological collection of the MGUP since then ([Gemmellaro 1866](#)). The figure of the mandible depicted in Fig. 2C is indeed the one reported in [Fabiani \(1928\)](#). However, no further information on this mandible has been published since.

A list of the Sicilian fossiliferous localities that yielded hippopotamid remains, modified from [Martino and Pandolfi \(2022\)](#), is provided in Supporting information S1. The terminology used for the dentition followed [Boisserie *et al.* \(2010\)](#), while the measurement protocol followed [Mazza \(1995\)](#). The mandible from Amoroso was compared with *H. pentlandi*, *H.*

melitensis, *H. creutzburgi*, *H. amphibius* (extant and fossil), *H. antiquus*, and *H. tiberinus* [= *Hippopotamus* ex gr. *Hippopotamus antiquus* in [Mazza and Bertini \(2013\)](#) and following publications] from direct observations (R.M. and L.P.) and published data ([Reynolds 1922](#), [Hooijer 1950](#), [Accordi 1955](#), [Melentis 1965](#), [Boekschoten and Sondaar 1966](#), [Caloi *et al.* 1980](#), [Caloi and Palombo 1983](#), [Kahlke 1989, 1997](#), [Mazza 1991, 1995](#), [Galobart *et al.* 2003](#), [Martinez-Navarro *et al.* 2010](#), [Mazza and Bertini 2013](#), [Athanasios *et al.* 2018](#), [Martino *et al.* 2023, 2024a](#)). The fossil *H. amphibius* specimens are not abundant, and the ones analysed were reported from Barrington (England), Fosso Malafede (Italy), and Cava Montanari (Italy) ([Reynolds 1922](#), [Caloi *et al.* 1980](#), [Mecozzi *et al.* 2023](#), [Martino *et al.* 2024a](#)). We did not include *H. minor* in the dataset because this species is rather peculiar, showing strong adaptations to the insular environment and extreme dwarfism ([Marra 2005](#), [Lyras *et al.* 2025](#)). All the measurements are available in Supporting information S2. All the analyses presented in this manuscript were developed in the RStudio environment ([R Core Team 2019](#)). The Principal

Component Analysis (PCA) was performed on the values of the mandible and greatest length and breadth of the third lower molar using the R packages *factoextra*, *FactoMiner*, *ggbiplot*, and *ggfortify* (Lè *et al.* 2008, Vu 2011, Husson *et al.* 2016, Tang *et al.* 2016, Kassambara and Mundt 2017). By linearly transforming the data into a new coordinate system through a PCA, the principal components that capture the most significant variation in the dataset were easier to identify. The potential for similarities or differences among the different species in the PCA space was also assessed through PERMANOVA, as implemented in the pairwiseAdonis and vegan R packages (Dixon 2003, Martinez Arbizu 2020). We also conducted a Linear Discriminant Analysis (LDA) on the PCA values to further test the dataset using the R package MASS (Venables and Ripley 2003). LDA aimed to find a linear combination of values, called predictors, which maximized the difference between two or more groups (in our analyses *H. pentlandi*, *H. amphibius*, *H. antiquus*, and *H. ex gr. H. antiquus*) while minimizing the variability within each different group. To effectively perform an LDA, the dataset was divided into train (70%) and test (30%) sets. The former set, which comprised the known species, was utilized as a training set to construct the discriminant function, the purpose of which was to capture the differences between the various analysed species. The test set, comprising the Amoroso specimen, was subsequently included in the discriminant function to ascertain to which analysed species it was more closely related to. The R packages *ggplot2*, *devtools*, and *tidyverse* were further utilized for a better visualisation (Wickham *et al.* 2016a, b, 2019).

3D methodology

The 3D model of the mandible from Amoroso was obtained through close-range photogrammetry. Overall, 1162 pictures were imported into the Agisoft Metashape Professional (1.7.0) software. The 3D model obtained has 874,408 faces. The 3D model of the specimen MGUP GA1 is available on MorphoSource (see Data Availability). The latter model was then included into a large 3D dataset, including 32 models of adult specimens of *H. pentlandi*, *H. amphibius*, *H. antiquus*, and *H. ex gr. H. antiquus* (see Supporting information S3). A juvenile specimen of *H. pentlandi* (IGF4010V) was also included in order to check the shape variability between adults and juveniles. The 3D specimens were digitized by R.M. and L.P. using two hand-held scanners, an Artec Eva (accuracy 0.1 mm) and an Artec Space Spider (accuracy 0.05 mm) and using photogrammetry principles. Some additional specimens were downloaded through the online repository Sketchfab (see Supporting information S3). The collected data were analysed using the principles of geometric morphometrics in 3D (GMM) (Adams *et al.* 2004). The shape of the sagittal cross-section of the mandibular symphysis was analysed using semilandmark curves digitized in Avizo 7.1. The applied protocol for 3D GMM analysis followed Martino *et al.* (2024b). The shape of the mandibular sagittal cross-section is diagnostic in Hippopotamidae (Boisserie 2005), and therefore potentially of interest for further study. The semilandmark configurations were then translated, rotated, and scaled to unit centroid size through a generalized Procrustes analysis (GPA) (Rohlf and Slice 1990, Bookstein 1991). To better visualize the results of the GPA, a PCA was subsequently performed. The R

packages used for the GMM analyses were *scatterplot3d*, *shapes*, and *ade4* (Ligges and Mächler 2002, Dryden and Mardia 2016, Dray and Siberchicot 2017).

Acronyms representing institutional provenance of the examined specimens are as follows: IGF-Museo di Storia Naturale, sezione di Geologia e Paleontologia, Università degli Studi di Firenze (Florence, Italy); MCP-Museum of Casal de' Pazzi (Rome, Italy); MCZR-Museo Civico di Zoologia di Roma (Rome, Italy); MGUP-Museo di Geologia Gemmellaro (Palermo, Italy); MSNM-Museo Civico di Storia Naturale di Milano (Milan, Italy); MSNUP, Museo di Storia Naturale e del Territorio, Università di Pisa (Calci, Pisa, Italy); NHMMZ-Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz (Mainz, Germany); NOVA-FCT-DCT-Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, Universidade NOVA de Lisboa (Lisbon, Portugal).

Anatomical abbreviations throughout the manuscript: c, lower canine; i, lower incisor; m, lower molar; p, lower premolar.

Measurements abbreviations used in the manuscript are as follows: AB, anterior breadth; B, greatest breadth; BFi, inner breadth of the rostral fan; Bfo, outer breadth of the rostral fan; H2P, height of the mandibular corpus at the level of the p2; H4P, height of the mandibular corpus at the level of the p4; H3M, height of the mandibular corpus at the level of the m3 hypoconulid; hypB, hypoconulid breadth; L, greatest length; LM3i, posterior border of the m3 alveolus to the first incisor alveolus length (measured to the most anterior point of the alveolus border); LS, length of the mandibular symphysis; p2–p4, length of the premolar series; m1–m3, length of the molar series; p2–m3, length of the teeth series; PB, posterior breadth.

RESULTS

SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Family Hippopotamidae Gray, 1821

Genus *Hippopotamus* Linnaeus, 1758

Species *Hippopotamus amphibius* Linnaeus, 1758

MORPHOLOGICAL DESCRIPTION

The almost complete mandible MGUP GA1 collected from Amoroso is robust, exhibiting massive canines and alveoli for the first incisors (Fig. 3). In lateral view the mandibular corpus is stout and relatively tall, though not particularly elongated (Fig. 3A, E). The ventral profile of the mandibular corpus is straight and slightly convex. The canine process is notably well developed and both canines are complete and large. The ascending rami are not preserved. The angular process connects with the lower profile of the mandible with a slightly arched angle. The mandibular symphysis is short and sturdy, and its sagittal cross-section is pear shaped. In dorsal view the fan is broad, and it widens at the p2–p3 level (Fig. 3B). The rami are slightly divergent. The dental arches follow a sigmoidal development, exhibiting minimal distance between the rami at the p2–p3 level (Fig. 3B). In anterior view the alveoli of all the four incisors are clearly



Figure 3. Mandible from Amoroso. A, left lateral view. B, dorsal view. C, right m2 and m3. D, left m2 and m3. E, right lateral view. F, anterior view. Scale bars 5 cm.

visible (Fig. 3F). The diastema between the two i1s is small, whilst the one between the i1s and the i2s is almost non-existent in comparison. The diastema between the i2s and the canines is more developed. The cross-section of the i1s is subcircular, while that of the i2s is more elliptical, with the labio-lingual length greater than the mesio-lateral. The canines are massive, showing convergent ridges on the enamel surface that extend towards the tip of the tooth (Fig. 3A, E). In the medial view a shallow longitudinal groove is visible on the enamel surface (Fig. 3F). A less evident groove is also visible on the lateral surface of the tooth (Fig. 3A, E). Furthermore, the enamel displays faint transversal lines. The cross-section is D shaped.

The m2s present a moderate degree of wear, as evidenced by the presence and preservation of all four cuspidal (Fig. 3C, D). The enamel is thick and crenulated. The wear surface of the hypoconid of the left m2 is fused with the distostylid. A trefoil wear pattern is evident in all the cuspidal, with the exception of the entoconid, which displayed a simpler wear pattern, almost subcircular or in the shape of a figure 8. The cingulid is also strong, forming shelves mesially and distally. The m3s are rather stout, with thick crenulated enamel and five slightly worn cuspidal. The four main cuspidal, with the exception of the entoconid which exhibits a comma-shaped wear pattern, have a trefoil-shaped wear pattern analogous to that observed in the m2s. The distal cuspidal, the hypoconulid, has a sub-circular wear pattern

on the right m3 (Fig. 3C), while on the left m3 the wear pattern is more cruciform shaped (Fig. 3D). The cingulid is strong and crenulated. The m3 cingulid formed a strong post-entostylid and a clearly discernible post-ectostylid. The anterior outlets of the transverse valley are V shaped, whilst the posterior outlets are U shaped.

The wear surface of the m2s and the m3s suggest that the specimen from Amoroso belongs to group XIV or XV (Laws 1968). The individual was presumably between 24 and 33 years old at the time of death (Laws 1968). The m2s exhibit moderate to heavy wear with dentine between cusps not continuous (group XIV). Conversely, the m3s exhibit dentine on the hypoconulid as in group XV, whereas in group XIV dentine was still not exposed.

