

The *Hippopotamus* remains from the latest Early Pleistocene site of Cava Redicicoli (Rome, central Italy)

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ABSTRACT - *The Quaternary record of hippopotamuses is extremely abundant, yet there are still conflicting opinions about their systematics and evolution. The main diagnostic characters of fossils and extant hippopotamuses are recorded in the skulls, while the distinct morphological features between species are less evident in dental and postcranial remains. When hippopotamus skulls are not available, taxonomic identification is often chronologically-based. Herein are described for the first time the hippopotamus remains of the historical museum collections from the latest Early Pleistocene site of Cava Redicicoli, housed in the Museo Universitario di Scienze della Terra, Dipartimento di Scienze della Terra, Sapienza Università di Roma and Istituto Italiano di Paleontologia Umana, Anagni. This material, although formally never morphologically studied, has been referred in the literature either to *Hippopotamus antiquus* (considering *Hippopotamus major* as a synonym of *H. antiquus*) or to *Hippopotamus ex gr. antiquus*.*

*Morphological and biometric comparisons with other Pleistocene hippopotamuses permit to attribute the studied material to *Hippopotamus cf. antiquus*. Biometric analysis of teeth and complete postcranial bones shows that the size of fossil hippopotamuses is quite variable, with the largest dimension for the European fossils recorded from the Villafranchian and the Epivillafranchian. The rich sample from the Cava Redicicoli provides new data regarding the morphological and biometric variability of this group during the large faunal renewal that occurred during the Early-Middle Pleistocene transition.*

INTRODUCTION

Throughout the Quaternary, hippopotamuses, together with proboscideans and rhinoceroses, were among the largest terrestrial mammals in European ecosystems. The fossil record of *Hippopotamus* in Europe is extremely rich, with a few nearly complete skeletons found in anatomical connection (Faure, 1985; Caloi et al., 1980; Mazza, 1991, 1995). Despite their abundance, the systematics and the evolution of Quaternary European hippopotamuses are still debated (Caloi et al., 1980; Faure, 1984, 1985; Mazza, 1991, 1995; Galobart et al., 2003; Mazza & Bertini, 2013; van der Made et al., 2017a, b). Apart from the Mediterranean islands, three forms have been recognised: *Hippopotamus antiquus* Desmarest, 1822; *Hippopotamus tiberinus* Mazza, 1991; and *Hippopotamus amphibius* Linnaeus, 1758. *Hippopotamus antiquus* and *H. tiberinus*, although different in body size, show a similar skeletal morphology so much that Petronio (1995) considered them synonyms. Moreover, many fossils from the early Middle Pleistocene sites of Europe have been attributed to *H. ex gr. antiquus* (Mazza & Bertini, 2013; Pandolfi & Petronio, 2015). On the other hand, *H. antiquus* and *H. amphibius* differ morphologically in the cranium (e.g., relative size and proportions, length of sagittal crest) and in the mandible (length of the horizontal ramus, profile of the ventral margin in lingual view; Caloi et al., 1980; Mazza, 1995; Pandolfi & Petronio, 2015), although diagnostic characters for postcranial elements are rather unappreciated (Mazza, 1995).

The earliest appearance of *Hippopotamus* in Europe is recorded from the Early Pleistocene site of Coste San Giacomo (Anagni basin, central Italy; Bellucci et al., 2012; Sardella et al., 2018), dated at 2.233 ± 0.032 Ma (Florindo et al., 2021). However, several authors (Marra et al., 2018; Martino & Pandolfi, 2022) argued that the fossil, since it was found *ex situ* in the field, could come from a younger deposit overlying the main fossiliferous level. Other remains referred chronologically to the earliest Pleistocene were found in the Elis area (Greece; Athanassiou, 2022 and references therein), Fontana Acetosa (Italy; Cassoli & Segre Naldini, 1984), Chiusi Basin (Italy; Cusani Politi, 1966, 1971; Mazza, 1995; Pandolfi & Petronio, 2015) and Senèze (France; Mazza & Rustioni, 1994). These records attested the first dispersal of *Hippopotamus* on the European continent during the Early Pleistocene (“Hippo Event” *sensu* Iannucci et al., 2023a). Over the late Villafranchian, *H. antiquus* became a common species of mammalian palaeocommunities in Europe (Caloi et al., 1980; Mazza, 1991, 1995; Galobart et al., 2003; Fidalgo et al., 2021; Adams et al., 2022). Epivillafranchian records (late Early Pleistocene) of hippopotamuses were found in Britain: Westbury Cave (Adams et al., 2022); France: Durfort (Bourdier, 1961), Le Vallonet (Moullé et al., 2005), Saint-Prest (Guérin et al., 2003); Germany: Untermassfeld (Kahlke, 2001; Kierdorf & Kahlke, 2020), Würzburg-Schalksburg (Kahlke, 1989); Georgia: Akhalkalaki (Kahlke, 1987); Italy: Cese di Preturo (Mazza, 1995), Colle Curti (or Collocurti; Mazza & Ventura, 1995), Madonna della Strada (Cava

Santarelli toponym; Mancini et al., 2012), Slivia (Benussi & Melato, 1970); Spain: Barranco León-5 and Fuente Nueva-3 (Martínez-Navarro et al., 2010), Cal Guardiola and Vallparadís Estació (Madurell-Malapeira et al., 2010 and references therein).

Hippopotamuses survived in this territory until the Last Glacial, when the extinction of the late Quaternary megafauna took place (Mazza, 1995; Petronio, 1995; Gliozzi et al., 1997; Mazza & Bertini, 2013). However, the disappearance of the hippopotamus (*H. amphibius*) and the straight-tusked elephant (*Palaeoloxodon antiquus*) in the palaeontological record is still uncertain, as their last occurrences are strongly linked to climatic changes in the Late Pleistocene. In the Italian Peninsula, the presence of these taxa after the Marine Isotopic Stage 5 (MIS) is questionable, since most of these fossils are of uncertain age due to doubtful stratigraphical contexts (Mecozzi et al., 2021a; Pieruccini et al., 2022).

One of the striking features of mammals is their response to glacial/interglacial fluctuations by modifying their body size. This is an important palaeobiological indicator, which may provide information about terrestrial ecosystems and environmental conditions (Mazza & Bertini, 2013; Adams et al., 2022). Notwithstanding this, the possible size variation between the species of *H. antiquus* and *H. amphibius* (the former larger than the latter; Caloi et al., 1980; Mazza, 1995; Palmqvist et al., 2008, 2022) is poorly investigated. Mazza & Bertini (2013) identified three different size patterns for Quaternary hippopotamuses: large-sized specimens during the Early Pleistocene; small-sized specimens during the Middle Pleistocene; large-sized specimens during the early Late Pleistocene.

This paper describes for the first time the large sample of hippopotamus from the latest Early Pleistocene site of Cava Redicicoli (Rome, central Italy), nowadays destroyed by urbanization, and preserved today at the Museo Universitario di Scienze della Terra, Dipartimento di Scienze della Terra, Sapienza Università di Roma (MUST, including the former Museo di Paleontologia di Roma, MPUR) and the Istituto Italiano di Paleontologia Umana, Anagni (IsIPU). Morphological comparison of the sample from Cava Redicicoli with other hippopotamus fossils from the Early to Late Pleistocene of Europe and extant specimens of *Hippopotamus amphibius* is carried out. Biometric analyses are performed in order to test differences in size between fossil and extant taxa, and to investigate the dimensional trend through time. The revision of historical collections has always been considered important in palaeontological research because it offers the possibility to describe unpublished material or to revise previously studied fossils. Considering the museum collections recovered from the so-called Campagna Romana (the urban area and outskirts of Rome), this approach is crucial because most of the fossiliferous deposits were destroyed or buried below anthropogenic deposits (Mecozzi et al., 2021b; Romano et al., 2021; Iurino et al., 2022; Iannucci et al., 2023b). Due to its rich fossil record, the Campagna Romana, which includes also Cava Redicicoli, represents a key area for the study of vertebrate assemblage evolutionary trends and palaeoenvironmental reconstructions during the Early-Middle Pleistocene Transition (EMPT; e.g.,

Iannucci et al., 2021a; Mecozzi et al., 2020, 2021b; Strani et al., 2021).

TAXONOMIC QUESTIONS AND BIOCHRONOLOGY OF FOSSIL HIPPOPOTAMUSES

The taxonomic identification of hippopotamuses is challenging due to the lack of complete crania between 0.5 and 0.1 Ma and the uncertain age of several samples, as well as the poorly mapped features in dental and postcranial bones.

