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The Middle Pleistocene Hippopotamus from Malagrotta (Latium, Italy): New Data and Future Perspectives

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Abstract: The Middle Pleistocene was characterized by the presence in continental Europe of at least two different species of hippopotamus: *Hippopotamus antiquus* and *H. amphibius*. Although suspected, the presence of both hippopotamuses in the same geographical area has not yet been proven. The following manuscript describes findings from Malagrotta (Rome, central Italy), dating back to the time span between 0.45 and 0.38 Ma. These findings offer new insights into the Middle Pleistocene period. The fragmented mandible has a slender and low corpus, the humerus is robust with a deltoid tuberosity placed medially on the diaphysis, the unciform shows a facet for the MCIV wider than the one for the MCV and the calcaneum is clepsydra-shaped. The morphological characteristics of the sample are closer to those of *H. antiquus*, despite the fact that the morphometric measurements are smaller than those of the samples coming from Valdarno (Italy), Untermaßfeld (Germany) or Colle Curti (Italy). Considering all the information, the material from Malagrotta is here attributed to *H.* cf. *antiquus*, indicating the survival of the European hippopotamus until at least 0.38 Ma in central Italy. The coexistence of *H. amphibius* and *H. antiquus* in the same geographical area is also discussed.

Keywords: quaternary; Italian peninsula; Hippopotamidae; taxonomy

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1. Introduction

Hippopotamidae family members are nowadays restricted to Africa and represented by *Hippopotamus amphibius* Linnaeus, 1758 [1] and *Choeropsis liberiensis* Morton, 1849 [2]. However, the diversity of this family was greater in the past, and hippopotamus representatives were widespread in Europe, Asia, and Africa [3]. Continental Europe was characterized by the presence of at least two different species during the Pleistocene: *H. antiquus* Desmarest, 1822 [4] and *H. amphibius*. *Hippopotamus antiquus* was a large European hippopotamus which was most likely related or evolved from the African *H. gorgops* [5–8]. *Hippopotamus antiquus* was present in almost all Europe [9–16]. The first appearance datum (FAD) of *H. antiquus* is still highly debated but it was firmly established in the Upper Valdarno area (Tuscany, Italy) around 1.9–1.7 Ma [17]. The last appearance datum (LAD) of the European hippo is estimated to be around 0.45 Ma in Portugal, which thanks to its geographical position and climate, probably acted as a glacial refugium ([16] and references therein). The LAD age of 0.45 Ma proposed for *H. antiquus* based on the evidence from Portugal is in agreement also with its presence in the roughly contemporaneous locality Marathousa-2 of the Megalopolis Basin of Greece, which again acted as a glacial refugium for several animals, including hippopotamuses [18]. *Hippopotamus amphibius* probably arrived in Europe during the Middle Pleistocene, and it persisted until the Late Pleistocene [13,16,19]. It should be noted that during Pleistocene another disputed species, *H. tiberinus*, has been described from different localities of Europe by Mazza [20,21]. The holotype of *H. tiberinus* was collected from La Maglianella (Rome, Italy), a locality geographically close to Malagrotta. Other remains ascribed to *H. tiberinus* were listed from German localities, such as Jockgrim, Eich, Mosbach, spanning from Early Pleistocene to Late Pleistocene [20,21]. However, *H. tiberinus* was later considered an invalid species by Petronio [22]. More recently, Mazza and Bertini [23] defined the latest and more advanced *H. antiquus*, previously referred to *H. tiberinus*, as *H.* ex gr. *H. antiquus*. Van der Made et al. [24] hypothesized a possible synonymy of *H. tiberinus*, *H. gorgops*, *H. georgicus*, and *H. sirensis*, the latter ones described from Georgia and Algeria, respectively. The taxonomy of *H.* ex gr. *H. antiquus* or *H. tiberinus* is therefore complicated and poorly understood.

The documentation of hippopotamids in Europe during the Middle Pleistocene is limited, mostly due to the scarcity of chronologically constrained localities and taxonomically relevant specimens [11,13,16]. Among the areas most intensively studied by palaeontologists, Italy probably represents one of the most important palaestrae for studying Middle Pleistocene fossiliferous localities [25,26]. In particular, the Latium area (central Italy) has numerous fossil sites from the Middle Pleistocene period that include hippopotamids. Among them, Cava Arnolfi (MIS 18.2–17.3), Muratella di Mezzo (MIS 18.2–17.3), Campo di Merlo (MIS 18–17), Casal Selce (MIS 15), Via Portuense (MIS 15), Maglianella (MIS 15), Via Aurelia km 18.7–19 (MIS 13), Via Aurelia km 18.9 (MIS 13), Collina Barbattini (MIS 13), Via Aurelia km 19.3 (MIS 13), Castel di Guido (MIS 11), Sedia del Diavolo (MIS 8.5), Prati Fiscali (MIS 8.5), Monte Sacro (MIS 8.5), Saccopastore (MIS 7), upper level of Torre in Pietra (MIS 7), and Casal de' Pazzi (MIS 7) [21,22,27–33]. Hippopotamid remains from Malagrotta (Latium, Italy) were first described by Caloi and Palombo [34]. Unfortunately, the sample from Malagrotta was limited to a vertebra and a fragmented metacarpal, which did not allow for a specific attribution. Therefore, the specimens from Malagrotta were assigned to *Hippopotamus* sp.

Here, we describe for the first time, new additional hippopotamid remains from Malagrotta which provide important information on the variability of Hippopotamidae representatives during the Middle Pleistocene. The remains from Malagrotta shed light on the latest *H. antiquus* individuals that inhabited Europe before their extinction. The Malagrotta specimens provide evidence of the late persistence of the European hippopotamus species in Europe and raise questions about its possible coexistence with *H. amphibius* in the Italian Peninsula.

Geological Setting

Malagrotta is a locality situated within the area of Rome, Latium, central Italy (Figure 1A). The sedimentary succession of Malagrotta, hosting both lithic artifacts and fossil remains, was firstly described by Caloi and Palombo and Cassoli et al. [34,35]. The taxa recovered from Malagrotta and reported by Caloi and Palombo [34] include *Elephas antiquus* (=*Palaeoloxodon antiquus*), *Equus caballus* (=*Equus ferus*), *Canis lupus*, *Dicerorhinus* cf. *hemitoechus* (=*Stephanorhinus hemitoechus*), *Sus scrofa*, *Hippopotamus* sp., *Cervus elaphus*, *Dama* cf. *clactoniana*, *Capreolus capreolus*, *Bos primigenius*, *Castor* sp., and *Oryctolagus* sp. However, Marra et al. [27] argued the presence of *C. lupus* and re-assigned the fragmented molar to *Canis* sp.

Several recent investigations have attempted at reconstructing the exact location and the stratigraphic context of the Malagrotta site [27,28,36,37]. Indeed, a rather confused picture emerged from previous literature, with two different stratigraphic schemes reported by Cassoli et al. [35] and Caloi and Palombo [34]. A location map in Caloi and Palombo [34] failed to match any actual outcrop in the field.