MORPHOLOGICAL AND MORPHOMETRICAL COMPARISON

Qualitative morphological comparison: The mandible collected from Amoroso (Figure 4A) is well preserved and therefore of particular interest. According to Accordi (1955), in *H. pentlandi* the height of the mandibular corpus is notably low, in contrast to the Amoroso mandible, where the mandibular corpus is comparatively tall and robust. The replica of the mandible from the Cannita Cave (Fig. 4F),



Figure 4. Comparison of different mandibles in lateral view. A, MGUP GA1, *Hippopotamus amphibius* from Amoroso. B, SMUC D3980, *H. amphibius* from Barrington (modified from Reynolds 1922, mirrored). C, MGUP SC7, *H. pentlandi* from San Ciro Cave. D, MGUP SC8, *H. pentlandi* from San Ciro Cave (mirrored). E, MSNM V2(10), *H. pentlandi* from Cannita Cave. F, MGUP 24915, replica of the complete composite skeleton of *H. pentlandi* from Cannita Cave. Scale bars 5 cm.

currently stored in the Museo Gemmellaro (Palermo, Sicily), exhibits a distinctive slender mandible with a comparatively low mandibular corpus when compared to the one from Amoroso. Caloi and Palombo (1983) defined the overall aspect of *H. pentlandi* mandibular corpus as more elongated than that of *H. amphibius*. Another mandible depicted in Capasso Barbato and Petronio (1983) and collected from Cannita Cave also shares a slender aspect, with a mandibular corpus rather low, in comparison to *H. amphibius* (Fig. 4E). The authors described the mandible of *H. pentlandi* from Cannita Cave as being taller than in *H. antiquus* but slightly lower than in *H. amphibius*. It is a commonly held view that *H. antiquus* is distinguished by a more slender and longer mandible when compared to *H. amphibius* (Fig. 4B) (Caloi et al. 1980, Mazza 1995). Despite the fragmentation of the mandibles collected from San Ciro Cave (Fig. 4C, D), a

mandibular corpus that is more robust and taller than in *H. pentlandi* from Cannita Cave is evident. In contrast, the mandibles of *H. antiquus* collected from Valdarno, Colle Curti, and Cal Guardiola Lower Unit are more slender and longer than the *H. amphibius* mandibles from Cava Montanari, Barrington, and Fosso Malafede (Reynolds 1922, Mazza and Ventra 2011, Mecozzi et al. 2023, Fidalgo et al. 2024, Martino et al. 2024a). Mandibles attributed to *H. ex gr. H. antiquus*, such as the remains described from Maglianella and Ortona, are much slenderer than in *H. antiquus* (Mazza 1991, 1995, Agostini et al. 2005). No complete mandibles of *H. melitensis* are known, while the mandible of *H. creutzburgi* figured in Marra (2005), in lateral view, is more slender than that of *H. antiquus*. Moreover, this species exhibits a short diastema between the p2 and the c, contributing to the mandible's distinctive short anterior portion.

Capasso Barbato and Petronio (1983) reported that the mandibles from Cannita Cave display a convex ventral profile of the mandibular corpus and an anteriorly arched angular process. Moreover, the dental arches exhibit a double curvature, with maximum concavity observed at the m2 level and maximum convexity in correspondence of the p3. In the Amoroso specimen the ventral profile of the mandibular corpus is straight or slightly convex and the teeth development is sigmoidal, as described in the specimens reported by Capasso Barbato and Petronio (1983). The isolated mandibles depicted in Accordi (1955) show a rather straight ventral profile of the mandibular corpus, a narrow rostral fan, small canines, and rather short symphysis. In contrast, the mandible of the mounted skeleton from Cannita Cave, despite severe deformity, clearly exhibits a convex profile. The rostral fan of the mounted skeleton's mandible is not particularly wide, and the length of the symphysis is short. The canine processes are well developed. In comparison to the Amoroso mandible, the first incisors and canines are less massive. The rostral fan is wider, and the symphysis is longer in the specimen from Amoroso than in *H. pentlandi* from Cannita Cave. *Hippopotamus antiquus* is typically distinguished by a convex ventral profile of the mandibular corpus, an angular process displaying a right angle, dental arches with a uniformly curved development, and a narrow rostral fan (Caloi *et al.* 1980, Petronio 1986, Mazza 1995). It is evident that the aforementioned characters are not exhibited by the specimen from Amoroso. In general, a greater number of characters (including the angular process with an anteriorly arched angle, the dental arches with a sigmoidal development, and a wide rostral fan) are shared by the Sicilian specimen and *H. amphibius*. The island species *H. creutzburgi* from Crete clearly differs from the Amoroso mandible in several morphological characters. A notable distinction between *H. creutzburgi* and the Amoroso specimen is the extremely narrow rostral fan, which does not widen laterally, a characteristic typical of the former species. Other distinguishing features of the latter species include a short symphysis, an i1 and i2 of similar size, and a small canine (Marra 2005).

Unfortunately, all the incisors are missing in the specimen from Amoroso. Nevertheless, some characters remain visible. The i1 section is round, as seen in *H. pentlandi* specimens described by Accordi (1955). However, it should be noted that this character is shared by the majority of the Pleistocene European species. It is noteworthy that Di Patti and Piccione (2004) documented some juvenile specimens of *H. pentlandi* from Cannita Cave exhibiting the hexaprotodont condition, a character previously reported exclusively in *H. amphibius* (Hooijer 1942). Regarding the lower canine, Accordi (1955) also acknowledged a massive c in certain specimens of *H. pentlandi*, asserting that males and females evidently differed in the dimensions of this tooth. This character is notably evident in *H. amphibius*, in which the size of canines represents one of the few anatomical features influenced by sexual dimorphism (Shannon *et al.* 2021). Following the study of Shannon *et al.* (2021), the large canines of the mandible from Amoroso indicate that this individual was most likely a male. The specimen designated as MGUP 24915 displays small canines, which are indicative of the specimen likely being a female individual. The canines of *H. pentlandi* from Cannita Cave possess a groove on the mesial side, but do not

exhibit an additional groove on the lateral surface. This feature has been reported in some *H. amphibius*. According to Caloi and Palombo (1983), in *H. pentlandi* the canines typically exhibit deep convergent ridges on the lateral surfaces. However, there are also specimens where the ridges were poorly developed and parallel. As demonstrated in Marra (2005), the lower canines of *H. creutzburgi* usually exhibit parallel ridges. In general, the grooves on the enamel surface are rather variable in *H. antiquus* and *H. amphibius*, and therefore this character seems not diagnostic at species level (but see discussion in Blandamura and Azzaroli 1977, Mecozzi *et al.* 2023).

The m2 and the m3 in *H. pentlandi* characteristically exhibit a comma-shaped entoconid (Fig. 5A, F–I, K–O), a feature that is observed in *H. antiquus* (Fig. 5E) and in select fossil *H. amphibius* specimens (Fig. 5C, D) (Mazza 1995, Marra 2005). However, in some of the m3s figured by Accordi (1955), the entoconid does not appear to be comma shaped, but rather more complex in its morphology. Stylids are generally common in hippopotamids, particularly the entostylid (Mazza 1995). The latter is typically strong in *H. antiquus* (Mazza 1995). However, Capasso Barbato and Petronio (1983) did not mention the presence of posterior stylids in the m3s from Cannita Cave. However, a subsequent deeper analysis of the material stored at the MSNM and collected from Cannita (Fig. 5L, N, O) and in the MGUP (Fig. 5K, M) did indeed highlight the presence of this character. Some of the m3s figured in Accordi (1955) show the post-entostylid and the post-ectostylid, as observed in the m3s of the Amoroso specimen. The outlets of the transverse valley can be either V shaped or U shaped, and therefore are not diagnostic (Mazza 1995). The overall shape of the MGUP GA1 is comparable to that of MGUP SC7 from San Ciro Cave (Fig. 5F). The comparison between these two latter specimens is facilitated by the similarity of their wear. In general terms, the wear surface and the enamel of the specimens from Sicily are more complex than in other specimens, and this is also the case for extant *H. amphibius* (Fig. 5B). The m3 of *H. melitensis* depicted by Marra (2005) (Fig. 5J) exhibits a slightly greater degree of wear and tear in comparison to the two m3s of the mandible from Amoroso. However, the general shape in *H. melitensis* is similar to the one of *H. pentlandi*, whereas the overall size is smaller than in the Sicilian species. The hypoconid in *H. melitensis* do not have a trefoiled wear pattern, as in the specimens from Amoroso. Moreover, in the m3 of *H. melitensis* the hypoconulid is comma shaped, whereas *H. pentlandi* is typically distinguished by more complex wear patterns (Marra 2005). A well-developed post-entostylid is also visible. In the m3 figured by Marra (2005), the presence of an entostylid is also supposed.

Morphometrical comparison: It is unfortunate that there is a paucity of mandibles available for morphometrical study of *H. pentlandi*. In the scatterplot LS vs. Bfo (Fig. 6) the specimen from Amoroso falls within the variability of *H. amphibius*, and close to the specimens collected from San Ciro Cave. The specimen from Cannita Cave plots in a distinctly different morphospace, exhibiting values that are remarkably smaller and potentially influenced by deformation. The values of Bfi are analogous to those from San Ciro Cave, whereas the specimens collected from Cannita Cave are considerably smaller and approximate the value of *H. creutzburgi*. The values of H4P and