Considering the fossil record of Italy, two skulls were assigned to a new species, *Hippopotamus tiberinus* Mazza, 1991. The first, a partial skull from Maglianella (C. 601) lacking the muzzle, is the holotype of this species (Mazza, 1991); the second, an almost complete skeleton from Sant'Oreste (MPUR/V 1950), is the paratype (Mazza, 1991). The latter specimen, however, had been previously referred to *H. antiquus* by Caloi et al. (1980).

Other remains from Middle Pleistocene localities of Germany (e.g., Mosbach and Jockgrim) were also attributed to this taxon (Mazza, 1991). Subsequently, Mazza (1995) assigned two other crania from Maglianella (specimens n. 321 and n. 322) to *H. tiberinus*. Petronio (1995) challenged these attributions, stating that the morphology of the skull C. 601 from Maglianella falls within the range of variability of *H. antiquus*. He also stated that the skull from Sant'Oreste is slightly crushed due to taphonomic processes, and several parts were reconstructed during restoration work. Thus, he attributed this specimen to *H. antiquus*, confirming the assignation previously reported by Caloi et al. (1980). Therefore, according to the hypothesis of Petronio (1995), *H. tiberinus* should be considered a synonym of *H. antiquus*.

After that, European hippopotamuses from the Middle Pleistocene have been generally referred to *Hippopotamus* ex gr. *antiquus*, an attribution that reflects the problematic taxonomic issue. However, it is worth noting that no morphological differences between *H. ex gr. antiquus* and *H. antiquus* have been identified (Caloi et al., 1980; Mazza & Bertini, 2013; Pandolfi & Petronio, 2015; van der Made et al., 2017b). Thus, pending further systematic and phylogenetic studies, the use of *H. ex gr. antiquus* (or *H. tiberinus*) should be discouraged. Recently, a model seems to have prevailed in the literature (Petronio, 1995; Kahlke et al., 2011; Martínez-Navarro et al., 2015; Pandolfi & Petronio, 2015; Konidaris et al., 2018; Kierdorf & Kahlke, 2020; Adams et al., 2022; Martino & Pandolfi, 2022), involving two species of *Hippopotamus* for the Pleistocene record of Europe: *H. antiquus* (= *H. major* = *H. amphibius antiquus* = *H. tiberinus* = *H. ex gr. antiquus*); and *H. amphibius* (= *H. incognitus* = *H. amphibius incognitus*). Considering that these two species are morphologically well distinguishable, the same scheme has been also adopted in this work.

A different phylogenetic framework for the European hippopotamuses was proposed by van der Made et al. (2017b) which includes three species: *H. antiquus* (shortly before 2.0-1.8 Ma), *H. tiberinus* (1.2-0.5 Ma), *H. amphibius* (from 0.5 to Late Pleistocene). This hypothesis, however, has not encountered consensus among the scientific community.

The extinction of *H. antiquus* is also an open issue regarding hippopotamuses, reflecting uncertainty about the taxonomic identification of isolated remains (often chronologically based) and the unconfirmed earliest dispersal of *H. amphibius* in Europe. While this issue was already raised by Cusani Politi (1980) and Faure (1985), and by various authors over the last forty years, a consensus has not been reached yet. So far, the sample from Maglianella, chronologically referred to the Middle Pleistocene (MIS 15) by Marra et al. (2014), represents the latest attested occurrence of *H. antiquus* in the European record.

Following the hypothesis of Mazza (1995), the first appearance of *H. amphibius* in Europe is from the early Late Pleistocene site of Barrington (MIS 5; United Kingdom). Another skull attributed to *H. amphibius* was found in the area of Tor di Quinto (Rome) (Caloi et al., 1980; Mazza, 1995; Petronio, 1995; Martino & Pandolfi, 2022) and is part nowadays of the historical collection of the MUST. However, its uncertain geographical provenance and stratigraphical context is still highly debated. In fact, Petronio & Pandolfi (2015) proposed that the skull was recovered from the Middle Pleistocene site of Cava Nera Molinaro (MIS 13), a hypothesis shared by Martino & Pandolfi (2022). If the age of the skull from the area of Tor di Quinto is indeed MIS 13, this would represent the earliest record of *H. amphibius* in Europe. On the other hand, Fabiani & Maxia (1953) proposed a different hypothesis, suggesting a different toponym, Cava Montanari, another quarry in the area of Tor di Quinto, whose chronostratigraphical setting has never been described. The revision of the geographical provenance, as well as the stratigraphical and geological data of this locality, is needed to clarify the earliest dispersal of *H. amphibius* in Europe. The revision of this skull and its geographical provenance and stratigraphical context were undertaken in the frame of a restoration work of the fossil vertebrates stored at MUST, including the specimen from the area of Tor di Quinto.

CAVA REDICICOLI AND THE HISTORY OF RESEARCH

The deposit of Cava Redicicoli (CR henceforth) was located in a quarry of the district of Bufalotta, in the urban area of Rome (Latium, central Italy, Fig. 1a-b). During the second half of the 1900's and in the early 2000's, this area has been heavily urbanised due the construction of Rome's beltway ("Grande Raccordo Anulare", Fig. 1b) and a large shopping centre ("Porte di Roma"). As a result, the deposit was destroyed or buried under anthropogenic deposits. Although the exact geographical position of the quarry is unknown, the toponym "Redicicoli" indicates a portion of territory northeast of Rome (Fig. 1c), called Tenuta di Redicicoli. The analysis of the historical topographic map of Rome (IGM 1936) recorded only one quarry ("Cava", black circled in Fig. 1c) in this area, located along the Settebagni road. Thus, it can be assumed that the position of CR probably coincided with that of the "Cava" circled in Fig. 1c.

The long stratigraphical sequence (Fig. 1d) exposed by intensive quarrying activities was firstly described

by Blanc et al. (1955). The succession comprised, from bottom to top: basal blue clay; fluvial gravels with clay; silty-clay levels interbedded by a layer of small pebbles; tuffaceous deposit with intercalations of diatomite levels. The mammal fossils were recovered from the fluvial gravels with clay between 1950 and 1956 (the year of excavation is generally written directly on each fossil).

The mammal list (Tab. 1) was first reported by Blanc et al. (1955). Caloi et al. (1979) carried out the first palaeontological study, and they proposed the distinction of two levels to explain the presence of typical taxa from both the Villafranchian and the Galerian. Subsequently, Di Stefano et al. (1998) formalised the chronological subdivision of the mammal fauna, and distinguished between Redicicoli 1, referred to the Pirro Nord Faunal Unit (late Villafranchian, late Early Pleistocene), and Redicicoli 2, referred to the Isernia Faunal Unit (early Galerian, early Middle Pleistocene). The hypothesis of Di Stefano et al. (1998) was also followed by Petronio et al. (2011). A different opinion was suggested by Palombo et al. (2003) who considered the fossils from CR as collected from a single level. This interpretation was later confirmed by Milli & Palombo (2005) who, citing an unpublished manuscript of Blanc, proposed that the mammal assemblage of CR came from a single fossiliferous level. A new chronostratigraphical assessment of CR described by Marra et al. (2014) supports the hypothesis of Palombo et al. (2003), identifying a single bearing-fossil fluvial gravel with clay levels, referred to the latest Early Pleistocene. According to Marra & Florindo (2014), the fluvial gravel with clay layers of CR is correlated with the Ponte Galeria 1 Formation (MIS 20-19). Florindo et al. (2007) dated two tephra layers (in other deposits of Campagna Romana) intercalated at the gravel-clay transition to the aggradation phase of the Paleo-Tiber in Rome (803 ± 8 ka and 783 ± 10 ka), whereas Marra et al. (2014) indicated an age between 808 ± 6 ka and 788 ± 9 ka. Finally, further radiometric dates were reported in Pandolfi & Marra (2015), constraining CR mammal fossils between 806 ± 6 ka and 788 ± 9 ka. Although the ages slightly differ, all three papers constrain the CR fossil-bearing level to the latest Early Pleistocene.

However, it must be stressed out that Marra et al. (2014) did not completely exclude the presence of at least two distinct faunal assemblages, since other authors reported the presence of sedimentary sequences in the proximity of CR referred to MIS 17 (calcareous mud deposits) or MIS 15 (brown sandy silt deposits) between fluvial gravels with clay layers and the overlying volcanic deposits. In these younger deposits, however, the presence of fossils has never been documented.