In fact, the faunal assemblage stored in the Museo Civico di Zoologia di Roma and attributed to the Malagrotta site must be considered as the result of repeated surface collections on different stratigraphic sections located south of the Via Aurelia, between km 16–16.5, ca. 1 km west of the actual toponym (Figure 1) [36].

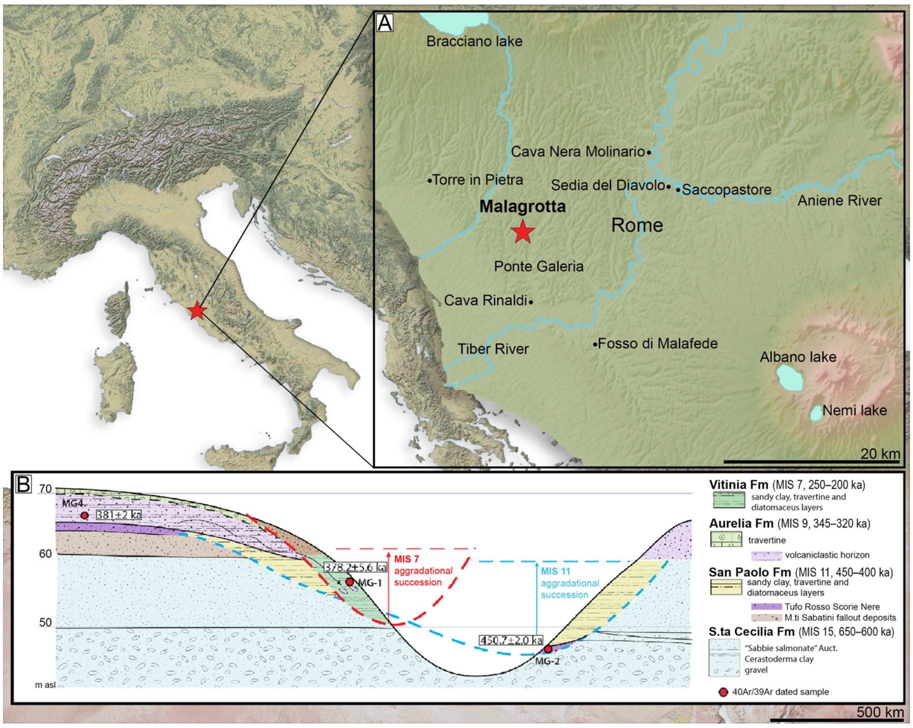

Figure 1. Localization of Malagrotta site. (**A**) Geographical map of the area of Rome, red star for Malagrotta. (**B**) Geological setting of Malagrotta (modified from Marra et al. [37]).

Detailed stratigraphic studies and $^{40}Ar/^{39}Ar$ dating of numerous samples allowed Marra et al. [37] to highlight the occurrence of two distinct glacio-eustatic sedimentary cycles in this area, spanning 450–250 ka, corresponding to the MIS 11 and MIS 7 aggradational successions (San Paolo and Vitinia Formations [38]). However, dating of the volcaniclastic material adhering to a bone fragment part of the preserved faunal assemblage gave an age of 378.2 ± 5.6 ka, while the pyroclastic flow deposit at the base of the stratigraphic section described in Caloi and Palombo [34] was dated at 450.7 ± 2.0 ka [36], suggesting a homogeneous provenance of the faunal remains from the MIS 11 aggradational succession. In particular, the assemblage described in Caloi and Palombo [34] can be dated to ca. 450 ka, while the sedimentary horizon from which the fossils described in Cassoli et al. [35] were collected is most likely a MIS 7 succession, but the faunal remains are reworked from the previous sedimentary cycle which includes sedimentary and volcaniclastic horizons spanning 450–378 ka.

2. Materials and Methods

The hippopotamid remains collected from Malagrotta and considered in this work are stored in the Museo Civico di Zoologia di Roma, Italy (MCZR). The material includes several cranial elements, including hemimandibles and isolated teeth, abundant fragmented vertebras and costae and postcranial bones, such as humeri and tarsal and carpal bones. For the complete list, see Supplementary Material Table S1:

The morphological terminology for the teeth follows [39]. All the postcranial remains were measured following the protocol reported by Mazza [21] (see Supplementary Material Figure S1). The remains from Malagrotta were compared with extant *H. amphibius* (e.g., from Congo River), fossil *H. amphibius* (e.g., Barrington, Tor di Quinto), *H. antiquus* and closely related forms (e.g., from Upper Valdarno, S. Oreste, La Maglianella), and *H. gorgops* from direct observations (R.M. and L.P.: Supplementary Table S1) and published data [9,16,20–23,29,40–49]. All the measurements are reported in Supplementary Material Table S2. All the analyses were developed in the RStudio environment [50]. Data analyses and visualization: devtools and ggplot2 [51,52].

Institutional abbreviations—IGF, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Università degli Studi di Firenze, Florence, Italy; MCZR, Museo Civico di Zoologia, Rome, Italy; MG, Museu Geológico de Lisboa, Lisbon, Portugal; MGGC, Museo Geologico Giovanni Capellini, Bologna, Italy; MNCN, Museu Nacional de Ciencias Naturais, Madrid, Spain; MPUR, Museo di Paleontologia, Sapienza, Università di Roma, Rome, Italy; MSNCC, Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa, Italy; NHMMZ, Naturhistorisches Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz, Germany; MNHN, Muséum National d'Histoire Naturelle, Paris, France; SMUC, Sedwick Museum of the University of Cambridge, United Kingdom.

Anatomical abbreviations—m, lower molar; P/p, upper/lower premolar; MC, metacarpal; FT, facet.

Measurements abbreviations—AB, anterior breadth; B, greatest breadth; H3m, height of the horizontal ramus or corpus at the level of the m3 hypoconulid; hypB, hypoconulid breadth; L, greatest length; PB, posterior breadth; BP, proximal breadth; BD, bread of the distal epiphysis; DP, proximal depth; BS, smallest breadth of the shaft; BT, breadth of the trochlea; DDl, depth of the lateral portion of the distal epiphysis; DDm, depth of the medial portion of the distal epiphysis; h, height; l, greatest breadth; Bmin, smallest breadth of the diaphysis.

3. Systematic Palaeontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Hippopotamidae Gray, 1821
Genus *Hippopotamus* Linnaeus, 1758
Hippopotamus cf. *antiquus* Desmarest, 1822

4. Results

4.1. Morphological Description

4.1.1. Mandible

MCZR PV 2010.2690 is a fragmented right corpus with a m3 missing the hypoconulid (Figure 2A–C). In lateral view, the ramus is slender and shallow. MCZR PV 2010.2690B (Figure 2D–F) is a fragmented left corpus with an almost complete m2 and a well preserved in situ m3. Both the right and the left ramus look slender. Both mandibles share a partially preserved ventral profile of the corpus with a straight-concave development.

4.1.2. Teeth

MCZR PV 2010.2690 includes a fragment of an upper canine (Figure 2G,H), well recognizable thanks to a posterior groove (Figure 2H), giving to the tooth a bilobate cross-section. The enamel is rough and longitudinally striated.