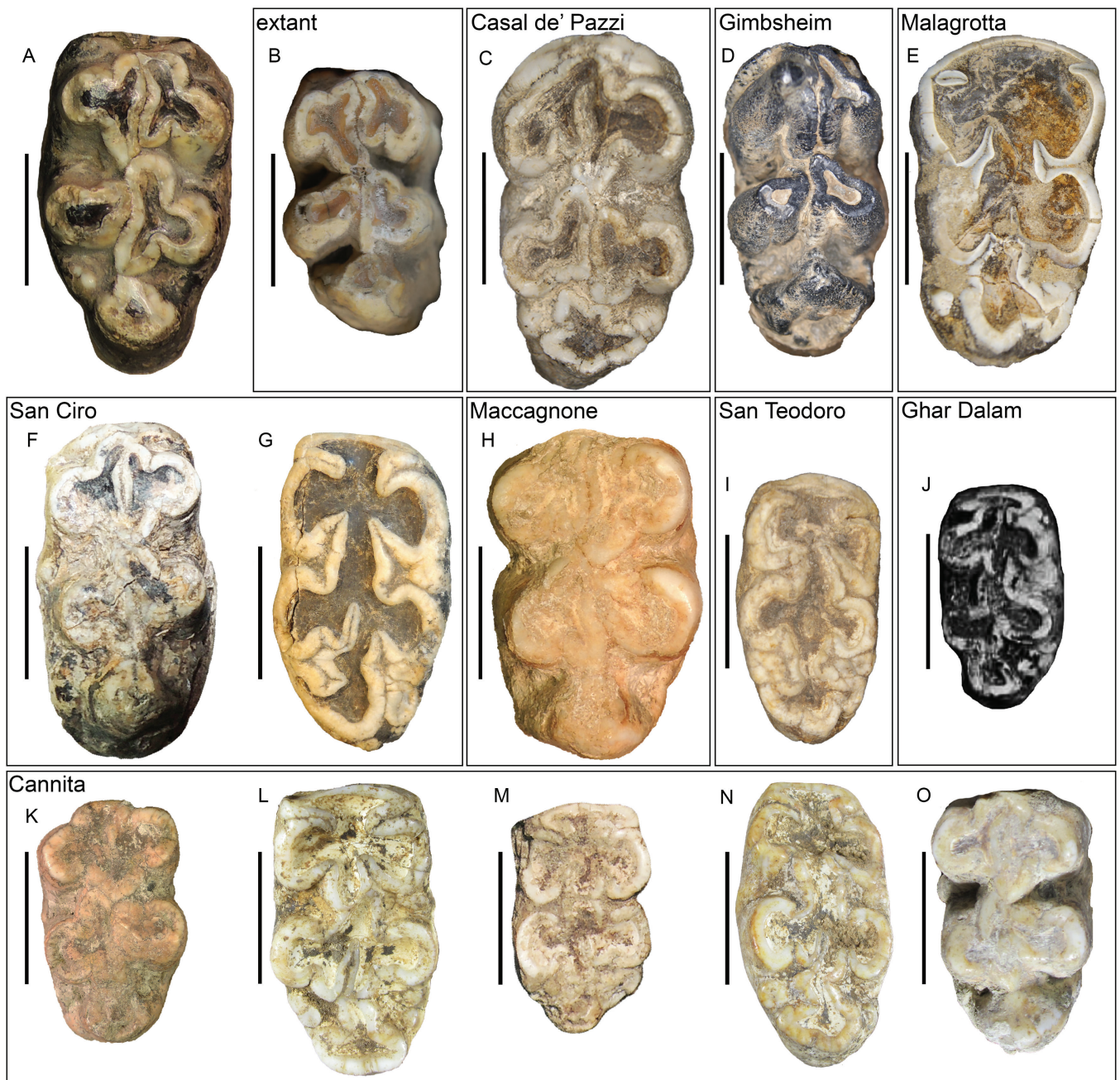


Figure 5. Comparison between different m3s belonging to the family Hippopotamidae. A, MGUP GA1, *H. amphibius* (Middle–Late Pleistocene, Amoroso). B, NOVA-FCT-DCT-5375, *H. amphibius* (extant, Angola). C, MCP CdP110, *H. cf. amphibius* (Middle Pleistocene, Casal de' Pazzi). D, NHMMZ PW1992/74-LS, *H. amphibius* (Late Pleistocene, Gimbsheim). E, MCZR PV 2010.2690B, *H. cf. antiquus* (Middle Pleistocene, Malagrotta). F, MGUP SC7, *H. pentlandi* (Middle–Late Pleistocene, San Ciro Cave). G, MGUP SC35, *H. pentlandi* (Middle–Late Pleistocene, San Ciro Cave). H, MGUP 635, *H. pentlandi* (Middle–Late Pleistocene, Maccagnone Cave). I, MGUP ST329bis, *H. pentlandi* (Middle–Late Pleistocene, San Teodoro Cave). J, *H. melitensis*, modified from Marra (2005) (Middle–Late Pleistocene, Ghar Dalam). K, MGUP CNFC022, *H. pentlandi* (Middle–Late Pleistocene, Cannita Cave). L, MSNM V9-4, *H. pentlandi* (Middle–Late Pleistocene, Cannita Cave). M, MGUP CN50, *H. pentlandi* (Middle–Late Pleistocene, Cannita Cave). N, MSNM V9-3, *H. pentlandi* (Middle–Late Pleistocene, Cannita Cave). O, MSNM V9-10, *H. pentlandi* (Middle–Late Pleistocene, Cannita Cave).

H3M of the Amoroso mandible fall within the variability of *H. amphibius*, whilst the specimens from Cannita Cave are smaller (see Supporting information S2). The differences in the ANOVA using LS, H3M, m1–m3, and p2–m3 are statistically significant (see Supporting information S2). However, the only values that are significantly different from the ones of the mandible

of Amoroso are *H. antiquus* LS and p2–m3 measurements. Furthermore, *H. pentlandi* exhibits distinct variations when compared with both *H. antiquus* and *H. amphibius*, while *H. amphibius* diverges from *H. antiquus*. The dimensions of incisors and canines are significantly influenced by sexual dimorphism, thereby rendering morphometric comparisons challenging

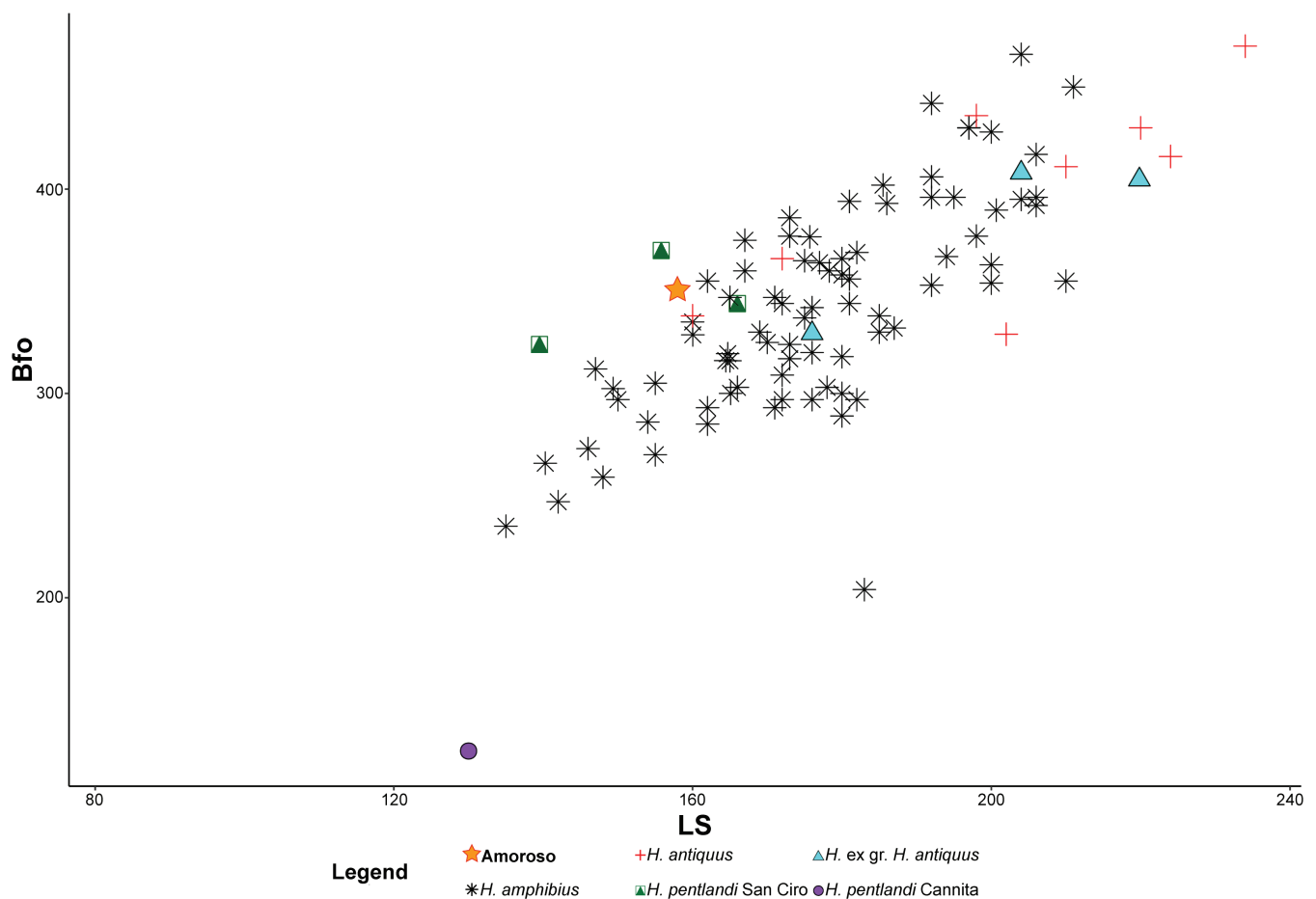


Figure 6. Scatterplot of length of the mandibular symphysis (LS) vs. outer breadth of the rostral fan (Bfo) (in mm).

(Shannon *et al.* 2021). With regard to the i1s, the measurements of the specimens from Amoroso (i1apD, 68.59 mm; i1m1D, 65.95 mm) fall within the variability of *H. amphibius* (i1apD, mean 45.85 mm; i1m1D, mean 41.27 mm) and *H. pentlandi* collected from San Ciro Cave (i1apD, mean 54.14 mm; i1m1D, mean 46.61 mm) (see Supporting information S2). The measurements of *H. pentlandi* material from Cannita (i1apD, mean 37.8 mm; i1m1D, mean 33.5 mm) are significantly smaller than the previously mentioned specimens. The only i1 available measurement belonging to *H. creutzburgi* (i1m1D, 22 mm) is also notably smaller compared to all the fossil and extant specimens analysed (see Supporting information S2). In contrast to the mandible, a greater number of isolated teeth from *H. pentlandi* can be compared to those from Amoroso. In the scatterplot B m2 vs. L m2 (Fig. 7A), the specimens from Amoroso fall within the variability of *H. amphibius*, whilst the variability of *H. pentlandi* is characterized by lower values. The smaller *H. pentlandi* m2s are all recovered from Cannita Cave and Contrade d'Imera. As anticipated, *H. creutzburgi* is smaller than *H. pentlandi*. The measurements for *H. melitensis* reported by Marra (2005) are more closely aligned with *H. creutzburgi* and *H. pentlandi* from Cannita Cave rather than with the specimens from Amoroso. The results of the analysis indicate that the differences between the values of both L and B of the m2s are statistically significant. It is noteworthy that the L values of *H. pentlandi* (different localities and Cannita Cave) and the Amoroso specimens exhibit a statistically

significant difference (for detailed results, see Supporting information, S2). The difference in the MANOVA analysis using the B and L values of the m2s is also statistically significant. The scatterplot of L and B of the m3 (Fig. 7B) is of particular interest. The Amoroso specimens exhibit a degree of variability that encompass both *H. amphibius* and *H. pentlandi*. However, the values of *H. pentlandi* that are more closely aligned with Amoroso are the San Ciro Cave specimens, while the majority of the smaller specimens are all from Cannita Cave. The differences in the ANOVA analyses using L and B values of the m3s are also statistically significant. However, no differences are detected between the specimens from Amoroso and *H. antiquus*, *H. amphibius*, *H. ex gr. H. antiquus*, *H. melitensis*, and *H. pentlandi* (Cannita Cave, San Ciro Cave, and different localities). A MANOVA analysis utilizing L and B of the m3s also highlight statistically significant differences (see Supporting information S2).