The long-standing debate created different opinions, but being the mammal remains found and excavated by Blanc, the fossils will be here considered as collected from a single level, and the chronostratigraphical assessment proposed by Pandolfi & Marra (2015) will be followed (Fig. 1e). Although the fossils from CR have been attributed to different taxa during the last decades, the remains have been never formally studied and described. An exception is the revision of the rhino sample carried out to Pandolfi & Marra (2015), which confirmed the presence of *Stephanorhinus* sp., and

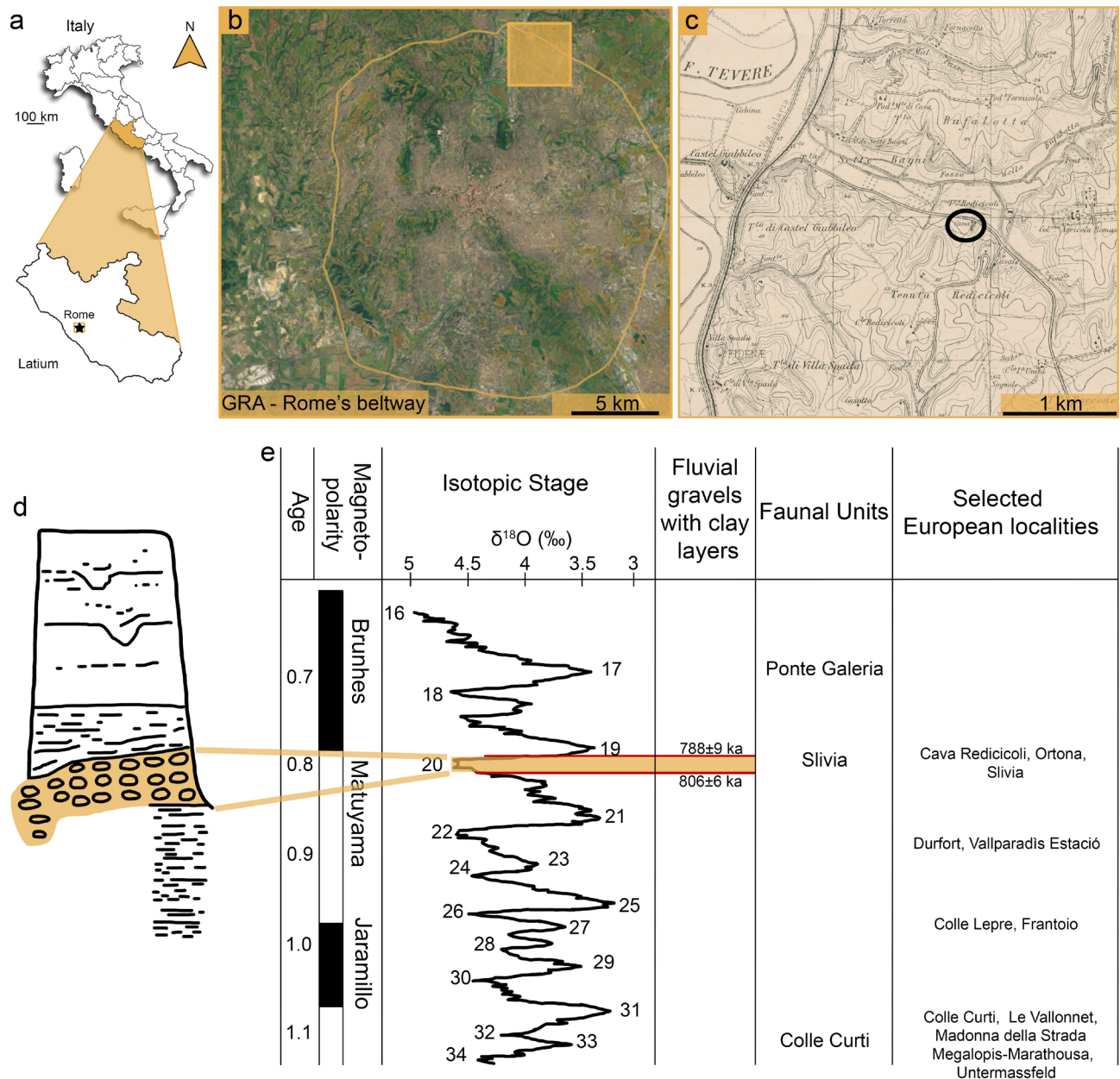


Fig. 1 - a) Geographical position of Cava Redicicoli (black star). b) Urban area of Rome with the position of Redicicoli district (orange circle). c) Historical map with the probable position of the Cava Redicicoli (black circle; modified from IGM, 1936). d) Stratigraphical log of Cava Redicicoli (modified from Blanc et al., 1955). e) Geochronological setting of fossil-bearing fluvial gravels with clay layers of Cava Redicicoli.

Stephanorhinus hundsheimensis. An extensive revision of the CR fossil sample is still underway, with the aim of updating the taxonomical attribution and adding important information on terrestrial ecosystems during the latest Early Pleistocene.

MATERIAL AND METHODS

The fossil remains described in this work were recovered between 1950 and 1956 by Alberto Carlo Blanc, during geopalaeontological surveys carried out in the urban area of Rome (Blanc et al., 1955). The studied material is housed in the Museo Universitario di Scienze

della Terra, Dipartimento di Scienze della Terra, Sapienza Università di Roma (MUST, including the former Museo di Paleontologia di Roma, MPUR), with a provisional progressive catalogue number (SN-/FS or SN-/LJ). Some of these fossils bear a number written on the bones indicated as “(ex. -)” when present. Only an isolated lower third molar is stored at the Istituto Italiano di Paleontologia Umana (IsIPU-CR1).

The taxonomic attribution of the CR hippo specimens was carried out by morphological and biometric comparison of the studied material with corresponding specimens of other fossils and extant *Hippopotamus* (Caloi et al., 1980, Faure, 1985; Mazza, 1995; Georgitsis et al., 2022).

Reference	Name	Biochron	Age	Mammal faunal list
Blanc et al. (1955)	Cava Redicicoli			<i>Canis etruscus</i> , <i>Dama nestii</i> , <i>Leptobos etruscus</i> , <i>Equus</i> cf. <i>stenonis</i> , <i>Hippopotamus amphibius</i> , <i>Rhinoceros</i> sp., <i>Elephas</i> sp.
Caloi et al. (1979)	Cava Redicicoli	late Villafranchian-Galerian	late Early - early Middle Pleistocene	<i>Archidiskodon meridionalis</i> , <i>Equus</i> cf. <i>stenonis</i> , <i>Equus stehlini</i> , <i>Dicerorhinus</i> cf. <i>etruscus</i> , <i>Dicerorhinus</i> sp., <i>Hippopotamus major</i> , <i>Dama nestii eurygonos</i> , <i>Dama</i> sp., <i>Cervus</i> sp., <i>Megaceros</i> sp., Bovidae
Di Stefano et al. (1998)	Redicicoli 1	late Villafranchian	late Early Pleistocene	<i>Bison (Eobison) degiulii</i> , <i>Equus</i> aff. <i>altidens</i> , <i>Mammuthus meridionalis</i>
	Redicicoli 2	early Galerian	early Middle Pleistocene	<i>Megaceroides</i> cf. <i>solihacus</i> , <i>Stephanorhinus hundsheimensis</i> , <i>Bison schoetensacki</i>
Palombo et al. (2001)	Redicicoli	Epivillafranchian	late Early Pleistocene	Hyaenidae indet., <i>Mammuthus (Archidiskodon) meridionalis</i> , <i>Equus altidens</i> , <i>Stephanorhinus hundsheimensis</i> , <i>Hippopotamus</i> ex gr. <i>H. antiquus</i> , <i>Pseudodama</i> sp., <i>Megacerini</i> indet., ? <i>Bison</i> cf. <i>B. (Eobison) degiulii</i> , <i>Bison</i> sp. aff. <i>B. schoetensacki</i>
Petronio et al. (2011)	Rome-Redicicoli 1	late Villafranchian	late Early Pleistocene	<i>Mammuthus meridionalis vestinus</i> , <i>Axis eurygonos</i> , <i>Bison degiulii</i>
	Rome-Redicicoli 2	early Galerian	early Middle Pleistocene	<i>Axis eurygonos</i> , <i>Stephanorhinus hundsheimensis</i> , <i>Hippopotamus antiquus</i> , <i>Equus altidens</i> , <i>Praemegaceros solihacus</i> , <i>Bison schoetensacki</i>

Tab. 1 - Mammal taxa from Cava Redicicoli reported in previous works.

The dental terminology adopted in this work follows Mazza (1995) and Boissierie et al. (2010), while the postcranial terminology follows Mazza (1995).

Due to the fragmentary state of preservation, four lower molars cannot be precisely identified (M_1/M_2 ; SN11/FSa, SN11/FSb, SN41/FSd, SN41/FSe).

In accordance with Mazza (1995), six dental variables have been considered: length (L) and breadth (B) for upper and lower incisors and canines, and outer length (OL), inner length (IL), anterior breadth (AB) and posterior breadth (PB) for the upper and lower premolars and molars.