The specimen MCZR PV 2010.2690 includes a highly worn out right P2/P3 (Figure 2I–K). The P2/P3 has rough and wrinkled enamel. On the lingual side, the cingulum is more developed (Figure 2K), whilst on the labial side, it is poorly visible (Figure 2I). The cingulum is strong and pustulated distally and well-developed mesially. The P2/P3 shows two almost complete straight roots. A further fragment of a highly worn out molar suggests that the Malagrotta specimens belonged to an adult individual.

MCZR PV 2010.2690 includes several fragments belonging to a right canine (Figure 2L), that is still partially embedded in the mandible. The enamel is finely striated longitudinally. There are also fragments of a right lower canine, with a well recognizable deep groove on the mesial side (Figure 2M). MCZR PV 2010.2690 includes a left first incisor particularly massive and straight (Figure 2N). Most of the incisor is covered by cement. The visible enamel is longitudinally striated and with feebly transversal lines. The wear-surface of the incisor is well visible dorsally.

Figure 2. Cranial remains of *H.* cf. *antiquus* from Malagrotta. Fragmented right hemimandible with an m3 MCZR PV 2010.2690. (**A**) Labial view; (**B**) lingual view; (**C**) dorsal view. Fragmented left hemimandible with an m2 and an m3 MCZR PV 2010.2690B. (**D**) Labial view; (**E**) lingual view; (**F**) dorsal view. Fragmented upper canine MCZR PV 2010.2690. (**G**) Posterior view; (**H**) cross-section. Right P2/P3 MCZR PV 2010.2690. (**I**) Labial view; (**J**) occlusal view; (**K**) lingual view. Fragmented left lower canine MCZR PV 2010.2690. (**L**) Mesial view. Fragmented right lower canine MCZR PV 2010.2690. (**M**) Lateral side. First left lower incisor MCZR PV 2010.2690. (**N**) Dorsal view. P1 MCZR PV 2010.2690B. (**O**) Occlusal view; (**P**) posterior view. Scale bar = 5 cm.

MCZR PV 2010.2690B includes several remains. Among these specimens, there is a slightly worn out p1 (Figure 2O,P), characterized by a single root and a single cuspid, curved dorsoventrally. The p1 has crenulated enamel and is hollow internally. MCZR PV 2010.2690B also includes a highly worn out m2. The enamel is thick and crenulated. No other characters are visible.

The MCZR PV 2010.2690 right m3 (Figure 2C) embedded in the mandible is particularly worn out, as are the previous teeth. The enamel is thick and continuous between the anterior and posterior cuspids. The cingulid is not particularly well developed. The hypoconulid is missing. The m3 MCZR PV 2010.2690B (Figure 2F) is also particularly worn out. The wear between the anterior and posterior cuspids is continuous. The enamel is wrinkled and thick. The hypoconulid has a well visible post-entostylid and a post-ectostylid. The cingulid is more poorly developed on the lingual side than in the labial one.

4.1.3. Humerus

The right humerus MCZR PV 2010.2691 is fragmented, and it lacks most of the proximal part (Figure 3A–C). The humerus is robust in anterior view (Figure 3A), with a laterally expanded deltoid tuberosity and a not particularly well-developed humeral crest. The coronoid fossa is deep. The trochlea is oblique, and the epicondylar crest has a well-developed lateral tuberosity. In medial and lateral view (Figure 3B), the bone displays a thick diaphysis. In posterior view (Figure 3C), the olecranon fossa is deep and not particularly wide. MCZR PV 2010.0074 is a right humerus fragmented into three pieces (Figure 3D,E). The proximal epiphysis of the bone has a thick lateral tuberosity with a bicipital groove that is neither particularly deep nor wide. The articular head is wide and well developed while the neck is not very prominent. The lateral tuberosity is well visible and tall. In distal view (Figure 3E), the medial epicondyle is robust, and the lateral one does not protrude very far outwards. In posterior view (Figure 3D), the olecranon fossa is fairly deep and not particularly wide as in the previous specimen.

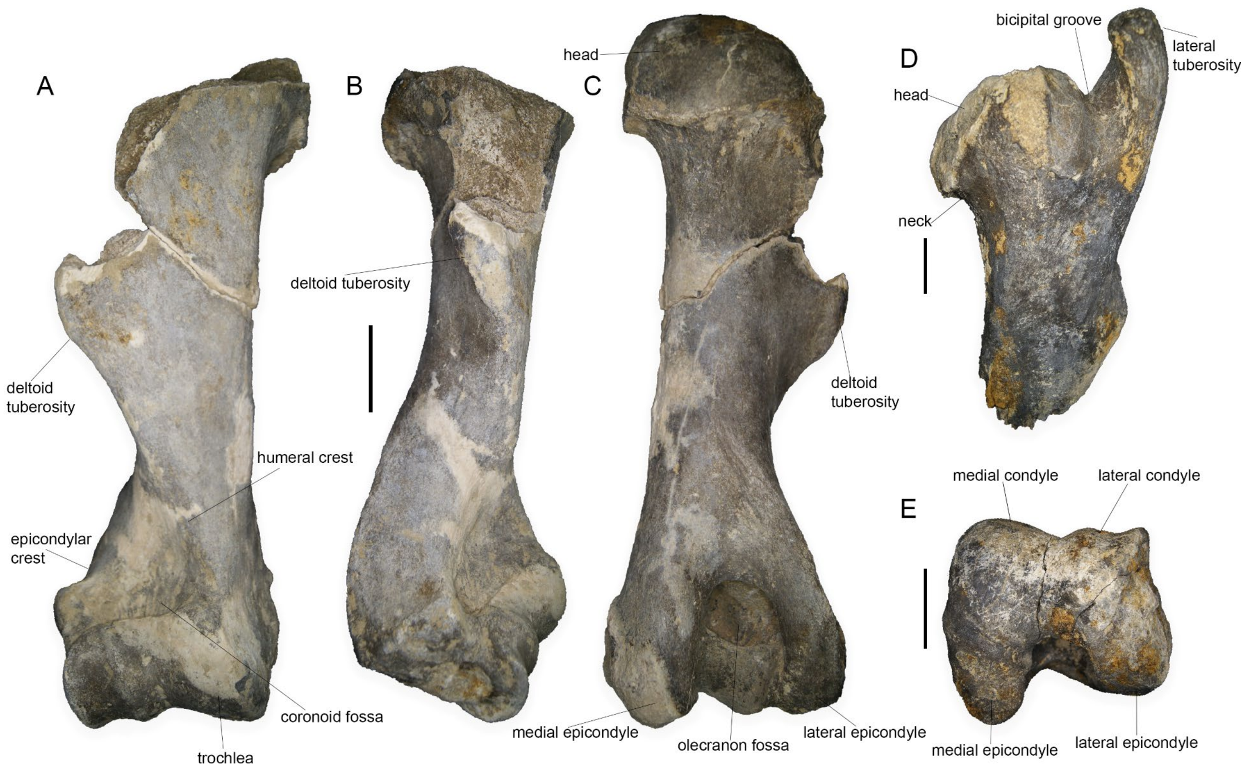

Figure 3. Right fragmented humerus MCZR PV 2010.2691 of *H.* cf. *antiquus* from Malagrotta. (**A**) Anterior view; (**B**) lateral view; (**C**) posterior view. Right fragmented humerus MCZR PV 2010.0074. (**D**) Posterior view; (**E**) distal view. Scale bar = 5 cm.