PCA and LDA

In order to conduct further testing of the measurements obtained from the sample, both PCA and LDA were performed. Both analyses take into consideration LS, Bfo, Bfi, L m3, and B m3 values. PC1 account for 66.4% of the total variability, while PC2 accounted for 15.7% (> 80%) (Fig. 7C). The specimen from Amoroso falls within the variability of *H. amphibius* and is close to *H. pentlandi*. It is important to note that the two Sicilian hippos in the present sample are from San Ciro Cave; data for

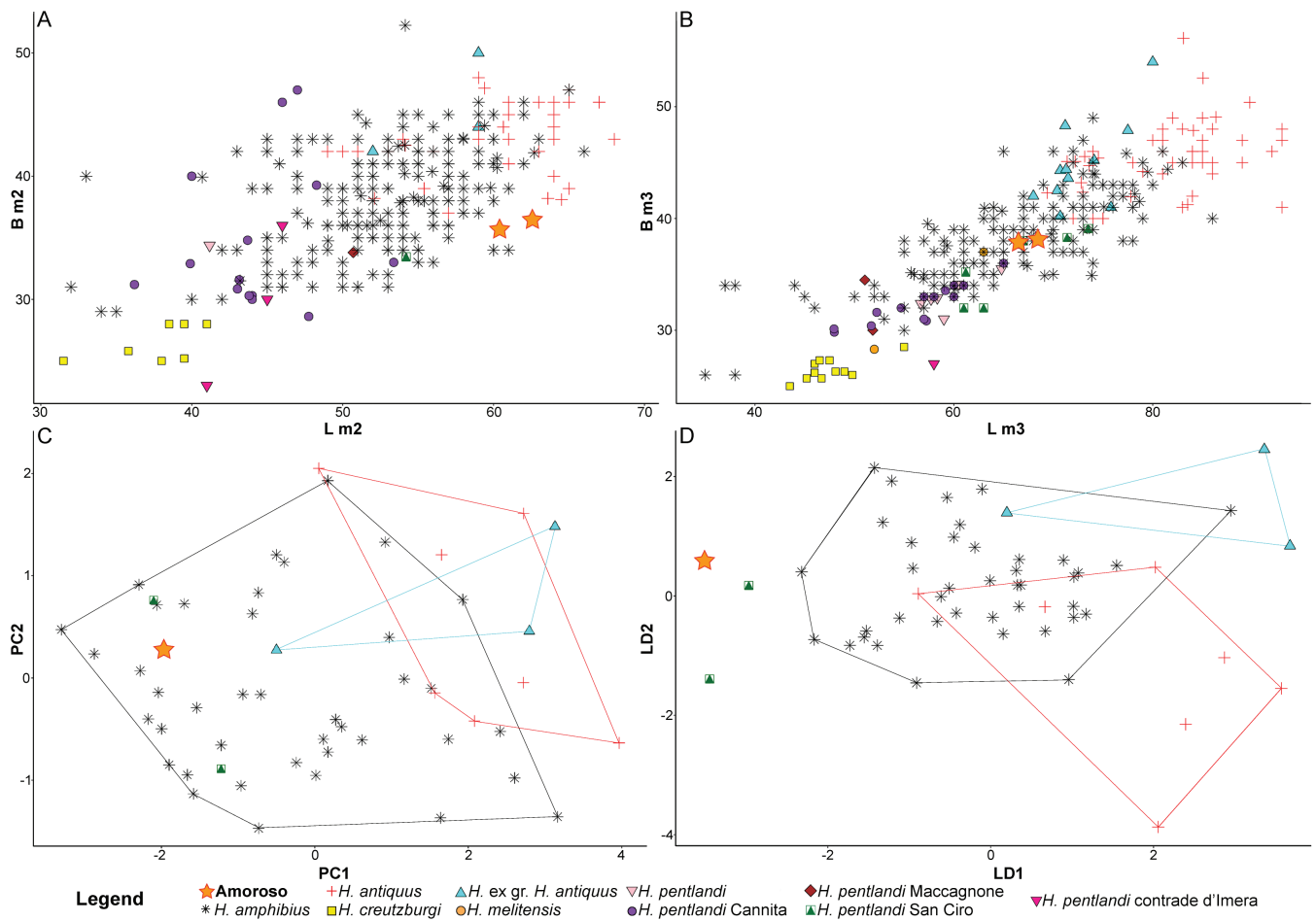


Figure 7. A, scatterplot greatest length (L) vs. greatest breadth (B) m2 (in mm). B, scatterplot greatest length (L) vs. greatest breadth (B) m3 (in mm). C, PCA analysis performed on the values of length of the mandibular symphysis (LS), outer breadth of the rostral fan (Bfo), inner breadth of the rostral fan (Bfi), greatest length of the m3 (L m3), and greatest breadth of the m3 (B m3). PC1 (66.4%) vs. PC2 (15.7%). D, LDA analysis performed on the same values of the PCA, LD1 vs. LD2.

the specimens collected from Cannita Cave or any other Sicilian locality are not available. *Hippopotamus antiquus* is distinguished by higher values of PC1 in comparison to *H. amphibius*. *Hippopotamus ex gr. H. antiquus* is plotted within the variability of the extant species and *H. antiquus*. The variables exhibiting the highest absolute correlation with the first and second axis are Bfo and LS. PERMANOVA analysis indicates that statistically significant differences can be observed exclusively between the values of *H. antiquus* and *H. amphibius*.

We also performed a LDA using the same dataset as the PCA to further test the morphometrical variability of the examined hippopotamid specimens (Fig. 7D). The predicted group for the Amoroso specimen is *H. pentlandi* (San Ciro Cave), with an accuracy of 75%. The Amoroso specimen and *H. pentlandi* are distinguished by notably negative values of LD1. In contrast to the variability exhibited by PCA, the values of *H. amphibius* are less subject to variation. *Hippopotamus amphibius* displays both negative and positive values of the LD1. By contrast, *H. antiquus* displays greater variability than *H. amphibius*, predominantly exhibiting positive LD1 and negative LD2 values. This analysis indicates a high degree of similarity between the values of the Amoroso and the *H. pentlandi* mandible from San Ciro Cave.

However, it is noteworthy that certain values of *H. amphibius* demonstrate a close proximity to those observed in Amoroso and *H. pentlandi* specimens from San Ciro Cave. It is important to reiterate that the present analysis is based exclusively on specimens from San Ciro Cave, with no additional localities having been considered. The current bibliography does not report any complete or undeformed mandibles from Cannita Cave.

3D Geometric Morphometrics

We performed GMM analyses using mandibles of different continental species and island species (Fig. 8). The character under investigation is the mandibular symphysis, as it is a diagnostic character in different Hippopotamidae species, following Boissarie (2005). In the results of our PCA analysis the positive PC1 values are indicative of a robust and predominantly sub-circular symphyseal cross-section, while the negative PC1 values are associated with a thin and elongated shape. Positive PC2 values are linked to a pear-shaped symphyseal cross-section, while conversely, negative PC2 values are characterized by a more elongated and taller posterior portion of the cross-section if compared to positive values. The Amoroso mandible exhibits a degree of variability that falls within the range of *H. amphibius*.

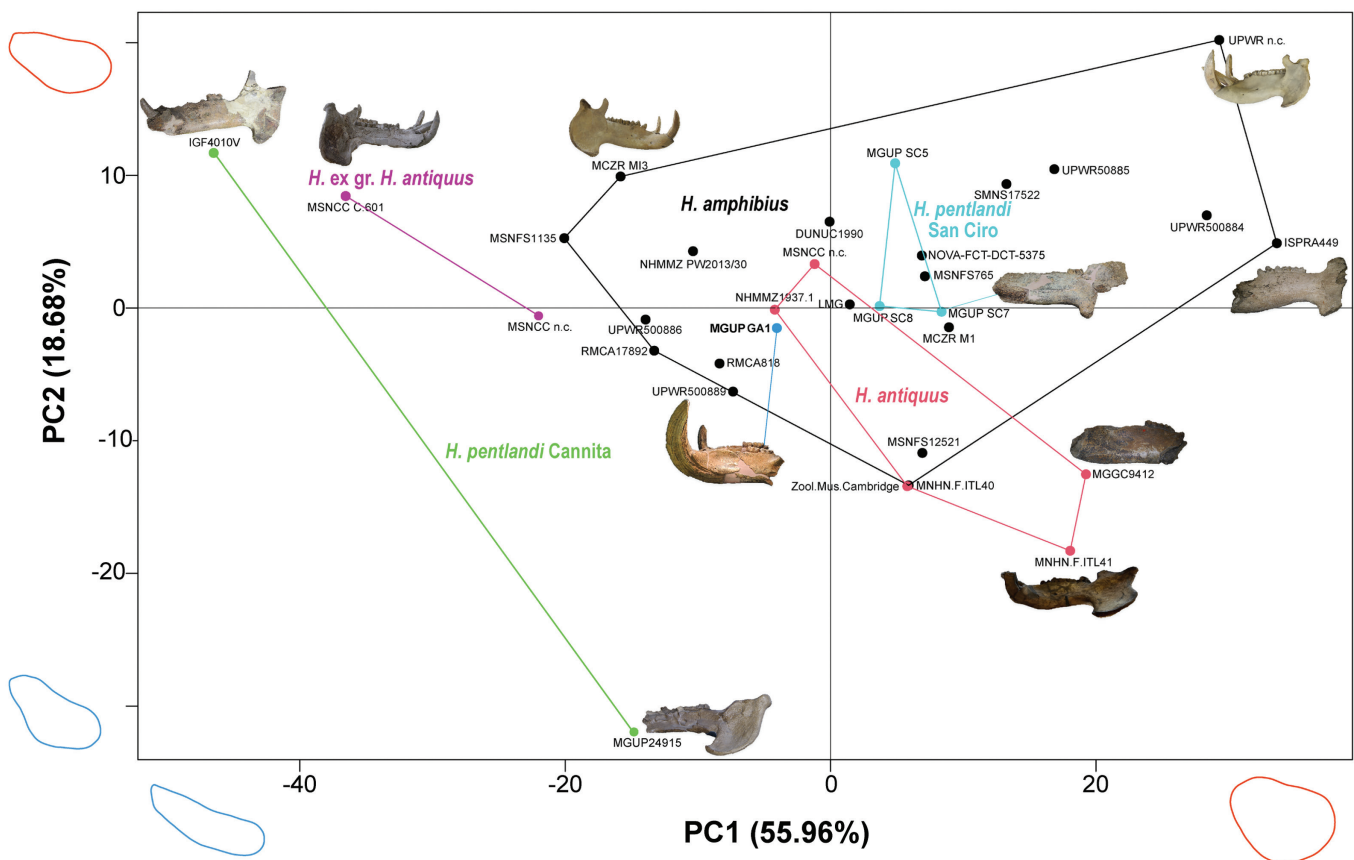


Figure 8. 3D GMM results performed on the symphyseal cross-section of different mandibles ascribed to *H. pentlandi* from Cannita (in green), *H. pentlandi* from San Ciro Cave (in light blue), *H. ex gr. H. antiquus* (in pink), *H. amphibius* (in black), and *H. antiquus* (in red). In blue the mean shape of the PC1- and PC2-, in red the mean shape of the PC1+ and PC2+.

However, it is also closely related to both San Ciro Cave and *H. antiquus* specimens. The mandible from Cannita Cave plots further away from all the specimens present in our sample, as well as a juvenile mandible (IGF4010V) collected from the same Sicilian locality. An important shift in mandibular shape during the ontogenetic growth of *H. amphibius* was previously discussed by Martino et al. (2024b), who suggested a shift in shape occurs between the stage III and more adult individuals. Nevertheless, further specimens must be incorporated into the analysis to achieve a comprehensive understanding of the ontogenetic growth of *H. pentlandi*. The specimens assigned to *H. ex gr. H. antiquus* deviate from the variability observed in both the extant specimens and *H. antiquus*. However, the specimen IGF4010V and MSNUP C.601 shared a similar cross section of the mandibular symphysis.