Moreover, 28 variables have been measured on the postcranial elements have been measured: Humerus: physiologic length (PL), smallest breadth of the diaphysis (BS), breadth of the trochlea (BT), breadth of the distal epiphysis (BD), depth of the lateral portion of the distal epiphysis (DDI), depth of the medial portion of the distal epiphysis (DDm); Radius/ulna: length of the radius + ulna (Lru), greatest length of the radius (Lr), physiologic length (PL), depth of the anconeal process (DPa), depth of the olecranon (Do), breadth of the proximal articular surface of the ulna (BPau), breadth of the proximal

epiphysis of the radius (BPr), smallest breadth of the shaft of the radius (BSr), depth of the shaft of the ulna (DSu), breadth of the distal epiphysis of the radius (BDr), distal breadth of the radius + ulna (BDru); Femur: smallest breadth of the diaphysis (BS); Tibia: greatest length (TL), smallest breadth of the diaphysis (BS), breadth of the distal epiphysis (BD), depth of the distal epiphysis (DD); Astragalus: lateral length (LL), medial length (ML), greatest length (L), proximal breadth (BP), greatest breadth (B), distal breadth (BD).

Literature data on fossil hippopotamuses from European Pleistocene sites and extant *H. amphibius* were considered (Mazza, 1995; Kahlke, 2001; Galobart et al., 2003; Mazza & Bertini, 2013). Extant material of *H. amphibius* stored in the Museo di Anatomia comparata "Battista Grassi", Sapienza Università di Roma (one complete mounted skeleton and one complete skull, both exposed in the Museum) and the Laboratorio PaleoFactory, Sapienza Università di Roma (one complete skull) was also included. The biometric data published by Faure (1985) were not considered in this work because the measurements were taken differently from Mazza (1995) and later studies.

GENERAL REMARKS

The analyzed material consists of 89 remains, including isolated upper and lower teeth and postcranial remains, some of these are complete (Tab. 2).

Given the total lack of archives and historical documents, there are no provenance data about the CR fossils. As reported by Milli & Palombo (2004), the mammal assemblage of CR (not only the hippopotamus remains) shows uniform state of preservation and fossilization features. This could further support the hypothesis that the fossils were collected from a single level.

The hippopotamus remains considered in this study are generally well preserved, although some elements are partially encrusted by a yellow-greyish sediment with small pebbles. Some postcranial remains show evidence of surface abrasion or flutiation, which suggests some transport before the final burial. Another taphonomic element of the water transport effect on CR bones, that can be inferred based on observations from laboratory, is the absence of articulated postcranial bones. The lack of weathering would exclude a prolonged exposure of the bones prior to burial. No evidence of bite marks or human butchering and exploitation was detected.

Only one juvenile specimen was identified, a fragment of femur (SN37/FS), representing 1% of the sample.

SYSTEMATIC PALAEOLOGY

Order ARTIODACTYLA Owen, 1848
Family HIPPOPOTAMIDAE Gray, 1821
Genus *Hippopotamus* Linnaeus, 1758

Hippopotamus cf. *H. antiquus* Desmarest, 1822

MORPHOLOGICAL DESCRIPTION

Upper teeth (Fig. 2 and Fig. S1 of the Supplementary Online Material; see measurements in Tab. 3)

CANINE: SN29/FS (EX. 7), SN40/FSA (EX. 4), SN40/FSB (EX. 5), SN47/FSA (EX. 6), SN56/FSD (EX. 3) - The upper canine is fairly labiolingually elongated, and it shows a deep sulcus in the central portion of the teeth on the lingual side. The enamel ridges and grooves on the tooth surface are slightly marked and fairly parallel along the lateral faces.

THIRD PREMOLAR: SN42/FSG (EX. 30) - The P³ shows a robust main cusp, with a slightly worn crown. The mesial and distal cingula are quite marked, whereas the labial and lingual ones are absent. A robust pillar is present in the central portion of the lingual side of the tooth and a second, less prominent, can be observed on the disto-lingual margin of the tooth.

FOURTH PREMOLAR: SN42/FS E (EX. 31), SN42/FS F (EX. 35) - In occlusal view, the P⁴ shows a triangular shape and a prominent main cruciform cusp. The lingual, mesial and labial cingula are quite marked, whereas the distal ones are absent.

FIRST MOLAR: SN42/FS H (EX. 32) - The only preserved M¹ from CR shows an advanced worn crown, which

Anatomical portion	Number of specimens	
	MUST	IsIPU
Upper canine	5	
Upper premolar	3	
Upper molar	4	
Lower incisor	9	
Lower canine	31	
Lower molar	10	1
Scapula	1	
Humerus	9	
Radius & Ulna	5	
Pelvis	1	
Femur	4	
Patella	1	
Tibia	3	
Astragalus	2	
Total	88	1

Tab. 2 - *Hippopotamus* cf. *antiquus* remains from Cava Redicicoli stored at the MUST and the IsIPU.

prevents to detect the morphological features. However, its size (OL 51.5 mm, IL 49.4 mm, AB 40.4 mm, PB 41.0 mm) suggests an anatomical identification as M¹. The outline in occlusal view is rectangular in shape.

SECOND MOLAR: SN42/FS I (EX. 28), SN42/FS L (EX. 27) - The M² has a trapezoidal shape in occlusal view, with the mesial breadth slightly larger than the distal. All the main cusps, paracone, protocone, metacone and metaconule, show a trefoil-shaped pattern. The cingulum is quite marked along the mesial, distal and meso-labial margins of the tooth, whereas it is less developed along the disto-labial and lingual margins. Pillars are present, although rather weakly, at the level of the transverse valley, both on the lingual and labial sides.

THIRD MOLAR: SN31/FS (EX. 6) - The M³ has a trapezoidal shape in occlusal view, with the mesial breadth slightly larger than the distal one. The paracone and protocone show a trefoil-shaped pattern, whereas the metacone and metaconule are comma-shaped. The mesial cingulum is well developed and continues along the mesial portion of both lingual and labial cingula. On the other hand, the distal cingulum is weakly developed, but in the central portion it shows a stylid-like morphology (distostyle). The lingual and labial outlets of the transverse valley are U-shaped.

Lower teeth (Fig. 2 and Fig. S2; see measurements in Tab. 3)

FIRST INCISOR: SN33/FS (EX. 39), SN49/FS (EX. 36), SN50/FS (EX. 40), SN51/FS (EX. 38), SN56/FS (EX. 37) - The lower I₁ is the largest incisor teeth. The section of the teeth is oval, while the wear of the upper part of the crown on the lingual side is advanced in all teeth.

SECOND INCISOR: SN30/FS (EX. 42), SN41/FSA (EX. 41), SN41/FSB (EX. 44), SN41/FSC (EX. 43) - The lower I₂ is mesiodistally elongated and it shows a deep sulcus along the lingual margin.



Fig. 2 - Dental remains of *Hippopotamus* cf. *antiquus* from Cava Redicicoli. SN47/FSa, upper right canine in lingual view. a) SN28/FS, lower right canine in lingual view. b) SN48/FS, lower left canine in lingual view. c) SN50/FS, lower right first incisor in medial view. d) SN42/FSg, upper right third premolar in occlusal view. e) SN42/FSf, upper right fourth premolar in occlusal view. f) SN42/FSi, upper left second molar in occlusal view. g) SN42/FSl, upper right second molar in occlusal view. h) SN31/FS, upper right third molar in occlusal view. i) SN32/FS, lower right third molar in occlusal view. j) SN42/FSa, lower right third molar in occlusal view. k) SN42/FSb, lower left third molar in occlusal view. l) IsIPU-CR1, lower left third molar in occlusal view. Scale bar is equal to 3 cm.