4.1.4. Vertebra

There are several fragmented vertebras stored in the MCZR. Among them, the best-preserved specimen is MCZR PV 2010.2677, a fragmented thoracic vertebra (Figure 4A). In posterior view, the neural spine is tall and almost complete, at its base the postzygapophyses are visible. The posterior face of the centrum is perfectly rounded with well-developed articular fossettes for the head of the rib on both sides of the centrum. The left transverse process is preserved while the right one is absent.

4.1.5. Scaphoid

The scaphoid MCZR PV n.c. shows a well-defined tuberosity in distal view, while in medial view (Figure 4B), the proximal articular facet for the radius is wide and slightly antero-posteriorly concave. In distal view (Figure 4C), there are two well-developed facets, one for the trapezoid and one for the magnum, while a third one for the trapezium is less developed.

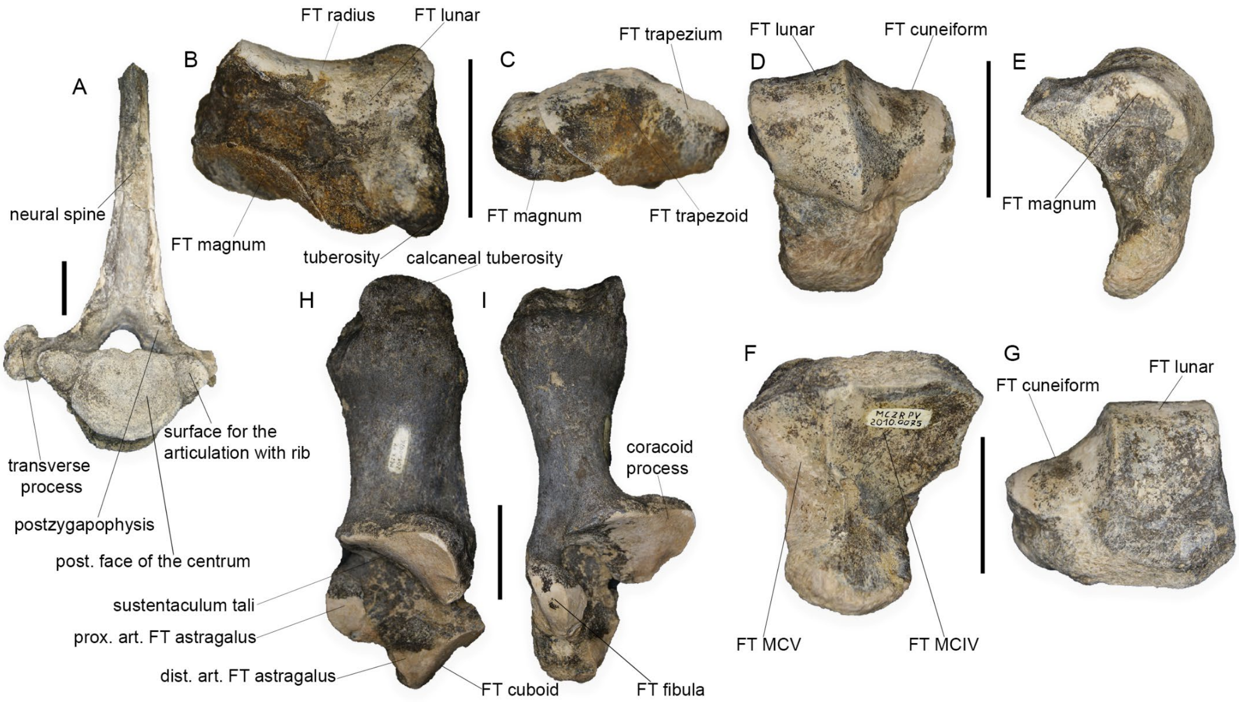

Figure 4. Thoracic vertebra MCZR PV 2010.2677 of *H.* cf. *antiquus* from Malagrotta. (**A**) Posterior view. Left scaphoid MCZR PV n.c. (**B**) Medial view; (**C**) distal view. Right unciform MCZR PV 2010.0075. (**D**) Proximal view; (**E**) medial view; (**F**) distal view; (**G**) anterior view. Right calcaneum MCZR PV 2010.0076. (**H**) Medial view; (**I**) anterior view. FT, facet. Scale bar = 5 cm.

4.1.6. Unciform

MCZR PV 2010.0075 is a right unciform almost entirely preserved. In proximal view (Figure 4D), the semilunar facet is trapezoidal, while the cuneiform facet is wider and lateromedially concave. The crest between the two facets is well developed. The lunar facet extends further distally than the facet for the cuneiform. In medial view (Figure 4E), the magnum facet is well visible, as well as a smaller facet for the MCIII. In distal view (Figure 4F), the almost complete articular facet for the MCIV is wider than the facet for the MCV. The latter facet is anteriorly and posteriorly well developed, extending for almost all the length of the bone. In anterior view (Figure 4G), the difference in height between the two articular facets is remarkable.

4.1.7. Calcaneum

In medial view (Figure 4H), the right MCZR PV 2010.0076 calcaneum is particularly robust and elongated. The calcaneal tuberosity is well developed, as well as the facets for astragalus and the sustentaculum tali. In proximal view, the calcaneal tuberosity displays a trochlea-like groove medio-laterally developed. In anterior view (Figure 4I), the largest facet is the one on the sustentaculum tali, which displays a triangular outline. The coracoid process is fairly protruding. The facet for the cuboid is wide and slightly concave. There is a deep groove between the facets for the astragalus. The facet for the fibula is well developed.

4.2. Morphological and Morphometric Comparison

4.2.1. Mandible

The horizontal rami (MCZR PV 2010.2690 and MCZR PV 2010.2690B) are shallow in lateral view, giving the mandible a rather slender aspect. The same development of the corpus is also observed in specimens IGF1043, IGF771, MGGC9412, and MGGC9416 from Valdarno (Italy), NHMMZ1937.1 from Mosbach (Germany), and MG3665 from Condeixa (Portugal), ascribed to *H. antiquus*. The slender aspect of the mandible is one of the diagnostic characters of *H. antiquus* [21,29]. As pointed out by Caloi et al. [29], mandibles of extant hippos are more robust and taller in lateral view. The specimen from Malagrotta is also extremely thin, resembling the mandible MSNCC C601 from La Maglianella, ascribed by Mazza [20,21] to *H. tiberinus* (=*H.* ex gr. *H. antiquus*). The mandibles of *H. amphibius* from the Late Pleistocene of Barrington (England) are particularly robust with a high corpus (in Reynolds [40], pls II-III, SMUC D3980), similar to those of the more recent *H. amphibius*. The ventral profile of the corpus in the studied specimens from Malagrotta is straight, slightly concave, similar to the aforementioned specimens of *H. antiquus*. However, as pointed out by Mazza [21], this character can be intraspecifically variable in *H. amphibius* and *H. antiquus*, and therefore not strongly diagnostic.