DISCUSSION

Taxonomical attribution of the Amoroso mandible

The mandible MGUP GA1 differs from *H. pentlandi* from Cannita Cave in having a sturdy and tall mandibular corpus and an overall shorter mandible in lateral view. The mandible of *Hippopotamus creutzburgi* differs from the Amoroso specimen in exhibiting an extremely narrow rostral fan that does not widen laterally, a short symphysis, i1s and i2s of similar size, and a small canine (Marra 2005). The angular process of the Amoroso mandible

has an anteriorly arched angle, dental arches with a sigmoidal development, and a wide rostral fan, characteristics shared with *H. amphibius*. No clear diagnostic differences were identified in the m2s and m3s of the different species analysed. However, a more complex wear surface and the presence of stylids on the cingulids are observed in *H. pentlandi* and fossil species, in contrast to the extant *H. amphibius*. *Hippopotamus melitensis* has a comma-shaped hypoconulid (Marra 2005), while in the other specimens analysed from Sicily it is cruciform shaped.

The morphometric analysis revealed a clear distinction between the specimens collected from Cannita Cave and those from Amoroso, the latter exhibiting a close resemblance to some specimens found in San Ciro Cave and to *H. amphibius*. The teeth and mandible measurements taken from the Cannita Cave specimens are notably small, suggesting that a more thorough revision of the hippopotamid fauna collected from this locality is necessary. The values of both *H. melitensis* and *H. creutzburgi* are smaller than those of *H. pentlandi* from both Cannita Cave and the hippopotamids collected from other Sicilian localities. The PCA and LDA confirm a close affinity between the specimens from San Ciro Cave and those from Amoroso material, with the former exhibiting a strong resemblance to *H. amphibius*. Unfortunately, no specimens from Cannita Cave were included in our analyses, since undeformed and rather complete mandibles are not described in literature. The 3D GMM analysis further highlights the significant differences between the

specimens collected from San Ciro Cave and Amoroso and those from Cannita Cave. It is evident from our morphological, morphometrical, and 3D GMM analyses that the specimens from Cannita Cave are rather unique and diverge significantly from those found in Amoroso and in San Ciro Cave.

In consideration of the preceding discussion, the mandible from Amoroso is found to be more analogous in terms of dimensions and morphology to *H. amphibius* rather than to *H. pentlandi* collected from Cannita Cave. The material included in this study, which was obtained from San Ciro Cave, also exhibits a greater degree of similarity to the variability of *H. amphibius* rather than to that of *H. pentlandi* collected from Cannita Cave. Despite the observed similarity in variability between the mandible from Amoroso and the material from San Ciro Cave, distinctive morphological or morphometrical characters that would enable a clear differentiation from *H. amphibius* are absent. Consequently, we can tentatively ascribe the mandible from Amoroso to *H. amphibius*.

Systematics and morphological variability of Sicilian hippopotamuses: insights and challenges

Despite the extensive documentation of the historical presence of hippopotamuses in Sicily, these large semi-aquatic mammals have received only limited attention in scientific research (Martino and Pandolfi 2022 and references therein). The majority of studies on Sicilian hippopotamuses were conducted during the 20th century (Scinà 1831, Fabiani 1928, 1932, 1934, Accordi 1955, Bonfiglio 1983, Caloi and Palombo 1983, 1986, Capasso Barbato and Petronio 1983, Petronio 1995, Petruso and Taschetta 2011, Martino and Pandolfi 2022). However, more recently, there has been a decline in interest, with the focus shifting towards the reconstruction of the hippopotamus diet and morphological functional adaptations to island life (i.e. Bethune *et al.* 2019, Georgitsis *et al.* 2022a, b).

The majority of the hippopotamid material from Sicily has been referred to a single species, *H. pentlandi*. Nevertheless, the evidence supporting this attribution is inconclusive. Despite the widely accepted fact that Sicilian hippopotamuses are smaller than those found in the Middle to Late Pleistocene mainland, *H. pentlandi* lacks a holotype. This is because von Meyer (1832) did not provide a formal systematic palaeontological description or images of this species when he erected it. The International Commission on Zoological Nomenclature asserts that ‘every name published before 1931 must be accompanied by a description or a definition of the taxon’ (ICZN 1999). In light of this, *H. pentlandi* is therefore not a valid species. Due to the ambiguity surrounding its systematics, the species *H. pentlandi* has been utilized for over a century as a ‘waste basket’ taxon, signifying all the small-sized hippopotamid material coming from Sicily. This approach, however, fails to address the challenges inherent in identifying the mainland ancestor, or determining whether a single, or multiple ancestors colonized the island. This is a salient issue given that both *H. amphibius* and *H. antiquus* are known to have inhabited the continent during relevant temporal periods. An early attempt to clarify the characters of the Sicilian species was made by Thenius (1954), who defined *H. pentlandi* as smaller than *H. amphibius* but bigger than *H. melitensis*. The author also highlighted that the third lower molar of *H. pentlandi* was characterized by a connection between the protoconid

and metaconid, and by the absence of connection between the paraconid and the hypoconid. Nevertheless, Accordi (1955) demonstrated that these molar characters are rather variable in *H. pentlandi* from Cannita Cave, and therefore not diagnostic at a specific level. Accordi (1955) thus proposed the description provided by his work on the material from Cannita Cave as a new definition for the species *H. pentlandi*. Consequently, the species *H. pentlandi*, with its distinctive characters and morphometrical values, should henceforth be understood as *H. pentlandi sensu Accordi (1955)*.

A number of studies were conducted on the Sicilian fossil fauna, with a particular focus on the *H. pentlandi* populations. Falconer (1860) documented the presence of two distinct hippopotamus species in San Ciro Cave. The author also documented that more than 40000 kilograms of predominantly hippopotamus material had been extracted from San Ciro Cave and subsequently destroyed. Consequently, a substantial proportion of the skeletal material from San Ciro Cave is no longer available for study, which significantly complicates the analysis of the variability of the hippopotamids from this locality. Accordi (1955) also recognized the occurrence of two different hippopotamid taxa in Cannita Cave, based on an i1, two upper canines, and an upper molar. Furthermore, Accordi (1955) identified the presence of a species closely resembling *H. amphibius* from different fossiliferous localities of Sicily documented in extant literature (Scinà 1831, Seguenza 1900, De Gregorio 1924, 1925).

Ciofalo and Battaglia (1888) described a series of bones originating from Contrade d’Imera (Termini Imerese), including 10 maxillary and mandibular fragments, premolars, molars, and a substantial quantity of post-cranial material. The measurements of the teeth reported for the hippopotamus from Contrade d’Imera are small, with values that are similar to those of the Cannita Cave specimens. It is important to highlight that a portion of the material described by Ciofalo and Battaglia (1888) can be attributed to juvenile specimens, rendering size differences uninformative.

The findings of the hippopotamid fossils at San Cusmano (Melilli, Siracusa), as documented by Accordi (1957), are distinctly smaller than the average size recorded from Cannita Cave. The author proffered two plausible explanations for this discrepancy. The first explanation suggests that the remains of Cannita Cave ascribed to *H. pentlandi* were sourced from multiple levels, leading to a composite collection of both *H. amphibius*-like and *H. pentlandi*. This would consequently lead to a greater morphometric variability of *H. pentlandi* from Cannita Cave. The second explanation posits that the Melilli population was more homogeneous, primarily consisting of small *H. pentlandi*. Consequently, other Sicilian localities would therefore have been characterized by the occurrence of both *H. amphibius*-like and *H. pentlandi*, resulting in a larger average size.

Capasso Barbato and Petronio (1983) advanced the argument that the hippopotamid species from Sicily should have rather been indicated as *Hippopotamus amphibius pentlandi*. The authors proposed a division of the presence of *H. amphibius pentlandi* in Sicily into three distinct stages. The first stage was distinguished by the co-occurrence of *H. amphibius pentlandi*, *Megaloceros messinae*, and *P. antiquus*, with the former exhibiting a size closely resembling its continental counterpart. A second phase was characterized by the presence of *H. amphibius*

pentlandi and *Palaeoloxodon mnaidriensis* (or *Palaeoloxodon* sp.), with both the hippopotamus and the elephant exhibiting a reduction in size (e.g. specimens from Cannita Cave). A third phase was then characterized by the absence of the hippopotamus and the presence of a well-differentiated fauna including *Palaeoloxodon* cf. *mnaidriensis*, *C. elaphus siciliae*, *C. lupus*, *S. scrofa*, *C. crocuta spelaea*, *B. primigenius*, *Bison priscus*, *Panthera leo spelaea*, and *U. arctos*. However, this hypothesis is in contrast with the faunal list of the *Palaeoloxodon* sp. FC, which highlighted the presence of hippopotamus together with the previous listed fauna (Bonfiglio et al. 2002, Larramendi et al. 2020, Mangano et al. 2020). In Mangano et al. (2020) the material of *H. pentlandi*, *U. cf. arctos*, and *Palaeoloxodon* sp. was collected together in San Teodoro Cave, similarly to the fossil remains retrieved from Amoroso.

Caloi and Palombo (1983) argued that *H. pentlandi* should not be considered as a subspecies of *H. amphibius* since it is characterized by several distinctive apomorphies, including zygomatic arches that are not particularly broad, a long upper canine-second upper premolar diastema, and a short dental series. Other characters visible in *H. pentlandi*, such as the elevated and more posterior orbits and protruding condyles, are common in *H. antiquus*. The mandibular corpus is typically longer and lower than in the common hippo and the ventral profile is generally sub-rectilinear. Furthermore, the horizontal rami become more subvertical than in the continental hippos, and the mandibular condyle and the coronoid process share a similar vertical height. It is also noteworthy that Caloi and Palombo (1983) identified numerous apomorphies in the post-cranial elements of *H. pentlandi*. The characters identified by Caloi and Palombo (1983) include a humerus with a poorly inclined trochlear axis, an ulna olecranon exhibiting a minor inclination, a femur characterized by a more developed lesser trochanter, a talus exhibiting a more protruding lateral lip, and metapodials displaying an articular surface that is more developed in the anterior view. In more general terms, the authors identified several morphological key differences between *H. pentlandi* and *H. amphibius*, highlighting that *H. pentlandi* possesses bones with distal epiphyses that are more developed transversally, an elongated radius and tibia in respect to the femur, reduced central metacarpals, and elongated central metatarsals. According to Caloi and Palombo (1983), all the aforementioned cranial and post-cranial characters arise from a combination of unique adaptations and a decrease in size.