CANINE: SN10/FSA (EX. 17), SN10/FSB, SN10/FSC, SN10/FSD, SN10/FSE, SN12/FSA, SN22/FSA, SN22/FSB (EX. 15), SN22/FSC, SN28/FS, SN39/FSA, SN39/

FSB (EX. 11), SN39/FSC, SN39/FSD, SN46/FSA, SN46/FSB, SN46/FSC, SN46/FSD, SN46/FSE (EX. 1), SN46/FSF (EX. 2), SN46/FSG (EX. 10), SN47/FSB (EX. 13), SN48/FS

Catalogue number	Tooth	Side	L	B	OL	IL	AB	PB
Upper teeth								
SN29/FS	C ^x	Dx	60.8	41.6				
SN47/FSa	C ^x	Dx	48.3	36.7				
SN42/FSg	P ³	Dx			41.7	42.0	23.6	33.0
SN42/FS _e	P ⁴	Dx			34.5	31.3	25.9	30.4
SN42/FS _h	M ¹	Dx			51.5	49.4	40.4	41.0
SN42/FS _i	M ²	Sx			52.5	51.7	52.9	
SN42/FS _l	M ²	Dx			53.8	55.8	54.0	47.0
SN31/FS	M ³	Dx			55.0	53.5	55.2	47.3
Lower teeth								
SN33/FS	I ₁	Dx	45.8	50.1				
SN50/FS	I ₁	Dx	40.7	42.3				
SN51/FS	I ₁	Dx	47.3	54.9				
SN56/FS _e	I ₁	Dx	52.7	52.6				
SN30/FS	I ₂	Sx	35.9	31.1				
SN47/FS _b	C _x	Sx	59.8	33.4				
SN48/FS	C _x	Sx	58.6	36.0				
SN62/FS	C _x	Sx	63.6	42.4				
SN63/FS	C _x	Sx	55.5	34.0				
SN55/FS _c	C _x	Dx	88.5	52.9				
SN42/FS _d	M ₁	Dx			41.8	41.4	33.7	32.0
SN41/FS _f	M ₂	Sx			55.1	50.9		
SN32/FS	M ₃	Dx			81.5	80.7	44.3	42.8
SN42/FS _a	M ₃	Dx			89.5	88.0	47.8	45.6
SN42/FS _b	M ₃	Sx			82.8	83.9	46.2	43.6
IsIPU-CV1	M ₃	Sx			86.7	86.3	48.9	49.7

Tab. 3 - Measurements (mm) of upper and lower teeth of *Hippopotamus cf. antiquus* from Cava Redicicoli (for abbreviations see Material and methods).

(EX. 79), SN55/FS_A, SN55/FS_B, SN55/FS_C (EX. 9), SN56/FS_A, SN56/FS_B, SN56/FS_C (EX. 16), SN62/FS (EX. 14), SN63/FS (EX. 12) - The C_x is mesiodistally elongated with a triangular section. A large and deep groove is present in the central portion of the lingual side. The enamel ridges and grooves on the tooth surface are slightly marked and fairly parallel along the lateral faces. The wear of the upper portion of the crown is advanced in all teeth.

FIRST MOLAR: SN42/FS_D (EX. 33) - The only preserved M₁ from CR shows an advanced worn crown, which prevents to detect the morphological features. However, its size (OL 41.8 mm, IL 41.4 mm, AB 33.7 mm, PB 32.0 mm) suggests an anatomical identification as M₁. The outline in occlusal view is rectangular in shape.

SECOND MOLAR: SN41/FS_F (EX. 29) - The only M₂ preserved in the CR sample is fragmentary and the wear of the crown is advanced, and only a few features can be observed. The metaconid is comma-shaped, the mesial cingulum is marked, and the outlets of the transverse valley are V-shaped in lingual view, with a weak pillar along the lingual margin.

THIRD MOLAR: SN32/FS (EX. 24), SN42/FS_A (EX. 23), SN42/FS_B (EX. 22), SN42/FS_C (EX. 25), IsIPU-CR1 - The M₃ is the longest molar of hippopotamuses. All four teeth show a homogeneous morphology. The metaconid and

protoconid are trefoil-shaped, and the postmetacristid is in contact with the prehypocristid. The hypoconid is trefoil-shaped with the posthypocristid not elongated distally, whereas the entoconid shows a comma-shaped pattern. The hypoconulid is cruciform-shaped. The labial outlet of the transverse valley is V-shaped, whereas the lingual outlet is U-shaped. The mesial and distal cingula are well marked, while the labial and lingual cingula are absent. Two pillars are present along the labial margin with the distal one quite robust. The wear of the crown is low in IsIPU-CR, moderated in SN32/FS and SN42/FS_A, and advanced in SN42/FS_B.

Postcranial elements (Fig. 3 and Figs S3-S8; see measurements in Tab. 4)

SCAPULA: SN73/FS (EX. 80) - SN73/FS corresponds to a fragment of a scapular corpus. In lateral view, it shows robust scapular spine and along the cranial margin the scapular notch is weakly marked. Medially, no diagnostic features are detected.

HUMERUS: SN34/FS (EX. 52), SN35/FS (EX. 57), SN53/FS (EX. 53), SN68/FS (EX. 50), SN71/FS (EX. 55), SN74/FS (EX. 51), SN78/FS (EX. 58), SN788/LJ, SN789/LJ - The proximal epiphysis is preserved only in SN788/LJ, but both major and minor tubercles are absent. The head of



Fig. 3 - Postcranial remains *Hippopotamus cf. antiquus* from Cava Redicicoli. SN788/LJ, right humerus in cranial (a) and dorsal (b) views; SN21/FS, left radius-ulna in dorsal view (c); SN790/LJ, tibia in cranial view (d); SN25/FS, left astragalus in plantar (e) and dorsal (f) views; SN27/FS, right astragalus in plantar (g) and dorsal (h) views. Scale bar is equal to 5 cm.

the humerus is circular in proximal view. The neck gently reaches the head of the humerus, forming an obtuse angle. Cranially, the deltoid tuberosity is quite marked. The distal epiphysis is well preserved in SN788/LJ, SN798/LJ and SN71/FS. In cranial view, the coronoid fossa is broad and deep and the lateral epicondylar crest is well marked, ending in a robust lateral epicondyle. The proximal border of the trochlea creates a large angle, according to the transversal plane, which is smaller than the maximum breadth of the distal epiphysis. Caudally, the olecranon fossa is very deep and large with the medial and lateral margins divergent, its outline is slightly triangular in shape. The medial epicondyle is more distally elongated than the lateral one.

RADIUS AND ULNA: SN21/FS (EX. 45), SN57/FS (EX. 46), SN58/FS (EX. 49), SN59/FS (EX. 47), SN61/FS (EX. 48) - The radius-ulna are fused along their length. SN21/FS consists of a complete radius-ulna bone, but the surface is strongly abraded, which limits the differentiation of

the several morphological traits. The proximal epiphysis of the radius shows the radial articular facet bearing two fossae for articulation with the humeral trochlea, the medial larger than the lateral one, separated by a weak coronoid process in proximal view. In cranial view, the diaphysis tends to be wider near the distal epiphysis. The lateral portion of the distal epiphysis is incomplete. In distal view, the poor state of preservation prevents a complete description of the carpal articular surface, although it appears mediolaterally elongated and proximally developed.

The ulna lacks the anconeal process, while the olecranon is fragmented. The latter is proximally elongated and slightly oriented caudally. In cranial view, the trochlear notch includes a large and well developed medial articular surface with humeral trochlea, as well as a small lateral one. These surfaces are separated by a large and deep radial notch. The diaphysis is stout and displays

Catalogue number	Side											
Humerus		PL	BS	BT	BD	DDI	DDm					
SN71/FS	Dx		68.3									
SN788/LJ	Dx	508.7	76.5	125.3	177.8	110.5						
SN789/LJ	Dx		67.9	98.2*				144.1				
Radius & ulna		Lru	Lr	PL	DPa	Do	BPau	BPr	BSr	DSu	BDr	Bdru
SN21/FS	Sx	411.2	278.4	262.7		102.2	91.9	101.2	58.9	53.0	177.7	165.8
SN57/FS	Sx						96.6	108.3	63.0	63.9		
SN58/FS	Dx				146.5	109.4	102.0	109.5				
SN59/FS	Sx				118.7	102.2*						
SN61/FS	Sx								64.0			
Femur		BS										
SN37/FS	Dx	70.4										
SN52/FS	Dx	80.8										
SN72/FS	Sx	79.3										
Tibia		TL	BS	BD	DD							
SN69/FS	Dx		55.4	91.9*	65.2							
SN790/LJ	Dx	378.2	74.6	10.7.6	75.2							
Astragalus		LL	ML	L	BP	B	BD					
SN25/FS	Sx	105.6	98.4	118.7	84.0	108.1	98.8					
SN27/FS	Dx	108.7	98.6	121.2	91.0	102.7	103.2					

Tab. 4 - Measurements (mm) of postcranial bones of *Hippopotamus* cf. *antiquus* from Cava Redicicoli (for abbreviations see Material and methods). An asterisk indicates approximate measurements.

a columnar development. In distal view, only the articular surface with cuneiform can be detected, which is broad craniodorsally and narrow mediolaterally.

PELVIS: SN70/FS (EX. 79) - SN70/FS consists of a fragmented pelvis, including the acetabulum and part of the corpus of the ischium. The acetabulum is oval in shape bearing an oval-shaped foramen at the level of its proximal margin.

FEMUR: SN37/FS (EX. 60), SN52/FS (EX. 61), SN67/FS (EX. 62), SN72/FS (EX. 63) - In the studied sample, both proximal and distal epiphyses are not preserved. In SN37/FS, the proximal epiphysis is disarticulated, which indicates that this specimen is a young individual. The bone is columnar with a rounded diaphysis. Although the proximal epiphysis is missing, in caudal view the trochanteric fossa is broad and the femoral neck is slightly convex, while the lesser trochanter is stout. The diaphysis is quite circular along the lateral margin, displaying a large and deep supracondylar fossa that reaches the distal epiphysis.