4.2.2. Teeth

Anterior teeth, lower incisors and canines, have no diagnostic characters, and are therefore not suitable for morphological comparison [21]. In the Malagrotta specimens, the enamel is finely striated, and the development of the ridges is not investigable since the canines are severely fragmented. The development of the enamel ridges has been used as a diagnostic character if concomitant with other observations by Caloi et al. [29]. According to the latter and to Petronio [22], these ridges on the enamel are usually parallel and shallow in *H. antiquus*, while deeper and anteriorly convergent in *H. amphibius*. However, Blandamura and Azzaroli [5] observed several *H. antiquus* canines from Valdarno, and both morphotypes were present. Therefore, the enamel ridges should not be considered as diagnostic in *Hippopotamus* species. The P2/P3 is highly worn out, and therefore difficult to analyze. The absence of a cingulum on the labial side in our specimens is a common feature in Hippopotamidae (Mazza, 1995) [21].

The available m2 MCZR PV 2010.2690B is highly worn out to detect any diagnostic characters. The m3s are partially worn out and diagnostic characters are not visible. However, Mazza [21] highlighted the presence of a strong postero-lingual pillar (post-entostylid) robust in the m3 of *H. antiquus*, a character that is also observed in MCZR PV 2010.2690B.

The L and PB of the m2 (L, 51.2 mm; PB, 39.8 mm) and m3 (L, 72.1 mm; PB, 41.45 mm) from Malagrotta fall within the variability of *H. amphibius* (m2: L, 54.99 mm; PB, 39.49 mm; m3: L, 70.09 mm; PB, 37.88 mm) and *H. antiquus* (m2: L, 60.37 mm; PB, 43.23 mm; m3: L, 81.12 mm; PB, 42.65 mm). However, the PB and AB of m3 (AB, 45.35 mm; PB, 41, 45 mm) are close to the variability of *H. antiquus* (AB, 45.02 mm; PB, 42.65 mm) (Figure 5A).

4.2.3. Humerus

The humerus MCZR PV 2010.2691 (Figure 6B) has a deltoid tuberosity located more mesially than in *H. amphibius* (Figure 6A), a character recognized by Mazza [21] in *H. antiquus* (Figure 6C,D). The development of the deltoid tuberosity in *H. amphibius* is also visible in SMUC D3980 (in Reynolds [40], p. 25, Figure 9B). In the specimen examined, the coronoid fossa is deep, and the trochlea is slightly inclined as in *H. antiquus* [21,48]. The bone is particularly robust medially and laterally, unlike *H. amphibius*, which is characterized by a slender diaphysis [21,48]. In posterior view, the olecranon fossa is not particularly wide and is deeper and more mesially developed than in *H. amphibius*. The latter character was also pointed out by Mazza [21], who defined the outline of the olecranon fossa as more triangular in *H. antiquus*. The medial epicondyle is more distally developed than the lateral one in *H. amphibius* (Figure 6A) rather than in *H. antiquus* (Figure 6C,D), and similar to MCZR PV 2010.2691 (Figure 6B). In distal view, the lateral epicondyle of the humeri MCZR PV 2010.2691 and MCZR PV 2010.0074 resembles the specimen MSNCC n.c. from La Maglianella and the lateral epicondyle is a little less bulging than in *H. amphibius* [21]. However, the specimen MGGC9420 attributed to *H. antiquus* shows a strongly protruding lateral epicondyle and a stronger medial epicondyle than in the humeri from Malagrotta. The plot BT vs. BD (Figure 5B) shows that the values of the Malagrotta specimens are close to both the extant and the European species. However, the values for BS and DP fall exclusively within the variability of *H. antiquus*. The dimensions of the humeri herein analyzed (BD, 144–146.5 mm; DP, 200 mm; BS, 73.8 mm) are closer to those reported by Faure [8] of *H. antiquus* (BD, 146–185 mm; DP, 188–216 mm; BS, 73–82 mm) than those of *H. amphibius* (BD, 117–145 mm; DP, 140–195 mm; BS, 52–65 mm). The dimensions of the humerus from Malagrotta are close to the humerus collected from Huescar-1 (late Early Pleistocene, Spain), even though the latter is a juvenile [16,53]. The ANOVA tests reveal that the statistical differences between the BD and DDm are significant ($p < 0.001$) for *H. amphibius* and *H. antiquus*, while no statistical differences were recognized for the BT and DDl.