In Bonfiglio (1992), the hippopotamus remains from Acquedolci (Messina), also called San Teodoro Cave, were indicated as falling towards the lower end of the morphometric variability of extant hippopotami, with post-cranial elements that are stouter than in *H. amphibius*. The Acquedolci material is particularly abundant, comprising more than 20 individuals, including 14 adult crania. Among these remains juvenile individuals are also well represented, with a femur and a metapodial found in anatomical connection with their distal epiphyses intact. The silty matrix of the fossiliferous layer, the abundance of *H. pentlandi* material, the absence of erosion, and the occurrence of elements in anatomical connection suggest the presence of a palaeolacustrine basin in the area (Bonfiglio 1992). Furthermore, the presence of well-preserved juvenile hippopotamid bones provides compelling evidence for their autochthonous nature, as these skeletal elements would not have been capable of surviving

transportation processes. However, it is regrettable that no further studies have been conducted on the morphology and morphometry of the abundant material from Acquedolci.

Petronio (1995) analysed the post-cranial hippopotamid material coming from Puntali Cave (Palermo). The hippo material from this locality was primarily found in association with *P. mnaidriensis* and *C. elaphus siciliae* and was assigned to the late Middle–Late Pleistocene. The hippopotamid remains described by Petronio (1995) exhibit greater morphological and morphometric similarities to *H. amphibius* rather than to *H. pentlandi*. In accordance with this observation, the author ascribed the material analysed from the Puntali Cave to a subspecies of the extant hippo, indicated as *H. amphibius* ssp. Furthermore, Petronio (1995) identified significant variations between hippopotamid remains collected from Tindari, Malatucca Cave, Maccagnone Cave, San Teodoro Cave (or Acquedolci), and Puntali Cave in comparison to material originating from Cannita Cave and Melilli. The hippopotamid elements described from the former localities were larger than those from Cannita Cave, with dimensions and morphologies that were more similar to *H. amphibius*. Petronio (1995) emphasized the imperative for a comprehensive re-evaluation of the intermediate-sized hippopotamid forms identified in Tindari, Malatucca Cave, Maccagnone Cave, San Teodoro Cave, and Puntali Cave, which, according to the author, most likely also represented a subspecies of the continental *H. amphibius*.

In addition, a number of small specimens of *H. pentlandi* were documented at site K22 (San Vito lo Capo, Trapani) (Petruso and Taschetta 2011). The fauna from the latter deposit exhibits smaller dimensions than those from Cannita Cave. The authors of the study hypothesize that the reduced size of the hippopotamid material collected from the K22 locality, which represents the westernmost occurrence of hippos in Sicily, may be attributed to elevated selective pressure resulting in morpho-functional alterations of the limbs (Caloi and Palombo 1994).

In light of the current state of the art, the systematics of the Sicilian hippo are challenging to evaluate. However, it is evident that two distinct taxa likely inhabited Sicily during the Quaternary. One of these taxa can be distinguished by an elongated cranium, narrower zygomatic arches, and a shorter sagittal crest when compared to *H. amphibius*. Its mandible exhibits a more elongated and lower mandibular corpus compared to the common hippo, while the position of the mandibular condyle and the coronoid process are more or less of the same level. This taxon is distinguished by a number of post-cranial diagnostic characteristics, as listed by Accordi (1955) and Caloi and Palombo (1983, 1986). It is notable for its comparatively small size in comparison to *H. amphibius*. The available evidence suggests that this taxon was predominantly present in Cannita Cave, San Vito lo Capo, Melilli, and most likely Contrade d'Imera. The first morphotype can be designated as *H. pentlandi sensu* Accordi (1955). Conversely, a second taxon is characterized by morphologies and morphometrics that are more analogous to *H. amphibius*, exhibiting a size comparable to that of small to medium-sized common hippopotamuses. Falconer (1860), Accordi (1955, 1957) suggested that is likely that both morphotypes (*H. pentlandi* and *H. amphibius*) were present in Cannita Cave and San Vito Cave. In the stratigraphic log reported in Di Patti and Piccione (2004), based on the information

mentioned in Fabiani (1934), the hippopotamid remains from Cannita Cave were collected from a well-defined fossiliferous stratum. Therefore, the material later studied by Accordi (1955) was most likely sourced from the same level. The presence of an hippopotamid more closely resembling *H. amphibius* than *H. pentlandi* was also reported in Puntali Cave by Petronio (1995). The study herein presented confirms the presence of *H. amphibius* in Sicily during the Middle–Late Pleistocene. Accordingly, as also hypothesized by Capasso Barbato and Petronio (1983), the continental form *H. amphibius* most likely dispersed several times into Sicily, and that would explain why the size of the hippopotamuses sourced from the same cave is sometimes highly variable. Further research on hippopotamid material from Sicily is required to facilitate a comprehensive understanding of their systematics.

CONCLUSION

The mandible described from Amoroso in this work provides significant data on the cranial morphological and morphometrical variability of hippopotamids in Sicily. The Amoroso mandible, known from the 19th century, had never been described in detail but, until to now, has represented one of the best-preserved hippo mandibles ever found in Sicily. The mandible under consideration in this study is notable for its robust and tall mandibular corpus, its overall short mandible, and its wide rostral fan. The angular process exhibits an anteriorly arched angle, while the dental arches are characterized by a sigmoidal development. A thorough morphometric analysis reveals a significant disparity between the specimens gathered from Cannita Cave and those from Amoroso, the latter exhibiting characteristics closer to samples from San Ciro Cave and to extant *H. amphibius*. The 3D GMM application also highlights a significant discrepancy between the specimens from Amoroso and San Ciro Cave and the ones collected from Cannita Cave. The Amoroso specimen falls within the variability of *H. amphibius* and is closely related to the variability found at San Ciro Cave. Following a thorough examination encompassing both morphological and the morphometrical analyses, the mandible from Amoroso can be tentatively ascribed to *H. amphibius*. The Amoroso mandible thus supports the hypothesis that at least two distinct species of hippopotamids inhabited Sicily during the Quaternary period. Based on the presence of elephant and bear remains, usually found in the *Palaeloxodon* sp. FC (or Maccagnone FC), in association with the mandible from Amoroso, it is plausible to assume that *H. pentlandi* and *H. amphibius* cohabited in Sicily during the Middle–Late Pleistocene. The remains of the small *H. pentlandi* are abundant from Cannita Cave, Melilli, Capo San Vito, and most likely Contrade d’Imera. However, a thorough reassessment of the extensive material from Cannita Cave is essential to definitively rule out the possibility that *H. pentlandi* may be a subspecies of *H. amphibius* rather than a distinct species. Moreover, further studies on the abundant material from localities such as Maccagnone Cave, San Ciro Cave, Puntali Cave, Malatucca Cave, Za’ Minica Cave, and San Teodoro Cave (also known as Acquedolci) are required to gain a comprehensive understanding of the systematics of the hippopotamids from Sicily.

SUPPORTING INFORMATION

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

S1: List of hippopotamid occurrences in Sicily.

S2: Measurements of hippopotamid mandibular and dental material, statistical analyses and related references.

S3: List of 3D mandible models used for the 3D GMM analysis.

ACKNOWLEDGEMENTS

The authors thank M. Aiglstorfer, Landeshauptstadt Mainz Naturhistorisches Museum of Mainz (NHMMZ, Germany); F. Alhaique, F. Carinci, and R. Rossi, Museo delle Civiltà di Roma (ISPRA, Italy); C. Marangoni, Museo Civico di Zoologia Roma (MCZR, Italy); P. Agnelli, Museo Storia Naturale di Firenze sezione La Specola (MZUF, Italy); E. Cioppi and L. Bellucci, Museo di Storia Naturale dell’Università degli Studi di Firenze, sezione di Geologia e Paleontologia, Firenze (IGF, Italy); M. Contessi, Museo Geologico Giovanni Capellini Bologna (MGGC, Italy); C. Sorbini, Museo di Storia Naturale e del Territorio, Università di Pisa, Calci, Pisa (MSNUP, Italy); Dal Sasso C., Museo Civico di Storia Naturale di Milano (MSNM, Italy); S. Merker and E. Amson, Staatliches Museum für Naturkunde Stuttgart (SMNS, Germany); E. Ferreira (DCT, FCT-UNL); and J.A. Moita and R. Dias, Museu Geológico de Lisboa (MG, Portugal). The authors also thank D. Fidalgo and an anonymous reviewer who helped improve the quality of this manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

FUNDING

R.M. is funded by the Fundação para a Ciência e a Tecnologia (FCT) (2021.08458.BD, <https://doi.org/10.54499/2021>), an Erasmus + grant [29191(532)105/2022/SMT], and SYNTHESIS + [DE-TAF-TA4-063 2022]. This research was also supported by the FCT, I.P through the Research Unit UIDB/04035/2020 (Geobiotec, DOI: 10.54499/UIDB/04035/2020). This work is part of the project P2022RZ4PL funded by the European Union—Next Generation EU, call PRIN 2022 PNRR (granted to L.P.). M.R. thanks the Stimulus of Scientific Employment, Individual Support – 2018 Call grant by the Fundação para a Ciência e a Tecnologia (Portugal, CEECIND/02199/2018) and GeoBioTec.

DATA AVAILABILITY

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. All the data used in this paper are available in the Supporting information. The 3D model of the investigated mandible is available on MorphoSource: <https://www.morphosource.org/concern/media/000729949?locale=en>.

REFERENCES

- Abbate R, Cimino A, Oieni A. I geomorfositi dell’area pedemontana dei monti Billiemi (Palermo): contributi idrogeologici e geofisici. *Thalassia Salentina* 2006;29:281–300.
- ICZN International Code of Zoological Nomenclature. Fourth edition adopted by the International Union of Biological Sciences. London,