PATELLA: SN36/FS (EX. 69) - The bone is triangular in shape in cranial view. Caudally, the morphology of the medial articular surface is trapezoidal and it is larger than the lateral one. The latter has a rectangular shape and it is proximo-distally elongated. Proximally, the insertion point of the muscle quadriceps femoris is rectangular in shape with a deep portion located near the medio-cranial margin. The medial process is stout and curved caudally.

TIBIA: SN60/FS (EX. 67), SN69/FS (EX. 66), SN790/LJ (EX. 75) - In general, the bone is relatively short and stout. The proximal epiphysis is preserved only in SN790/LJ, but it is incomplete. In cranial view, the tibial crest is robust and becomes less evident distally after the half of the diaphysis. In plantar view, the medial intercondylar

tubercle is weakly projected proximally, while in proximal view it appears stout and mediolaterally elongated. The medial articular surface is semi-circular in shape. Cranially, the medial malleolus is projected distally, whereas the lateral border of the bone appears as a crest-like and it ends in a weakly developed lateral malleolus. Medially, the notch of the distal epiphysis profile is relatively narrow and deep. The medial groove of tibial cochlea has a deep triangular shape, whereas the lateral one shows a less deep rectangular shape in distal view.

ASTRAGALUS: SN25/FS (EX. 71), SN27/FS (EX. 72) - Two specimens are complete. Dorsally, the lateral crest of the proximal trochlea is slightly elongated proximally than the medial one, with a relatively broad trochlear pit. A large and deep fossa occupies the central part of the bone, which extends up to both its lateral and medial margins. However, the opening of the lateral margin is larger than the medial margin. As such, the proximal trochlea surface is well separated by the distal trochlea one. The distal trochlea is deep, with a central crest which separates the cuboid articular surfaces from the navicular one. Laterally, the distal articular facet for calcaneus has an oval shape, while the proximal facet for calcaneus and the facet for fibula is flat. In plantar view, a proximal groove separates the proximal trochlea from the plantar facet for the articulation with the sustentaculum tali of the calcaneus. The latter is in contact with the distal trochlea.

MORPHOLOGICAL COMPARISON

The main diagnostic characters for fossil hippopotamuses are recorded on the skull (Caloi et al.,

1980; Mazza, 1991, 1995), although no cranial remains are preserved in the CR material. As to teeth configuration, *H. antiquus* and *H. amphibius* do not show significant morphological differences except for size. The only exception concerns the enamel ridges and grooves on the surface of the canines, which are fairly parallel along the lateral surfaces in *H. antiquus* and convergent forward in *H. amphibius* (Blandamura & Azzaroli, 1977; Caloi et al., 1980). All upper and lower canines of CR show enamel ridges and grooves quite parallel, therefore similar to *H. antiquus*. However, Mazza (1995) found a large variability of enamel ridges and grooves arrangement in fossil and extant hippopotamuses, thus suggesting that this character cannot be considered diagnostic for species identification purposes.

Conversely, clear-cut morphological criteria for the postcranial bones of hippopotamuses are still lacking, although a preliminary attempt was proposed by Mazza (1995). Following this work, several features referred to *H. antiquus* were identified in the CR material. These features are: a triangular-shaped outline of the olecranon fossa and a marked oblique orientation of the trochlea of the humerus in dorsal view; short and robust radius-ulna, with wide proximal and distal epiphyses of the radius and well-developed medial and lateral articular surfaces with radius of the ulna; short and stout tibia, with a pronounced tibial crest becoming less evident near the distal epiphysis; the lateral length of astragalus much longer than the medial length and well separated proximal trochlea surface from the distal trochlea surface.

Opposite postcranial features are instead characteristic of fossils and extant *H. amphibius* (see Mazza, 1995). These features are: a parallel-sided shape outline of the olecranon fossa and less oblique orientation of the trochlea of the humerus in dorsal view; slender radius-ulna, with narrow both proximal and distal epiphyses of the radius

and less developed medial and lateral articular surfaces with radius of the ulna; slender tibia, with a pronounced tibial crest which is less evident close to middle part of the diaphysis; the lateral length of astragalus slightly longer than the medial length and contact between the proximal trochlea surface and the distal trochlea surface.

Recently, Georgitsis et al. (2022) added new morphological data on postcranial remains of extant specimens of *H. amphibius*, based on four skeletons housed in the mammalogy collection of the Royal Museum for Central Africa (Belgium). The authors observed that the tibial crest reaches the distal epiphysis in the tibia and the proximal trochlea surface is well separated from the distal trochlea surface in the astragalus.

BIOMETRIC COMPARISON

The biometric comparison of fossil and extant hippopotamuses shows differences among the groups considered. The values of the OL of M_3 of the Villafranchian and Epivillafranchian samples of *H. antiquus* are separated from the Galerian sample of *H. antiquus* and both extant and fossils of *H. amphibius*, the former having larger teeth (Fig. 4a). The fossils of the CR sample (all four belonging to adult individual) fall within the variability of the Villafranchian specimens of *H. antiquus* and are slightly larger than the Epivillafranchian specimens. The plot of M_3 shows no differences in the OL/AB ratio between the groups considered, with specimens distributed along the same diagonal (Fig. 4b).

On the other hand, the differences in size are more variable in the postcranial bones. In general, Villafranchian and Epivillafranchian specimens of *H. antiquus* show the largest size, whereas fossil and extant of *H. amphibius* are usually reduced in dimensions. The humerus of the CR

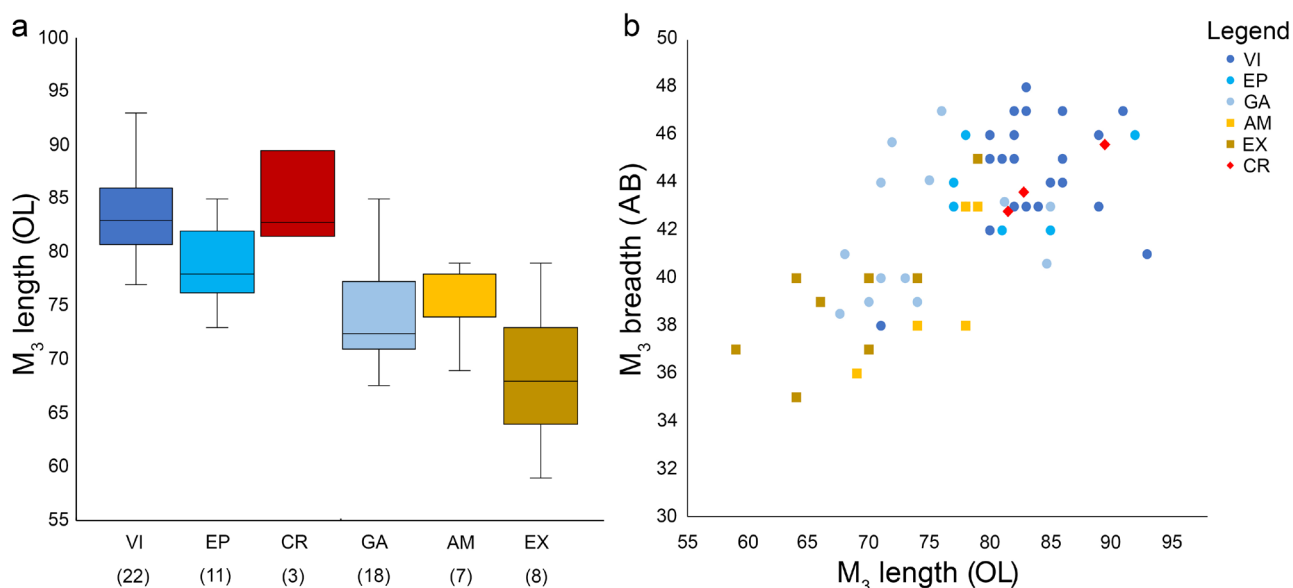


Fig. 4 - Boxplot of the M_3 outer length (OL, mm) of fossil *Hippopotamus* of Europe and extant specimens of *H. amphibius* (number of specimens in the brackets). a) Plot of outer length (OL, mm) vs anterior breadth (AB, mm) of M_3 of fossil and extant *Hippopotamus* (b). Colors: blue - Villafranchian sample of *H. antiquus*; azure - Epivillafranchian sample of *H. antiquus*; red - sample of Cava Redicicoli; light blue - Galerian sample of *H. antiquus*; orange - Aurelian sample of *H. amphibius* (including only Barrington sample); dark orange - extant sample of *H. amphibius*.

sample shows a large size, which is comparable only to the largest specimens of Villafranchian *H. antiquus* (Fig. 5a). Regarding the radius-ulna, the CR specimen shows the smallest dimension among the fossil *H. antiquus*, thus falling only within the variability of extant *H. amphibius* (Fig. 5b). The tibia of CR is generally smaller than the Villafranchian and Epivillafranchian specimens of *H. antiquus*, and it is slightly larger than the Galerian specimens of *H. antiquus*, whereas it falls within the upper variation range of extant *H. amphibius* (Fig. 5c). Finally, the size of the astragali of CR sample is consistent with the lower variation range of the Villafranchian specimens of *H. antiquus* and the upper variation range of the Galerian specimens of *H. antiquus*. Moreover, they are smaller than the Epivillafranchian specimens of *H. antiquus* and larger than extant specimens of *H. amphibius*.