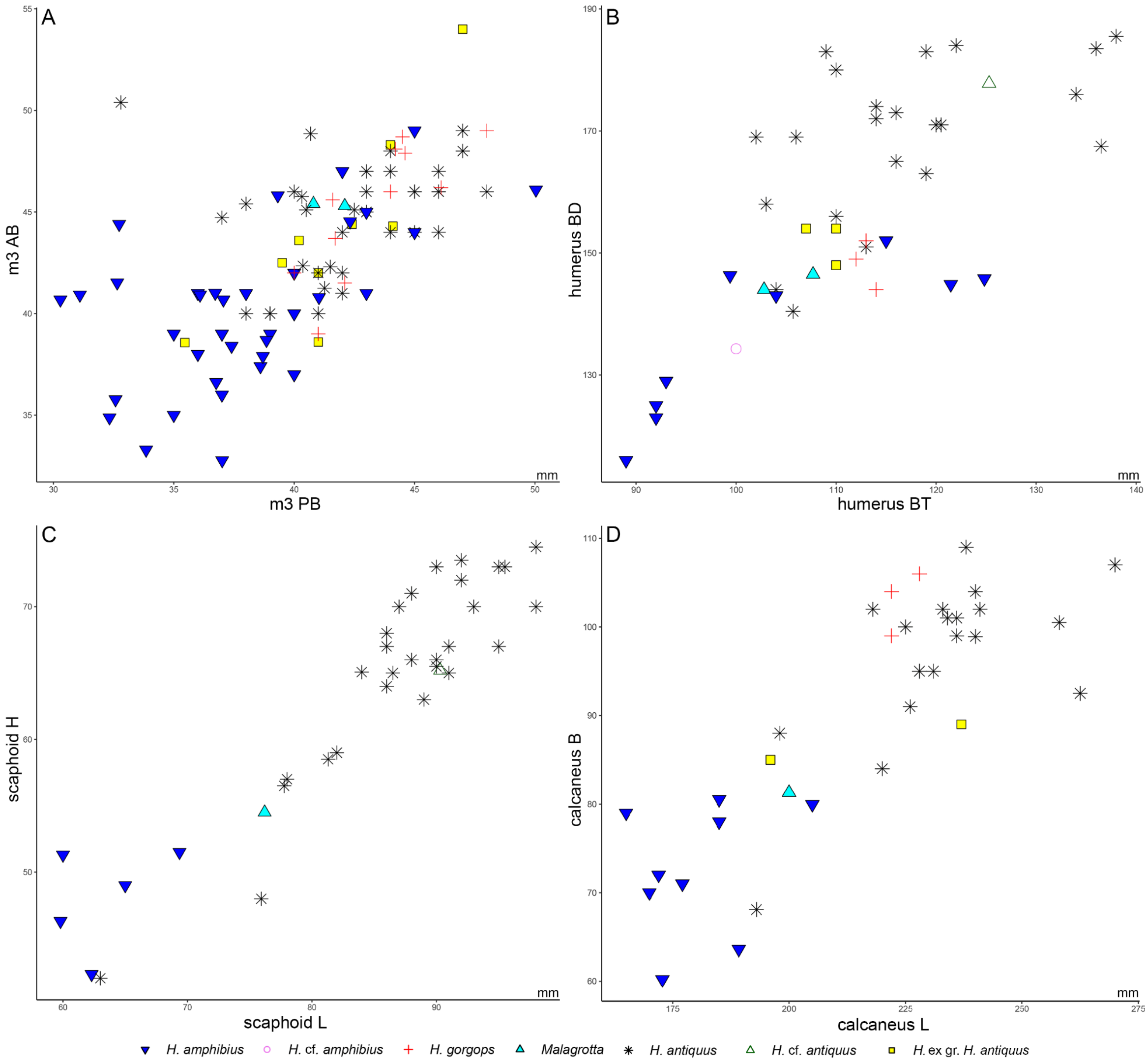

Figure 5. Scatterplots: (**A**) m3 PB vs. AB; (**B**) humerus BD vs. BT; (**C**) scaphoid H vs. L; (**D**) calcaneus L vs. B. All the measurements are in mm. For all data see Supplementary Material.

4.2.4. Scaphoid

The scaphoid from Malagrotta has a more concave radius facet than *H. amphibius*, but less concave than in *H. antiquus* (NHMMZ PW 1991/1-LS, copy of IGF1043, NHMMZ1957/650 and NHMMZ1957/574). In medial view, this facet is also more trapezoidal than in MCZR PV n.c. from Malagrotta and *H. amphibius*. In lateral view, the scaphoid from Malagrotta, similarly to those of *H. antiquus*, has a clepsydra shape, due to the presence of a constriction that runs antero-posteriorly in the medial portion of the bone. This feature is also present in *H. amphibius*, but it is less stressed. The overall morphology of the scaphoid from Malagrotta is closer to that of the scaphoids collected from Mosbach (Germany) and referred to as *H. antiquus*. The morphometric analysis suggests that the dimensions of the Malagrotta specimen (L, 76.2 mm; h, 54.5 mm) fall within the variability of *H. antiquus* (L, 87.26 mm; h, 65 mm) (Figure 5C). The ANOVA tests are significant for both the L and h values of the scaphoid ($p < 0.001$) for *H. amphibius* and *H. antiquus*.

Figure 6. *H. amphibius*: (**A**) humerus posterior view; (**A1**) humerus anterior view; (**E**) unciform distal view; (**F**) unciform anterior view. (MNCN n.c., recent). Malagrotta specimens: (**B**) humerus posterior view (MCZR PV 2010.2691); (**G**) unciform distal view; (**H**) unciform anterior view (MCZR PV 2010.0075). *H. antiquus*: (**C**) humerus posterior view (IGF1043 modified from Mazza, 1995 [21]); (**I**) unciform distal view; (**J**) unciform anterior view (NHMMZ1959.553, Mosbach sands, Germany). *Hippopotamus* ex gr. *H. antiquus:* (**D**) humerus posterior view; (**D1**) humerus anterior view (MSNCC n.c., La Maglianella, Italy), scale bar = 5 cm. (**K**) Hindlimb of *H. amphibius* (MNHN AC-A7986, recent), scale bar = 8.5 cm. 1, Development of the deltoid tuberosity. 2, Olecranon fossa. 3, Height between the medial and the lateral epicondyle. 4, Crest between the FTMCIV and FTMCV. 5, Development of the FT for the cuneiform.

4.2.5. Unciform

MCZR PV 2010.0075 is morphologically similar to the unciform of *H. antiquus* (NHMMZ PW 1001/1-LS). In distal view, the unciform from Malagrotta (Figure 6G), as well as NHMMZ1959.553 (Figure 6I), is more robust than the one of *H. amphibius* (Figure 6E).

In MCZR PV 2010.0075 and NHMMZ1959.553, the facet for the MCIV is wider than the one for the MCV, the latter being more limited laterally. In contrast, in *H. amphibius*, the facets for the MCIV and MCV have a similar size, with a crest between the facets placed more medially. The articular facet for the MCIV is slightly curved in MCZR PV 2010.0075, as well as in NHMMZ1959.553, while in *H. amphibius*, it is almost flat [54]. In anterior view, the facets for the lunar and for the cuneiform in the Malagrotta specimen (Figure 6H) are more like the facets displayed by NHMMZ1959.553 (Figure 6J), attributed to *H. antiquus*. In *H. amphibius*, the difference in height between the facet for the cuneiform and the one for the lunar is less stressed and the facet for the cuneiform is less concave (Figure 5F). In anterior view, the area under the articular facets is probably where the dorsal intercarpal and mediocarpal ligaments attach [54]. This area is bigger in *H. antiquus* (NHMMZ PW 1991/1-LS and NHMMZ1959.553) and in the Malagrotta specimen than in *H. amphibius*. The morphometric comparison highlights that the dimensions of the Malagrotta specimen (L, 86.4 mm; l, >77.4 mm; H, 61.7 mm) are close to both *H. amphibius* (L, 80 mm; h, 48.76 mm; l, 72.77 mm) and *H. antiquus* (L, 103.94 mm; h, 68.79 mm; l, 95.51 mm) (see Supplementary Material Table S2). However, most *H. amphibius* remains are characterized by lower values of h (height) than the Malagrotta specimen, which is closer to the variability of *H. antiquus*. The ANOVA tests highlighted that differences between L and h are both statistically significant ($p < 0.0001$) for both *H. amphibius* and *H. antiquus*.

4.2.6. Calcaneum

In medial view, MCZR PV 2010.0076 shows a proximal portion particularly robust and protruding, as in *H. antiquus*, while in *H. amphibius*, this feature is not well stressed. The diaphysis in *H. antiquus* and in MCZR PV 2010.0076 is clepsydra-shaped, while in *H. amphibius* is columnar-like. The Malagrotta specimen is characterized by a fairly protruding coracoid process, similar to *H. antiquus*. Moreover, in MCZR PV 2010.0076, the proximal articular surface for the astragalus projects out of the dorsal margin of the bone, as observed in *H. antiquus* (NHMMZ PW 1991/2-LS), contrary to *H. amphibius* [55]. The overall aspect of the bone, and in particular, the protruding proximal-most end also fits the description of KYP4-332 by Athanassiou et al. ([48], p. 187, Figure 7J) ascribed to *H. antiquus*. Moreover, the calcanei from La Maglianella have several features in common with the specimen from Malagrotta. The coracoid process is protruding, the bone is clepsydra-shaped, the proximal articular facet for the astragalus is projecting out of the dorsal margin and the proximal end of the bone is prominent. The morphometric comparison highlights that the specimen from Malagrotta (L, 200 mm; B, 81.3 mm; Bmin, 34.9 mm; BP, 66.3 mm; DP, 63.5 mm) is close to the variability of both *H. amphibius* (L, 180.12 mm; B, 72.7 mm; Bmin, 35 mm; BP, 81.56 mm; DP, 66.79 mm) and *H. antiquus* (L, 233.03 mm; B, 95.93 mm; Bmin, 38.27 mm; BP, 71.86 mm; DP, 67.03 mm) (Figure 5D). The ANOVA tests highlighted that differences between L and B are both statistically significant ($p < 0.0001$) for the extant hippo and *H. antiquus*.