- UK: International Trust for Zoological Nomenclature, 1999; **xxix** + 306.
- Accordi B. *Hippopotamus pentlandi* von Meyer del Pleistocene della Sicilia. *Palaeontographia Italica* 1955; **L**:1–52.
- Accordi B. Nuovi resti di ippopotamo nano nel Pleistocene dei dintorni di Siracusa. *Atti Accademia Gioenia di Scienze Naturali in Catania* 1957; **XI**(6):99–109.
- Adams DC, Rohlf FJ, Slice DE. Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology* 2004; **71**:5–16. <https://doi.org/10.1080/11250000409356545>
- Agostini S, Bertini A, Caramiello S et al. A new mammalian bone bed from the lower Middle Pleistocene of Ortona (Chieti, Abruzzo, central Italy). *Proceedings of the Giornate di Paleontologia* 2005; **12**:1–5.
- Alessi G. Memoria sulle ossa fossili ritrovate in ogni tempo in Sicilia, e recentemente in Siracusa, con osservazioni geologiche storiche filosofiche. *Atti dell'Accademia Gioenia di Scienze Naturali di Catania* 1833; **7**:199–242.
- Anca F. Note sur deux nouvelles grottes ossifères découvertes en Sicile en 1859. *Bulletin de la Société Géologique de France* 1867; **17**:684–695.
- Athanassiou A, Michailidis D, Vlachos E et al. Pleistocene vertebrates from the Kyparissia lignite mine, Megalopolis Basin, S. Greece: Testudines, Aves, Suiformes. *Quaternary International* 2018; **497**:178–197. <https://doi.org/10.1016/j.quaint.2018.06.030>
- Bada JL, Belluomini G, Bonfiglio L et al. Isoleucine epimerization ages of Quaternary mammals of Sicily. *Il Quaternario* 1991; **4**:49–54.
- Basilone L, Di Maggio C. Geology of Monte Gallo (Palermo Mts, NW Sicily). *Journal of Maps* 2016; **12**:1072–1083. <https://doi.org/10.1080/017445647.2015.1124716>
- Battaglia A, Ciofalo S. Scoperte paleontologiche presso Termini Imerese (Sicilia). Lettera al prof. G. Gemmellaro. *Bollettino del R. Comit. Geol. d'Italia* 1883; **4**:229–231.
- Bethune E, Kaiser TM, Schulz-Kornas E et al. Multiproxy dietary trait reconstruction in Pleistocene Hippopotamidae from the Mediterranean islands. *Palaeogeography, Palaeoclimatology, Palaeoecology* 2019; **533**:109210. <https://doi.org/10.1016/j.palaeo.2019.05.032>
- Bivona Bernardi A. Breve relazione sugli ossi fossili trovati non a guari vicino Palermo. *Giornale Officiale Palermo* 1830; **26**.
- Blandamura F, Azzaroli A. Ippopotamo Maggiore di Filippo Nesti. *Accademia nazionale dei Lincei-Memorie Scienze Fisiche* 1977; **XIV**:169–188.
- Boeschoten GJ, Sondaar PY. The Pleistocene of the Katharo basin (Crete) and its hippopotamus. *Bijdragen tot de Dierkunde* 1966; **36**:17–51. <https://doi.org/10.1163/26660644-03601002>
- Boisserie JR. The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): a review based on morphology and cladistic analysis. *Zoological Journal of the Linnean Society* 2005; **143**:1–26. <https://doi.org/10.1111/j.1096-3642.2004.00138.x>
- Boisserie JR, Lihoreau F, Orliac M et al. Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae): *Kenyapotamus* and hippopotamid origins. *Zoological Journal of the Linnean Society* 2010; **158**:325–366. <https://doi.org/10.1111/j.1096-3642.2009.00548.x>
- Bonfiglio L. Prima campagna di scavo dei depositi a mammiferi pleistocenici dell'area della grotta di S. Teodoro (Acquedolci, Messina, Sicilia). *Geologica Romana* 1983; **22**:271–285.
- Bonfiglio L. Campagna di scavo 1987 nel deposito pleistocenico a *Hippopotamus pentlandi* di Acquedolci (Messina, Sicilia nord-orientale). *Bollettino della Società Paleontologica Italiana* 1992; **30**:157–173.
- Bonfiglio L, Berdar A. Elefanti pleistocenici del litorale dello Stretto di Messina, revisione e nuove osservazioni. *Quaternaria* 1969; **11**:255–261.
- Bonfiglio L, Violanti D. Prima segnalazione di Tirreniano ed evoluzione pleistocenica del Capo Peloro (Sicilia nord-orientale). *Geografia Fisica e Dinamica Quaternaria* 1983; **6**:3–15.
- Bonfiglio L, Mangano G, Marra AC et al. Pleistocene Calabrian and Sicilian bioprovinces. *Geobios* 2002; **35**:29–39. [https://doi.org/10.1016/s0016-6995\(02\)00046-3](https://doi.org/10.1016/s0016-6995(02)00046-3)
- Bonfiglio L, Di Maggio C, Marra AC et al. Bio-chronology of Pleistocene vertebrate faunas of Sicily and correlation of vertebrate bearing deposits with marine deposits. *Alpine and Mediterranean Quaternary* 2003; **16**:107–114.
- Bonfiglio L, Esu D, Mangano G et al. Late Pleistocene vertebrate-bearing deposits at San Teodoro Cave (North-Eastern Sicily): preliminary data on faunal diversification and chronology. *Quaternary International* 2008; **190**:26–37. <https://doi.org/10.1016/j.quaint.2007.10.019>
- Bonfiglio L, Rosso A, Herridge V et al. Pleistocene caves of eastern Sicily coast: exceptional archives to reconstruct the history of the island's biota. *Geosciences* 2022; **12**:258. <https://doi.org/10.3390/geosciences12070258>
- Bookstein FL. *Morphometric Tools for Landmark Data*. New York, NY: Cambridge University Press, 1991.
- Burgio E, Di Patti C. I vertebrati fossili della Grotta di San Teodoro (Acquedolci, Sicilia). *Naturalista Siciliano* 1990; **XIV**:1–19.
- Burgio E, Oliva N, Scalone E. La collezione vertebratologica della Grotta dei Puntali presso Carini (Palermo, PA). *Naturalista Siciliano* 1983; **7**:67–79.
- Burgio E, Costanza M, Di Patti C. I depositi a vertebrati continentali del Pleistocene della Sicilia Occidentale. *Naturalista Siciliano* 2002; **XXVI**:229–282.
- Caloi L, Palombo MR. Osservazioni sugli ippopotami nani delle isole del Mediterraneo. *Geologica Romana* 1983; **22**:45–83.
- Caloi L, Palombo MR. Osservazioni sui caratteri biometrici del cranio di *Hippopotamus pentlandi* von Meyer della grotta della Cannita (Sicilia) e degli ippopotami pleistocenici dell'Europa occidentale. *Hystrix, the Italian Journal of Mammalogy* 1986; **1**:137–159.
- Caloi L, Palombo MR. Functional aspects and ecological implications in Pleistocene endemic herbivores of Mediterranean Islands. *Historical Biology* 1994; **8**:151–172. <https://doi.org/10.1080/10292389409380475>
- Caloi L, Palombo MR, Petronio C. Resti cranici di *Hippopotamus antiquus* (=H. major) e *Hippopotamus amphibius* conservati nel Museo di Paleontologia dell'Università di Roma. *Geologica Romana* 1980; **19**:91–119.
- Capasso Barbato L, Petronio C. Considerazioni sistematiche e filogenetiche su «*Hippopotamus pentlandi*» von Meyer, 1832 (Mammalia). *Atti della Società italiana di scienze naturali e del museo civico di storia naturale di Milano* 1983; **124**:229–248.
- Chilardi S, De Dominicis A, Zampetti D. La frequentazione preistorica di Grotta Emiliana (Erice, Trapani). *La frequentazione preistorica di Grotta Emiliana (Erice, Trapani)* 2012:275–288.
- Ciofalo S, Battaglia A. Sull'*Hippopotamus pentlandi* delle contrade di Imera. *Termini Imerese: Tipografia Fratelli Amore via Monte* 2:1888.
- Cuvier G. *Sur les ossements fossilés d'Hippopotame. Recherches sur les ossements fossiles de quadrupèdes*. Paris: Deterville, 1812.
- De Gregorio A. Mammiferi quaternari di Sicilia. *Annales de Géologie et de Paléontologie* 1924; **Parte I**:3–10.
- De Gregorio A. Mammiferi quaternari di Sicilia. *Annales de Géologie et de Paléontologie* 1925; **Parte V**:38–43.
- Desnoyers J. *Recherches géologiques et historiques sur les cavernes et particulièrement sur les cavernes a ossements*. Paris: Imprimerie de Bourgogne et Martinet, 1845.
- Di Patti C, Calandra V. Il censimento del patrimonio paleontologico siciliano. *Il Naturalista Siciliano* 2004; **S. IV 28**:895–917.
- Di Patti C, Piccione S. La collezione vertebratologica della Grotta della Cannita (Misilmeri - Pa) conservata presso il Museo Geologico 'G.G. Gemmellaro' di Palermo. *Naturalista Siciliano* 2004; **XXVIII**:947–963.
- Dixon P. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* 2003; **14**:927–930. [https://doi.org/10.1658/1100-9233\(2003\)014\[0927:vaporf\]2.0.co;2](https://doi.org/10.1658/1100-9233(2003)014[0927:vaporf]2.0.co;2)
- Dray S, Siberchicot MA. *Package 'ade4'*. Lyon, France: Université de Lyon, 2017.
- Dryden IL, Mardia KV. *Statistical Shape Analysis: with Applications in R*. Chichester, UK: John Wiley & Sons, 2016.
- Fabiani R. Cenni sulle raccolte di Mammiferi Quaternari del Museo Geologico della R. Università di Palermo e sui risultati di nuovi