DISCUSSION

Taxonomical attribution

The morphological analysis carried out in this work permits to describe for the first time the large hippopotamus sample from Cava Redicicoli, which has been referred in the literature to *H. antiquus* (Caloi et al., 1979, *Hippopotamus major* considered as synonym of *H. antiquus*; Petronio et al., 2001) or *Hippopotamus* ex gr. *antiquus* (Palombo et al., 2003). Upper and lower canines show a parallel development of enamel ridges and grooves on the tooth surface. This feature was considered diagnostic for *H. antiquus* by Blandamura & Azzaroli (1977) and Caloi et al. (1980). By contrast, Mazza (1995) recognized a large variability of enamel ridges and grooves arrangement: prominent and convergent enamel ridges were more frequently observed in fossil and extant *H. amphibius*, whereas both morphotypes are found approximately with the same frequency in *H. antiquus*. Mazza (1995) concluded that the variability found within the two species discourages the use of this character for taxonomic purpose.

Additional morphologies were identified in the CR postcranial bones, such as a marked oblique orientation of the trochlea in the humerus, a well-defined tibial crest, becoming less evident towards the distal epiphysis, a well-separated proximal trochlea surface and the distal trochlea surface in the astragalus. All these characteristics are generally observed in *H. antiquus*, whereas opposite morphologies were commonly detected in *H. amphibius*. In particular, the two astragali, considered by Mazza (1995) the most diagnostic skeletal element for the identification of fossil hippopotamuses, exhibit morphological characteristics which are typical of *H. antiquus*. However, two of the features proposed by Mazza (1995) for *H. antiquus* were rarely observed also in extant specimens of *H. amphibius* (Georgitsis et al., 2022; see Morphological comparison section).

As mentioned above, the main characters for fossil and extant hippopotamuses are recorded in cranium and mandible (e.g., Caloi et al., 1980; Mazza, 1995). When fossil skulls are unavailable, taxonomic identification is often based on chronological grounds. On the other hand, the non-description of dental and postcranial remains severely limits the morphological knowledge, as

evidenced by the absence of widely accepted unambiguous criteria for these elements. Therefore, considering the fact that the studied material shows a certain affinity to *H. antiquus*, the CR sample is ascribed to *Hippopotamus* cf. *antiquus*.

Size variability

Hippopotamuses are considered among the most important indicators of palaeoenvironmental and climatic conditions. The long persistence of this group in Europe and its rich record offer the possibility to investigate whether hippopotamuses experienced fluctuations in size driven by climatic change. Modern hippopotamuses are found exclusively on the African continent, in suitable wetland habitats. Their occurrence in the fossiliferous deposits of Europe indicates the presence of permanent water bodies, humid climatic conditions and annual temperatures warmer than present (Candy et al., 2006, 2010). Although the faunal assemblages in which hippopotamuses occurred have often been referred to an interglacial stage, their presence cannot itself be considered an indicator of warm climate conditions (e.g., Russo Ermolli et al., 2010; Bellucci et al., 2012; Mazza & Bertini, 2013; Adams et al., 2022).

During the late Early Pleistocene and the early Middle Pleistocene, there was a progressive increase in the amplitude of climate oscillations, with the shift from a 41 kyr to 100 kyr orbital rhythm (Lisiecki & Raymo, 2005; Maslin & Ridgwell, 2005; Clark et al., 2006). This led to an increase of the long-term average global ice volume and the establishment of a strong asymmetry in the global ice volume cycles. This climatic change is known as the Early-Middle Pleistocene Transition (EMPT), a phase that lasted about 1 Ma (ca 1.4-0.4 Ma; Head & Gibbard, 2015). This interval is marked by one of the major faunal renewals that occurred in Europe, from the Villafranchian to the Galerian, leading to the formalisation of a new biochron, known as the Epivillafranchian (1.2-0.9 Ma; Kahlke, 2001, 2006, 2007, 2009; Bellucci et al., 2015). The faunal renewal in the mammal palaeocommunities of the EMPT triggered the extinction of several Villafranchian taxa and the arrival of Galerian newcomers, such as *Cervus elaphus* Linnaeus, 1758, *Sus scrofa* Linnaeus, 1758, and *Crocota crocuta* (Erxleben, 1777) (e.g., Gliozzi et al., 1997; García, 2003; Madurell-Malapeira et al., 2010; Sardella & Petrucci, 2012; Bellucci et al., 2015; van der Made et al., 2017b; Iannucci et al., 2020, 2021b; Walker et al., 2020). *Hippopotamus antiquus* persisted in Europe during the EMPT and represented one of the common elements of European terrestrial ecosystems, as well as one of the few survivors of the Villafranchian mammal faunas. Mazza & Bertini (2013) hypothesised that the climatic oscillations of the EMPT affected the size of hippopotamuses, with larger specimens found during the Early Pleistocene and smaller specimens during the Middle Pleistocene. Larger hippopotamuses did not appear again until the early Late Pleistocene, a period characterised by a warm climate.

The comparison of M_3 provides a reliable indication of the size variability of fossil hippopotamuses, as their teeth are not affected by sexual dimorphism, with the exception of the canines (Laws, 1968; Mazza, 1995; Shannon et al., 2021). The result of the biometric comparison carried out in this work confirmed the presence of the largest