4.3. Taxonomic Attribution

The mandible from Malagrotta in lateral view is particularly shallow and slender, with a partially preserved concave ventral profile of the corpus. *Hippopotamus antiquus* has a mandible slenderer and shallower than *H. amphibius*. The latter is characterized by a stronger and robust mandible in lateral view [16,21,29] Mandible slenderness is a character even more stressed in *H. tiberinus*, defined as *H.* ex gr. *H. antiquus* in Mazza and Bertini [23]. Unfortunately, all teeth from Malagrotta are severely worn out, and therefore diagnostic characters are not easily recognizable. Nevertheless, the m3 MCZR PV 2010.2690B shows a post-entostylid that in Mazza [21] is listed as characteristic of *H. antiquus*. The morphometric analysis on the available teeth is also poorly diagnostic at specific level.

The humerus MCZR PV 2010.2691 is strong and robust, it has a deltoid tuberosity placed mesially, a deep coronoid fossa, and a slightly inclined trochlea. It also shows an olecranon fossa with a triangular outline and not particularly wide. All these characters are also observed in *H. antiquus* [21,48]). The mesially placed deltoid tuberosity as well as an olecranon fossa with a triangular outline are even more visible in specimens ascribed to *H.* ex gr. *H. antiquus* (sensu Mazza and Bertini [23]. Morphometrically, the humerus from Malagrotta is closer to the variability of *H. antiquus* [9,21,40,49]. The scaphoid MCZR n.c. from Malagrotta displays a facet for the radius more concave than *H. amphibius* but less concave than in *H. antiquus*. The overall aspect of the scaphoid is closer to the ones collected from Mosbach sand (Germany), ascribed to *H. antiquus*. Morphometrically, the scaphoid from Malagrotta falls within the variability of *H. antiquus* [21,23,46,54]. The unciform MCZR PV 2010.0075 is robust, with a facet for the MCIV wider than the one for the MCV, as in *H. antiquus*. The former facet is also slightly curved, while in *H. amphibius* is usually flat [54]. The tuberosity of the scaphoid is well developed, while in *H. amphibius* is usually less stressed [54]. The value of h falls within the variability of *H. antiquus* [9,21,42,46,54]. The calcaneum MCZR PV 2010.0076 has a clepsydra-shaped diaphysis, while in *H. amphibius* is more columnar-shaped (see Supplementary Material Figure S2). The coracoid process and the proximal articular surface for the astragalus in MCZR PV 2010.0076 are fairly protruding as in *H. antiquus*. All the latter characters are also common in *H.* ex gr. *H. antiquus* specimens. Dimensionally, the calcaneum from Malagrotta is closer to *H. amphibius*, displaying smaller dimensions than *H. antiquus* [9,21,40,46,48,55]. The available measurements for *H.* ex gr. *H. antiquus* are close to the one of MCZR PV 2010.0076.

The analyses performed allow us to recognize that the Malagrotta specimens share several morphological traits with *H. antiquus*. However, the size of most hippo remains is fairly modest, closer to the variability of *H. amphibius*. For this reason, the Malagrotta specimens are here ascribed to *H.* cf. *antiquus*. It should be noted that the specimens analyzed show a clear affinity with fossil material ascribed to *H.* ex gr. *H. antiquus*.

5. Discussion

5.1. Size and Climatic Conditions

The hippopotamus from Malagrotta is characterized by a smaller size when compared to the remains from Valdarno (Italy) dated 1.9–1.7 Ma ([2,13] and references therein), Untermaßfeld (Germany) dated ca. 1.07 Ma [9,56,57], and Colle Curti (Italy) dated ca. 1 Ma (lower part of MIS 31 in Mazza and Ventra [58]) (see Supplementary Material Figure S1). The dimensions of the specimens from Malagrotta are closer to the ones of *H. tiberinus* (=*H.* ex. gr. *H. antiquus* in Mazza and Bertini [23]) collected from La Maglianella (Italy, 0.6 Ma), Mosbach-2 (Germany, Middle Pleistocene), and Jockgrim (Early Pleistocene, Germany) [21]. Dimensionally, it can be also noted that the Malagrotta teeth have affinity with the remains from Condeixa (Portugal, ca. 0.4 Ma in Fidalgo et al. [16] and references therein), Megalópolis Basin (Greece, Middle Pleistocene in Athanassiou [11]), and Fuente Nueva-3 and Barranco León-5 (Spain, 1.3 ± 0.1 Ma in Martínez Navarro et al. [59]). As already pointed out by Mazza and Bertini [23], the size of hippopotamuses may have experienced fluctuations driven mostly by climatic change. For the latter authors, hippopotamuses were characterized by larger sizes during warm and humid stages and became way smaller under colder and drier (non-optimal) environmental conditions. One of the smallest specimens of *H. antiquus* was described from Ortona (Italy), from an interval between MIS 19 and MIS 17 [23,60]. Several remains were unearthed from this locality, among them the most outstanding one is an almost entirely preserved mandible of an adult hippopotamus [60]. Mazza and Bertini [23] highlighted that the small dimension of the hippopotamus collected from Ortona, ascribed to *H.* ex. gr. *H. antiquus*, was probably affected by non-optimal environmental conditions. However, body size changes in hippopotamuses should be better investigated, and effects related with distributions of water bodies, seasonality, interspecific competition, or specifical faunal compositions should be tested in the future. The size of the m2 (L, 54.8 mm; PB, 44 mm) and the m3 (L, 79 mm; B, 44.2 mm) from Ortona are close to the values of the Malagrotta specimen (m2: L, 51.2 mm; PB, 39.8 mm; m3: L, 72.1 mm; B, 45.3–45.4 mm).

A study with a similar conclusion to Mazza and Bertini [23] was also carried out by Fidalgo et al. [14] on the hypoplasia of hippopotamids teeth. In the Hippopotamidae representatives from Untermaßfeld, among the largest sized examples of *H. antiquus* ever, the dental enamel hypoplasia (DEH) reported is not severe nor prevalent [61]. Remains from Collecurti are also poorly affected by DEH, while sites dated to ca. 0.9–0.86 Ma, characterized by a long and severe glacial phase, show a high incidence of DEH [14]. The incisor collected from Malagrotta MCZR PV 2010.2690 shows feebly transversal lines on the enamel that might be caused by hypoplasia. Some of the hippopotamid remains (upper and lower canines) collected from La Maglianella (0.6 Ma, Italy) also show the presence of enamel hypoplasia.

The studies of Mazza and Bertini [23] and Fidalgo et al. [14] confirm that there is probably a correlation in hippopotamids between size and hypoplasia, with seasonality and environmental conditions affecting them. However, further studies are needed to quantify and characterize the variability of size of hippopotamuses correlated with the different environmental conditions of Pleistocene, in particular after the Jaramillo sub-chron.