- assaggi esplorativi. *Bollettino Associazione Mineralogica Siciliana* 1928;IV:24–34.
- Fabiani R. Risultati di alcuni scavi nella Grotta di Zà Minica presso Capaci (Palermo). *Atti della Reale Accademia delle Scienze Lettere e Belle Arti di Palermo* 1931;17:1–8.
- Fabiani R. *Risultati di alcuni scavi nella Grotta della Za' Minica presso Capaci (Palermo)*. Palermo: Scuola tipografica Boccone del povero, 1932.
- Fabiani R. Notizie preliminari sui risultati di uno scavo paleontologico nella Grotta della Cannita (Palermo). *Bollettino di Scienze Naturali ed Economiche di Palermo* 1934;16:3–7.
- Falconer H. On the ossiferous Grotta di Maccagnone near Palermo. *Paleontological Memoirs and Notes* 1860;16:99–106. <https://doi.org/10.1144/gsl.jgs.1860.016.01-02.10>
- Faure M. *Hippopotamidae (Mammalia, Artiodactyla) d'Europe occidentale*. Lyon: Université Claude Bernard, 1983.
- Faure M. *Hippopotamus incognitus* nov. sp., un hippopotame (Mammalia, Artiodactyla) du Pléistocène d'Europe occidentale. *Geobios* 1984;17:427–437. [https://doi.org/10.1016/s0016-6995\(84\)80017-0](https://doi.org/10.1016/s0016-6995(84)80017-0)
- Faure M. Les hippopotames quaternaires non-insulaires d'Europe occidentale. *Nouvelles archives du Muséum d'histoire naturelle de Lyon* 1985;23:13–79. <https://doi.org/10.3406/mhnl.1985.1058>
- Faure M, Guérin C. Plaidoyer pour l'espèce sicilienne *Hippopotamus pentlandi*. *Atti Accademia Peloritana dei Pericolanti, classe I di Scienze Fisiche Matematiche e Naturali* 1989;67:297–317.
- Fazello T. *De rebus Siculis decades duae, nunc primum in lucem editae. His accessit totius operis index locupletissimus*, Palermo, apud Ioannem Matthaeum Maidam et Franciscum Carraram, 1558, 1–616.
- Fidalgo D, Madurell-Malapeira J, Martino R *et al.* An updated review of the Quaternary *Hippopotamus* fossil records from the Iberian Peninsula. *Quaternary* 2024;7:4. <https://doi.org/10.3390/quat7010004>
- Galobart A, Blaya E, Madurell J *et al.* Resultats de la segona fase d'actuacions (1999–2005) als jaciments paleontològics del Plistocèn inferior d'Incaral. *Paleontologia i Evolució* 2003;34:153–173.
- Gemmellaro GG. Sulla grotta di Carburanceli. Nuova grotta ad ossame ed armi in pietra dei dintorni della Grazia di Carini. *Giornale di Scienze Naturali ed Economiche* 1866;1:255–264.
- Georgitsis MK, Liakopoulou DE, Theodorou GE. Morphofunctional examination of the carpal bones of pygmy hippopotamus from Ayia Napa, Cyprus. *Anatomical Record* 2022a;305:297–320. <https://doi.org/10.1002/ar.24738>
- Georgitsis MK, Liakopoulou DE, Theodorou GE *et al.* Functional morphology of the hindlimb of fossilized pygmy hippopotamus from Ayia Napa (Cyprus). *Journal of Morphology* 2022b;283:1048–1079. <https://doi.org/10.1002/jmor.21488>
- Gray JE. On the natural arrangement of vertebrate animals. *London Medical Repository* 1821;15:296–310.
- Guérin C. *Ordre des Artiodactyles. Famille des Hippopotamidae*. Paris: Les Grands Mammifères Plio-Pléistocènes d'Europe. Masson Ed., 1996.
- Hooijer DA. On the supposed hexaprotodont milk dentition in *Hippopotamus amphibius* L. *Zoologische Mededelingen* 1942;24:187–196.
- Hooijer DA. The fossil Hippopotamidae of Asia, with notes on the recent species. *Zoologische Verhandlungen* 1950;8:1–124.
- Husson F, Josse J, Le S *et al.* Package 'factominer'. *An R package* 2016;96:698.
- Kahlke RD. Die unterpleistozänen *Hippopotamus*-Reste von Würzburg-Schalksberg. *Quartär-Internationales Jahrbuch zur Erforschung des Eiszeitalters und der Steinzeit* 1989;39/40:67–94.
- Kahlke RD. Die *Hippopotamus*-Reste aus dem Unterpleistozän von Untermaßfeld. *Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen)*, Teil 1997;1:277–374.
- Kassambara A, Mundt F. Package 'factoextra'. *Extract and visualize the results of multivariate data analyses* 2017;76:10–18637.
- Larramendi A, Zhang H, Palombo MR *et al.* The evolution of *Palaeoloxodon* skull structure: disentangling phylogenetic, sexually dimorphic, ontogenetic, and allometric morphological signals. *Quaternary Science Reviews* 2020;229:106090. <https://doi.org/10.1016/j.quascirev.2019.106090>
- Laws RM. Dentition and ageing of the *Hippopotamus*. *African Journal of Ecology* 1968;6:19–52. <https://doi.org/10.1111/j.1365-2028.1968.tb00899.x>
- Lê S, Josse J, Husson F. FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software* 2008;25:1–18.
- Ligges U, Mächler M. Scatterplot3d - an R package for visualizing multivariate data. *Journal of Statistical Software* 2002;8:1–20.
- Linnaeus C. *Systema Naturae*. Stockholm: Laurentii Salvii, 1758.
- Lyras GA, van der Geer BGM, Kafousias MS *et al.* On the cranial anatomy of the smallest insular hippopotamus (Cyprus, Pleistocene). *Bollettino della Società Paleontologica Italiana* 2025;64:337–348. <https://doi.org/10.4435/BSPI.2025.17>
- Mangano G, Insacco G, Bonfiglio L *et al.* New finds from San Teodoro Cave: an updating of the Middle Pleistocene fossil record from Acquedolci (north-eastern Sicily). *Palaeobiodiversity and Palaeoenvironments* 2020;100:1065–1076. <https://doi.org/10.1007/s12549-020-00430-7>
- Mannino G. *Guida alla preistoria del Palermitano: elenco dei siti preistorici della provincia di Palermo*. Palermo: Istituto siciliano studi politici ed economici, 2008.
- Mannino G, Zava B. Le Grotte della Falesia di Malatacca-Benfratelli (Palermo). *Bollettino Accademia Gioenia Scienze Naturali* 1994;27:5–15.
- Marra AC. Ippopotami insulari del Pleistocene del Mediterraneo. PhD dissertation, University of Modena, 1998.
- Marra AC. Pleistocene hippopotamuses of Mediterranean islands: looking for ancestors. In: *Proceedings of the International Symposium 'Insular Vertebrate Evolution: the Paleontological Approach'*, Mallorca, SP, 2005. Balearic Islands, SP: Societat d'Història Natural de Balears 2005;12:193–204.
- Martinez Arbizu P. 2020. *pairwiseAdonis: Pairwise multilevel comparison using adonis*. R package version 0.4.1.
- Martinez-Navarro B, Rook L, Papini M *et al.* A new species of bull from the Early Pleistocene paleoanthropological site of Buia (Eritrea): parallelism on the dispersal of the genus *Bos* and the Acheulian culture. *Quaternary International* 2010;212:169–175. <https://doi.org/10.1016/j.quaint.2009.09.003>
- Martino R, Pandolfi L. The Quaternary *Hippopotamus* records from Italy. *Historical Biology* 2022;34:1146–1156.
- Martino R, Ríos M, Mateus O *et al.* Taxonomy, chronology, and dispersal patterns of western European Quaternary hippopotamuses: new insight from Portuguese fossil material. *Quaternary International* 2023;674:121–137.
- Martino R, Marra F, Beccari V *et al.* Middle Pleistocene *Hippopotamus amphibius* (Mammalia, Hippopotamidae) from southern Europe: implications for morphology, morphometry and biogeography. *Quaternary Science Reviews* 2024a;331:108613. <https://doi.org/10.1016/j.quascirev.2024.108613>
- Martino R, Zanolli C, Fidalgo D *et al.* Talking heads: disentangling the shape changes of the large extant hippopotamus during its ontogenetic development. *Integrative Zoology* 2024b;20:665–669. <https://doi.org/10.1111/1749-4877.12850>
- Marziano C, Chilardi S. Contribution to knowledge of the Pleistocene mammal-bearing deposits of the territory of Siracusa (southeastern Sicily). In: *Biosphere to Lithosphere, Proceedings of the 9th ICAZ Conference, Durham, UK, August 2002. Abstract p. 94–109*. Oxford, UK: Oxbow Books; 2002;1:94–109.
- Mazza P. Interrelations between Pleistocene hippopotami of Europe and Africa. *Bollettino della Società Paleontologica Italiana* 1991;30:153–186.
- Mazza P. New evidence on the Pleistocene hippopotami of western Europe. *Geologica Romana* 1995;31:61–241.
- Mazza PPA, Bertini A. Were Pleistocene hippopotamuses exposed to climate-driven body size changes? *Boreas* 2013;42:194–209.
- Mazza PPA, Ventura D. Pleistocene debris-flow deposition of the hippopotamus-bearing Collecureti bonebed (Macerata, Central Italy): taphonomic and paleoenvironmental analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 2011;310:296–314. <https://doi.org/10.1016/j.palaeo.2011.07.022>

- Mecozzi B, Iannucci A, Mancini M *et al.* Reinforcing the idea of an early dispersal of *Hippopotamus amphibius* in Europe: restoration and multidisciplinary study of the skull from the Middle Pleistocene of Cava Montanari (Rome, central Italy). *PLoS One* 2023;**18**:e0293405. <https://doi.org/10.1371/journal.pone.0293405>
- Melentis JK. Über *Hippopotamus antiquus* Desmarest aus dem Mittelpleistozän des Beckens von Megalopolis in Peloponnes (Griechenland). *Ann. Geol. Pays Helléniques* 1965;**16**:403–435.
- Owen R. Description of teeth and portions of jaws of two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *Hyopbovinus*) discovered by the Marchioness of Hastings in the Eocene Deposits on the N. W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London* 1848;**4**:103–141.
- Pentland W. Note contenant la détermination des ossements fossiles des cavernes voisines de Palerme. *Annales des Sciences Naturelles* 1832;**1** Série:208–211.
- Petronio C. Nuovi resti di ippopotamo del Pleistocene medio-inferiore dei dintorni di Roma e problemi di tassonomia e filogenesi del gruppo. *Geologica Romana* 1986;**25**:63–73.
- Petronio C. Resti inediti di ippopotamo della Grotta dei Puntali (Carini, Palermo). *Geologica Romana* 1995;**31**:265–272.
- Petruso D, Taschetta F. New data on the Middle Pleistocene endemic Sicilian hippo. *Natura Rerum* 2011;**1**:5–20.
- R Core Team. R: a Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing, 2019.
- Reynolds SH. A Monograph on the British Pleistocene Mammalia VOL. III, Part I. *Hippopotamus*. *Monographs of the Palaeontographical Society* 1922;**74**:1–38. <https://doi.org/10.1080/02693445.1922.12035586>
- Rhodes EJ. ESR dating of tooth enamel. In: Basile B, Chilardi S, (eds), *Siracusa, le Ossa dei Giganti. Lo Scavo Paleontologico di Contrada Fusco*. Palermo: Lombardi, 1996, 39–44.
- Rohlf FJ, Slice D. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 1990;**39**:40–59. <https://doi.org/10.2307/2992207>
- Scinà D. *Rapporto sulle ossa fossili di Mardolce e degli altri contorni di Palermo*. Palermo: Reale Tipografia di Guerra, 1831.
- Seguenza L. *L'Hippopotamus pentlandi Falconer di Taormina*. Taormina: Tipografia dell'Etna, 1900.
- Shannon G, Sadler P, Smith J *et al.* Contrasting selection pressure on body and weapon size in a polygynous megaherbivore. *Biology Letters* 2021;**17**:20210368. <https://doi.org/10.1098/rsbl.2021.0368>
- Tang Y, Horikoshi M, Li W. ggfortify: unified interface to visualize statistical results of popular R packages. *The R Journal* 20162016;**8**:474–485. <https://doi.org/10.32614/rj-2016-060>
- Thenius E. Ueber die Alterseinstufung der Arsenalterrasse von Wien; *H. pentlandi* and seine Vertbarkeit für die Stratifizierung der Arsenalschotter. *Mitt. Geol. Gesell.* 1954;**45**:135–146.
- Valguarnera M. *Discorso dell'origine ed antichità di Palermo e dei primi abitatori della Sicilia e dell'Italia*. Palermo: Gio. Battista Maringo, Stampator Camerale, 1614.
- Venables WN, Ripley BD. *Modern Applied Statistics with S*. New York, NY: Springer, 2003.
- von Meyer H. *Palaeologica zur Geschichte der Erde und ihrer Geschöpfe*. Frankfurt-An-Mein: S. Schmerber, 1832.
- Vu VQ. ggbiplot: a ggplot2 based biplot. R package version 0.55 755, 2011. <http://github.com/vqv/ggbiplot>
- Wickham H, Chang W, Wickham MH. 2016a. 'ggplot2', *Elegant Graphics for Data Analysis*. Springer-Cham, 2016a. <https://doi.org/10.1007/978-3-319-24277-4>
- Wickham H, Hester J, Chang W, Bryan J. Devtools: tools to make developing R packages easier. R package version, 2016b. <https://github.com/r-lib/devtools>
- Wickham H, Averick M, Bryan J *et al.* Welcome to the Tidyverse. *Journal of Open Source Software* 2019;**4**:1686. <https://doi.org/10.21105/joss.01686>