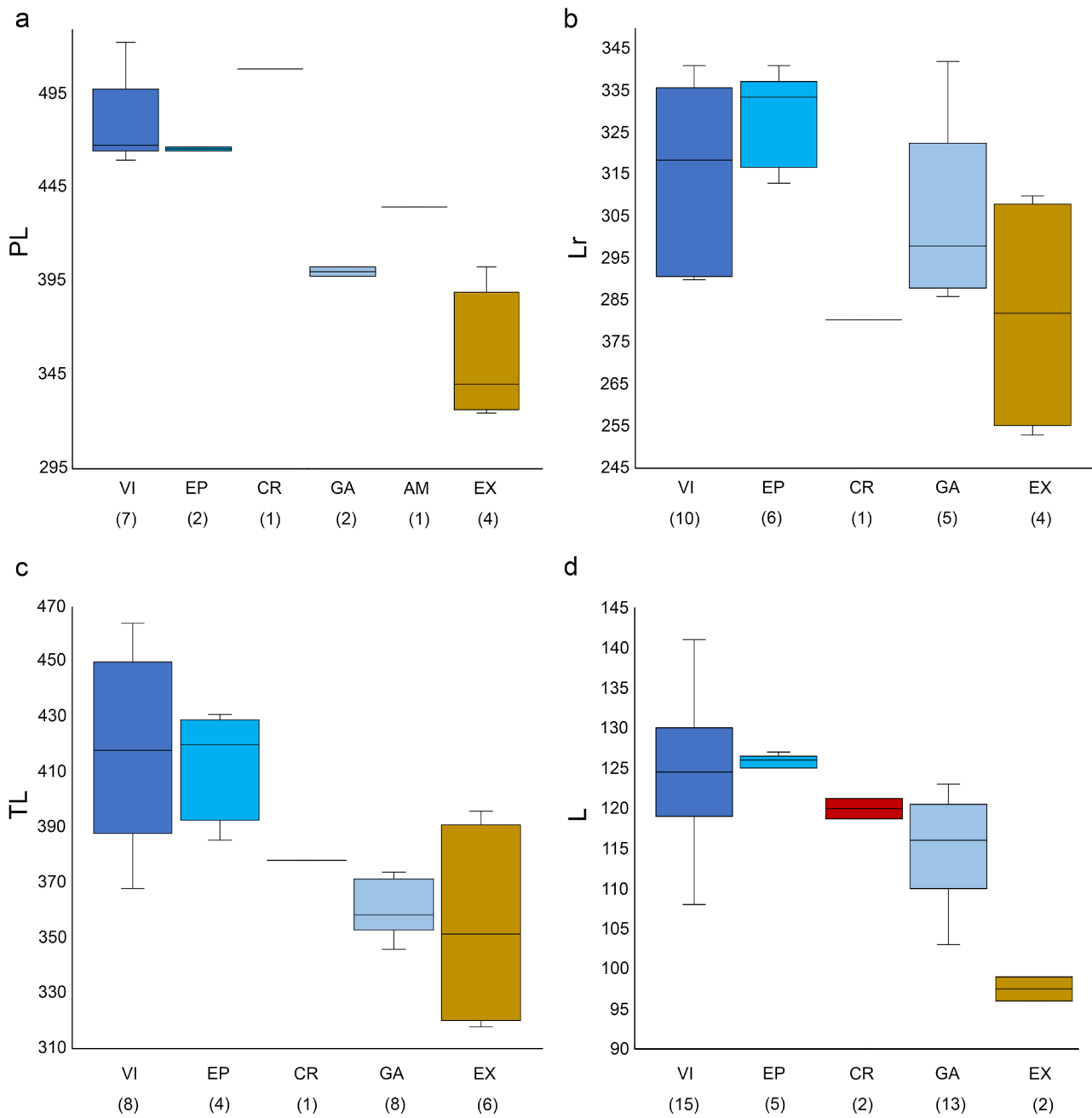


Fig. 5 - Boxplot of physiologic length (PL, mm) of the humerus (a), greatest length of the radius (Lr, mm) (b), greatest length (TL, mm) of the tibia (c), greatest length (L, mm) of the talus (d) of fossil *Hippopotamus* of Europe and extant specimens of *H. amphibius*. Colors: blue - Villafranchian sample of *H. antiquus*; azure - Epivillafranchian sample of *H. antiquus*; red - sample of Cava Redicicoli; light blue - Galerian sample of *H. antiquus*; orange - Aurelian sample of *H. amphibius* (including only Barrington sample); dark orange - extant sample of *H. amphibius*. Number of specimens within brackets.

size specimens attested during the Villafranchian and Epivillafranchian, including the CR sample (Figs 4-5). Fossil and extant specimens of *H. amphibius* show a small size, partially overlapping the Galerian sample of *H. antiquus* (Fig. 4). Based on the fossil remains from Barrington, Mazza & Bertini (2013) suggested that the fossil sample of *H. amphibius* reached a large size in the Late Pleistocene. On the contrary, the boxplot of M_3 length (OL) and the plot of M_3 length (OL) and breadth (AB) show that the specimens from Barrington (the only fossils included in the Aurelian sample of *Hippopotamus*

amphibius in Fig. 4) are similar in size to the Galerian sample of *H. antiquus*. The four specimens from CR show a large size which falls within the range of Villafranchian group of *H. antiquus*, and only in the upper part of the range of the Epivillafranchian group of *H. antiquus* (Fig. 4).

Postcranial bones are generally less represented than the cranial remains (including teeth). Therefore, the results of the biometric comparison could be affected by sample size. Nevertheless, the general trend observed in the postcranial elements is consistent with that observed in the M_3 , with the smaller specimens found in the

Galerian and extant specimens of *H. amphibius*. The size of the CR specimens is instead quite variable, with a large humerus, similar to the Villafranchian specimens, a relatively medium size for the astragalus, but a small radius-ulna and tibia.

How can these marked size differences of CR be explained? Looking at other abundant fossils records of hippopotamuses, similar conditions can be observed. The samples from Incarcal (Galobart et al., 2003) and Untermassfeld (Kahlke, 2001; Kierdorf & Kahlke, 2020), which include respectively 280 and 848 remains, are suitable for testing size variability. The measurements of the two radio-ulnae from Incarcal differ greatly (Lr: IN-I 199 = 341 mm; IN-I 752 = 290 mm; Galobart et al., 2003), but their differences (ca. 50 mm) are similar to those reported for extant *H. amphibius* (Lr: min = 253 mm; max = 310 mm; Mazza, 1995). The tibiae from Untermassfeld also differ (TL: IQW 1979/15 117 = 431 mm; IQW 1980/16 885 = 427 mm; IQW 1979/15 118 = 420 mm; IQW 1979/15 124 = 385.5 mm; Kahlke, 2001), but, also in this case, the difference between the largest and the smallest is ca. 50 mm, which is approximately the same as that observed for extant *H. amphibius* (TL: min = 318 mm; max = 396 mm; Mazza, 1995). Other examples of variation include the femora from Castel di Guido (greatest length = 490-569 mm; mean = 499.2 mm; three specimens; Mazza & Bertini, 2013) and Valdarno Superiore (greatest length = 608-700 mm; mean = 636.2 mm; seven specimens; Mazza & Bertini, 2013).

In extant mammalian taxa, males are generally larger than females. The same consideration goes for *H. amphibius* (Mazza, 1995; Eltringham, 1999; Mazza & Ventura, 2011; Mazza & Bertini, 2013; Shannon et al., 2021). However, extant hippopotamuses show a reduced sexual dimorphism (Eltringham, 1999; Mazza, 1995; Mazza & Ventura, 2011; Mazza & Bertini, 2013), and, as demonstrated by Shannon et al. (2021), males are only slightly heavier (5%), longer (2%) and taller (7%) than females. The authors found a clear separation between the sexes exclusively in the jaw and canines, where males are much larger than females (44% and 81%, respectively). Size sexual dimorphism in canines was also observed in previous studies (Laws, 1968; Mazza, 1995; Mazza & Ventura, 2011). These differences have been interpreted as sexual selection, favouring an increased weapon size (Mazza, 1995; Shannon et al., 2021). Regarding the postcranial elements, there is a lack in clear-cut dimensional separation between sexes. Therefore, sex bone identification based on size is not recommended, at least if the specimen falls within the upper part of the male range or in the lower part of the female range (Mazza & Bertini, 2013). Taking into account these considerations, sexual dimorphism does not seem to explain alone the overall size differences observed in the Pleistocene hippopotamuses of Cava Redicicoli. In fact, the humerus is one of the largest among extinct hippopotamuses and the tibia and, especially, the radius-ulna are far below the range of variation of the Villafranchian and Epivillafranchian *H. antiquus*.

Another interesting point is the relationship between size and age noted by Shannon et al. (2021), providing a new key for understanding size variation of fossil hippopotamuses. In fact, hippopotamuses increase in size

until approximately 17 years of age, with males continuing to grow but not females. On the other hand, the maximum height is reached at approximately 15 years of age. Body length, body mass, and shoulder height continue to increase after reaching adulthood (individuals 10 years of age; Shannon et al., 2021), thus demonstrating that adults show an increasing size trend between 10 and 20 years of age. The same dimensional differences have been observed in adult specimens from CR, which appear to be influenced not only by sex but also by age. This new interpretation could even explain a similar large variation recognized at Castel di Guido (Mazza & Bertini, 2013), Incarcal (Galobart et al., 2003), Untermassfeld (Kahlke, 2001) and Valdarno Superiore (Mazza & Bertini, 2013), also considering that after the fusion of the epiphyses it is not possible to estimate the age of a hippopotamus fossil bone, thus preventing their identification as subadult/young adult/adult. Combining sex and age, the humerus of CR can be tentatively ascribed to a large adult male, while the radius-ulna and tibia may belong to a young adult, probably female.

CONCLUSION

The hippopotamus remains of the rich historical museum collection from the latest Early Pleistocene site of Cava Redicicoli are described herein for the first time. Clear-cut morphological criteria for dental and postcranial elements of hippopotamuses are still lacking, and only a first attempt was reported by Mazza (1995). This limited knowledge urges caution, and therefore the CR sample is tentatively referred to *Hippopotamus cf. antiquus*.

The biometric comparison carried out in this work highlights that the size of the CR postcranial bones is quite variable being strongly affected by two factors: sex and age. The observed dimensional differences represent a limit for assessing the possible size response to glacial/interglacial fluctuations based on postcranial elements.

On the other hand, the analysis of the lower third molar, not affected by sexual dimorphism, provides a reliable framework for the size trend of hippopotamuses during the Quaternary. The results of this work partially support the hypothesis of Mazza & Bertini (2013), who recognised large-sized hippopotamuses during the Villafranchian and Epivillafranchian, including the CR sample. Nevertheless, no clear biometric differences were observed between Galerian *H. antiquus* and fossil and extant *H. amphibius*.

Finally, the *Hippopotamus* record from the CR provides valuable palaeoecological information, as this group is considered an important indicator of palaeoenvironmental and climatic conditions. Their occurrence indicates the presence of permanent water bodies, humid climatic conditions and annual temperatures potentially several degrees higher than present.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data of this work are available on the BSPi website at: <https://www.paleoitalia.it/bollettino-spi/bspi-vol-622/>

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