5.2. How Many Hippopotamids in Europe during the Pleistocene?

Hippopotamids during the Middle Pleistocene in Europe are poorly represented, and the dispersal of *H. amphibius* is unclear. Recently, Mecozzi et al. [19] re-described a skull of a hippopotamid (MPUR/V 149) collected from the area of Rome, previously attributed to *H. amphibius* ([13,29] and references therein). The exact location of the remains is unknown, but through an analysis of the sediment recovered from the skull, Mecozzi et al. [19] concluded that most likely it was collected from Cava Nera Montanari, dated between 560 and 460 ka. However, a more precise age constrain of 535–500 ka was established by Marra et al. [27] based on the fact that the sedimentary succession cropping out at Cava Nera Montanari (also known as Cava Nera Molinario) is firmly correlated with the MIS 13 aggradational succession (Valle Giulia Formation [38]), due to the intercalation of the Tufo del Palatino pyroclastic-flow deposit. As it has been verified for the site of Malagrotta (see Section Geological Setting and references therein), most of the fossil remains stored in the different repositories in Rome (see, for example, the material from Ponte Milvio, and the several attempts to stratigraphically locate the fossil remains from the urban area of Rome such as Di Stefano et al. [62]; Marra et al. [27]; Mecozzi et al. [19]) are catalogued according to the site of collection, without regard to the complex stratigraphic setting of each location. Evidently, at the beginning of the 20th century, there was no awareness about the wide time interval that the so-called "Tiber terraces" (i.e., the fluvial-lacustrine deposits outcropping along the flanks of the Tiber Valley and its tributaries in Rome) span. They actually comprise the aggradational cycles MIS 13 through MIS 7, spanning 535–200 ka ([63] and references therein). This is the case of Cava Nera Montanari, where an about 12 m tall quarry cut exposed the deposits Valle Giulia Formation at the base and those of the Vitinia Formation at the top, separated by the channeled pyroclastic-flow deposit of Tufo Rosso a Scorie Nere (452 $\pm$ 2 ka) ([64] see also Figure 6 in Mecozzi et al. [19]). Therefore, there is no objective way to say if the collected fossil remains come from the lowest or the uppermost horizon, also considering that the fluvial lacustrine deposits of the two aggradational successions of MIS 13 and MIS 7 are barely distinguishable [65]. Following that, the occurrence of *H. amphibius* in Italy during the MIS 13-MIS 11 is questionable and its presence during MIS 10-8 is also not strongly supported by the available data [13]. However, *H. amphibius* was well established in the Italian Peninsula during the late Middle Pleistocene and the early Late Pleistocene [13]. The presence of *H. amphibius* in Spain is reported from the TD8a level, 602 $\pm$ 92 ka of the Gran Dolina deposit [66,67]. However, the attribution is based on an isolated incisor, and therefore it should be more cautiously ascribed to *Hippopotamus* sp. Other paleontological sites with *H. amphibius* remains from the Iberian Peninsula include Solana de Zamborino (0.48–0.3 Ma in Álvarez-Posada et al. [16,68]), Las Jarillas (0.45–0.4 Ma in Baena Escudero et al. [16,69]) Aridos I de Arganda (MIS 11 in Blain et al. [70,71]) and Mealhada (0.2–0.13 Ma in Fidalgo et al. [16]). *Hippopotamus* ex gr. *H. amphibius* is reported from France in Levallois (301–242 ka) and Celle-sur-Seine, ascribed to MIS 11 [10,72,73]. However, the remains from France have never been described or compared and their attribution is therefore dubious. In Greece, remains of *H. amphibius* were reported from Late Pleistocene deposits, although its presence in earlier deposits has yet to be proven [11].

If *H. amphibius* was already present around 0.5 Ma in the Latium area as assessed by Mecozzi et al. [19], that would also mean that the extant hippo and *H.* cf. *antiquus* concurrently inhabited the same area. The co-existence of *H. amphibius* and *H. antiquus* was already taken into consideration by several authors, but not supported by data [16,19,23]. The presence of two different hippopotamus species is interesting since it has been rarely documented in Africa and South East Asia. Pandolfi et al. [74] described the presence of two hippopotamuses, *H. gorgops* and aff. *H. karumensis* from Buia (Eritrea) around 1 Ma. As underlined by the authors, the two species occupied the same geographical area but probably different ecological niches. Also, Harris [44] reported the presence of three hippopotamids, *H. gorgops*, aff. *H. karumensis*, and aff. *H. aethiopicus*, from different members of the Koobi Fora Formation and the Nachukui Formation (Kenya). However, up to now, no two species of the same *Hippopotamus* genus have been documented in fossiliferous localities in Africa or Europe. Considering what was stated before, further studies on the latest *H. antiquus* should be carried out to fully understand its ecological niche and adaptations.

6. Conclusions

The mid and late Early Pleistocene was a period particularly favorable for hippopotamids. They were present in almost all Europe and a large amount of hippopotamid specimens were recovered from different fossiliferous sites. During the Middle Pleistocene, the presence of hippopotamids in the fossiliferous localities dropped, and their variability during that period is less known. The material herein studied from Malagrotta (Rome, Italy) displays morphological characteristics closer to *H. antiquus*, such as a slender and low corpus of the mandible, a strong and robust humerus with a deltoid tuberosity placed medially on the diaphysis, a unciform with a facet for the MCIV wider than the one for the MCV, and a clepsydra-shaped calcaneum. However, the dimensions of the remains from Malagrotta are rather small for an *H. antiquus* specimen, but close to the variability of *H. tiberinus* (=*H.* ex gr. *H. antiquus*). The remains from Malagrotta are therefore ascribed to *H.* cf. *antiquus*. *Hippopotamus antiquus*, the big European species, was characterized by larger dimensions during the Early Pleistocene, as testified by remains collected from Untermaßfeld, Valdarno, and Colle Curti. During the Middle Pleistocene, *H. antiquus* became smaller and more slender, probably for climatic conditions not particularly favorable, as confirmed by material from Megalópolis Basin (Greece) and Condeixa (Portugal).

The age of the *H.* cf. *antiquus* from Malagrotta is estimated between 451 $\pm$ 2 ka and 378 $\pm$ 6 ka (MIS 12-MIS 10). The LAD of *H. antiquus* is placed around 0.45 Ma in Portugal and Greece, but Malagrotta specimens testify that probably the large European hippopotamid disappeared slightly after 0.45 Ma, surviving at least in the central Italian Peninsula.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/quat7010013/s1. Supplementary Material Table S1: List of all specimens from Malagrotta stored in the MCZR. Supplementary Material Table S2: Measurements from Malagrotta and data for scatterplots shown in Figure 5. Supplementary Material Figure S1: Measurements protocol following Mazza (1995) [21]. Supplementary Material Figure S2: A, Calcaneum of *H. amphibius* (SMNS6717.2.4.68.11, Late Pleistocene, Oberrhein, Germany). B, Calcaneum of *H.* cf. *antiquus* (MCZR PV 2010.0076, Middle Pleistocene, Malagrotta, Italy). C, Calcaneum of *H. antiquus* (MSNCC n.c., Early Pleistocene, Valdarno, Italy). D, Calcaneum of *H.* ex gr. *H. antiquus* (MSNCC n.c., Middle Pleistocene, La Maglianella, Italy). 1, Dorsal development of the sustentaculum tali. 2, Clepsydra shape of the corpus calcanei.

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